[SQUEAKING]
[RUSTLING]
[CLICKING]

NANCY

## KANWISHER:

All right, so we're going to talk about number. I got a little carried away with the behavioral work on number because I just think it is so awesome. And I think it's, frankly, a little more interesting than a lot of the neural work. So this is going to be sort of a behaviorally heavy lecture.

But let's start by thinking about why we have number and what we use it for. And the first thing to realize is that we use concepts of number and quantity like all the time. Most obviously, if you're, say, getting change at a store. I guess that doesn't really happen very much anymore. People are going to forget how to subtract because they just put their credit card or bump their phone or whatever they do. But anyway, it used to be that you handed over this stuff called money and that coins came back and that was the subtraction involved.

We use it to tell time or to fail to tell time, as in my case this morning. To choose the larger of two objects, that's a continuous idea of quantity, not a discrete idea of number. To choose the shortest line at a grocery store, right, and all of those kinds of things are comparing quantities.

And we also take these basic ideas of number and quantity and we build on them in modern societies to do all kinds of amazing things like engineering. Like all of modern science is highly quantitative, like all of computer science. And so these are really fundamental ideas.

And animals, it turns out, are capable of mastering very simple but sophisticated understandings of number and even arithmetic computations. They can learn about order and number and quantity. OK, and they need to for lots of reasons.

So here, just a brief overview of some of the situations where animals need concepts of number and quantity in the wild. Foraging, right, so animals spend a lot of time rooting around for food over here, rooting around for food over there, deciding when to keep rooting around here despite diminishing returns and go somewhere else where there's unknown pay off, unknown amounts of food. So that's a whole math of foraging behavior. OK, so that deals with the rate of return of the food at each location and the amount and the quality. And you can imagine a whole math to optimize the amount of food.

They also need to know about number and quantity when they form teams, which many animals across taxa do in different ways. So schooling fish can quickly pick out the more numerous school of fish to join. And that's what they want to do because your statistics are better if they're a predator if you're in the larger school than the smaller school, right? So your chance of getting eaten is reduced just dividing by the number of options.

And then there's all kinds of animals that take into account the size of groups of their own species or other species when making decisions about how far to run or who to chase or who to predate on or who's at risk of predating upon you. So lions hunt in teams. And they have to work together. They have actually whole strategic situation where different lions play different parts like a football game. And they have to decide which groups of predators to take on based on numerical advantage.

And my favorite is the n plus one frog, the Tungara frog that lives in the rainforest in Puerto Rico. And it literally one ups other frogs, the males do in trying to impress the females. And so what happens is that one frog will start calling out. One male frog will start calling out trying to sound all hot to the gals. And then another frog will one up him by doing that call but elaborating on it by adding an extra call or an extra component.

So for example-- [FROG CALL] OK, so that's one dude calling out. And not to be outdone, the next guy calls back. [FROG CALL] And apparently, if you follow these guys, they pretty systematically add one to the previous frog's call, right, up to a point. The point being approximately four. So it's not like 100 and 101 . But it happens. OK, so that's just a broad overview of some of the cases that understandings of number and quantity arise in natural environments without training.

So we want to know how is all this computed in the mind and brain. And so what are the foremost thinkers on this topic is Stan Dehaene, shown here. And he wrote in a very widely cited book, actually review article and book quite a while ago, 20 years ago, he said, animals, young infants, and adult humans possess a biologically determined, domain-specific representation of number. So this is a very kind of extreme, hardcore claim. We will see at the end of the lecture that he has backed off that claim.

OK, so a couple of things, biologically determined, he's kind of implying innate, right? Domain-specific, I've avoided this phrase, for the most part, because it's kind of like jargon gobbledygook. But it's actually so entrenched in our field that it's worth knowing what it is.

Domain-specific is just this idea of functional specificity that I've been talking about. But you can apply it to not just a piece of brain like, does this patch of brain process only faces? You can also apply it to a mental process even if you don't know what its actual brain basis is. So do we have special mental machinery for thinking about numbers that's distinct from our machinery for face recognition or navigation or language or whatever else? OK, so that's what domain-specific means. And it's worth knowing because you'll encounter it in other contexts.

OK, so in more detail, Stan says, a specific neural substrate, located in the left intraparietal area, is associated with knowledge of numbers and their relations, which he defines as number sense. The number domain is a prime example where strong evidence points to an evolutionary endowment of abstract, domain-specific knowledge in the brain because there are parallels between number processing in animals and humans. Again, kind of hardcore claims.

Not just is there this so he doesn't quite say innate, but he's strongly implying innate. I mean, that's evolutionary endowment, that basically means innate, right? It's an evolved ability that lives in a particular part of the brain. OK?

So who would a thunk, right? Number, right? You think of number as something you get taught in school. But no, he's saying it's really part of your biological endowment. It has a particular brain region. And all of that may be if not completely independent, it may exist without explicit training. OK? So that's quite a claim.

So what does number sense mean exactly? Well, what Stan and others in the field mean by number sense, it's a bunch of things. First of all, the idea that for human adults to have number sense, that means they can represent large numerical magnitudes without verbal counting, right? So counting is an interesting thing. But we're going to leave it aside for the moment.

Number sense is a more general idea that's going to apply to animals and infants without explicit counting. OK, so you can have some way of representing that there's a lot of things here. And there's fewer things there.

Second of all, these representations are approximate. And the ability to discriminate two of them depends on the ratio of those two, not the absolute difference. OK, and I'll show you in more detail what I mean by that. It's a deep fact about number sense and actually all of perception, pretty much.

Further, the idea is that these representations are abstract. They're not just, say, a particular visual form. Like approximately 13 looks like this. No. They're going to generalize across modality, OK, and space and time.

Next, these mental representations of number can be used in operations. Even without counting and being explicitly informed, you can add approximate numbers. You may be thinking, what the hell am I talking about? But I'll show you in a second.

So for example, I'm going to show you two sets of dots next. And you're just going to shout out first if the first set of dots had more, if there were more dots in the first array and second if the second array had more dots. OK, ready? Here we go. Boom. Boom. Second. Duh.

OK, let's try another one. Duh. And another one. Uh huh. Another one. I noticed the volume decreasing. And I noticed some hesitancy. Actually, I'm not sure about that one.

OK, so how did you do that? What did you do? Did you go 1, 2, 3, 4, 5? No. I tried to do it, so there wasn't time to do that. How'd you do it?

## AUDIENCE:

I kind of tried to see like the density, like how close all the dots were.

NANCY

## KANWISHER:

## AUDIENCE: It seems to be OK.

NANCY
KANWISHER:
OK, what Jack is pointing to is a really important thing in thinking about number, which is that number is confounded with area extent. How much total yellow stuff is on the screen? And it's confounded with density.

And this is a big problem in people who want to do research on number. And so what they usually do is you can't totally unconfound those things. But you can unconfound them one at a time.

So you can vary the size of the objects. And you can vary the density across trials. So no one of those cues will enable you to do it fully. This example isn't great that way because they were all the same size, right?

OK, but so the point is, without explicitly counting, and God knows what you do it, how you do it, you just feel like you have a sense of roughly how many. Everybody got that sense? OK, so that's what we mean by number sense is that sense that you can just look at something and have a sense of roughly how many. Like you don't know if it's 19 or 18 , but you know it's not 13 , right? OK, right. Oh, and you guys all got quieter when the numbers got closer together. OK? It gets harder when the numbers are closer together.

OK, so in experiments that have quantified this, lots of people have looked at this. Here's one that I was involved in way back. Just like you did, this is the task here that you guys just did. And here are some of the data we got. So let me walk you through this.

This is accuracy on a bunch of different comparisons. 16 dots versus 32 dots, people are pretty much $100 \%$ correct. OK? This is just normal human adults.

16 versus 24 , great. 16 versus 20 , pretty good. 16 versus 18 , now we're really dropping. 16 versus 17 , forget it. Can't do it. OK? So performance falls off as the numbers get closer together. OK?

So that's sort of intuitive. But now let's consider these are all comparing to 16. Here, we compare to eight. Eight versus 16. Eight versus 12. Eight versus 10. Eight versus nine. You see the same fall off as the numbers get closer together. OK?

So far, so good. But now we can ask, what determines that fall off? Is it the absolute difference or the ratio? And the way we tell is we plot the ratio of those two curves, and we look at performance. And we see they are spot on top of each other.

That tells us that it is not the absolute difference that determines your ability to do this but the ratio of the numbers of dots. OK? It's sort of intuitive, right? But it's amazing how clear the result is. Everybody get that?

OK, so this is a really deep fundamental fact about perceiving approximate number. And it's actually, more generally, a fact about perception. It's called Weber's law. And it just means that the discriminability of, in this case, two numbers, two numerosities, depends on their ratio, not their absolute difference.

The exact same thing holds for evaluating which of two stimuli is brighter, which of two objects is heavier, which of two sounds is louder. They all follow. The ability to do that is a function of the ratio of the, two not the absolute difference. Yeah?

## AUDIENCE:

[INAUDIBLE] with the size of the dots?

NANCY
KANWISHER:
So in this experiment, we varied the sizes every which way and the density. As I mentioned before, you can't completely unconfound both size and density within each trial. But across trials, you can muck them up. So you can ask whether people are doing it by size or by density. OK? And we did all that here.

OK, so this is not shocking yet. It's just kind of a basic, deep, clear fact about whatever our mental representation of number is, that it's this approximate thing. It's pretty good. And its precision scales with the magnitude.

OK, all right, so this has been quantified in lots and lots of experiments. And this is called the Approximate Number System, or ANS. And the standard test that's been used in lots of studies to measure people's kind of number acuity is a lot like what I just showed you.

You show an array like this. And you say, are there more yellow dots or blue dots? And people very quickly say yellow, in this case. And then you ask for a case like this. And they're a little slower, right? And here, you can see that the sizes have changed and have been orthogonalized.

OK, so the ratio of yellow to blue dots is called the Weber fraction, right? This is this idea of Weber's law that determines your accuracy from just that ratio. And so you can measure people's Weber fraction, their ability to do this task, their kind of number precision.

And what you find is, first of all, that there's very big individual differences. OK? Now, this is interesting. It's like things that we've seen in other domains. There are very big individual differences in navigational ability. There are very big individual differences in face recognition ability.

And in both of those cases as well, there are people who are just so bad at it, from an early age, that it's like a syndrome. In this case, it's called developmental dyscalculia. I think I didn't fit it into the navigation lectures. But there's a whole kind of developmental disability in navigation that's called developmental topographic agnosia. People were just always really awful at knowing where they are, right? And I did mention developmental prosopagnosia. People were just always awful at face recognition.

In each of these cases, in the apparent lack of any evidence of brain damage and in the absence of differences in IQ or other abilities. So it seems like each of those abilities has a very broad range. At the bottom end of the range, it's really kind of affects your life you're so bad. And it's unrelated to other abilities.

And I think that's pretty interesting because it goes along with the idea that those mental abilities are really distinct parts of mind and brain. You can have a crappy number sense, and it doesn't mean that you're bad at other things. You just have a crappy number sense. It's a separate system, right? OK. Approximate number sense develops slowly. It's best at age 30. You guys are still on the upswing. We won't talk about me.

This is what do we have here? This is Weber fraction. So the Weber fraction is what that ratio needs to be for you to be fairly accurate on whatever criteria they chose. And so a small fraction means you're better. And so it goes down. And this is age here, best at 30. And this is reaction time, which goes up for everything. What a bummer. Anyway.

Interestingly, early ability with approximate number on this kind of a test predicts later math ability with very different kinds of organized math that you learn in school. So here's a study that looked at that. They asked whether this early approximate number sense is predictive of later arithmetic ability.

And so in this case, they did a task like this. And their measure, they didn't use the task I just showed you. This is another thing you can do with little kids. You just flash this up. And you just ask them, how many dots are there? And they have to say four, right? And you just measure reaction time. It's pretty basic. OK?

And so then what you do is you run this on kindergarteners. And you define groups that are slow, medium, or fast at this task. OK? So then you follow them. And you look at them later, in this case, at age nine and six years.

And what you see is, even these older kids, who are defined by the slow, medium, or fast group in kindergarten, this is now their accuracy at arithmetic tasks four years later. Yeah? So it's not just some weird little task that psychophysicists made up to measure God knows what. It's predictive of your later arithmetic ability. OK? So it matters.

So the speed of this dot estimation task at kindergarten is not associated with later abilities of other kinds, like Raven matrices, which is one of the standard measures in an IQ test, right? It's a nonverbal and non-number kind of task. Or ability to name digits or letters or other things that you can test kids on in however old they are, nine years. OK? So it's specifically predictive of later arithmetic ability. Everybody with me? So it matters.

All right, and that suggests that there would be ways to intervene in dyscalculia. Potentially, you could catch the kids early who are destined to have a hard time and maybe figure out what you could do about it. And there are efforts underway to do that. OK? OK.

OK, so I'm going to show you. We're exploring these various number abilities. I'm going to show you something interesting about symbolic numbers. So far, we've been telling you about nonsymbolic numbers. That means just dot arrays.

Now we're going to deal with symbolic numbers. I'm going to flash up a bunch of numbers. And you're just going to say bigger if it's bigger than 65 or smaller if it's smaller than 65. Really easy. But you're going to shout it out loud and clear. Ready? Here we go.
AUDIENCE: Smaller.
NANCY
KANWISHER:

## AUDIENCE: Bigger.

## NANCY Good.

## KANWISHER:

AUDIENCE: Smaller. Bigger. Smaller. Bigger. Smaller. Bigger.

NANCY OK, did you guys see what happened there? Did you feel what happened? When the numbers get closer to 65,

## KANWISHER:

 you're slower. Now you think about it, why the hell is that, right?If you run this in Matlab, it's not going to take longer to tell you that 63 is smaller than 65 than it takes to tell you that eight is smaller than 65 , right? I assume. I haven't tried it. But I doubt it.

So what does that mean? That means that even when you are dealing with symbolic numbers, numbers that you have this whole elaborate edifice you've been trained on how to operate with these guys, especially you guys, you are still invoking some kind of notion of the continuous quantity. You haven't totally left that idea behind and moved off into some abstract space. You're still, even in doing this very literal, exact symbolic number task, you find it easier when the numbers are farther apart than when they're closer. Yeah, Talia?

## AUDIENCE:

NANCY
Could it be because of the number you chose? So if you chose the numbers 60, let's say, I feel like we read left to right. And they maybe have a good concept for the number of digits that we see. So when we see a number like 62, we have to read both the digits instead of just the one.

Yeah, but all the ones I showed were at least two digits.

Yeah. But when you read, like when you see a number like 25, you see the two. And then you automatically like know that.

OK, fair enough. OK, that's a good counter explanation. But you guys were slow even with 58 . I think, right? We could test that. I'm pretty sure all this has been tested pretty carefully. I don't know this literature totally thoroughly. But I doubt-- it's a good alternative account. And there might be some effect.

But I think it's-- oh, in fact, in fact, actually, there is, yeah, I have data coming up next. But right. Blah, blah. OK, here's the data. OK? It's pretty continuous. So I think your good, plausible alternative doesn't seem to capture very much of it. OK?

So yeah, this is what you guys just did. And does everybody get how this kind of reveals that even when you think you're doing this kind of more symbolic abstract thing, you're still tapping into some kind of continuous notion? Yeah? OK.

So that says not only does your ability to do that in kindergarten predict your ability to do arithmetic later, it says, even now as highly trained MIT students who do all kinds of much more sophisticated math than this, you're still invoking that same kind of continuous sense of approximate number or something like it. OK.

All right, so where have we gotten? We started with this checklist of what number sense might mean. And I've argued that you adults can represent large numerical magnitudes without verbal counting, that these numbers are approximate, and that your ability to discriminate them depends on the ratio, not the difference. And I've sort of loosely told you that these experiments are generally done unconfounded from things like area and that they refer to the discrete number

OK, what about these other questions here? I haven't really shown you how abstract they are or whether you can actually use them in arithmetic operations. OK, so how would we tell that? Well, here's an experiment that we did way back.

We did the very same task I did on you guys before, which has more, except the first thing was an array of dots. And the second thing was a series of tones. OK? Series of tones presented faster than you could count. Beep, beep, beep, beep, beep, like that, right? OK.

And so you might think that if people are doing some literal perceptual thing that this would be just like freaking impossible, right? But it's not. Accuracy is just about the same, maybe a hair lower, but almost the same with the cross-modal comparison of which has more than with the within modality one, visual dots to dots or tones to tones. This is dots to dots and tones to tones. And that's across. It's a little bit surprising.

So that shows you that whatever you're tapping into is a pretty abstract representation. It's not tied to vision. It's not tied to hearing. And it also completely eliminates worries about density or area or stuff like that because that doesn't work here at all. OK? All right.

OK, can you do operations on these? Sure. Why not? You can give people a dot array and a dot array and then tell them to add and ask whether the sum of those is greater or less than that. Let's try it. OK, here we go. Everyone ready? Consider, is the sum of this plus this greater or less than this.

Yeah. OK? And I really didn't leave you time to count. And so whatever you were doing in adding, you weren't adding symbolic numbers. You were adding these approximate amounts. OK? Well done.

And then we could go crazy and do it across modalities. I'm going to ask you to add dots to tones and ask whether the sum is greater or less than that. We won't do it. But it turns out, people are just as good at that. Amazing, huh?

So where has this gotten us? This told us that whatever this approximate number sense that we all have, it's damned abstract. You can compare it across sensory modalities pretty much as well as within. And you can perform operations with it. You can do addition. And you can also do subtraction just as straightforwardly. OK? So that's pretty cool.

But in all of these studies and the demos with you guys, these are done on people with years and years of training in arithmetic. And so we really want to know, are these things-- is any aspect of this system innate? Is it present in very young infants? And to what extent do animals have these abilities? OK?

Well, how would we find out whether they're present in infants? Well, there's a bunch of ways. But looking direction and looking time are the key cues you have with newborn infants. And so here's a study that was done on four-day-old infants.

And what they did was they presented-- they had a familiarization phase. This is done cross modally. OK? So they present either sets of 12 sounds, to, to, to, to, 12 , right, of those, or ra, ra, ra, ra, present a bunch of those to infants. Or they present sets of four taking the same total duration, to, to. It's just a coincidence that it's to. This is, I think, done in French. So anyway, the infants won't be confused by the sound to.

So during that, you then show the infants these arrays. And you ask what they look at more. OK? They're not told the task. There's no way to tell them a task. It's just something they do.

And what you find is, in the four versus 12 case like here, that's four versus 12 , the infants look more at the congruent number then the incongruent number. OK? So again, they're comparing across modality. They're hearing some number of syllables. And they're selectively looking at the corresponding number of visual forms. No instruction. No nothing. Four days old. Amazing. OK?

So they can do that if the comparison is four versus 12. They can do it if it's six versus 18. But they kind of can't do it very well. I mean, it's significant, but it's not very good if it's four versus eight. OK? So they have some sense of number. But it's very approximate. Yeah?
AUDIENCE: Did you say they looked at the one that matches the number, or they hear the sound that goes with it?
NANCY Matches. That's congruent means match. Looking time on congruent versus incongruent.
KANWISHER:

AUDIENCE: Isn't that kind of different from--

NANCY From adaptation.

## KANWISHER:

## AUDIENCE: Yeah.

It is. It is totally different from adaptation. And herein lies a classic annoyance for developmental psychologists. Because sometimes kids match. And sometimes they show adaptation. And you kind of don't know. Sometimes you don't know which way it's going to go.

I don't know. Heather, do we have any insights about how you know which way it's going to go? Or you just try and experiment and you find out and yeah? Yeah. Yeah.

It does mean you have to be careful. Because if you run a whole experiment on a smallish number of infants-and it's usually hard to get enough because people have to drive in with their kids. And this, how do you find them? And there's other developmental labs who have all the kids. And it's like you're always running experiments with barely enough kids, right?

And so that means there's a problem here. Because if you would take the result in either direction, that's a statistical problem. You gave yourself two shots at it, right? And so you have to statistically discount your finding because it could have gone either way. That is if your prior hypothesis is it has to go in one direction, you're on stronger footing. But you just suck it up and run a few more kids. Yeah?

OK, so good. So this also shows that ratio dependence, right? They're better at it with the big differences than the small differences. OK? OK, so that's infants having this very, very early, at least in very crude form.

What about animals? OK, so let's meet Mercury the macaw. Here's Mercury the macaw.

## [VIDEO PLAYBACK]

- To a human, the order of the symbols shown on the above screen are obvious. We have all learned from a young age which of these symbols represented--
[END PLAYBACK]

NANCY Oh, what a good birdie.
KANWISHER:
[VIDEO PLAYBACK]

- --the lowest number and which the highest. However, for Mercury, the blue-headed macaw we see here, he has had to learn by trial and error the specific order to press these symbols to get a piece of food. It took him quite a long time.

Mercury's brother Mars can do a bit better than that. He has begun to learn the more general concept. That is the symbols will always have an order. So when presented with a new list, he was able to rapidly decipher the order of new symbols, in this case kingfisher, warhead, hawk, hummingbird.

Pressing randomly on the screen would have led to him receiving the correct answer less than $1 \%$ of the time. He's clearly doing better than that. This is interesting, as it shows the very basic aspects of cognition related to numbers are present in an animal that is very distantly related to humans.
[END PLAYBACK]

OK, mostly, I just showed that because it's cute. But it's impressive ordering. OK? Still, he's kind of slow. I think it only goes up to four things. OK, so now we're going to meet the chimp Ayumu, who lives in Kyoto and who's the son of a very famous chimp named Ai, who was like a number wiz. But anyway, here's Ayumu.
[VIDEO PLAYBACK]
[END PLAYBACK]


#### Abstract

NANCY I know. I can only catch the first three. And then it's like I can't even tell if he's correct, except from the tone. KANWISHER: Pretty good. [VIDEO PLAYBACK]


[END PLAYBACK]

NANCY Oh, got one wrong. Anyway, mostly gets them right. Pretty impressive, huh? OK, so that's cool. And order is KANWISHER: clearly relevant. It's part of the space. But it's not the same as quantity or number, right?

OK, so now we're going to skip to the honeybee, just for kicks because this paper just came out a month ago. And I think it's awesome. Honeybees have 1 million neurons. And if you're impressed, don't be impressed. Remember like a mouse has 100 million. And we have 100 billion. OK? Six orders of magnitude. OK, so 1 million is like not-no. eight orders of magnitude. So 1 million is not that many, right?

OK, and further, these guys branched off from us, evolutionarily, a very long time ago, 600 million years ago. So they're tiny little guys, not very many neurons, totally different kind of thing. Who would think they have any kind of numerical abilities? Of course, they wouldn't, right?

Oh, and yet, they can do arithmetic. OK, so here's the design. So here's what these guys did, this wonderful lab in Australia. I love this stuff. OK, so they trained these honeybees.

This was a chamber like this. Honeybees fly into the chamber. And they see a number in a color right here. It's blue. And it's two. OK? And then there's a little entry hole. And they can choose to play or not play.

If they go into the chamber, then they're in this interior space, where they get to make a choice between that pattern and that pattern. OK? And there's a little pole underneath each pattern. And if they light and they land on the pole, they can get some liquid. OK?

So in the blue case, they're rewarded over trials. That if it's blue, that means they should add one to this number. And hence, that would be the correct answer. And that's the incorrect answer. OK? That would be amazing. Yeah? And if they choose the wrong number, they get some nasty quinine. OK?

All right, in contrast, if the shape out front is yellow, then they have to subtract. So that means they have to keep track of this number and go in there and choose that number minus one. All right? OK, so keep in mind, oh, so they balance the total surface area. It doesn't look like in this figure. But it says in the method section they did. I believe them.

And further, realize that when the bee is in here, he has to be holding that number in memory and adding one to it or subtracting one to it to figure out what to choose here. So this is pretty sophisticated. It's not like they're side by side, right? OK, and yet, they're pretty good at it. Here's accuracy over training trials. By 100 trials, they're over 80\% correct. Pretty amazing, isn't it?

OK, so then, in any good animal or infant cognition study, you want to show whether it generalizes. So then they test the same ability with new numbers. I forget what this range was. But it went one to four or something like that. And then they go to five or six, just to generalize the numbers, and different shapes than were used in the training trial.

And the accuracy is around mid 60s. It's not quite as good. But it's still very good. They're not being reinforced here. And they're still doing the task.

Now, what are the pink and blue bars? OK, so you might think, well, is a bee just going to the one that has more or less? So instead of learning add one, he's learned go to the larger number, larger than the one that you saw at the entry chamber, or go to the smaller number.

But no, that's not what they're doing. Because the pink bars show the performance when both of the options are in the same direction, right? So the thing is blue. So he's doing addition.

And he sees a two. And he goes in, he has a choice between three or four. He can only do that if he knows the difference between adding one and just taking the thing that has more, right? And he's well above chance in the pink bars.

OK, so he's not just saying, choose the one that has more or the one that has less. He's adding one, pretty accurately, I mean sort of accurately. Better than chance. OK?

All right, now that's pretty cool. But adding one, subtracting one, it's cool. But do they really have abstract concepts? Do they understand the concept of zero? OK, so paper was published last year arguing that they have the concept of zero. Here's how it goes.

Same lab trains them, in this case, just on greater than or less than. So the bees are given a choice like this. And one set of bees is trained on greater than and one is trained on less than. So this set of bees trained on greater than chooses this one and then this one and then this one and so on. OK? Another set of bees is trained to do the opposite. All right?

OK, so that's the training phase. Then we want to test in a generalized situation. So now they're tested with different shapes and different numbers, so threes and fours were. Maybe threes weren't used. I forget. There's some numbers in here that were not used before.

OK, so you test them with new shapes. And here is accuracy for less than or greater than. Chance is $50 \%$. And they're $75 \%$. Not bad. OK? So they get more than or less than.

OK, now we want to test the generalization. OK, oh, yes, sorry. This is where they changed the range of numbers. So the bees had not dealt with sixes before. So now they still have to do greater than or less than with a new numerical range. And they're still well above chance. OK?

So then finally, they test zero. OK? So the bees that have to do less than have to say which of those is correct, all right? And you can see-- where did it go? Where's the zero one? Right here. And they're well above chance for both less than and greater than. OK?

So we could quibble about whether that's a concept of zero. But the cool thing is these bees had not been tested with a blank card before. And they spontaneously get the idea that that is less than one or two or three or anything else. Yeah? So arguably, they have a concept of zero with no training and only 100 million neurons.

OK, so all of that is in trained animals. And we can see some of these kinds of abilities even with untrained animals. And I will tell you just one more animal experiment because it's my all-time favorite ever and the simplest one in the whole set.

This was done a long time ago by Church and Meck. So here's what they did. This is done in rats. They have a training phase, where they train the rats to press the two lever if they see two light flashes or hear two sounds. And they press another lever, the four lever if they see four lights or hear four sounds. OK?

That's kind of basic animal training. It's a rodent. They're good at this. No big deal. But then after the animals have learned this, they spontaneously throw, in the testing phase, a trial with two lights and two sounds.

And the rats press the four lever, first time. No training. No nothing. Spontaneous addition. Spontaneous abstraction across tones and lights. Pretty awesome, huh? So it's not just that you can reveal these abilities with elaborate training.

OK, so we have all of these different kinds of evidence of an abstract number sense. And they're present in newborn infants. And they're present in animals. And they just seem to be part of our basic cognitive machinery, machinery that we share with animals.

So how are they implemented in the brain? OK, so a little neuroanatomy reminder of some basics. This is a weird angle of a brain. It's kind of like this, kind of back of the head, front of the head, temporal lobe, frontal lobe around the corner. Everybody oriented?

There is one of the longest sulci in the brain that starts about here. On me, it goes like this. And it curves around like that. It's back here. It goes up. And it curves over. OK?

It's called the intraparietal sulcus. And I mention that just because it's in a lot of the number literature. You saw it in the paper you guys read for last night.

And above it is the superior parietal lobule. And below it is the inferior parietal lobule. And none of that matters other than that a lot of the action is in the parietal lobe, particularly up here around the intraparietal sulcus. OK?

All right, so studies that have looked at this includes some classical studies of patients with brain damage and something called acalculia. That means loss of ability to calculate. OK? And so there's two basic kinds of acalculia that are really interestingly different.

So there's one acalculic patient who has left parietal lobe damage, that same region I just talked about. And this person is bad at approximation. So the kinds of dot array tasks that I gave you guys, this guy, after brain damage right here, is really bad at that kind of stuff.

And interestingly, he's more impaired on subtraction than multiplication. So for example, hes worse at, what is seven minus five than what is seven times five? So think about that for a moment. And think about what that might mean, especially in light of another acalculic patient who has a very different presentation.

He's got left temporal damage. His approximation is fine. So all those kind of dot array kind of tasks and tone tasks that I told you about, he's good at. This guy shows the opposite. He's more impaired at multiplication than subtraction. So do you guys have any-- oh, so first of all, you put these two patients together, and what do you have?

| AUDIENCE: | Double dissociation. |
| :--- | :--- |
| NANCY | Yeah? What? |
| KANWISHER: |  |
| AUDIENCE: | Double dissociation. |

NANCY Double dissociation. Right. Two patients with opposite patterns of deficit, right? If we just had one, then we could KANWISHER: maybe tell a story. But it wouldn't really know. But we have two, and they have opposite patterns. And now that really kind of constrains the interpretation. David.

AUDIENCE: Can the first person add fine?

NANCY Good question. He's not very good at adding.
KANWISHER:

## AUDIENCE: Oh.

## NANCY Thoughts? What do you think it means?

KANWISHER:

## AUDIENCE: It might mean that the addition and subtraction [INAUDIBLE] use the same like--

NANCY Used what?

## KANWISHER:

## AUDIENCE: Like they use the same area.

NANCY Yeah. So one hypothesis is that addition and subtraction are just a different beast than multiplication. Different
KANWISHER: parts of the brain do those things. Totally possible. But there's a kind of more intuitive interpretation.

AUDIENCE: Well, I think people tend to memorize times tables.

NANCY Bingo. Bingo. Often, like the right answer is something that's like right in front of you. Just think about, what is it KANWISHER: like to do that? How do you do seven times five? You don't think about the meanings of the numbers. You just blurt out 35. Right? Right? It's not a very rich number task. I mean, it's a number task. But it's a concrete, rote, verbally memorized thing. Right?

And so the idea is that those verbalized concrete number facts are in one domain. One set of brain damage would impair those. And it's a different thing to impair the actual representation of numerosity. And the idea is that this person is the one with the real damage to the approximate number system. Right? Yeah?

AUDIENCE:

NANCY

## KANWISHER:

## AUDIENCE:

## NANCY

KANWISHER:

## AUDIENCE:

NANCY
KANWISHER:

## AUDIENCE:

NANCY
KANWISHER:

## AUDIENCE:

NANCY

## KANWISHER:

Does that mean that patient can be it is a problem doing the seven times five normally. But when they ask for summing seven for five times, they're not very good.

Yeah. Well, I think the approximate number system might have a tough time dealing with summing seven five times. So yeah, it has limits, right? It can deal with it can add two approximate things. But you might really lose your mind if you tried to do a whole string of it. Yeah? Yeah?

If he was working on the same digits, like maybe seven plus seven or seven minus seven, expect him to maybe do that fairly easily if that's the case, right?

Say more.

If it's a case that his approximate--

Yeah, yeah. Yeah.

He should be able to do seven minus seven fairly easy. Because you know that when you subtract the same things, you're going to get zero.

Yes. But it's an interesting question, actually, whether that would be part of that system or whether that's kind of more abstract formal thing you learn. So I think it depends how you do it, right?

So one of the ways-- I didn't talk about this. But those same experiments adding, say, adding dots to dots, those were also done with little kids. And there, what you do is you show-- I don't really remember what it is. But you show some array of things, and you hide it behind a screen. And then you show another array and hide it behind the screen. And then you reveal the screen. Like how many things are there? That kind of stuff works spontaneously.

So it might tap into that system. I think that's an interesting question. I'm not totally sure how it would go. Yeah? So the second person is bad at recall across the board? Or is it just with numbers?

Just with numbers. Yeah. I mean, there's always a little bit messy. The patient literature is always like some other random stuff. And how do you account for that? And there's lesions in other places. But to a first approximation, these are reasonably number-specific deficits. All right?

OK, so that's a bit of a hint from the neuropsychology literature. But there's mainly these two patients and some other like messier ones. And so one wants to use neuroimaging to get a better picture of it.

Of course, that's been going on for a long time. And so here's one of the early papers from Stan Dehaene's lab. This is a top view of the brain. So this is this parietal zone. And this is what is often referred to as the horizontal segment of the intraparietal sulcus. hIPS to its friends. And it's that sulcus I talked about that goes up like this. It kind of curves over. And it's like this bit right there. OK? That little orange strip.

And so what he's saying in this review article from a long time ago is that that region is activated only when you do calculation. He means basic arithmetic in this case. Not when you do all these other things.

But when this paper came out, I'm like, yeah, right. I don't think so. I can't tell you how many experiments I've run and seen big ass activations right there on tasks that have nothing to do with numbers. So looks good. Sounded good. He got away with it for a while. And it's not true. Yeah?

## AUDIENCE:

NANCY

## KANWISHER:

## AUDIENCE:

## NANCY

## KANWISHER:

So is the reason sort of high enough that you can zap it?

Terrible. Being filmed too. He's a really smart, nice guy. I just like when people are a little bit fast and loose and make a big claim, which you can tell at the time isn't quite right. It's a little bit annoying. Anyway. Sorry. Go ahead.

Yeah. Is the region high enough that you can zap it?

Ah. We're getting there. Yes, indeed, you can. But let's do a little more basic stuff first. OK, so the claim is that this hIPS thing is the locus of the approximate number system. That was the early claim. OK. And for further, the claim implicit in this article in this figure is that it's involved in numerical representations only, not any of these other things, grasping tasks, manual tasks, eye-movement tasks, et cetera, et cetera, et cetera.

OK, really? And as I mentioned, like me and lots of other people had seen it looks like the same regions activated in all kinds of other situations, especially those involving reasoning about spatial location. You guys got short shrift six weeks ago. I meant to talk about the parietal lobe and its role in high-level vision. And it just somehow went by the boards. But all this stuff is involved in aspects of vision, particularly spatial vision, knowing what is where. OK?

And so there's an alternate view, which is that there's no specific brain region that's specifically all only involved in discrete number per se. Instead, there's a common region for processing magnitude of almost any dimension, whether discrete or continuous, right, that approximate number system or your exact number system, and that it builds on previous representations of space. OK? For example, the number line, right?

So you guys read this article for last night. And just to review what the key point was, this is, again, the kind of aerial view with the parietal lobe here. And that's the hIPS region, yeah, that was in the previous slide. And you can see it's this horizontal part of that sulcus way up in the parietal lobe.

And the yellow and green means that there's overlapping activation for both symbolic calculation, that's like with symbols, and for nonsymbolic calculation. That's like dot arrays stuff like that, right? And so it's activated for both of those.

And the point of this paper is, first of all, that there's also overlap with the eye-movement system, right? And so here, they're really asking, is this spatial representation kind of co-opted in your representation of number using a kind of spatial number line, right? It makes perfect sense. Animals need a representation of space. It's like extremely basic, right? And once you have that, you can co-opt it and represent numbers in that same spatial code.

And as you guys all read, the cool result from that paper, which is also from Stan Dehaene's lab, is that when you take that region right in there, you take those voxels in there, and you train them on making leftward versus rightward saccades. So now you have a classifier that looks at the pattern of activation there, can distinguish a leftward versus a rightward versus saccade. I'm just reviewing this. Hopefully it was clear enough.

That same classifier can then distinguish subtraction versus addition. Did you guys all get that from the paper? Yeah? It's pretty cool, isn't it? Anyway, so that's kind of nice evidence that the same spatial system that's used in spatial attention and eye movements has been co-opted to represent numbers as well. OK. All right, so I just wanted to incorporate that. In case anybody missed what the paper was about, those were the key points.

Other early studies have asked more directly this question of whether different kinds of magnitude are all represented together in the brain. And this study is quite clever. They used a variant of the fact that I showed you guys before.

Remember when saying whether the number is greater or less than 65, it's harder when it's closer to 65 than when it's farther from 65. OK, even though I was showing you symbols, that was key thing, right? So that's called the distance effect, right? And that's true for all comparisons.

And so this study exploits that distance effect. And they use stimuli like this. And they ask, which one is larger? And it could be larger in absolute size. Like the two is larger here. Or it can be larger in number meaning like the seven is larger.

OK, so in different blocks, you're saying, which one is physically larger? Which one is numerically larger? Which one is brighter? That would be this one here. And then they just have a control with letters. OK?

And so then-- sorry. The design is slightly complicated. So there's these three main tasks and a control task. But then within each, they have the difficult version and the easy version. And the difficult version is when the comparisons are close, two similar brightnesses, two similar numbers, two similar sizes versus two larger ones. OK? So that's what all this garbage shows.

OK, so then you do that subtraction. You look, and you say, OK, what parts of the brain are more active when you do the difficult versus easy number comparison? Like saying, which is larger? It's not that difficult. But two versus three versus two versus seven. OK?

And so what they find is that similar regions of the brain are active for all three of those kinds of comparisons. OK? So it's not like you get just one for symbolic number or for the two magnitude tasks. All of those different kinds of magnitude activate the same regions.

And so the conclusion is that number and size and brightness engage a common parietal spatial code, OK, an overlapping region for all of these. Does that make sense? OK. And so that shows, in this case, that it's not just symbolic number but also magnitude. Which one is bigger, right? It's kind of continuous magnitude idea. OK? OK.

Right. So one worry is that, in each of these cases, they're comparing a difficult condition to an easy condition. And so maybe the regions they got are just engaged in any kind of task difficulty. Maybe if they had done a syntactic task on language stimuli that was difficult versus easy, they would get the same things. From this experiment, we don't know. We'll talk more about that in a couple weeks when we talk about language, right?

But here's at least one control that deals with that sort of and which does a TMS experiment, as you suggested a while back. OK, so this is kind of cool experiment. I mean, it's weird, but sort of cool. OK, so what do they do?

They use-- OK, so they have, again, an easy task and a hard task. Again, it's the thing greater or less than 65. Not very hard, right? The hard one it's that hard. But so is it greater or less than 65 ? And it's either a symbolic number, or it's a dot array. You can't really see it, but there's a bunch of teeny dots in there. Or in the other condition, they have to say whether that ellipse is more horizontal or vertical. OK?

And so you spend a lot of time, before you run the experiment, measuring reaction time and accuracy to balance difficulty within the easy conditions and balance difficulty within the hard conditions. OK? So then what they do is they do something called offline TMS. OK?

Offline TMS, I didn't talk about this much before. The standard kinds of TMS, you stick the coil right on the subject's head. There's a subject doing a task on a monitor. And somebody is standing there holding the coil. It's really kind of rudimentary.

And right at a key point of the trial, you deliver a zap to disrupt that part of the brain. And you find out how much that interferes with performance on that task. That's the standard online kind of TMS thing.

But there's also offline TMS, where you zap people at a slow rate for like 10 minutes. And then the idea is that you've kind of generally disrupted that piece of brain for, say, another 10 minutes. It's a little bit scarier. But it's just like 10 minutes, right?

OK, and so that way, you don't have to be quite so fancy about the precise timing. You can just kind of reduce its effectiveness for a whole 10 minutes. OK, so that's what they did here, offline TMS. So you sit there and get zapped for 10 minutes slowly here. And then you do some math tasks. OK.

OK, so what they find is that zapping the left intraparietal sulcus disrupts the magnitude tasks on both numbers and dots. But it doesn't mess up the shape tasks with the ellipses, even though the ellipses are balanced for difficulty. OK? So that's at least a little bit of an argument that it's not just about generic difficulty, at least in this experiment. OK?

All right, I think that's what I just said. So that's some evidence for a role of at least the left intraparietal sulcus in both symbolic and nonsymbolic number. Again, nonsymbolic number just means dots without Arabic numbers, not just any difficulty.

All right, so that's all very nice. But it's crude as hell, right? We found these big, blurry chunks of brain that are implicated. And we zapped a big chunk of brain and slightly reduced performance. It's like, OK, better than nothing. But it's not very impressive.

What are the actual neurons doing in the brain? Well, now it becomes really important and useful that this approximate number system that I've been talking about is also present in animals. And that means we can use animal models.

And we can record from individual neurons in the parietal lobes of monkeys when they do number tasks to find out what actual neurons are doing. OK? And so there's a guy named Andreas Nieder, who's been doing this for a long time. And he has some pretty remarkable data.

And so he starts by training monkeys to do a number task. So here's what the monkey sees. Monkey sees a sample, some number of dots. And then there's a memory delay, in this case, one second. And then he has to do a matching task and choose that array, not this array. OK?

So he's got to remember that there's three dots and choose the right three. And notice that the sizes and configuration of the dots have changed. So we have to do something more like remember three in whatever mental monkey E's version of three exists. OK?

OK, simple matching tasks. Then he records from neurons in the parietal and frontal cortex in monkeys. And he finds neurons that are sort of specific for number.

OK, so here's time in that task. This is the time that the sample is presented right here. And here is the response of a single neuron that likes two more than anything else. OK? And that too, notice, is all different kinds of spatial arrangements and sizes of the dots. What's common about all of them is that it's two.

Next best, it likes four. OK? And it generalizes across number from there. So it's approximate. It's not like high for two and zero for everything else. It's got a kind of generalization gradient. But it prefers two. OK? So that's a number neuron. Yeah?

OK, here's a six neuron. This neuron likes six. Here it is same task during presentation of trials here. Red is six. Next closest is like eight and maybe 10. So it also generalizes as well, but it responds more to six than anything else. Pretty awesome. Huh?

OK, now that doesn't tell us how it was computed, right? So finding a single neuron that does something spectacular is thrilling. We all love it. It's great fun.

And we're closer to the neural circuit because we found a neuron that seems to be part of the action. But notice it doesn't tell us how that neuron made that computation, right? What are the circuits that led into it, that enabled it to be specific to six or two? But it's still cool.

OK, but next, we want to know, how abstract are those neurons? This is just dot arrays. OK? And they're just presented in one array. So next, Andreas Nieder trains his monkeys to keep track of the number of things that happen over time.

It's not a spatial array. It's a temporal sequence. OK? So we have to see that there's four things coming in here and then choose the array that matches with four. OK?

See how this is the way to ask how abstract those number neurons are. Are they really representing the abstract magnitude of two or six or whatever it is. Or are they representing something about the shape of a two-type array or a six-type array.

OK, and they can also test over different modalities. So now they present four different tones. And the monkey has to choose the four dots. OK? Now it's both over time and over sensory modality.

So how abstract are those number neurons? OK, they're pretty abstract. So here are a few number neurons. Cell one is in the blue colors. And here is its response in light blue to dots, one dot, two dots, three dots, four dots.

And here is the same cell responding to sounds. It's specific to one, both for sounds and dot arrays. Isn't that cool? And you see the green cell is selected for two, whether in dots or sounds, and so forth. Pretty cool, huh? So these are very abstract number neurons. Does that makes sense? OK. OK.

OK, now these monkeys are trained on number tasks. So you might think that these kinds of abstract number neurons-- and they're trained to do the generalization from tones to arrays. So maybe those neurons wouldn't live in their brains if they hadn't been trained to do that.

But I don't have time to show you all the data. But in subsequent work, the same team has recorded from monkeys before any training. And you find similar number of neurons.

So it does seem like these are things that exist in-- and remember that's consistent with what I said before, which is that a lot of these number abilities are present in animals without any training and in newborns. And so it makes sense that some of those neurons would be around even in advance of any training.

## AUDIENCE:

How many neurons did they have to look at it to find?

NANCY

## KANWISHER:

Oh, that's a good question. I forget what percent it is. We could look it up in the Nieder paper. Yeah. It's not like you record from thousands, and you find 10 , right?

Remember they know where to look from, first, the human lesion literature and then the human functional imaging literature. And then there's also monkey neuroimaging literature where you can have monkeys doing dot tasks. So you can know where to look. Because the brain's a big place. If you're just sticking electrodes all over, God help you, right?

So they know to go up in that parietal lobe if that region is homologous between humans and monkeys. And there's a lot of other evidence that that region is homologous. So they know how to get in the right zone. And I'm sure, once in the right zone, they're not all number neurons. I'm sure it's a relatively small percent. But it's not a trivial percent. Yeah?

## AUDIENCE:

Do we have sense for how fractions are represented? Because all of these seem to be discrete. Or [INAUDIBLE], any ideas?

NANCY
KANWISHER:
Yeah. Well, it's tricky because, certainly, at the single unit level, you'd have to either find some natural version where monkeys think about fractions naturally or teach them about fractions, which would be really hard. Because, for some reason, fractions are just really hard.

Like all the people who study math education, it's like the key problem is, how do you get kids to understand fractions? I don't know why they're such a tough thing. But apparently, it's like a real dividing line, the kids who get fractions and the kids who don't.

So I'd have to think. But, occasionally, there are patients with electrodes in their brains. And one could look at that. Actually, I took this slide out, but there's a paper that came out last year where they found number neurons in humans as well.

I took it out because I didn't know how to integrate it in the lecture. Because the number neurons are deep in the medial temporal lobe, far from the parietal lobe. And it's like, I don't know how that fits. I don't know if that's the same thing or something else.

But anyway, there are at least some number neurons that have been found in humans. And you could, in principle, look for number neurons up in the parietal lobe. In fact, I have a guy I'm trying to collaborate with. I'm begging him to collaborate with me. He's got two people who have arrays of electrodes chronically implanted right up in this region here because they are paralyzed.

They had spinal damage. And like Michael Cohen's lecture, he's got arrays of electrodes where he's trying to use the neural responses there to direct robot arms. And so there's two of these people who have these chronically implanted things. I'm like, oh, please, please, please, can I collaborate with you and get responses from your patients' neurons? Was there a question over here a moment ago? Sorry. I thought I saw a hand go up.

OK, so let me wrap up. So I've been arguing that this approximate number system is shared with animals and newborns. It's a pretty basic system that lots of animals have. It follows Weber's law, which you should remember. I don't like testing you guys on esoteric facts. But Weber's law is a very fundamental fact. And you should know it about perception and, in particular, about number.

It tells you that the ability to discriminate two numbers goes as the ratio, not as the difference of those numbers. And that these approximate magnitude representations measured both behaviorally and neurally in humans and animals are very abstract to the particular objects, to the modality, to whether they come in over space or time, et cetera, whether they're represented in symbols or arrays of items. OK?

I mentioned that there are big individual differences in humans in the precision of the approximate number system. And that is predictive of later arithmetic abilities independent of IQ. And we talked about the horizontal segment of the intraparietal sulcus as a key locus for the approximate number system in humans, including number-specific neurons.

And we also talked about, both in some of the papers I mentioned and the paper you guys read, that there seems to be that that approximate number system up here in the parietal lobe, so far, doesn't seem to be one of these extremely specialized systems like faces and motion and navigation, which may turn out to be less specialized later with pending more data. But at the moment, we can already see that these number representations overlap a lot with representations of space, shown perhaps most dramatically in the paper you guys read showing cross decoding between eye-movement direction and arithmetic operations.

OK, hang on. I'm almost done summing up. Number neurons, we talked about that. Yes, so we'll give the last word to Stan Dehaene, who started off with this very extreme view and has evolved to a still interesting but slightly less extreme view.

He says, the brain treats number like a specific category of knowledge requiring its own neurological apparatus in the parietal lobe. But when it comes to subtler distinctions, such as number versus length, space, or time, the specificity of hIPS vanishes. No part of hIPS appears to be involved in numerical computations alone.

In fact, he goes further to say that the human brain, in general, is neither anisotropic white paper, like equipotential, where all the regions are equivalent, nor a neat arrangement of tightly specialized and wellseparated modules. All right? Anyway, OK, there was a question. Sorry.

AUDIENCE: [INAUDIBLE] just then having this, I guess, easier time with approximate numbers, given more of an interest in that.

NANCY
KANWISHER:

That's a really, really good question. And I am sure there are data on that. And I don't know what they are. But I will go look. I always say that. But, Dana, will you send me an email right now to go look up whether the prediction from childhood ANS to adult arithmetic abilities has to do with an interest or you might say just an emotional response. Like if you suck at it, it feels bad. And you become avoidant, and you get all dysfunctional about it, right?

We all have-- I mean, most of us have domains where we do that. And math phobia is a real thing. And who knows. It could start in there. So yeah, good question. I don't know. I will look that up. Other questions? OK, see you guys on Wednesday.

