

The following content is provided under a Creative Commons license. Your support will help MIT OpenCourseWare continue to offer high quality educational resources for free. To make a donation or view additional materials from hundreds of MIT courses, visit MIT OpenCourseWare at [ocw.mit.edu](https://ocw.mit.edu).

**ABBY NOYCE:** One of the things we've been talking about when we're talking about how vision and the visual system works is that the visual system is not very interested in places where the world is all the same. Clear blue sky, clear smooth surfaces, your visual system looks at that and says I don't need a whole lot of information to give you a perception about this.

But it really pays a lot of attention to places where things change, where there's motion, where there's edges, where color changes, where there's lines. And we're going to talk today a little bit about the neural processes that manage to grab onto these sorts of features.

So you guys talked yesterday about ganglion cells, right, in the retina? Yes, no.

**AUDIENCE:** Yes.

**AUDIENCE:** Are those rods and cones?

**AUDIENCE:** She mentioned it.

**ABBY NOYCE:** OK. So what happens is-- we'll back up then. So there's a bunch of different layers of cells in the retina, right? Here's the back of an eyeball. Here's all of our photoreceptors, rods and cones. And then in here, there's a bunch of different layers of neurons. Neurons, and there's some that do horizontal processing and more. Lots of neurons.

So the retina is this sheet, right? It's got photoreceptors furthest to the back of the eye, and then it does this preliminary processing. And one of the things that is important here is that this set of neurons that is closest to the inside of the eye-- if you look straight in through somebody's pupil, this would be the surface of the retina that's closest to you. Remember, the photoreceptors are on the back, and the layers of processing come forward-- are called ganglion cells. And ganglion cells are the ones that actually bundle all their axons together and line up and form the optic nerve, right?

So ganglion cells have a particular kind of receptive field. A cell's receptive field is the part of the field of vision that it responds to. So for a given-- any given photoreceptor is responding usually to a very small part of the visual field. These have this very small and very simple receptive field.

They respond-- if there is light there, they change their response. If there is not, they go back to their baseline. And some of them respond to different colors preferentially, but for the most part, they have these very simple receptive fields.

Ganglion cells, on the other hand, because of what's called lateral inhibition, have center-surround receptive fields. So each ganglion cell is looking at a little bit of the visual world and this is kind of the classic representation of an on-center ganglion cell.

So this is a cell that would respond if it's looking at a dark surface or a dark screen like this, and it had a little white dot right where the center of the receptive field is-- this is an excitatory center and an inhibitory surround. So this ganglion cell would respond a whole lot to this sort of stimulus.

Whereas if it's looking at just a blank field, then the excitatory center is still going to get stimulated, but the inhibitory surround is also going to get stimulated. And so the excitatory and inhibitory stuff that's feeding in cancels out.

So you can think of this as if we're looking in the fovea in the center of your eye, where all the receptive fields are really small because your visual system is doing detail, it might look something like this.

We've got one cone. That's not what it looks like, I know. They've got all that squiggly stuff. And this cone-- and we've got our ganglion cell down here. And this cone is feeding in an excitatory impulse to that ganglion cell, and that's going to be the center of this ganglion cell's receptive field. But all of the cones that surround this cone would be feeding inhibitory impulses to the ganglion cell.

And this is just straight up excitatory and inhibitory synapses, right, like we talked about last week? So that if just this cone gets stimulated, then there's only an excitatory input coming into that ganglion cell, and the ganglion cell will, in turn, fire. If there's input coming in from both the center and the surround, then the mix of excitatory and inhibitory is going to actually decrease, probably average out to zero, the way most of these are weighted.

If the cell is looking at a stimulus that just looks like that, so that only the inhibitory part is stimulated and the excitatory part isn't getting anything, then it's going to actually decrease its baseline firing rate. So all these cells kind of have a base firing rate that if they're not getting any kind of stimulation, they just tick, tick, tick. They just go every so often. And then that rate

will increase as the cell gets more excitatory stimulation, or it can actually decrease as the cell gets more inhibitory stimulation.

So ganglion cells, we get on-center. We also get off-center ganglion cells. These are inhibitory in the center and excitatory in the surround. Just like the on-center, the off-center cell, if it's looking at a plain field like this, it's not going to respond very much. The excitatory and the inhibitory parts cancel out. But this cell will be inhibited by the single white dot and excited by the ring with the dark dot.

So they're responding to opposite sorts of simulations, but in both cases, they're not responding to these kind of featureless fields. They're responding to places where the visual system is doing something more-- where the visual stimulus is doing something more interesting.

So like I said, so ganglion cells are the cells whose axons run all the way down the optic nerve, back into the lateral geniculate nucleus of the thalamus, and from there, they get passed to a new set of-- they terminate there. They synapse onto more neurons, and those neurons go to primary visual cortex.

So did Xander show you guys the scintillating grid illusion with the black squares and the white grid in between them? Did you talk about what causes that?

**AUDIENCE:** She said no one knows.

**AUDIENCE:** No, not that one. That was the other one.

**AUDIENCE:** No, she said no one knows for that one. Yeah.

**ABBY NOYCE:** So to some extent, it can be explained by looking at the ganglion cells. The other kind of classic example of this-- I wish I had my slides-- is what's called the mock band illusion, where if you put rectangles of light gray and dark gray next to each other, then right at the border between them, the light gray one looks lighter and the dark gray one looks darker compared to the rest of the rectangle. And again, this kind of ganglion cell response can explain some of that.

So that there scintillating grid, if you've got-- new piece of board. You've got your boxes, right? Box, et cetera. That's a lot of chalk dust.

So think about what's happening-- think about what's happening to ganglion cells with-- let's just think about on-center ganglion cells as they hang out here. So an on-center ganglion cell that's scooched right up against the edge of one of these boxes, so center-surround, its center is going to get inhibited by the white part of the grid that it's on. The center is going to get excited by the white part of the grid that it's on, right?

And half of the surround is going to be inhibited but the other half isn't, so the excitatory part still trumps the inhibitory part. So this ganglion cell will actually respond more than a ganglion cell that's only looking at the white part because of how part of its inhibitory surround is not being exposed to the white. Part of its inhibitory surround is looking at the black portion of the square.

And one of the things that people think is happening with this here scintillating grid illusion is that ganglion cells that are here and here and all around it, that are scooched right up against the edges of the squares are firing more than a ganglion cell that's out here in the middle of the intersection. So it ends up looking like the bits that are between the squares are brighter than the bit that's in the middle.

So that's one theory. And I like it as an example of how you can take this really simple properties of a particular class of nerve cells and what it responds to, line a couple of them up together, and hey, look, a perceptual effect, and perceptual effects are cool.

**AUDIENCE:** Do we know which ones are on-center and which are off-center?

**ABBY NOYCE:** You can test it. I mean, the way people find these is-- and you've got both. The way people have found them is you've got your classic anesthetized cat lying on a table, and you're showing it little dots of light. And you're sticking an electrode into the cat's retina, actually or-- yeah, probably directly into the retina or maybe into the optic nerve and picking up the axons-- and measuring what sorts of stimuli are causing these cells to fire and which aren't. Which is how you find that each cell has a very specific region of the visual field that it looks at, and it responds in one of these two characteristic patterns.

So ganglion cells, scintillating grid. So people knew for quite some time, probably from the early 20th century, that ganglion cells have this receptive field pattern. And people were trying to figure out how cells in visual cortex respond and how cells in the thalamus and the lateral geniculate nucleus respond.

Remember, your information pathway goes like eye to V1, right? So the thalamus here is taking in the sensory input, doing a little bit of processing, and passing it along to cortex. There's also actually an awful lot of information that comes from all of these other parts of visual cortex that goes back to the thalamus.

So there's a lot of top-down influence on the thalamus, and nobody is exactly sure what that processing is doing. Some theories are kind of like it lets you compare what you're currently looking at to what you were looking at a moment ago, so you can see things like motion and changes and direct your attention to it.

LGN also seems to be involved. You've got a reflex, more or less. So if you hear a loud noise off to one side, you'll usually turn and look at it. And that seems to be auditory information coming into the lateral geniculate nucleus, coming into the thalamus, at least from the auditory system, which tells the lateral geniculate nucleus to send you a signal to direct your visual attention over where you heard the noise coming from.

All right. So cells in the lateral geniculate nucleus have on-center and off-center receptive fields with, this is called center-surround antagonism, that pattern, where the center is doing one thing and the surround is doing the opposite. And the cells in the lateral geniculate nucleus have pretty much that same pattern of response. So a given cell will respond to a given thing.

Cells in the visual cortex, however, don't. They do something different. You guys, OK? So the classic example of this is two guys named David Hubel and-- shoot, what was his name? Like Thorston or something. Thorin, no, that's somebody else-- and Wiesel.

Hubel and Wiesel were researchers in the '50s, who were working with anesthetized cats, trying to find receptive fields for cells in the cat's primary visual cortex. So cat on table so that it's facing a screen. The cat's anesthetized so it holds still, and it has to look at the screen.

And they put little microelectrodes into these parts of visual cortex and tried showing the cat different kinds of stimuli, dots, lights dots, dark dots, dots in different parts of the visual field. all of the stuff that will make cells in the lateral geniculate nucleus so the ganglion cells in the retina fire like mad, right?

And it didn't work. And eventually, they managed to find one cell that sometimes when they showed it a dot, it responded to different parts of the visual field. And they didn't really think it

was the dot of light they were showing it that was the key stimulus.

So eventually, they managed to figure out that what was triggering the cell to respond was, as they pulled slides in and out of the side projector they were using-- old school technology here-- that as the edge of the slide kind of cast a shadow that moved across the screen, the cell was responding to that, to a line, the particular angle, in a particular part of the receptive field, moving in a particular direction or moving perpendicular to how the line was oriented. So and once they had found that, they said, hey, look, these cells are responding to something completely different than everything in the LGN and in the retina.

And pretty quickly, other people started working on this. And they've managed to find three different main types of cells in V1, and all of them are dependent, really picky about orientation. They're all basically line detectors of one kind or another.

And the simplest one are cells called simple cells, which respond to a line of a particular orientation or an edge of a particular orientation in a particular part of the visual field. So they're like all of-- like the cells earlier in the system, like the ganglion cells and the lateral geniculate cells, they're very picky about where in space their stimuli are. And these cells look for lines of a particular angle.

So how do you go from cells that look for this-- how do you take that kind of information and pass it along and build a line detector using this kind of preliminary cell?

**AUDIENCE:** Say if you're looking at one thing and then a line moving, I guess, would cause multiple cells to fire, like just one after another.

**ABBY NOYCE:** Yeah, good. So yeah, it looks like a lot of what's happening with motion detecting is where you get sequential firing over a particular area of the cortex.

Frogs actually have cells in their retina, really early in their visual processing system that look for just a small dot moving around. They've got fly detectors to help them find their food. So they've got cells that respond to motion of a small stimulus. We don't have those.

**AUDIENCE:** I think I read that frogs also they can't detect their food if it's absolutely still. So if it's a fly on the wall and it's not--