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PROFESSOR: I'll let you know, we'll probably have two quizzes next week. I want to give you a very simple quiz that I used to give every year in 914, in which you simply list the cranial nerves, their names, the number, the name, whether they're sensory, motor, or both.

There's a table, I believe, in the book. So let me look at that and we'll send an email around about that. I think it's very useful to know. It's just one of those outlines that you need to have in your mind. So when you encounter it--

AUDIENCE: I think I memorized it. I don't know if you asked or not.

PROFESSOR: Yeah. I learned a little mnemonic. I think I give it in the book. I just memorized the mnemonic, and then I had no trouble. Because you hear those names enough that it's easy enough to learn it.

All right, so auditory system. We had ended by talking a little bit about coding, frequency, and intensity and the auditory nerve. And then how it's the spatial map of the basilar membrane is preserved in the organization of the axons coming into the cochlear nuclei here.

And I want to just review the sensory channels, what happens to that information that comes in through the eighth nerve, the auditory component of the eighth nerve. We're not going to talk much about vestibular. But if you learn the auditory system, vestibular is not that different. It's less studied, but the hindbrain mechanisms are studied the most because they are important in some human problems.

And of course, to the neurologist dizziness is a common complaint that people have, and he has to understand something about that system. But then we want to get to

studying the two major ascending pathways. In the auditory system you can divide ascending pathways pretty early on. And the pathways more concerned with identifying patterns, generally temporal patterns of the stimulus, and they keep frequency separated all the way up to the auditory cortex.

And then pathways concerned with localization in space, [INAUDIBLE] for that. So this is the system that you gradually come to understand more and more as we go through this. These are the basic channels.

We talk about a reflex channel, just short pathways that begin in the cochlear nuclei. Mostly ventral cochlear nucleus, but both of the cochlear nuclei that just project to brainstem neurons that have pretty short reflex connections. And startle is just one of them.

And then the cerebellar pathways, which could be considered a type of lemniscal channel. You see it here. I show a pathway from the dorsal cochlear nucleus, as well as through a reflex.

And then the lemniscal channels. There are two major routes to the inferior colliculus, two separate routes. And the inferior colliculus projects heavily to the thalamus and the medial geniculate body. Medial because it's-- in the human, it's another bump, a geniculate structure that's medial to the lateral one. The visual input comes in from the retina.

There is a smaller route that's more prominent in the large mammals. It was actually discovered first in the chimp. But then they looked with more sensitive methods and they realized it's even there in the rat. A pathway directly from the dorsal cochlear nucleus to the medial geniculate body.

But then there's a route that we think may be older, that is here in gray. I show it coming from the trapezoid body primarily. Which gets its input, many neurons in the trapezoid body region here, which contains a lot of crossing fibers related to the auditory system.

That travels through the reticular formation also to these nuclei at the lateral

lemniscus. The axons continue forward through the midbrain, some of them go into the superior colliculus. They don't terminate in the main nucleus of the medial geniculus. They terminate in cells around it, including many cells that are multi-modal.

There are uni-modal regions, too. This It's just called part of the posterior group of nuclei. But it includes a nucleus that's called the medial nucleus of the medial geniculate body.

I just want to say a little more about the eighth nerve. You know that axons representing different frequencies terminate in this organized way in the two nuclei. The nerve comes in from below.

And then a similar thing happens in the ventral cochlear nuclei, anterior and posterior divisions, and in the dorsal cochlear nucleus. Where axons from different parts of the basilar membrane, different parts of the cochlea, terminate at different levels.

So if you penetrate this way, you'd see the representational frequency. Now if you look at one of these axons, it travels rostrocaudally through the nucleus. This would be like those rostrocaudal axons that I just showed you along here.

What they're showing in this picture, this is originally from Nelson Kiang here at MIT. He still comes to talks here. I met him just the other day. He did a lot of this work on the eighth nerve. And what he's showing in this picture is different cell types in the ventral cochlear nucleus.

And he investigated how these respond to a pulse of sound, graphed here. This is the tone burst. And here's how the eighth nerve axon responds.

A lot of the action potential is right at the beginning. And then it sort of levels off at a lower level. And you'll note here, if you look at the responses of these cells, there's one type that pretty much matches this. They call it a primary-like post-synaptic train of action potentials.

So my question is, how can that happen? Because normally, no matter where you are in the central nervous system, cells don't fire when there's only one action potential. There's got to be a lot of summation.

Either it's ready to fire because there's a lot of other excitatory input coming in. There's also some spontaneous activity. And if it's near the point where it's going to fire anyway and it might fire a little earlier if there's input. But how does this happen reliably? And why is reliability so important for those nerves?

It's important because it's used as a cue to position in space. Because the input from the two ears is compared. And I talk about the chick system, because it's a little simpler than the mammal and it's been easier to study. The studies are better for the chick than they are for the mammal.

You've got to know what the endbulb of Held is. These are endings of eight nerve axons on some of these cells. Cells like this, they're spherical bushy cells. In the chick they're just balled cells. During development they have a lot of dendrites. They pull them all in with development.

And this terminal distributes over the cell like a cup. There's a similar ending in trapezoid body that's called the Calyx of Held. They were both described by this anatomist Held. I used to call it the Calyx of Held and the cochlear nucleus.

But then I read the history and realized that he actually described the one in the trapezoid body. He also described this one, but didn't call it calyx. So people call it the endbulb of Held.

But you can see what's happening here. It forms multiple synapses. So many different synapses in one bump, one terminal enlargement. That means with the action potential one pulse here arrives. It causes simultaneous depolarization at many different points in that membrane.

So they all summate here at the axon hillock, and you end up with one action potential coming out. That's pretty unusual in the sense of central nervous system. These are just another summary of these connections through the thalamus.

And these are the summary of the thalamic projects then. Of course, the medial geniculate body projects to the auditory cortex in the temporal lobe. You also get projections to nearby areas from those posterior nuclei that are getting auditory input.

That's why when I diagram this this way, I show that these neurons outside of principle nucleus, in the medial geniculate body, I show them going to area 41. Whereas these other cells go primarily to the other areas, especially the areas ventral to the auditory cortex. These also get transferred connections from the auditory cortex.

Just remember that cells here and the medial geniculate body send axons that go not only to neocortex, but also into the amygdala, the lateral nucleus and amygdala. And I mentioned there are some visual projections like that too, to that lateral nucleus, the amygdala. And that's proved to be pretty important in learned fear in studies primarily of the rat.

This is what we've just looked at. And I think I just answered this question, why do some of the auditory nerve axons that terminate in the ventricle of the nucleus end in a giant terminal enlargement? To answer that you have to describe that endbulb of Held. What function does it serve? Can we get enough spatial summation so so one action potential results in one output action potential? And you need to know what the trapezoid body is. In pictures like this, I just show it as down here.

But if you looked at a cross section-- I really should have a mammalian cross section here, but they're easy to find. You find that the cells here, especially in the ventral cochlear nucleus, project to both sides, into cell groups in the trapezoid body.

There's a medial nucleus trapezoid body and lateral nucleus trapezoid body. And there you have, in mammals, there is another big Calyx of Held that preserves that one-on-one response to auditory input in generating the location information.

Let's look at it in the chick. Coincidence detectors is a good term for it. I created this table because some people have a terrible time if they only see the drawings. They got to have it all spelled out in words, so I created the table. All I'm doing here is putting words to those pictures that we've already gone over.

So now we'll follow the pathways involved in these two functions. We'll begin with the sound localization, which involves that precise timing we were just talking about. The pathway that is generating these differences, depending on where the sound is coming from in the azimuthal plane.

One of the major outputs is to the superior colliculus, where you have a map of the auditory world. The spatial map, that is neurons respond best to sounds coming from a certain position in space. And that position in space matches the area where the visual input is also triggering closer to the surface. The auditory input is coming in to the middle layers of the colliculus.

Somatosensory inputs are coming into the deeper layers, most of them below the auditory. And there you get a spatial map, too. Think of the coverage of the field around the animal's head by those enormous whiskers, the mystacial vibrissae of rodents. They protrude out into the visual field.

So yeah, you're only dealing with the space right next to the head. But that still matches the things they see beyond that. So they can anticipate something coming at them. They can anticipate a stimulus in the whisker that's located in the same area.

And then when we deal with pattern identification, that pathway from the dorsal cochlear nucleus goes directly to the thalamus, also by way of the inferior colliculus. But some of them go directly, and then to the endbrain. And most of the analysis of temporal patterns happens in the cortex.

So for location, I have here the eighth nerve. You go to the ventral cochlear nucleus. And these are the structures of the trapezoid body. So superior olive, and that's where you get neurons projecting to a number of places, including the

cerebellum. Even though the cerebellum. does get some direct input too.

And then from there you go to the nuclei, the lateral lemniscus, and inferior colliculus as we'll see, and the superior colliculus. Which itself, as we know, has projections into the lateral thalamus.

So in mammals it's the medial superior olive which is sensitive to precise time of arrival. That's just representing azimuthal position. I mean, the timing doesn't actually help the animal discriminate sounds above the horizontal plane or below.

They need other ways to do that. It's not as accurate. But by simple head movements they can generate cues. And because of the shape of the pinnae, the pinnae attenuate different sound frequencies differently, according to elevation.

So the sound actually has a slightly different effect on different neurons. And that is used in localization in the vertical plane. That's been studied in owls, where just the configuration of the feathers around the ears create those differences.

I don't know as much about that. It's not been as well studied. But we do know that there is a map in the vertical dimension as well as in the azimuthal direction.

So let me go through those studies in chickens. We've talked about this endbulb. That is here in this diagram of one neuron type on both sides in the cochlear nucleus of the chicken. So here's the axon coming in from the organ of Corti in the cochlea on the left side, and then on the right side. Here's the endbulb of Held.

So we know every action potential coming in here leads to one here. And note that these neurons have two projections. They branch. One goes to this nucleus laminaris. Obvious why it gets that name, because of its appearance. And then the other branch goes this way, goes to the ventral dendrites of the nucleus laminaris on the other side.

So this side, it projects to the dorsal dendrites. The ones on the other side project to the ventral dendrites. These cells will fire only if they get nearly simultaneous arrival of potentials from the two ears, from the two sides, from that cell pipe of nucleus

magnocellularis on both the left and right sides.

And I've noticed, when I've looked at the pictures in Golgi in a study of the chick-- this was Jhaveri and Morest at Harvard. They studied the development of this system, including the development of these big endbulbs. But they also pictured the magnocellularis cells.

And I've noticed that always the cells didn't go directly towards laminaris. They made this loop. Obviously designed to keep the timing nearly the same as the crossing axon. Now you, of course, would have to get slight differences in the length of the axon. That would be the simplest way, anyway, to get different positions in space.

The studies that have been published indicate that this one is kept more constant. And the crossing one is the one that varies a little bit systematically. So the result is a map of the azimuthal plane from directly to the left to right in front, and then on the other side to the other side. So you get the whole field represented only if you take both nuclei into account.

So there is no laminaris in the mammalian brain. But the lateral superior olive contains cells just like this. It was all more theoretical. It was theory for a long time. And the reason I use the chick studies is because that's where they finally were able to pin it down and make measures.

It was done by, that anatomical study I was telling you about by Jhaveri and Morest at the same time Tom Parks out of the University of Utah was studying the electrophysiology of that system in the chicks. And together they made a very powerful story. And one of the places these axons project is to the tectum of the midbrain. This is just speculation about how it evolved. You can read it if you're curious about that.

There is a second mechanism for sound localization involving, in mammals, the lateral superior olive. Did I say, I think I was supposed to say medial before. This one's the lateral. And that's responsive to differences in amplitude of the two ears.

Because, of course, that's an even simpler way. Obviously sound is going to be louder because the head's in the way of the other ear. So there is a slight difference in intensity, too. So that is also used.

But it's decoded in the lateral superior olive. And I don't know how that's handled in chicks. Because the study in chicks was focused on that nucleus that they could get to with their electrodes and find it in animal after animal, because it was located right dorsally.

This is all in the dorsal hindbrain of the chick. This is hard to get at in the mammal, because it's way down ventrally in the hindbrain. And they're very small nuclei. So it's difficult to do the study in mammals.

And then I mentioned how the owl uses different attenuation and different frequencies, and how head movements-- we use head movements a lot. When we hear sounds we may not even think about it sometimes. But we make slight movements of the heads. And we know this improves our localization ability.

Let's answer these questions. Distinguish between two prominent pathways to the auditory system. The lateral lemniscus and the breaking of the inferior [INAUDIBLE]. So I brought this picture from the [INAUDIBLE] system chapter. You can see those.

Here is the lateral lemniscus. You see the white there. It's the axons coming, they're actually mostly coming from down here. This bump here is the superior olive. The bump for the caudal here is the inferior olive.

The superior olive is the auditory pathway. And it includes the trapezoid body cells here. I should start here. You see the cochlea nucleus there? And you see that little-
- that's a nerve there.

Here come the axons. I've drawn an arrow to the cochlear nucleus. And there you go down to the trapezoid body in the superior olive. And then here you have pathways going to the inferior colliculus.

Some of them end a little before they get there, in the nuclei of the trapezoid body.

They follow that lateral lemniscus up. And then from there they follow-- I drew it a little too far, I guess-- they go into that bump. This is the breaking of the inferior colliculus.

You look carefully, you do see deeper shadows on either side. It is a white band there. So we're talking about then lateral lemniscus here, breaking the inferior colliculus here in blue. I've labelled those different components in different colors.

And that picture is in color in your book. But I wanted you to see that once you learn that anatomy, you can make these things out just looking at the surface of the brain. And it varies a lot, depending on how you adjust the light.

If you're working with another species and you want to get a picture like this, just get a really well-fixed brain, clear the surface of all the blood vessels, and just play with the light. And you'll end up seeing all these different things.

So here we can see all the auditory system things. I'll put that online with one without the arrows and one with the arrows. Where does information about location of sounds and sights converge in the subcortical structures of the CNS? Where would that be?

I was talking about visual, auditory, somatosensory, all in optic tectum or superior colliculus. Then I say what happens that the auditory and visual get out of register? How could that happen?

Well, it happens with development. As the head changes size that happens naturally. If you put prisms on an animal you cause the visual field to shift. The map of the retina in the tectum doesn't change. What changes is the auditory map.

The auditory map is the more plastic one. It shifts so it matches the visual one. A fascinating finding, initially by Mark Konishi in owls. He had prisms on the owls and he showed these effects.

But we should have realized something like that had to be happening in development. It would be very difficult. It's similar to what the cerebellum does, for

timing and controlling the motor system. But here it's in the sensory system.

So then in question nine here, I say characterize two separate functions of auditory system pathways extending through the brainstem. How is the separation of these two functions expressed from the endbrain? Even in transcortical pathways. Now that requires you to read a lot more of the chapter to get all those parts. But what am I talking about?

AUDIENCE: [INAUDIBLE].

PROFESSOR: So the location information is what we were just talking about. That's one of the functions. But what's the other major function? And the pathways are largely different.

AUDIENCE: Identifying.

PROFESSOR: Identifying auditory stimuli, which is done mainly by patterns. Because it can't be just frequency, right? I mean, if your child's voice changes, you want to still understand him. Even though he's talking in a full register below where he used to talk.

So we are responding to patterns, not to absolute frequencies. We respond to amplitude changes, and that might be important. But not nearly as important as temporal patterns and frequency, various kinds of complex frequency modulation.

I mentioned the experiments on location information getting to the colliculus. And here let me just add to that the studies of ablation of superior colliculus. These were done by me in the hamster. But they've then been done extensively in the cat as well.

Lesions don't just affect visual orienting. They affect auditory orienting. And they affect, more transiently, somatosensory orienting, too. The somatosensory recovers the best, even without the colliculus.

Why do you think it's just transiently affected? These are diaschisis effects. Tectum is big. And it's affecting brain stem mechanisms for orienting as well.

So initially you get the loss of the input from that big tectum. They lose everything. They're amazing animals when they first wake up from the surgery.

They can't orient to anything. Then they recover. They pretty soon are responding to their whiskers again.

AUDIENCE: What does their behavior look like when they can't orient to anything?

PROFESSOR: They're hunched up in the corner, but they are hungry. So the first thing they start responding to is stimulation around the lips. And then they start orienting to touches around the lips, around the mouth.

They will start turning a little bit, so they can see you're trying to feed them. These are the hamsters. Big advantage to using hamsters is they're so motivated to get those little seeds, you know. And they're also a lot cuter than rats and mice.

AUDIENCE: I don't know about that.

PROFESSOR: They're fun to study. [LAUGHTER]

The deficits in orienting towards sounds recovers a little bit to laterally placed sounds. There are hindbrain mechanisms that can turn the head in response to sounds, even without the tectum. It's wiped out at the beginning.

That then has a slower recovery than the somatosensory orienting, but it recovers. But the orienting to overhead stimuli is very dependent on the tectum. And they just don't orient to things above them.

They can show freezing responses to novel sounds. Because they're detecting them with the cortex. It's just making those movements that has changed.

And we have a lot of information on the pathways cortex, location information, auditory localization of sounds does reach the cortex as well. In fact, they've shown distinct cortical regions reached by location information and identification information

They are separate in the cortex. I've found there's a lot of pictures of this just in recent years. But this is a very clear one.

Here you have the primary auditory cortex. And then around the auditory cortex, we talk about the auditory belt cortex. The areas here in the rostral belt cortex are the ones sensitive to position. And the projections from there go into the posterior parietal cortex, the same regions that are getting visual.

It's not identical regions, they're adjacent regions. But then there are regions of convergence, too. The picture here doesn't show the convergence. And then from these regions, you have the pathways going to prefrontal cortex.

We talked about those for the visual system earlier. Same thing happens for audition. It goes right into those areas of the frontal eye fields. So it's getting not just visual, but auditory as well.

And some of the pathways don't even go through posterior or parietal. They go directly to prefrontal. And then in the rostral auditory belt cortex, you have pathways leading through the superior temporal gyrus to the amygdala. And from the temporal pole directly to the ventral prefrontal areas. Those same areas that themselves project to amygdala and hypothalamus.

So they show here how the visual pathways do a similar thing as we talked about in chapter 22. It was years after the discovery of the visual system pathways like that where people started paying attention to this in the auditory system. And then this was worked out.

Let's talk about auditory pattern detection. We still have a little time. Now we're talking more about dorsal cochlear nucleus. That's where you have their origins of the most direct pathways.

These are temporal information in the auditory input. It goes to main nucleus of the medial geniculate body. And from there through the auditory area primarily.

So when they map auditory cortex by physiology-- there are beautiful anatomical

maps too. Even the Golgi studies have seen this. The way neurons are arranged in both inferior colliculus and medial geniculate body is a very well organized system.

When you get up to cortex, it's been the physiologists that have dominated the field. And now we have physiologists studying the auditory system--d Josh McDermott here in the department.

And they've mapped these. Initially they looked for the tonotopic maps, just like in the cochlear nuclei. We already know that animals can discriminate different frequencies without the cortex. So I'm asking here in this question, describe several properties that have enabled investigators to distinguish multiple neocortical auditory areas.

The first one is frequency differences. A1 is a good illustration. But these are different positions, from rostral to caudal, different distances from the posterior suprasylvian sulcus.

Here's the posterior suprasylvian sulcus. Here's the middle suprasylvian, here's the anterior. So they measure from here, and they go across this cortex in in A1. And when they do that, at each position they find multiple best frequencies.

That is the frequency where you get the best responses in that neuron. The neuron does respond, though, to other frequencies, too. It's just that it's most sensitive at one frequency. So they use that for these maps.

But you can see that the envelope of the planes in this kind of graph do show up on a tonotopic map. It does respond to higher frequencies when you're further from the posterior suprasylvian sulcus. So that's what a tonotopic map is in the auditory system.

It doesn't mean it's a precise map. At any one position, you can get a lot of different frequencies. And there is a reason for that. It uses that information from other frequencies.

So here in the cat, which is by far the best studied animal for auditory system. And

Jeff Winer, who I know and was working with Kent Morest, the guy that did a lot of that work on the auditory system at Harvard, and Jhaveri was his student there. Winer worked with Morest in anatomy, and then also did a lot of physiology. And this is from one of his review papers.

He describes five tonotopic maps. And you see them here-- one, two, three, four, five. This light gray area in the picture. They all have this frequency difference when you go from one position to the other. Then there are three nontonotopic areas. They are the darker gray here.

This is anterior ectosylvian, and what we call auditory area two. So what does it respond to? Well, just like auditory cortex, it responds to frequency modulation of tones.

And then there's three multisensory areas. So they're not just auditory. They're really association areas. And they're these. Not the auditory system, people, they're really multisensory areas.

The visual areas are here. And unimodal visual areas, association areas, are in here. [INAUDIBLE] areas in this lateral gyrus. It's very peculiar in that they call it lateral gyrus when it's the most medial gyrus in the hemisphere. It's this gyrus.

And these are the unimodal association areas. And then multimodal areas. And then there's two limbic areas. We call it the insular cortex. It corresponds to insular in the monkey and humans.

And this temporal area here. This area is covering that area where the amygdala is located, by this neocortical area. It's not part of the amygdala. They are near cortical areas.

And then I mention here, there is separation of input from the two ears in the cortex. And then I ask about ablation effects. I say how are ablation effects in the auditory cortex of the cat related to word deafness after certain cortical lesions in humans?

Well, I like to start with the early electrophysiological studies. Because they're still

the best examples of what we mean by pattern selectivity. Let's look at this one.

I won't go over all the others, but I published some of them in the book. Here they have to one tone-- and here's the map of how it responds to single tones.

Here's the sound pressure levels, and notice that the minimal amplitude sound, it's responding best at one frequency here. That's how they get the tonotopic maps, by mapping single neurons like this. You can do it with larger electrodes, too, and still get some degree of mapping.

And notice how it responds to tone on, not to tone off. And it'll do that for a number of different frequencies. But obviously most sensitive here. But now look what happens if you give a tonal changing frequency. Frequency modulation, so it's going [WHISTLING UP AND DOWN LIKE A SIREN].

And it's responding always to the upward ramp of frequencies. And that's what we mean by temporal sensitivity. And there's many examples of that. Some of the examples are more complex.

Like here's one that always responds to the offset of the tone. Here's one that responds best to short tone, the up side of short tones. But to longer tones, it responds much more vigorously when the sound goes up.

This one doesn't respond to the long burst, but will respond to the short burst, but only after repeated presentations. So you get a lot of variability, always sensitive to temporal patterns. And Whitfield and Evans, who were the first to really comprehensively study this, have a simple model, which I've redrawn here to make it a little clearer, showing that once you have this frequency specificity in the cortex, by having inhibitory interneurons that are asymmetric in between these neurons, you can get, because of the inhibitory pathways, this neuron won't respond well when you're going high to low.

But when you're going low to high, the inhibition timing will not inhibit those adjacent neurons in time, so you will get a response. And again, of course you have to assume certain convergence in the neuron further on in the pathway. But because

they don't find neurons like this, output neurons, of the thalamus.

You do find them in the cortex. You know that it's got to have circuits somewhat like this in the cortical areas. And it involves these inhibitory interneurons, which remember arise in mammals from noncortical areas in development. But they migrate in. And there's a lot of inhibitory interneurons there in the cortex.

Now, if you ablate the cortex, you don't get rid of frequency discrimination. But you get profound defects in responses to patterns. You can train them to respond to very simple temporally modulated tones.

They fail to learn it after you ablate even just a one, or even just a more ventral area. They have a terrible time. These are highly interconnected areas, so of course you're getting large diaschisis effects, too.

A lot of these patterns appear to depend on these interconnections between these auditory areas. You can use pattern discrimination, you can use responses to novelty instead of habituation to novel sounds. You always get the same kind of result. They need the cortex to respond to temporal patterns.

So it's like humans with word deafness. Words are, of course, really complex temporal patterns. And humans can become word deaf with cortical lesions that affect auditory regions. I point out here another species.

Many years ago there were people, this was Capranica, I believe, at Cornell. He was studying the auditory system of bullfrogs. He found neurons that responded to the splash of another bullfrog entering the water. Talk about a complex pattern. That was a really good example.

I tried to find his publication on that and couldn't. But because he talked about it a lot, and we talked about in here at MIT when he was doing them, I'm sure it was a real finding.

There's been studies of squirrel monkeys and macaque monkeys. The squirrel monkey work was earlier. We heard a little bit about that yesterday from the

speaker here.

But then in 2008, using imaging methods, they found regions in the monkey temporal lobe that became active when other monkey voices were heard, but didn't respond to other sounds. Temporal patterns made by monkeys and their sounds was what this responded to. And they found that they can distinguish that area.

It responded differently to voices in different monkeys. They often would get them to habituate. Over time it responds less. But then a new monkey voice appears.

It doesn't have to be louder. It can even be softer. And suddenly that region responds again. So they can detect individual differences.

I took these quotes from a news report, but you can find the article in *Nature Neuroscience*, from the Nikos Logothetis laboratory. Nikos was here working with Peter Shor for a while on the visual system.

So of course we postulate that there are units like that in humans that respond selectively to [INAUDIBLE]. We are probably born with them, although we lose perhaps some of them with development that are not in our language.

And we know about hemispheric differences in humans, too, because we specialize for dealing with speech in the left hemisphere. This is also very plastic. So if very early in life a child loses his left hemisphere, if the lesion is early enough, he will develop speech in the right hemisphere.

It's very strange, though. If he just has a damaged left hemisphere-- this is not in my notes, just interesting to mention. If a child has damage that affects the left hemisphere, but it has to be totally wiped out, the hemisphere, to get speech to shift to the right hemisphere. So he'll end up with just bad speech.

So one of the treatments for severe problems in children is to actually ablate the entire hemisphere. It sounds horrible. But in fact, the behavioral result is better if they have really bad hemisphere pathology.

AUDIENCE: Why would that be?

PROFESSOR: I can find-- OK. We'll skip over the specializations now. We'll mention them a little bit next time.

They talk about echolocation a little bit. We saw that in chapter six. The structures became enlarged in bats and dolphins compared to the more visual animals.

And then you should learn a little bit about birdsong pathways. Especially with Michael Fee here in the building studying birdsong. And a little bit about speech.

And the pathways are very parallel, although the names are different in reptiles and birds than they are in mammals. But they have very clear regions of the endbrain that are auditory, just like the auditory cortex of the mammal. So we'll look at that briefly next time.