GERALD SCHNEIDER: OK, we talked about spinal reflexes last time. This is class 20, the second session on the motor system. And we're going to continue talking about spinal reflexes.

Last time, the slide that I just mentioned is this one. Right here, you can see I had crossed it out. It says lateral horn.

It made sense to them that when the spinal cord looks like that, that looks like it's the lateral horn. But this is actually an enlargement, and this is all ventral horn. The lateral horn is a tiny, little protrusion in the gray matter right at that location where I'm putting the cursor. Or it would be there, OK?

So these were our slides from last time. And today, we'll talk about the stretch reflex and talk about its function. Then we'll say a little bit about intersegmental organization in the cord and then plasticity in the cord. And I don't if we'll get to descending pathways, but we need to cover that in order to introduce the film that we're going to see on Friday on the function of descending pathways.

OK, so the stretch reflex. What is it? It's the reflex they always test in the neurology clinic with a jerk of the knee, the knee-jerk reflex. Now, that's just an example of a stretch reflex. All your striated muscles have stretch reflexes, OK?

If you suddenly stretch any muscle, you get a stretch reflex. But ordinarily, this reflex is operating not just as sudden stretches but to any stretch, OK? And let's talk about that. The sensory organ is called the muscle spindle. It's in the muscle and it responds to muscle stretch, OK?

So this is your textbook picture. It shows a little piece of the biceps muscle there. And it shows two kinds of sensory endings. There are endings in the tendons. And you see the enlargement here in the upper right.

The Golgi tendon organ is sensory axons that innervate the tendons and respond to tension in the tendon. OK, so the tighter the muscle, whether the muscle is short or long, it doesn't matter. If that tendon is tight, those tender organs will fire.

And what's its function? Well, if the muscle becomes so tight that the muscle is endangering itself or endangering the tendons or bones, it will cause the muscle to suddenly relax, OK? That's to protect your muscles and limbs, OK?

But there's also, in the muscle, in parallel with the long muscle fibers, there's little slender fibers called muscle spindles that contain not only muscle fibers, much smaller muscle fibers than the striated muscle fibers that give power to the muscle, but they contain sensory endings.

So for example, in blue here, they show a large axon that comes down and then wraps itself around the spindle, OK? It's designed to fire action potentials when the muscle is stretched, OK? Then there's a few other endings there.

And then there's also motor axons, the gamma motor fibers coming from gamma motor neurons in the ventral horn of the cord that innervate the muscle fiber. The intrafusal muscle fiber. "Fuse" is for the shape. So it's shaped like a spindle or a fuse, OK? So we call it the intrafusal muscle fiber if it's that fiber that tightens up the spindle.

And OK, so let's look at this picture now. Here, they show a muscle fiber and a spindle organ, which has smaller muscle fibers in it. So this is the main striated muscle fiber, OK? And this just represents the attachments to the bone on either side.

Now, if you stretch the muscle, what happens? You stretch the spindle too. OK, what'll happen is that the spindle afferent fibers will start firing. So will the Golgi tendon organ, the axons innervating the Golgi tendon organ when-- this just shows when the stretch occurs. So as soon as it's stretched, both of those afferents will fire, OK?

You say, well, then why did you need two endings? Well, you'll see. Here's a picture of when the muscle is contracted. So the alpha motor neurons that fire cause this muscle to shorten, OK?

When the muscle shortens, the Golgi tendon organ, of course, is going to fire because of the tension in the muscle. But now the spindle has become relaxed. If the muscle shortens, the spindle is not stretched. So it's going to fire very little, if at all, OK?

That rarely happens, except very transiently. Why? Because when this muscle contracts, the gamma motor neurons also fire and shorten the spindle to keep it sensitive to stretch. So its length is always being adjusted for the length of the muscle because we want it to be able to respond to a stretch that wasn't expected, OK?

And that system for controlling the length of the spindle, we call the gamma efferent system, coming from gamma motor neurons, smaller motor neurons in the cord. They shorten the spindle, which would adjust its sensitivity, keep it sensitive to sudden stretch, OK?

Now, why is that so essential? Why do we have to keep doing that? If you look in any nerve fiber innervating a muscle, you're going to find 30% of the axons are gamma axons-- axons from gamma motor neurons, much smaller than the axons in the alpha motor neurons, OK?

Well, think about it. If the spindles are a certain length and they stay that length, then any time the muscle sketches out-- let's say it's at a length. So the spindles are firing very little when my arm is in this position. And now I extend my arm. I'm lengthening the biceps muscle, OK? So the spindle won't fire at all.

But if I try to make it shorter-- I'm sorry. If I lengthen it, I'm stretching it, OK? And what'll happen? The spindle's organ will cause the afferents to fire. And the muscle will tend to move back to its position. Tends to keep the muscles in that position, OK?

If I shorten it, they're not going to fire if those spindles now don't change. But on the other hand, there are spindles in the extensor muscle too. So if the spindles are just set at a certain length, the limb will stay in one position or will try to, anyway, because of the muscle-to-muscle reflex.

The afferent from the spindle organ comes in through the dorsal root by a very large fiber, the largest fibers in the dorsal root the 1a afferents. Those axons go directly to motor neurons of the same muscle, OK? That's why we call it a muscle-to-muscle reflex, OK? That responds to muscle stretch, so we also call it the stretch reflex, OK? That is the monosynaptic reflex.

Every time we change position of the limb, we have to change the length of the spindles in order to keep the spindle sensitive and to allow the muscle to assume any position that we command it to assume, OK? So alpha-gamma coactivation is essential to the functioning of this system.

Now, in thinking about the function of the stretch reflex, the obvious thing is, well, it restores muscle length. Let's say I'm holding this, and something nudges me and disturbs me. Right away, if I'm trying to hold it in one position, it'll rise up again because of the muscle-to-muscle. I don't even have to think about it, OK? It will tend to restore muscle length.

It was thought that that must be the function of the stretch reflex. In fact, it was thought that, well, maybe we control our movements that way. We just change the spindle settings. And then the limb will try to go to the corresponding position. Seemed like a very good way to control the limbs, even with varying amounts of resistance to the movement.

But it was found in studies that no more than about 30% of the compensation due to disturbance of the limb when it's trying to hold a position, when you're trying to hold it in one position, is due to the stretch reflexes. Most of it, in fact, is due to the spring-like properties of muscle.

You can think of the limb this way, OK? If the green there represents my forearm, you can think of the muscles holding the limb in this position like springs connected on either side, OK? And those springs are tense, OK?

And so if the limb is disturbed, what happens? We push that down. The spring gets tighter, the upper spring. This spring gets looser, and it will spring back.

That's called the spring-like properties of muscle. And a major person in specifying the spring-like properties of muscles was Emilio Bizzi upstairs. They worked out many of those details.

Well, the springs have to have a certain amount of tension. And the tension is what's set by the muscle-to-muscle reflex. We call that tension "muscle stiffness," OK? Muscle stiffness. So muscle stiffness is simply how tight these springs are, how tense the muscles.

What's the other term? We usually talk about muscle tone. But resting tone is how tight the muscles are when you're at rest, OK? So does that change?

Try something. Put your hand on your arm so you feel both the biceps and the extensor muscles, the triceps, on the other side. OK, and now you move it in a relaxed way, OK? You won't feel the muscles now.

And now do this. Speed up the movement. And what happens? They tighten up on both sides, OK? Whenever you make faster movements, you get tighter springs, OK?

Now, what is that from? It's because the gamma efferents are firing. They tighten up. You get more action in the muscle-to-muscle reflex, OK? The muscle spindles are tighter, getting increased muscle stiffness or muscle tone.

Very important for fine control of movements. They have those springs tight. And in fact, we have good evidence that they're important in fine movement control If we look at both phylogenetic differences in animals and-- for example, we look at the iguana versus the frog, I can--

If you take a picture here of the spinal cord, let that be the gray matter on one side. OK, you find the large motor neurons in these animals that have dendrites that sometimes go way up into the dorsal horn, OK? And if you're a frog, these large afferent fibers coming in from the dorsal root, some of them will contact the very distal parts of those dendrites.

But if you're an iguana-- we'll make him purple here. If you're an iguana, these contacts are made much further down the dendrite, getting much tighter control of the motor neurons by the muscle-to-muscle reflex.

But the other thing and perhaps the stronger evidence-- the iguana, by the way, is a more advanced lizard. The frog is an amphibian. The iguana has much more complex hands and control of its hands than the frog, OK?

So that's just a correlation. But if we look at the density of muscle spindles in various muscles, we see that it's much greater in muscles of fine control. So you have many more spindles in the muscles of your fingers and your tongue than you have in the large muscles of your arm. And you wouldn't have so many in the muscles of the back. So it's mostly distal muscles.

So let's talk a little bit about, now, spinal cord organization. Remember the name that we give to connections that are formed within the cord, from one part of the cord to another part of the cord? So what we're talking about is the function of these propriospinal connections.

First of all, we have action patterns that are inherited, that are formed by connections made all within the cord, that, when they mature, we have these abilities. Now, what kind of patterns am I talking about other than withdrawal and stretch reflexes?

Well, it's been studied by physiologists who separate the brain from the spinal cord, and then they maintain-- this is usually done with cats. And they maintain them on a respirator. So they keep oxygenating the blood.

And they find that they have alternating movements of the limbs, walking movements. They find out that they have certain patterns. They call them reflex patterns. But if one leg, hind leg is flexed and the other, extended, you will get a similar pattern, as if they were walking in the upper limbs, OK?

All the basic movements of walking are there. And if you put the cat, put his hind limbs on a treadmill, and you activate the cord a little bit by stimulating the animal, OK? And that might be by a descending connection that you've spared.

But there are other ways to provide input. You can stimulate the animal around the anus, for example, and it will activate the cord enough that he will start stepping. And he will walk on the treadmill, even though he's got no connection with the brain. So it's got to be spinal. The whole thing has to be organized in the spinal cord.

The scratch reflex is another spinal reflex. We call it-- that is actually a fixed action pattern. If we put a stimulus, say, on the back of a cat, he will raise a hind limb in order to scratch it. He will actually scratch. And he will show the rhythmic movements of the scratching. Those rhythmic movements and the positioning of the limb are all controlled by spinal mechanisms.

Now let's talk about this, spinal modules of limb movement control. This has to do with how the descending connections control the position of limbs. In the Bizzi Lab a few years ago, they used, at that time, frogs. All the initial work was done with frogs.

They wanted an animal who had a large enough cord but also made very simple movements of the limbs that was easy to work with in the laboratory. So they used large bullfrogs, OK? And then later, they verified the work with rats, large rats. And I asked you to read a paper on that.

Basically, what they found-- they used this kind of setup, OK? They had a frog that they had clamped in position. And they put very tiny electrodes into the spinal cord, OK? They had one limb hooked up to a force transducer. And they could also measure tension in the muscles with electromyograms, OK?

And here, you see the limb in one position. And then they apply the spinal cord. And what they found was when they stimulate the certain part of the spinal cord with this tiny electrode, the limb will try to move, OK?

And what they're depicting in this kind of picture is that if they move the end of the limb here, the foot, into various starting positions and keep stimulating that same place, the limb seems to always move towards a certain position. We call that the equilibrium point. And so if the limb starts out in that equilibrium point and you stimulate the cord, it will stay there, OK? So it seems to move the limb towards one position.

And so they created these kinds of pictures, vector pictures, for various points of stimulation within the cord. And the interesting finding was that even though they stimulated many, many different parts of the gray matter, they found only a very limited number of positions. In other words, many neurons seem to all do the same thing. And they found that these neurons were distributed in longitudinal columns within the cord. And there were a limited number of those columns representing a limb, OK?

So the conclusion was that it constitutes a very elementary alphabet for producing complex movements. Now, how would that be? Well, they found that if you stimulate more than one of those columns, you get a vector sum of the result of the simulations done separately.

So with a limited number of columns like that, you could get many different kinds of movement and move the limb into various positions. Now, they don't know just-- there's not very many. And there's probably more in the rat.

And of course, they were dealing with only one plane of movement. So they've simplified the situation quite a bit. But it was a very basic discovery about spinal organization that simplified the problem of how descending connections are controlling movement.

OK. Now let's just go a little bit above the spinal cord, the rostral extension of the cord. In Latin, the spinal cord is the "medulla spinalis," the spinal marrow, the marrow of the spine, OK?

And the oblongation, the forward extension of that is the medulla oblongata, OK? So that's the caudal part of the hindbrain. And when reflexes involve the medulla oblongata, we call them suprasegmental because they're above the segment so that they involve connections above the segments of the cord where we have various reflexes controlled, autonomic system reflexes, for example, controlling blood pressure.

You say, well, what reflex controls blood pressure? Well, you have sensory axons innervating special, little organs around the branches of the aorta that detect carbon dioxide concentration in the blood. So if carbon dioxide goes up, you want to increase heart action to get more oxygen, OK?

That's the glomus flex, and that's a hindbrain reflex, and other types of reflexes that regulate heartbeat, OK? The heart will beat on its own without that. But these hindbrain reflexes are modulating it, speeding it up or slowing it down.

And then we have various protective reflexes. The gag reflex. Well, that has to do with swallowing, right? I think we triggered that once. Or a few of you brave souls did when you stuck your hand beyond the circumvallate papillae on the rear of your tongue to trigger that reflex, the gag reflex.

Vomiting is another reflex. What normally triggers vomiting? Why is it a reflex? Well, certain toxins, bad things, get into your blood from something you've eaten, OK?

And it gets into the hindbrain, to a place in the hindbrain where, unlike most areas in the brain, things from the blood can get in, right around the area postrema near the obex, OK? That caudal end of the fourth ventricle. And you trigger that response to vomiting. Very important for keeping us alive.

Reflexes and other mechanisms controlling breathing are also mainly hindbrain, though they involve the caudal midbrain, also. OK, and I will talk a little bit about breathing control just after the midterm, when we talk about rhythmic movements.

Now, you have other senses coming into the hindbrain too, like vestibular sense, auditory sense. An example of reflexes controlled by vestibular sense would be the righting reflex, which gets more than just-- is triggered not only by vestibular input but somatosensory input as well.

But that's the reflex where if we get knocked over, we tend to right ourselves. It's very obvious in an animal like a cat, which will tend to right itself, even in the air, OK? Any animal, if you knock him over, will tend to right himself with a combination of the vestibular and somatosensory reflexes.

And then, finally, the subject of your paper-- many fixed action patterns controlled by hindbrain. At the very simplest level, the eye blink, which is more than just a reflex because there's a drive that builds up and makes us want to blink. But it's very simple in its connections.

The swallowing reflex is also really a fixed action pattern, which also has a motivational component which builds up and involves over 20 different muscles, mostly controlled by various levels of the hindbrain and even the upper spinal cord.

And finally, we have many fixed action patterns resulting in facial expression, which also involve control of the tongue as well as the muscles around the lips and the whole face, controlled mainly by the facial motor nucleus. And there are seven.

We're not talking about the input side since many inputs from the limbic forebrain and visual system control facial expressions as well. We're just talking about the fixed action pattern, the output side, which is through the hindbrain.

OK, let's talk a little bit about plasticity and reflex connections. First, let me define post-tetanic potentiation. We talked about monosynaptic reflexes. You can enhance a monosynaptic reflex in the following way.

Say you first give a test pulse to the sensory fibers coming from a muscle, OK? And you will get a twitch of the muscle through the monosynaptic reflex. We're stimulating input fibers, OK? So we give a pulse, and we'll get a contraction of the muscle.

OK, now we stimulate with a tetanus. A tetanus means rapid-fire stimulation-- not just da, da, da, da, da, da, da, but [TRILLS]. OK, you stimulate rapidly. That's a tetanus.

OK, and if you do that for a little while and now give another single pulse, you'll find that you get a greater response than you did before because you have potentiated the monosynaptic reflex. That's post-tetanic potentiation.

And the much-studied long-term potentiation here of neurons in the central nervous system are really a very similar thing but not usually involving such rapid stimulation. But a potentiation of a synaptic connection that lasts a long time is called long-term potentiation, OK?

Now, you don't always get potentiation by stimulation, OK? It happens, of course, in conditioning procedures. It happens in many pathways. If you stimulate at the right rate, you'll get potentiation. But you often, if you get repeated stimulation, you get less and less sensitive connections. You get habituation.

So for example, if we have a novel stimulus that causes you to turn your head, OK? You hear a sound that you weren't used to. And you'll turn to see, what is that? So you figured out what it is. It elicited a response.

But what happens? If it keeps up, you habituate to it. And pretty soon, you're totally ignoring it. You might not even hear it anymore if it's an auditory stimulus.

And obviously, we habituate to the clothes we're wearing. We habituate to many stimuli that we just don't pay attention to anymore. That's a decreased sensitivity.

Well, in physiology, they discovered that some of those same connections, that if stimulated at one rate, you get potentiation, you get long-term potentiation. If you stimulate at a much slower rate, you'll get reduced sensitivity. So they call that low-frequency depression, OK? These are the physiological phenomena that correspond to the behavioral phenomenon of habituation or sensitization and reflex.

Now, if we just deal with the spinal cord, can it learn anything? Can you get anything besides this post-tetanic potentiation? OK?

So let me describe an experiment that was done that showed that the spinal cord is capable of some learning. It was based on a simple experiment where they took a cockroach, left him attached to a ganglion. Now, that's the cockroach's leg. And here's a beaker of water, OK? And here's the water.

And it's conductive. We put some salt in it, and it's conductive. OK, now we hook that up. We hook it up to a stimulator here, OK? We put one probe there. And the other probe will attach to the leg.

OK, so what happens? We've suspended the cockroach leg that way. And you don't even need the cockroach there. But you do need the ganglion that controls it. So you can have part of the cockroach-- the leg and the ganglion, OK?

So what happens? Well, the leg will extend. It's not going to stay flexed all the time. It will extend down into the water. And as soon as it touches the water, it gets a shock, OK? We have it hooked up to a stimulator, OK? So it closes the circuit, shocks the leg, and you get a withdrawal reflex, OK?

And then the leg will extend again. It will touch the water. And well, what'll happen is that eventually, the leg stays up.

Now, if you have another leg and you hook it up in series in that circuit, but it's stimulated in a way that's uncorrelated with the position of the leg, that leg doesn't learn to stay up. It's only where you have this-- the position of the limb is related to when the stimulus occurs that you'll condition it.

So Dr. Charlie Gross, former MIT professor-- had been for many years. Now a professor in the Department of Psychology at Princeton University-- with his students, did a similar experiment on the rat. Now, here they had the whole rat, but they made him a spinal rat or at least put the hind limb by doing a mid-thoracic section of the cord, OK?

So now, instead of just the cockroach, they had-- that was a rat leg, OK? But they hooked him up the same way. They were inspired by the cockroach work, OK? And again, they put another rat in the series, OK? So you can imagine how they would do that.

They put the other-- this is hooked to another rat over here, OK? And there's the rat foot. So now, if this is the first rat over here, whenever that rat extends its leg into the fluid, both legs get stimulated.

But the leg on the left is only being stimulated when the leg is extending into the water. The leg on the right is being stimulated at random because it's not moving in synchrony with the other rat. It's a separate rat, OK?

And what they discovered was the rat with the correlated stimulation gets conditioned, and the other leg doesn't. You might affect the responses a little bit of the one on the right there, but you don't get the conditioning that you do on the left. So they got some spinal conditioning.

Retention of that learning was not for very long. But it was for many hours, OK? So they did get conditioning in the spinal cord. So we know there's some simple learning, even within the spinal cord.

There's been other experiments on spinal control. And one favorite one that I like was done with crossing of nerves. Well, this is the last thing we'll talk about today. Sorry.

If you take the nerves to the foot and you sever the extensors and the flexors, cross them over, and get them to regenerate to the wrong muscles-- so now the nerve that would innervate flexors is now stimulating the extensors. It regenerates into the extensor muscles.

OK, so now when they regenerate, if you've done that to a rat, every time the rat wants to raise his foot, he lowers it. And when he wants to lower it, he raises it. And they've done that with monkeys and cats and rats.

Now, what happens? Over time, of course, all the feedback is wrong. So do they learn? Rats learn almost nothing. They maintain their uncoordinated movements because the spinal cord is not adapting to the abnormal feedback. It's not learning.

But in the monkey, they found that over time, the monkey learns to coordinate his limb again, OK? Does that mean the monkey spinal cord is more plastic than the rat spinal cord? Well, not necessarily, because these are not spinal animals.

So they tried, then, severing descending connections in those monkeys. And they found that as soon as the descending connections were severed, the monkey becomes like the rat. He shows the reverse.

All the adaptation, all the learning had taken place above the level of the spinal cord, OK? So even though we can get some simple conditioning at the level of spinal cord, it doesn't extend to this kind of adaptation to such a miswiring of the connections, OK?

All right, next time, we're going to talk about the higher systems, the role of descending pathways. And we'll describe the anatomy. And then we'll see a film of a famous experiment on monkeys.