If some of you don't have your quizzes yet, the graded quizzes, Michael and Hannah have them with them, so make sure you pick them up before you leave.

Now we've been going over readings from the Konrad Lorenz book that I posted online. I am going to give you a quiz on Wednesday covering that material. Very sparsely, of course, with only a few questions. If you've read it and listened to the classes, it should not be a difficult quiz. And there will also be a homework due early next week. I'll try to get that posted by Wednesday as well. So you'll have plenty of time to work on the homework.

Now this was the initial slide for the last class. We talked about the models. We talked about hierarchies. And chains of behavior. And we started with this topic, talking about spatial orientation by means of reflexes and what they call taxis, which are automatic orientation during locomotion. We've not talked about the role of cognitive behavior, the internal model, but we will do that today. And then finally we'll talk about the way organisms handle multiple simultaneous motivations.

So this was the last thing we talked about. A goldfish seems to pretty intelligently solve this problem. He's on one side of a barrier, food is on the other. He can see the food. So he moves towards it, but he runs into the barrier. But he has an automatic response to the barrier. It's a response called negative thigmotaxis. It's a kind of reflex involving locomotion, in which he moves away and changes directions. So he ends up moving along the barrier until he clears it. So he appears to know what to do, but in fact he's just using these simple automatic responses.

Now I asked at the end here, why does a dog often fail in such a situation? What does a dog do? The dog's here now. What does the dog do, trying to get to that food? And it's on the other side of a fence. Let's say an inexperienced dog-- because I'll admit that an experienced dog can learn methods of solving it. He can go around the end, but an inexperienced dog will not do that. At least not for quite a while. He will persist trying to get through that fence, long after the goldfish has already solved a similar problem.

So what does he do? What has the dog inherited that he can use to solve the problem? Without thinking about it, without learning anything? What does he do automatically? Come on, you have dogs. Some of you. Sorry?

He can dig with his paws.

Yeah, he either tries to jump over the fence or go under it. Frequently under it. They try to dig under the fence. And anybody that's kept dogs in a fenced backyard knows this problem. They do get out sometimes, and they frequently try to dig under the fence. Something that attracts them. Usually it's not food, because they're well fed if they're pets. For a male, it's usually female dogs. And I've had male dogs that either dig under fences or leap over them. Females are a little easier.

Does the dog ever solve the problem, an inexperienced dog? Well, he keeps trying, and eventually he's exhausted, and he gives up. And then he starts wandering around, and in his wandering, he does find the end of the fence. And then he will probably see that the food is still there, and he will get to it. It doesn't take more than once or twice of going through that, and the dog will learn. It's kind of trial and error learning, you could say. But he doesn't solve it when he's in a really highly motivated state, because then he's dominated by these instinctive behaviors.

Now think of the way dogs evolve initially as wolves, and they normally aren't confronted with things like fences. The barriers they're faced with, streams, lakes, ravines, mountains. I mean, they're certainly adapted to dealing with those things, but not things like fences. But yet they're also very intelligent. Is the fish then as intelligent as the-- more intelligent than the dog because it can solve those problems? Remember we talked about the intelligence of instinct. What seems like intelligent behavior, and we think of intelligence as involving cognition, may not involve cognition at all. It's simply instinctive behavior that's highly adapted to this situation.

So let's talk now about cognitive behavior. How do human languages give clues to the nature of what we call insight? We've got to think about what's insight is. And this is what Lorenz says about it. He quotes Porzig, who wrote in 1950 that our language translates everything that cannot be visualized into spatial concepts. It's not just done by my one language, but by all languages. Concepts for space and time use the same spatial terms. For orientation, all orientation is always concerned with both space and time. Of course we move through multiple spaces, both physical spaces and conceptual spaces. These are represented in our memory as both conceptual and physical spaces, our memory for them.

Because we think in conceptual spaces. And in fact, the part of the brain involved in what we call cognitive maps, we believe is involved-- there's plenty of evidence now from imaging studies-- is involved in both kinds of navigation. When we solve problems, or when we think about going somewhere physically, it involves association cortex and hippocampal formation in the temporal lobe.

So let's talk about this term, insight, now. If you search under Google, you can find how they deal with insight in animals. I did searches on insight in apes. Found examples of both chimp and gorilla problem solving. Some of them are well known, and I read some of these studies as a graduate student. It's very interesting because they get evidence that even in these apes, just like in humans, there's evidence that they form plans within some kind of an internal model of the world. And they can anticipate events. And they can consider alternatives and act on them. I think these websites that I'm giving here still work. These are some pictures that I found.

This kind of work-- this isn't from his studies, but the work was initiated by Wolfgang Kohler in World War I. And it was carried further by Paul Schiller, Peter Schiller's father, and later by his wife Claire Schiller. But this was the nature of the work. You see chimpanzees here? Here's a chimp that's using a stick to-- he's learning there that he can poke that stick under the fence and get at things.

The more famous problem was hanging a banana. This was done first with guerrillas. And here you see chimps solving a similar problem. There are bananas hanging up high. What is the chimp doing there? He's piling up boxes which were present in the pen. But they weren't piled up. They were scattered about. And the chimp eventually will pile the boxes up so he can do-- what do you see the chimp doing here? Climb up on the boxes. Looks like these are about to fall over. But he's reaching the bananas. There you see it happening too. Another one's involved also.

And Claire Schiller wrote an interesting analysis of this behavior. Because it had been interpreted as sort of [INAUDIBLE] problem solving, like they figured it out. They looked at the boxes, they looked at the bananas. They couldn't reach the bananas.

And they figured out in their minds that they could climb on boxes and get to it. But she asked, does that mean they were-- there's no instinctive behavior involved at all? She said she didn't think it meant that at all. Because chimps and gorillas both make nests, twice a day, at least. To sleep. They take naps in the middle of the day, they sleep at night. And every night they make a nest in a different place. They do the same thing for their naps. They construct these things. They pile leaves, branches, up in making the nest.

So they have that in their instinctive behavior. It's not that far from that to pile anything. Especially wooden boxes. And what the connection when they piled them, and they often don't-- they seem to be acting rather randomly. They almost seem to be forgetting about the bananas when they first play around on the boxes. But they figure out pretty quickly, they make the connection that they can get up a lot higher. So it's definitely a kind of insight. They do figure out-- they make that connection. They can get higher by piling the boxes. And they can use-- then they figure out it is a way to get at those bananas.

So when Lorenz talks about what he calls higher animals, he said he has the hypothesis that there's a higher control center in higher animals, he says, superimposed on all these orienting mechanisms. And of course the mechanisms for instinctive behavior. And also remembers changes in the environment and is able to judge the priority of incoming insight information.

Well, that's pretty general and difficult to get a grip on. How do you define a higher versus a lower animal? Can you think of any way to do that? It's not an easy issue. We already saw how a goldfish, you just use a single problem like that, you could say a goldfish is a higher animal than a dog. But most of us would realize that's not very likely. Think of the brain, for example. The dog has a extremely large endbrain compared to the goldfish. The lower parts of the brain, the midbrain is relatively larger in the goldfish. And the hindbrain is pretty similar, all the same basic structures. All the way from-- really across the vertebrates.

But the endbrains are very different. We know higher can't mean better adapted, because all existing species are highly adapted to their particular environmental niche. You could define it in terms of ability to anticipate. And these anticipation abilities we've talked about a little bit before, we mentioned it here, talking about the apes. And when we deal with anticipation, the ability to anticipate things in the future, we know the parts of the brain, the association areas of the neocortex that are primarily involved, and especially prefrontal areas, because they're involved in planning movement. Movement the animal will make in the future.

So we can ask now a neurological question. What animal has the relatively largest prefrontal cortex? And up until recently, if I'd given this question in this class, I immediately would have said, well, it appears that humans have the largest-- relatively largest prefrontal cortex.

But look here. I've drawn the prefrontal cortex. I've taken this from the literature. A study of a monotreme, an egg-laying animal. Very primitive in evolution. This is the echidna. And I've colored the prefrontal areas in pink. These are motor areas. This is a somatosensory area. Visual area. And auditory area. So you get an idea there of the relative size of the prefrontal cortex.

Now look at human. Look at the side view here. Prefrontal cortex here is in this model pink. There's somatosensory, motor, premotor, there's the prefrontal cortex. And now the posterior association cortex is very large. So if you took all the association cortex, OK, maybe human is even larger than echidna. But if you just took the prefrontal areas, the echidna beats us all. What does that mean?

Well, I wish I could answer it. There's almost no behavioral study of the echidna. And yet they're present in some of our zoos. It's only fairly recently, but that depends on how old you are. To you, it would be a long time ago when they first discovered these facts about the prefrontal cortex and the corresponding nucleus and thalamus, this MD area that projects to the prefrontal cortex. That's also huge in the echidna.

So the fact is, with that neurological substrate, the animal must've evolved that for some reason. What do humans use all this prefrontal cortex for? We know it's for planning, for future anticipation of events, as is posterior cortex. But it's the frontal where we plan our actions.

But there's one other thing we use that for. And that is the language system. It involves this region of the frontal lobe and this region of the posterior association cortex. Basically, auditory association areas, but also visual and somatosensory are part of it. In other words, multi-modal association areas and auditory association areas that are highly connected with that frontal lobe. Nothing like that in the echidna that we know of.

So humans, with the language system, it seems to be sort of superimposed on and highly connected with the other brain systems. And we know that it enables social communication. So in a sense, even the way it's connected is sort of a higher system. So is that a way to define higher and lower animals? Well, maybe. It's a possibility. And just pointing out how difficult this issue is. But at least because I'm a neuroanatomist as well as an animal behaviorist, I sort of can't help but use the anatomy to make a stab at it.

But I really would like to see-- I would like to do it myself if I had any echidnas around here to study.

Here's what I would guess. It can't be that it's a very social animal. We know frontal lobe-- and it's been proposed that frontal lobe became so big in humans because of social life. And that characterizes our higher cognition. Well, is the echidna there a very social animal? No. It's mostly a solitary animal. Course all these animals, even the solitary ones, have to mate, to reproduce. And so, yes, they have that. But they don't have the complex social life of humans. In fact of most primates.

What does he eat? He's an anteater. This is the Australian spiny anteater. What's so difficult about hunting ants? One is they're very small. They move very fast. And when you get them, they don't stay around very long. My guess is he can very rapidly not only see many, many ants, he can remember where they are. That takes our prefrontal cortex, we call it working memory. And he can guide multiple actions very, very quickly. And get as many ants as possible.

It seems awfully simplistic. Could that result in this enormous evolution? I don't know. But that's one of the things I would go after. That would be one thing I would like to test. I would like to observe their feeding behavior. Exactly how they do it. Compare other animals. Other anteaters, to see if they're as good as an echidna. And what kind of prefrontal cortex they have.

Let's deal with multiple simultaneous motivational states. And talk about how they resolve the conflict, if they do at all. And I think I've already pointed out that we don't always resolve our conflicts. Remember the model of Tinbergen, where he shows the hierarchy of instinctive behavior? And he shows at the lower levels, where you have multiple different actions at approximately the same level of a hierarchy of instinctive behavior. He shows these interconnections among them. Largely inhibitory connections. So that only one of them becomes dominant at any one time.

So the way you see that, what happens in behavior, if you deal with two very highly aroused states, you can get different ways to solve it. You might just superimpose them. So show examples of that. What happens if the motivation to approach, let's say it's a dog, and he's highly motivated to attack. But he's also afraid. So he's also highly motivated to run away. What does he do? Often you get a superimposition of the motor patterns, the fixed motor patterns of those two fixed action patterns. You can also get mutual inhibition. Which can lead to either one dominating, or you can get two states alternating. So you can get oscillations.

And then interestingly you can also get displacement activity. A third behavior that seems to have nothing to do with the motivational states underlying this. Suddenly a third behavior will emerge. And the animal shows displacement.

Let's talk about each of these. If you talk about approach and avoidance behavior in geese or in fish. It's very interesting. I think fish are about the most interesting. If you take a little cichlid fish, these beautiful tropical fish, and get an animal that's trying to approach food but also he's afraid, because there's something novel there that makes him avoid it.

What does the fish do? You can literally see a fish where the front end of the fish, represented by his pectoral fins, is moving back. And his tail is swimming forward. So you see the simultaneous appearance of elements of both fixed action, fixed motor patterns. Underlying these two different motivational states.

In geese, and you see this a lot when you're trying to feed geese, and you're novel to them. They want the food, but they're afraid of you because you're novel. You might be a danger to them. You can actually see oscillations of their neck. Like both actions are being simultaneously triggered. So you get this weird oscillation in the fish. You get a lot of trembling of the neck, as described by Lorenz.

I think that's not always clear when it's happening what it is. But that appears to be how it originated. The fish, it's clearer. Because you get both actions very clearly in different parts of the fish. The part that's closer tries to run away. The part that's farther, flees-- it tries to go forward.

Here's a superimpositions in the dog, where Lorenz has described his hypothesis of how gestures of threat behavior must've evolved in dogs. And this is his very nice illustration of it. He's showed the different expressions of a dog in silhouette, expressions representing increasing motivation to flee. So here's a dog that's purely afraid. Ears flattened back. Mouth fairly straight. Eyes not wide. If you're very familiar with dogs, you look at that, you say, that dog's afraid of something.

Here's the normal, calm dog. Here's increasing motivation to flee. Here's increasing aggression. So here's the dog that doesn't have any tendency to flee. See, his ears come forward. His lips curl. He shows his teeth. And he growls. That's the dog that you don't want to get any closer to. He's a dog about to attack.

But now with increasing motivation to flee at the same time, he shows a dog here that shows maximal aggression and maximal motivation to flee. You just superimpose the two types of actions. You get almost flattened ears, but not completely. They're still turned up at the ends as they are here in the very aggressive dog. He still is showing teeth, but notice nothing like this animal, where he's widened his mouth so you can see all his big teeth.

Here you don't see them all. In fact, his lips are curled back, more like this animal. And so forth. And he doesn't sound quite the same either . And this is a threatening dog. When you see dogs fighting, you'll see them threaten each other with this kind of expression. You see this superimposition of the two motivations.

I say here that mutual inhibition usually occurs between action patterns at the same level of organization. And Lorenz discusses this. I give you the page there. But so that only one can be expressed at any one time. But there is one action pattern that's almost always given absolute priority. What do you think that is? What's the action pattern you're most likely, and not just you but any animal, to give priority to? It's not sex. Life preserving. You're attacked by a predator that can kill you. You lose your other motivations, the motivation to flee the predator, to escape from the predator, will be absolutely dominant. And this is true in almost every animal.

If the animal has absolutely no predators, which is very unusual, you can imagine an animal that might not-- you might not see this tendency to flee. Maybe Tyrannosaurus Rex was like that. But they're pretty unusual, when you see that.

Mutual inhibition can also cause oscillation, as I mentioned before. Two fixed action patterns can oscillate. And this oscillation can become ritualized in evolution. They can become social signals. So these are examples. Here's a female pygmy or dwarf cichlid. Beautiful little fish. It's got a prepared nest site. And it's attracting a male. But how does it do that? It attacks the male, and then immediately reverses and tries to guide it to the nest. She gets his attention by attacking him.

And it's very similar in the male stickleback fish. We talked about that. The male stickleback fish builds the nest. Then he swims out, chooses a female that looks the most gravid, the most ready to lay eggs, because of her swollen belly. He'll pick the one, and they tested, remember, with the dummy stimuli, that he will tend to choose the one with the most eggs.

And he starts an attack, but then immediately changes his whole movement. It's become more ritualized in the male stickleback than in the cichlids. Because he has a very characteristic dance he uses. We call it a dance. It's a ritual kind of swimming. The zigzag dance. That the female has evolved a specific response to, a following response. And if she's the one he attacked, she's the one who'll pay the most attention and often will follow him to the nest. He leads her right into the nest. She swims through the nest and deposits her eggs, which elicits his following through the nest, and he inseminates the-- fertilizes the eggs.

So this ritualization is common in evolution, where you can trace the origins by looking at closely related species. Because in some species you'll find the ritual to be a little different or less ritualized perhaps. Just like in the cichlids here you don't find as much ritualization. As you find in the sticklebacks, where the females have evolved a very specific response to that male movement. And the movement itself is a little different from normal swimming behavior.

Talk about displacement activity. What are two situations where displacement activity occurs? There's a diagram of the causes of that, that I didn't try to reproduce here because it just doesn't go far enough in explaining it. And the reason it doesn't, is displacement activities are in some species it's always the same thing. Whereas the theory that you see outlined there by some computational ecologists really doesn't predict a species' typical nature of some displacement activities.

But when do they occur? Two simultaneous motivations. We mentioned this before. You want to stay in here while I'm going to stay at the very end. But you also want to leave. So what do you do? You do a third thing. You engage in other activities. You might increase the chewing your pencil. You might scratch your head. I'm impatient. I want to finish this lecture and leave. I might pace a little more. I might scratch my head a little more. These are all displacement activities. So when you have two simultaneous motivations, you often engage-- your likelihood that you will engage in the third thing are increasing.

And the thing we talked about before is when just one motivation is very high. But then something blocks the stimulus, that blocks the key stimuli that elicit the fixed motor pattern. So then like the bear, he's angry, but there's nothing to vent his anger at. So he vents it at anything near. A man who's extremely angry at his boss, but he's also afraid. Or his boss isn't right there. Or he becomes angry when he gets a letter from his boss. He gets very angry, but the boss isn't there. He can't take out his anger directly. He's likely to yell at his wife. He's likely to hit something. And so on and so forth.

Some people get so engaged in sports, they have a rubber baseball bat just to hit the TV with. They don't want to ruin their TV. They actually sell those. Do any of you have that?

But even if you don't that directly show that kind of displacement activity, you're likely to do something. Express some kind of action because of the motivation. After-discharge displacements are what they're called. It's a single motivation. It's highly aroused, but then no specific stimuli to elicit the normal fixed motor pattern. So other actions occur.

Displacement activity was originally given this long German name, ubersprungbewegungen. The springing over activity. Sparking over activity in German. And it was studied a lot by Tinbergen as well as by Lorenz. And these are the two situations that I was talking about.

Let's give examples of the species typical nature of displacement activities. First of all, here's ganders of three different types of geese that are in conflict between escape and defense of their nests. Very common conflict that the female goose is faced with. With the greylag goose, she engages in wing shaking. Very vigorous wing shaking. The pinkfoot goose, she engages in preening movements. Movements that have evolved for distributing oil from glands under her wing cover feathers. And distributing the oil on the flank feathers. The greater snow goose engages in bathing movements. And she'll do this right on dry ground, even though there's no water, no water to bathe with. Because it's displacement bathing.

Here's one that many of you have seen. Hamsters, in conflict. Especially if you're novel. Let's say hamsters are not always very kind. Yes, they're pets, but unless they're very familiar with you, you will see this kind of thing. You try to give them a seed. We know it's their favorite food, so they're very attracted to sunflower seeds. But you smell a little different. They're a little cautious. So they're in conflict. They approach. They avoid.

What do they do? Almost always they will start grooming. They'll show displacement grooming. And if you keep hamsters, you learn to discriminate between real grooming and displacement grooming. It's not always easy. Especially once the displacement grooming starts, it goes on for a long time in some cases. Because the grooming itself seems to calm them down.

But when they start their displacement grooming, it's so vigorous, it's more vigorous, more animated, than real grooming. And they don't always go through all the motions of real grooming. Just the ones with the larger movements. It becomes very obvious.

So similarly you can have displacement wing shaking and normal wing shaking. Normal oil distribution, displacement oil distribution, and so forth.

So think of the various examples of human displacement activities. I've just listed some of them here. Pacing the floor, we mentioned. Head scratching. Biting a pencil. I didn't mention the oscillations of a foot. Just saw the guy over here. OK. No. Nail biting. Nail biting often originates as displacement. Of course they can become habits. But they're displacement activity habits. So just like these birds, they show a certain thing, people can develop habits of showing certain displacement activities.

So why might displacement activities then sometimes become ritualized and actually undergo changes in evolution from the original fixed action patterns that they represent? Can you think of a reason? Because it leads to the next topic, next major topic we want to talk about. The changes occur because they conserve the social signals. It results in benefit, mutual benefit, because it can promote the survival of an animal if he can detect the displacement activities in another animal and realize that the animal's in some kind of conflict. So he then becomes more cautious, even if he doesn't notice what's causing all that in the first animal. It serves as a social signal.

So we'll talk about communication. And when we talk about mating behavior, we'll talk about courtship. And many courtship rituals that you observed in animals, originated as either displacement activities or as conflict resolution. Two simultaneous aroused fixed action patterns. And then you'll see the two fixed action patterns oscillating in the courtship ritual. Because courtship does involve both approach and avoidance. And often we see that in the ritual. We'll bring that up again when we talk about the courtship behavior.

A little more about the quiz. I know there's quite a bit of reading in Lorenz. But emphasize concepts I've talked about or at least mentioned in the class. One of the clues I can give you is I think I want to ask you something about those models. At least know what the major differences are between the Tinbergen models and the Lorenz models. I won't ask you about the computational models that have been done. We only talked in class about the Tinbergen and Lorenz models. But I also said they each have advantages. So you should know. What is the value of learning about both?

And if you focus on the study questions and the list of questions I've given you, most of them we've brought up in class, I think you'll be pretty well prepared.

And I'm not finished with the homework yet, because I want to add a couple of questions on the things we'll be covering the rest of this week. That's it for today.