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PROFESSOR: All right, a little less time today, because I gave you a little extra time on that since you were obviously needing a little more time. For this class and Friday's class, after a little bit on early evolution and behavior, we'll say a little bit about genetics and learning. Then mostly Friday we'll get to the topic of navigation and migration, how animals find their way on foraging trips and other behavior that involves movement quite a ways from their homes.

There's not much in the readings on these topics, but they come up in studies of the brain and certainly belong in a behavior class. I want to know the most basic multipurpose movement abilities of animals. We talked about multipurpose movement abilities already, but I want to know what are the multipurpose movement abilities that you find even in single-celled organisms. In fact, you find them all the way from protozoa to primates.

They're the ones we're familiar with besides elementary life support behaviors and movements within the cell, we have these. Even In protozoa you have locomotor activity for approach and avoidance, foraging, feeding, and for escape from predators. You have orienting movements in response to sensory inputs, and you have various kinds of grasping.

Grasping doesn't always mean manual grasping. It can be oral grasping, and so forth, and other kinds of grasping. If you're a snake, obviously it's either oral, or they have another means of grasping. Then you have various special purpose movements. These vary a lot more between species. Is that any different now for multicellular animals? Actually all those behaviors listed for the single-celled organisms apply to multicellular animals of all sorts.

I just want to point out that invertebrates, even if you just eliminate the entire forebrain, you find these basic movement abilities represented. They're represented in the midbrain. They're basic to the organization of the midbrain-- control of locomotion, control of orienting movements, and control of various kinds of grasping movements.

But what we've been calling the action-specific potential-- that is the motivation behind these movements, the motivations that usually lead to these various multipurpose movements-- then the forebrain is much more involved. I want to try to summarize basic support systems in very general terms, and then we'll talk about the regulators and controllers of behavior, which are really the motivational states of the forebrain.

I like the way the neuroanatomists here at MIT for many years while [INAUDIBLE] describe the basic supports underlying all behavior as stabilities-- three types of stabilities. What do we keep stable? We're talking about internal automatisms and reflexes, what we call the mantle of reflexes.

First of all, stability of the internal environment, the vital functions, respiration, breathing-- now does that involve behavior? Well certainly, very simple breathing behavior, of course, but if we have trouble breathing, we'll see other kinds of behavior to try to get enough oxygen. You have circulation of the blood. That's regulated by reflex actions. Regulation of the chemical environment-- the blood, the lymphatic fluids, the various extracellular fluids-- that involves reflexes. Feedback control systems-- homeostatic mechanisms, generally.

Then of course, we regulate temperature, and that involves reflex actions and involves fixed action patterns of various sorts. These vary somewhat across species, but there's some similarity in all the vertebrates. That's stability of the internal environment. Then we have stability in space, and this includes postural support-- various reflex actions that we've talked about. It includes maintaining balance and direction during locomotion, as well.

That all can be called stability in space. Some people would say it also includes other kinds of spatially-oriented behavior, including the orienting behaviors. Finally, stability in time-- if I just am talking about the level of automatisms, including reflexes and feedback mechanisms, then we're talking about-- we have to include, though, the temporal organization of the day-night cycle, the circadian rhythms, and their entrainment by the light-dark cycle, the cycle of the sun.

We have longer and shorter rhythms, as well, but the major thing is motivational persistence. Without our motivational states, animals in general would flit from one thing to the other, depending on what, at the moment, was dominant. But motivation tends to persist, and that gives some unity to current behavior. That's all part of stability in time, and it's all regulated pretty automatically.

Of course, stability in time can be extended a lot when you deal with forebrain mechanisms. I'm asking here for which of the three is the forebrain most important. I've already answered it, really-- it's stability in time. Above these basic support systems are the regulators of behavior, the basic controllers we call drives, motivational systems. And I want to just list them. Now you actually did this somewhat when you talked about ethograms. It's really a similar thing.

If we just talk about the various kinds of what behavioral neuroscientists would call the controllers, or regulators of behavior. We, for example, can start with ingestion, drives, or motivations, various related drives-- foraging, predation. Then a couple kinds of defensive behavior-- anti-predator motivation, first of all, and then second, social, defensive behaviors-- part of social behavior.

Then the various drives involved in reproduction-- I'm not saying each of these is a single drive, but we can group them. Then we have one that's often left out by ethologists, but not by Lorenz-- and it shouldn't be-- exploration of novelty. Novelty serves various roles, which we'll talk about in a minute.

Then various other motivations, including motivations for elimination, for shelter and nest construction, for sleeping, for play, various social motivations, and we have to add to all these innate behaviors, the learned motivations. Because with learning, we also can acquire motivations associated with learned behavior-- something which is not as well understood, but it's clearly something we have to deal with.

Just adding a little detail, ingestion drives would include both hunger and thirst-- the basic ones. And of course, you can get abnormal drives, too, but those are abnormalities acquired because of the reward involved and because of the availability of artificial things like drugs. But in fact, animals can also become abnormal in their hunger and thirst. That's why we talk about such things as food addiction, for example.

Then the other drives related to feeding are foraging, predatory attack, and various predators. Prying in starlings is a separate drive. Poking with a spine is separate in cactus finches, and so forth. Then for defensive behavior, the various anti-predator behaviors, we have both escape and avoidance, two somewhat separate. We're going to deal with that separately later on, and we'll see a video about escape behavior.

Then the various types of defense at the level of social behavior include territorial behavior, maintenance of a position in a hierarchy, achieving a position, maintaining it, improving it, and so forth. These all involve specific social motivations. And then various reproductive drives-- just some essential ones here-- pairing, involving, roaming or searching, advertising, selecting or responding, which we usually called mate selection. Then mating itself, brood-tending-- various aspects of parental behavior.

Exploration of novelty-- just point out some of the roles of that. It plays a role in security and defense. When we see something novel, an animal will interrupt his current behavior. If he didn't do that, he often would be caught. He improves his ability to detect the source of the predator and the nature of the predator by his orienting movements.

Of course animals, even if there's no predator turnaround, will explore novelty and expand what we call their cognitive map--- their map of the environment, their knowledge of the environment-- which is crucial for their ability to escape from predators. They're not escaping into an unknown area, but areas they know well, and they know the routes for getting back home or to getting to a hiding place.

It plays a role in ingestion. We talk about neophobia and neophilia. If animals are starving, they tend to be more neophilic-- that is, they will seek novel foods, whereas normally if food is relatively plentiful, they will be neophobic. They will avoid novelty. And it does play a role in sexuality, as well, more in some species than others. There's many other motivations that we've mentioned, some of them before.

This is another topic about genes and behavior, and I point out here at the beginning, that variations in a single gene can result in variations in behavior. I just want to know what kind of effects on the body does such a gene have to have. Well it's a very simple answer. If a gene has a specific effect on behavior, like it can be a gene-- if the animal has it, like a bee, he engages in cleaning out of the hive, and if he doesn't have it, he doesn't.

You have these two kinds of bees-- the hygienic bees and the non-hygienic bees. What has to be different? What does the gene have to cause? The gene, by itself, knows, in single cells, the single cells aren't controlling behavior. So why is behavior different? How can the gene result in differences in behavior? Very simple-- must be differences in the nervous system, right, because that's the way we inherit fixed action patterns.

Fixed action patterns depend on brain circuitry and other aspects of the brain, including hormones, for example, the chemical environment, and so forth. That's the kind of an effect it has to have. Generally, at least in invertebrates, the effect is on the central nervous system. And I point out, besides hormones here, it could be differences in sensory input and so forth that could result in changes in behavior-- that is if an animal inherited much higher sensory acuity or much lower thresholds to respond to certain types of inputs in the environment, it will change its behavior.

Going back to the bees, here, the hygienic bees-- what are they? Why does a bee colony need hygienic bees? What do those bees do? It's described in Scott quite clearly. These are the bees that are opening up the cells, pulling out dead or dying larvae, getting rid of them, dumping them out. But not all bees do that. At least if you observe, say, a colony of many hundreds of bees, you'll see only a certain percentage of them will actually do that. The others just don't.

Scott uses this as an example of genes in behavior, and he discusses it in terms of two genes. It's all based on one study that showed that you can create a colony where there's no hygienic bees, and you can have colonies with many more hygienic bees. The evidence is, from the paper he was studying, that it's based on two genes. Both tend to be dominant, and if they possess the non-dominant allele, then they will be hygienic.

But why are there two genes? Because there's two behaviors involved, and they apparently, according to this study, they inherit separately the ability to do one or the other. In order to find dead larvae or dying larvae, they have to be able to open the cell in the hive-- so he calls that uncapping-- and the other involves actually getting into the cell and pulling out the dead larvae.

That's another kind of behavior-- so two distinct behaviors. And the genetic studies indicate that you can have bees that will uncap, but won't clean out. And you can have other bees that won't uncap, but they will clean out dead larvae. That's why they concluded there have to be two separate genes. Then he goes on, and he points out that in a colony, you can have a colony, let's say, that contains all hygienic bees, but they don't all engage in hygienic behavior.

You can have a colony that involves half hygienic bees, but 50% of them don't engage in hygienic behavior. Furthermore, they engage in the behavior only when they reach a certain age, and the age at which they start their hygienic behavior will actually depend on the proportion of hygienic bees in the colony. If there's many more, they will engage at an older age. If there's very few, then they will start younger. He spells out the numbers for that.

I went to one of the studies he was using. The title I listed for you, there-- "Influence of Colony Genotype Composition on the Performance of Hygienic Behavior in the Honey Bee." They describe the creation of four colonies that had 25% hygienic bees, 100% hygienic bees, or 0% hygienic bees.

This is from their table, where they're summarizing many of the results. Here's the percentage of hygienic bees, and the 100n means 100% non-hygienic, so that's 0% hygienic bees. Here they're just listing the number of bees that are hygienic or nonhygienic. The nonhygienic ones are in parentheses.

You'll see that there are 1,600 bees. They adjusted the numbers in these four colonies-- so there are 1,600 bees in each of the four colonies. They went from being all hygienic and no hygienic, and then the in between ones here-- 400 and 1,200, and 800 and 800. Then here's the statistics on how many of them are actually engaging in hygienic behavior. You can see that if only 25% of them were hygienic, then almost 79% of them engaged in hygienic behavior. If half of them were hygienic, then almost 40%

If all of them were hygienic, only about 19% of them would engage in hygienic behavior in this study. Of course, if none of them were hygienic, then they are only looking at the hygienic behavior of the two kinds of bees. But they looked at the nonhygienic behavior-- sorry, nonhygienic behavior in hygienic and nonhygienic bees. It's very interesting, the nonhygienic bees actually do engage in some hygienic behavior, so that doesn't quite fit the genetic study.

That led me to look a little further, and I found another paper. It included one of the same authors, which is how I found it. It was published the same year in the *Journal of Comparative Physiology*, and it was entitled "Olfactory and Behavioral Response Thresholds to Odors of Disease Brood Differ Between Hygienic and Nonhygienic Honey Bees." They had a couple of different ways of looking at how sensitive they were to odors.

They were interested, of course, in their response to the odor of dying or dead larvae, and they found that the hygienic and nonhygienic bees showed different thresholds. The hygienic bees were much more sensitive to the odor. They had inherited different olfactory abilities. But it wasn't that the nonhygienic bees couldn't detect the odor of the dying larvae. They just had much higher thresholds, so it was more difficult for them to detect. So that may explain why the nonhygienic bees sometimes do clean out a cell of dead larvae.

They not only can smell, just not as well. But they can also engage in hygienic behavior, if they actually detect it. But usually they're not engaging in such behavior, because they don't notice it. That's probably much more efficient for a bee colony. You don't need all bees doing that. What you need the rest of them for? These are worker bees, and you want them to go out and get the nectar, bring it back to the hive, feed those larvae, because most of them, of course, are alive, unless the colony is suffering from some pathology, which does occur in bees.

The study completely neglected the topic that Scott had emphasized-- the difference between uncapping and removal behavior. This later study, in spite of one of the authors being the same, they didn't mention that. I'm not going to make any attempt to reconcile that. This is typical in science. They don't completely satisfy you with any study, but it did explain quite a bit about why some bees engage in the behavior and others don't.

A little more about genes and behavior-- we talk about genetic fitness. What is genetic fitness? Direct genetic fitness means how many offspring you have. That's one measure of your genetic fitness. We can also talk about inclusive fitness. How do we define inclusive fitness?

It was a major issue for Charles Darwin, this issue. How could sterile workers evolve in social insects? Sterile workers are not having offspring. Sterile workers are the daughters of a queen, but they share a lot of genes with that queen. In fact, because of the genetics of these hymenoptera, they usually share 75% with the mother. That depends, if she only mated with one male anyway.

We'll come back to this topic when we deal with sociobiology. It's been a major topic, and it's led to a number of new findings by a sociobiologist. The point is because of the work of those sterile workers, their work for the colony, promotes the survival and increase in their genes, which they share with their mother, the queen. They have inclusive fitness.

Similarly, if you have a human who has no offspring, it doesn't mean that his inclusive fitness-- the broader definition of genetic fitness-- isn't present. If he is doing something to promote the survival of his nieces and nephews, for example, of his sister, whatever you see, he's promoting the survival of his own genes. He shares 50% with his siblings. He shares 25% with his nieces and nephews. That's why the concept of inclusive fitness is so important. It's, in fact, necessary to explain the evolution of specific types of behavior.

Let's say a little bit about learning, and starting with very simple kinds of learning-- habituation and sensory adaptation. You should know the definitions of habituation and sensory adaptation. Scott's textbook describes briefly just habitation, not sensory adaptation. You can easily find an answer to that, and you should be able to give definitions of habituation. I'm asking a question there about habituation to different kinds of stimuli.

Let's just start with definitions for these two terms. In both cases, there's a decreased response with repeated presentation of the same stimulus. Say I'm touching your back of your hand. I'm sitting next to you, you know me well, and I'm jiggling my hand, and I'm touching you. You notice it at the beginning, but pretty soon you habituate to it.

Or did you? Maybe just adapt to it. Maybe it's sensory adaptation. What's the difference? Habituation is more central, and we can go to physiology and define it that way. It's closer to the motor side, and the level of the response depends on the degree of novelty. The more this stimulus occurs, the less and less novel it is, the more expected it is-- less and less response.

In the case of sensory adaptation, the actual-- and this usually happens right at the receptor level-- you get less and less response. The receptors are just not sending as many impulses to the central nervous system. It's a kind of fatigue. That's sensory adaptation, and when the stimulus stops, there's a gradual recovery.

The same is true for habitation. There is recovery, but the mechanism is very different. In the case of a habituation, it's really difficult to define it as a kind of fatigue, although people have thought of it as fatigue at the more central level. Think of examples of habituation, and tell me if you can habituate to both simple and complex stimuli. Can you habituate to several bars of Mozart?

You can certainly habituate to a ticking of a clock. You can habituate to cars going by. You live on a busy street like I do, pretty soon you're ignoring most of it-- a particularly loud truck goes by, something changes, yeah you notice it, but most the time, you're not even noticing that you're habituated to it. You don't normally notice the clock. You don't notice internal sounds in your body unless they change a lot. You habituate to it. What about the bars of Mozart? Can you habituate to it? Yes you can. You can habituate to complex stimuli, too.

In fact, in tests of habituation, it's when something changes that you get a new response. So in formal tests, you might use series of stimuli. They often use rhythmic stimuli, and they can then suddenly leave out one stimulus in the rhythm. It sounds different, and the animal or the person will make an orienting response.

You can respond to the sudden absence of the stimulus, any detection of novelty. Now what are the responses? We won't be able to get much beyond this today. All of these terms are used in describing responses to novel stimuli-- the arousal response, the orienting response, orienting reflex is commonly used, especially in the east. This has been studied a lot in Russia.

We talk about curiosity for novelty. That is also a response to novelty. There's responses at the autonomic level, involving the autonomic nervous system. What are those responses? Heart rate change-- it's usually a heart rate increase, but if the heart's beating very fast already, it will actually slow down-- altered breathing, increased muscle tension, basal dilation in the head, basal constriction in the limbs.

Interesting that it's different in the head and in the limbs. In the head, where you have only head senses, it's different than the limbs. You can specifically measure that. You can measure the volume of the finger, for example, with a plethysmograph. It's easy to hook up a cuff around the finger and measure the volume and record it in a pretty sensitive way, and you will see the basal dilation or basal constriction.

Then there's behavioral responses-- alerting responses-- orientation of the head, eyes, and ears. Exploratory behaviors-- so now we're not just talking about orienting and alerting. I'm talking about approach and manipulation, all behavioral responses to novelty. Then finally we have a motivation to seek novelty, especially in higher vertebrates. Exploratory behavior occurs caused by a motivation to seek novelty that we call the motivation of curiosity.

I want to point out here that a novel stimulus can be seen as a conflict between expected input and perceived input. If you look at it-- this is the way a cognitive psychologist would look at it-- and it corresponds very well to what's happening-- and I point out here that the autonomic changes are exactly the same as measured by a lie detector.

What does a lie detector measure? Lies cause a different kind of conflict. In both cases we're dealing with conflict, and in both cases, we get these same autonomic responses. If in a lie detection-- that's why the skill of the person administering the test is so critical. He can get the autonomic responses, just by introducing novelty, and he has to be very aware of that.

We'll start by talking more about other kinds of learning, including associative learning and conditioning next time.