Podcast Interview: Eran Amichai

PNAS: Welcome to *Science Sessions*, the podcast of the *Proceedings of the National Academy of Sciences*, where we connect you with Academy members, researchers, and policymakers. Join us as we explore the stories behind the science. I'm Matthew Hardcastle, and I'm speaking with Eran Amichai of Dartmouth College. Bats use echolocation to navigate and look for food by emitting a call, listening for the echoes of the call bouncing off objects, and then using the echoes to discern the position and composition of the objects. In a recent PNAS study, Eran and his colleague Yossi Yovel of Tel Aviv University in Israel explored whether a bat's knowledge of the speed of sound is innate or learned. The researchers raised a group of bats in a helium-enriched environment, where the speed of sound is much faster than in normal air. Whether the bats were raised in the helium-enriched environment or introduced to it later, they consistently underestimated the distance they had to cover to reach a target. This would suggest that the bats' grasp of the speed of sound is innate and inflexible. So how exactly do bats use echolocation? Listen:

Audio clip: [chirping at various internals and speeds]

PNAS: Eran, can you walk us through what we just heard?

Amichai: Okay. So, what I sent you was a slowed down recording of an echolocation sequence of a bat approaching a target and landing on it. You start with the bat just doing one chirp at a time at relatively long intervals, so it sounds "cheep, cheep, cheep, cheep." In a natural behavior, usually that will be done in the air, and we call that phase "search phase." And that is when a bat is searching for the target. Now, once the bat has acquired the target, either for landing or a prey item that it is trying to engage, we go into what is known as the approach phase. And the approach phase would be much shorter intervals and more strobes, groups of close-together calls, so it will be "cheep, cheep-cheep, cheep-cheep, cheep-cheep, cheep-cheep-cheep, cheep-cheep-cheep, cheep-cheep-cheep." And this is when the bat is trying to speed up the information update rate on its target. Okay? And you can imagine to yourself that you are walking in a room, and you have your eyes closed; and then you open your eyes for one second and close them; and walk in, opening them for a second and closing them. And that's okay, if you don't want to hit the walls, don't want to stumble into a chair or something. But then if somebody throws a ball at you and you need to catch it, you must have a much quicker rate in order to catch it, right; you need to change this still images sequence into a more [of a] video image. So that's what bats do when they are starting to engage a target: They up the speed of the information update.

And then at the last stage, which we call the buzz or the terminal phase, the bat is already very, very near the target. Usually it's around 50 centimeters or less, and it's trying to actively catch it or land on it. And it sounds, "Cheep, cheep, cheep-cheep, cheep-cheep, cheep-cheep-cheep,

cheep-cheep-cheep, [trill].” And that end, the “[trill],” that's what we call the feeding buzz or a buzz, and that's when the bat is at the shortest possible calls and the shortest possible intervals. And this is one of the great ways for us bat researchers to know what bats are doing, even in nature. When we're standing outside, we don't see the animal, but we can hear its echolocation, and we can still know what it is doing, at least to some degree.

PNAS: You say in your study that bats need to know the speed of sound to calculate distances during echolocation. In terms of animal behavior, why does it matter whether knowledge of the speed of sound is innate or learned?

Amichai: Right. So for almost any behavior that an animal displays along its life, and definitely with sensory behavior or sensory biology, each trait can evolve to be either innate or learned. And another level is that it can be either fixed or flexible, or plastic, throughout the animal's life. So those are two different levels, and not necessarily one side goes together. They could be innate but flexible, learned but fixed, or either one of those extremes. And there are pros and cons for each of those four corners, let's call it, and one of the biggest advantages of having a trait that is learned is that it becomes much easier to adapt it to changing environments. But it comes with a cost. And that cost is that, usually, there is a period in which that trait needs to be learned, needs to be practiced, before it can be fully functional. And that makes the organism much less independent during that period, more reliant, for example, on parental care, or simply that it takes longer for that animal to properly use that trait. Now, if you go to the other side—an innate trait—the big advantage is that you're born, and you're ready; you can immediately start using that trait. You don't need to wait. The disadvantage is that, many times, you're going to be stuck with exactly what you learned, and you cannot adapt it if something in the environment or something in your life changes.

PNAS: In your study, you raised two groups of bats under different conditions. One group was raised in normal air, and the other group was raised in helium-enriched air, called Heliox. Can you explain what you observed with these two groups?

Amichai: We had a group of pregnant female bats in helium-enriched air, in which the speed of sound is increased. And so that's the condition into which those pups were born. They have always heard echolocation, either their mother’s or their own, only in enriched helium air. And so that would give us the condition in which if this trait is reliant on learning or on experiencing the environment that will provide us with the conditions to have them, sort of quote unquote, calibrate their echolocation with increased speed of sound. And the way it happens is, especially in captive conditions, we have to train the bats to eat from a plate because this is not a natural condition for a bat. So what happens in nature is that, for the first, I guess, about 2 months, the pups only feed on milk from the mothers. And then they start exploring their environment, learning to fly, learning to hunt, while the mother gradually reduces how much milk she gives until they are weaned and they are independent. We had to train the bats ourselves to eat from a plate. Probably the most challenging part was training the pups to eat from a plate. The mothers learned very easily; the pups, it took a little longer. But once they had learned that, then they kept trying to fly to the target and eat from the plate that was on the target.

We compared their echolocation parameters to those of the pups that were born and raised in normal air. We always tested the pairs of one Heliox pup and one air pup together; they were at the same age and the same flight abilities, so we were comparing always at the same conditions. And we tried to see if there are any differences between the two, and then we switched places. So the Heliox pup would go to air, and the air pup would go to Heliox, and then we compare it again. And we found that basically everything was the same; there were no differences. When either the air pups or the Heliox pups were flying in Heliox—increased speed of sound—then we had lower parameters for echolocation because they were experiencing sensory error. And when they were in air, they had the normal or distance-appropriate parameters because they could assess the target range properly. And we did not find any initial differences that we would have expected between the air pups or the Heliox pups if there was a learning component to that.

PNAS: What did it look like when a bat’s flight was unsuccessful?

Amichai: There are two components to that. One is the flight itself, which we only touched upon in the paper, but it is important to understand. One thing that the Heliox does to the air is it makes it less dense. And when it's less dense, the bats or any flying animal would experience reduced lift. And the bats compensated for that by increasing the amplitude of their wing beats. So they would raise them higher and lower them lower and make up a larger wing beat to compensate for that loss of lift. Now when you look at unsuccessful flights at helium, or Heliox, you see that the bats basically fly and pass right underneath the target, and that's because they start preparing for the landing a little bit too early. And so they lose lift and pass underneath the target. That's presented us with a problem. And the problem was that we couldn't say which flight was unsuccessful because the bat simply couldn't compensate properly for the loss of lift and which failure is because of a sensory error, which is why most of our results are based on echolocation data. And that echolocation is from when the bat is still on the wall preparing to take off to the target, and it is basically preparing for the flight, focusing on the target. And we identified in a previous study two very, very helpful parameters to look at, which are the interval between the calls that the bat produces right before it takes off and also the duration of these calls. So this can tell us whether the bat looks further or closer away. So smaller parameters, shorter calls, shorter intervals, meaning that the bat thinks the target is closer to it. And longer parameters, longer durations, longer intervals, mean that the bat perceives the target as being farther away. So this is what we based most of our results on, and not on whether the bat managed to actually hit the target or not. And the interesting thing is that even in flights in Heliox when the bats did manage to hit the target, they still had a sensory error.

PNAS: So your results suggest a bat's knowledge of the speed of sound is innate. What is the significance of this finding for our understanding of bat behavior?

Amichai: I think it gives us a better understanding of two concepts. One is a little bit more understanding of how the bat's brain functions, and that's without having to go into the brain and put electrodes inside, just by recording the sensory behavior. So we know a little bit better about this function of the bat's brain. We know that this is probably fixed and not flexible, so there are no learning involved in this aspect. But I think a more interesting insight is into the intricacies of selections when you look at an evolutionary process of a trait. And in this case, we thought that we understand the pressures that are applied here. We thought that, oh, we have a trait that would benefit from being flexible, from being learned. And we expected—we were actually surprised by our results—we expected exactly the opposite, right? So we thought that we understood the sort of array of pressures on this trait, and we found that we were wrong. And we think that the reason is that the cost of these sensory errors is not that great. We are talking about very short distances. And because that error would be relative, the closer the bat gets to its target, the absolute distance of the error is smaller. So as the bat closes in with its target, it gets a more and more accurate perception of range, even if it does have a sensory error. And in the context of the natural behavior of a bat closing in on a target, almost always the bats overshoot the target and sort of scoop it up with its membrane, either the tail membrane or the wing membrane. And so it is very easy, even if you underestimate or overestimate a little bit, you already have that buffer, that you can have that mistake and still engage with your target successfully. But on the other hand, when you look at the ecological constraints of most bats, definitely in temperate zones, you see that there is a very limited period of time for the pup to get to independence and to get itself fattened up for winter. So there is definitely a big, big advantage to having that period of perfecting your echolocation as short as possible.

PNAS: You say in your study that bats encode the world in terms of time and not space. What exactly do you mean?

Amichai: When we move down to the small scale—to the short distances up to a few meters, which is relevant for a bat trying to catch a target, for a bat trying to avoid colliding with another bat, for a bat navigating within its cave, for example—so there, we think that the bat does not encode space in terms of distance, but in terms of time, specifically the time it takes for the echoes to return. Now, this is not our theory; we did not come up with it. It was described or suggested previously, but I think this is one of the first pieces of evidence that supports this theory: the fact that the bats never learned to update their sensory behavior, even when they experienced failure after failure, and even when they experienced success. So you would think that once the bat has succeeded in Heliox, it would sort of update, “Oh, I'm thinking that 2 milliseconds is this distance, but actually, it's that distance, and I can convert it to the proper distance.” So you would expect the brain to work that way, if it would have been converting those delays into distance. But because that never happens, we believe that this supports the hypothesis that when the bat is relying on echolocation, it never translates time to distance, it just stays in the time domain. So this is a different encoding of space. So we're not encoding it in centimeters, we're encoding it in milliseconds.

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