Finding Meaning in Sound: Auditory Perception and Adaptation

INTERVIEW WITH PROFESSOR FRÉDÉRIC THEUNISSEN

BY CAROLINE KIM, KIRA STERLING, AND ANANYA KRISHNAPURA

PROFESSOR FRÉDÉRIC THEUNISSEN

Dr. Frédéric E. Theunissen *is a professor in the Department of Psychology at the University of California, Berkeley and is the principal investigator of the Theunissen Lab. His work strives to understand how the brain recognizes and perceives natural sounds, such as human speech and animal vocalizations. In his research, he uses computational approaches as well as behavioral experiments to explain auditory phenomena and understand the neural representations of natural sounds. In this interview, we discuss his findings on auditory perception and adaptation in zebra finches and humans.*

BSJ: What drew you to the fields of neuroscience and psychology, specifically auditory science and perception?

FT: It was not a straight route to where I am now. I received my undergraduate degree in physics, but I was also interested in biology and evolution from the beginning of my studies. For a while, I thought medicine would be a good path for me, but then I realized that I liked research and the academic environment much better. In the 1980s, Donald Glaser, who was a physics professor at UC Berkeley and Nobel Prize winner for the invention of the bubble chamber, was trying to model the brain with neural networks. I went to his lab meetings, and I thought that applying a physics-based approach to tackling such a complex problem as presented by the human brain was a really fascinating project. I think a lot of physicists are a little naive because they think that clean, simple mathematical formulations can be easily applied to most projects, but it becomes more difficult to implement this kind of approach once you break into the complexities of biology. I was interested in the intricacies of his work, and that served as my first attraction to neuroscience and the study of the brain.

With regard to auditory science, I like to learn different languages, I enjoy music, and I am fascinated by animal communication and the evolution of language, so it was a natural transition into studying sounds. I study what the auditory system does, what happens in different stages of auditory processing, and how we can understand that processing—not just in terms of simple synthetic sounds that engineers produce, like pure tones and white noise, but particularly natural sounds. My first contribution to the field of neuroscience was to study how we can understand the different computations that are happening in different stages in the context of natural sounds. Now, we are pushing our questions even further, attempting to additionally understand the context of sounds that we produce for communication.

BSJ: What is a vocal signature, and how do animals use these signatures to distinguish individuals?

FT: Vocal signatures are mostly used in the context of animals where animals use them to identify each other. For example, emperor penguins live in huge colonies, and, to us, all the penguins might look alike. It turns out that they themselves also have a hard time recognizing one another, and the only way they can find their mate is often through these vocal signals. These very characteristic signals that they produce are their individual vocal signatures.

Passive voice cues can also be used to distinguish between individuals. For instance, one individual may have a vocal tract that is a little bigger or has different cavities compared to another's, leading to overall differences in voice. Your manner of speaking is another example of a passive voice cue. Individuals might use certain expressions in a way that is unique to them. Since you can recognize a person's speech based on these kinds of cues, they can also serve as an individual's signature.

BSJ: Between active and passive cues, is one more effective than the other in differentiating individuals?

Figure 1: Zebra finches.[2] *Zebra finches are commonly found in Central Australia, where they most likely evolved. The gray and bright orange-colored bird is highly social by nature and is considered to be incredibly adept at singing and producing vocalizations.*[3]

FT: Some active cues are more salient than passive ones. If your goal is to identify yourself, you can accentuate non-passive features. For example, I can say, "I am Frédéric Theunissen," and that can be my individual signature. That is a stronger cue for you than if you were to just listen to my voice for a while.

The flip side is that these cues are less flexible. Whereas the main purpose of active cues is to identify individuals, they do not carry much meaning beyond their initial use. Conversely, passive cues generalize very well. With voice recognition, I do not have to remind you every five minutes that I am Frédéric Theunissen because, at some point, you recognize my voice and know that I am the speaker.

BSJ: What initially drew you to studying zebra finches in particular?

FT: Zebra finches are the laboratory equivalent of mice for songbirds. One reason for this is that they are domesticated, which means they do well in captivity. Another is that they breed all year long, so you can maintain a colony of birds relatively easily. The lab in which I did my postdoctoral research worked with zebra finches to study the mechanisms of song learning and song production. As it turns out, they are a great species in which to study communication because they are social birds and have a rich repertoire of communication calls. In addition to songs, which the males produce to attract females, they have a repertoire of sounds for all kinds of communication: aggression, distress, and even different types of alarms.

When I started studying zebra finches, I was really focused on song learning and the ability to learn to vocalize, which is something that is pretty unique. Then, I realized we can study more than just how they learn to produce sounds by imitation. We can further explore how their auditory system as a whole is involved in determining signals, making decisions, producing sounds, and so forth. That opened the door to a lot of different questions in communication.

BSJ: In one of your experiments, you conditioned finches to discern recordings of vocalizations using a food-based reward system. Can you tell us more about the process of designing this experiment?

FT: It is hard to ask animals what they are thinking. Therefore, we study them in two ways, one of which is just by observation. For example, if we see that a bird only responds when his mate is calling, we can deduce that individual recognition has taken place.

Alternatively, we can also set up experiments to test certain ideas. These experiments fall under the category of "Go/No-Go" tasks. If the finch hears one sound, it performs the associated task to receive a reward. We noticed that these birds are both good at pecking and slightly impatient, so we taught them that in order to receive a reward, they must refrain from pecking when played a particular song. When the bird starts to hear a sound and knows it is not tied to a reward, it will peck in order to skip the trial and move on to the next. When it recognizes one of the rewarded sounds, then it knows it needs to wait in order to be rewarded with food. Thus, our experiments took the classic model of operant conditioning experiments and optimized it for the personality of zebra finches.

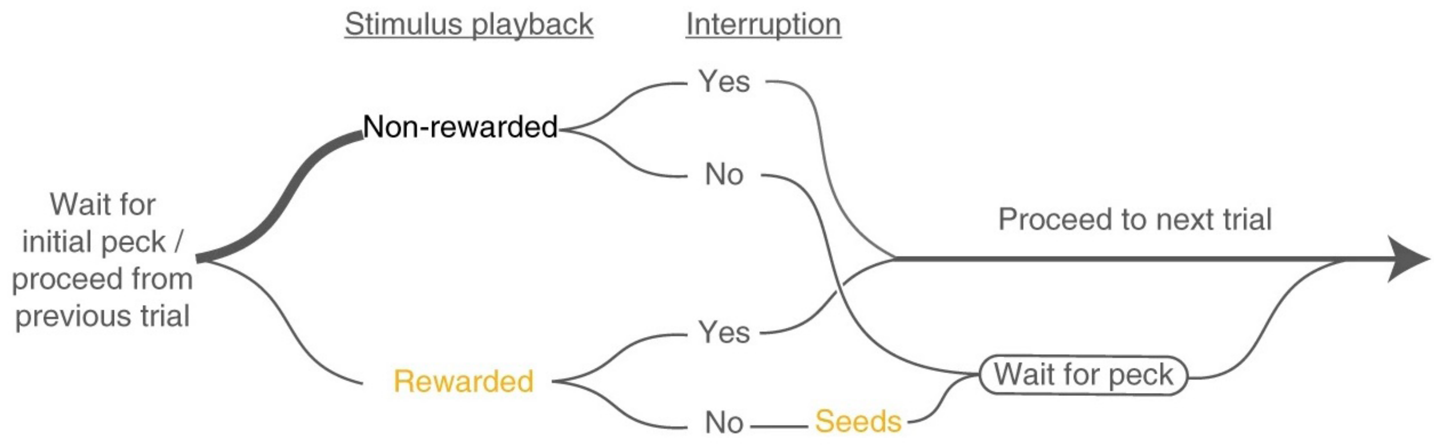

Figure 2: Flowchart depicting the sequence of the go/no-go task from the aforementioned zebra finch study.[4] *Finches pecked a keypad to initiate a sequence of vocalizations from one of two different bird vocalizers. One vocalizer is associated with a reward (Re), while the other is not (NoRe). Birds maximized their food reward by interrupting the NoRe vocalizer through pecking and refraining to interrupt the Re vocalizer through not pecking.*

BSJ: What can your research on their auditory perception tell us about the evolution of zebra finches?

FT: It is hard with sounds, and brains in general, to go back into the fossil record and make concrete claims as to how evolution has occurred. However, I can say a few things on how the brain of zebra finches has been specialized to do certain tasks. One striking result was the number of individuals that a finch could remember and how fast they could commit this to memory. It was very clear that this animal has a high capacity for building auditory memories. On top of memorizing the signatures of up to fifty different birds, these finches must also recognize different renditions of an individual's unique call, which can be a very difficult task. We do not know yet where these memories are stored in the birds' auditory systems and what allows them to store and recall memories so quickly. What we do know, though, is that even with complex natural sounds, they have a very efficient neural representation. We have shown this not just in one paper, but several times over the years when comparing natural and synthetic sounds.

BSJ: Can your research on zebra finches offer insight into how humans have created their methods of communication?

FT: I think finches and humans share a lot of similarities in terms of high-level auditory representation—that is, how we represent sounds internally. We can think of a sound not only as a pure tone of a given frequency but also as an auditory object, which is essentially a group of different sounds that can be attributed to a specific source. There exists a whole set of characteristics and qualities, beyond just pitch and amplitude, that allows a sound to be identified as a particular auditory object. For instance, we can say the word "hello" a thousand different ways, but they all represent the same auditory object in our mind. This mechanism of perception is highly advanced, but it seems so natural and automatic that we do not even think to realize it. We also see this level of perception occurring in other animals— in particular, we found that the response properties that we observed in human auditory neurons were mirrored in those of zebra finches as well.

At some point, though, you have to study humans if you want to learn about human language. It is fascinating to see at what point the human brain in particular has become this hyper-specialized, language-processing organ. Going from simply recognizing speech signals to processing language is something that is unique to only humans, and there is still a debate of where that line is.

BSJ: In "Rapid Adaptation to the Timbre of Natural Sounds,"[5] you mentioned that there are several characteristics that identify an auditory object, one of which is timbre. What is timbre, and what is its significance in speech*?

FT: What is interesting about timbre is that it is defined with a negative definition— it encompasses all aspects of sound beyond just loudness and pitch. Timbre is what makes a certain voice or instrument unique, and so it is key to identifying auditory objects. Some features of sounds, like frequency or amplitude, can be observed mathematically based on the features of a given sound wave. Timbre lies outside of these characteristics that are easily quantifiable and represents the quality of the sound or the set of characteristics that allows us to perceive them. There are a number of components that change the quality of the sound, but the reason why timbre is so important is because it serves as the key to identifying auditory objects. If we go back to our discussion about auditory objects, we can think of it as the shape and features of the sound, similar to how one would recognize the shape and features of a face. We can pronounce every single vowel of speech with the same pitch, intensity, and amplitude, but we would still be able to tell each vowel apart because each vowel is distinct in their timbre.

BSJ: What are the neural processes that support this auditory adaptation?

FT: There are all kinds of neural mechanisms that are both short-term and long-term. The depletion of neurotransmitters at the synapse are examples of short-term processes. You could also have a postsynaptic mechanism adaptation, where, if you always have the same calcium influx when you are transmitting information from one neuron to the other, the effect of that will decrease over time. So you can have levels at which adaptation can occur — it happens in your ear, all the way to your brain.

BSJ: In one of your initial experiments testing auditory adaptation, you primed participants with one of two sounds, and when asked to classify an intermediate sound between the two, listeners reported it sounding more like the one they were not primed with. Was there anything that surprised you about the results of this study?

FT: Our results were not particularly surprising, since previous work tells us that after sensory adaptation, we should expect to see an aftereffect. For example, if you stare at a waterfall flowing downwards and suddenly look elsewhere, everything seems to move upwards. This is the same phenomenon that is observed here, but in terms of sound rather than visual perception. Using a visual analogy, it would be as if after looking at pictures of planes and birds, you were shown a bird that was somewhat plane-like; you would perceive it as more bird-like. The part of it that was more unexpected was that adaptation happens for these pretty high-level features, like timbre, which is made of a lot of different components.

BSJ: What do you believe is the most rewarding aspect of your work, and what do you think is in store for future research on auditory perception?

FT: I think the most rewarding aspect of my work is that as I am discovering things, the kind of questions I have become richer. Every day, I get more amazed by the growing complexity of my work and the processes by which humans and animals are able to

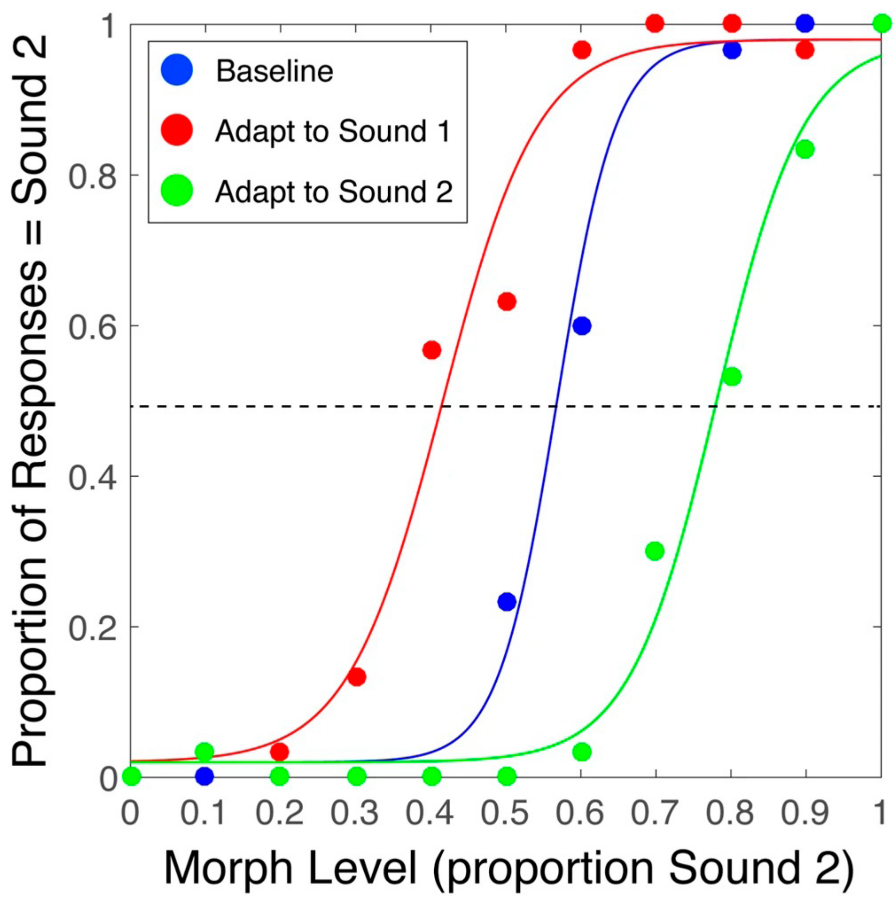

Figure 3: Results of intermediate sound perception based on primed sound.[5] *The x-axis indicates the composition of the intermediate sound that participants were given, in terms of how much it was composed of Sound 2. The three curves indicate whether participants were primed with Sound 1, Sound 2, or neither (baseline). The y-axis indicates the proportion of responses where participants indicated that the morph sounded more like Sound 2.*

perceive sounds. You start to gain an appreciation of these animals by doing this kind of research, and that, to me, is highly rewarding. But there is also the reward associated with being able to do this work with other people. In terms of what is in store for future research, we have a good understanding of auditory memories and representation, but we do not know exactly where they are stored and how they are formed. It might be useful to think about where memory is stored for words or how we are able to associate everyday phenomena with certain sounds. Hopefully, by the time I retire, I could solve at least one of these problems.

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** Though this study was conducted under the supervision of Professor Theunissen, the concept was developed and study performed by graduate student Elise Piazza.*