Neural mechanisms of echolocation in bats

Brain mechanisms of behavior (PSY 445)
Lecture 8

Required reading:

Further readings:
Chapter 2, Echolocation in Bats, in Behavioral Neurobiology by Thomas Carew.

The animal:
Bats are the most numerous order of mammals, and the most diversified of any animals on earth. This incredible evolutionary success is probably due to the huge advantage that echolocation gives them over their competitors by allowing them to fly and hunt in the dark. Several species are commonly studied in the lab, including the big brown bat, which is an FM bat, the horseshoe bat, and the mustache bat, which are CF-FM bats. The terms FM (frequency modulated) and CF (constant frequency) refer to their calls. An FM call is a short chirp that rapidly sweeps across a wide range frequencies (so it is a broadband signal). A CF call is much longer in duration (5-30 ms) and stays at a single frequency. CF-FM calls are a hybrid of the two, combining the advantages of both (which we will learn more about below).

2.2 Bats emit ultrasonic signals
The ultrasonic signals that bats emit can be recorded and plotted as shown. Here bat cries were measured as bats approached and captured their prey. (A) Some bats, like Eptesicus, use primarily FM signals. (B) Other bats, like Rhinolophus, use a combination of FM and CF signals. Note how the rate of the cry goes up dramatically as the bats near their prey. After Camhi 1984; data from Simmons, Fenton, and O’Farrell 1979.
Phases of pursuit and capture. Based on stroboscopic photographs at 100 ms intervals. Numbers indicate corresponding images of the bat and insect, tick marks indicate calls. In the approach phase, call rate is low, but the rate increases dramatically as the bat closes to within a meter, and are nearly continuous in the terminal phase. (Kick & Simmons 1984).

The behavior:

**Phases and sequence of echolocation:**

**Search phase:** Bat emits pulses at a steady, low repetition rate (~10 per second).

**Approach phase:** Bat turns head and ears toward target and increases call rate to ~50 per second.

**Tracking phase:** The bat now tracks the target with its head and ears. During this phase the bat observes target features to decide if it is an insect and is worth capturing.

**Terminal phase:** Call rate suddenly increases to ~200 per second, presumably for constant updating to allow accurate tracking at close range. Then the bat uses its wing or tail to scoop the insect into its mouth, and immediately returns to the search phase.
What can a bat detect using echolocation?

**Distance (range):** Bats measure distance by comparing the time of the emitted pulse to the time of the returning echo. Rapid FM sweeps are especially well suited for this, because the call passes through a wide range of frequencies, and is at each particular frequency for only an instant. Thus the bat can make a precise pulse-echo time comparison at each frequency point.

Bats can be trained in the laboratory to discriminate different targets for a reward. Jim Simmons, whose lab used to be on the 2nd floor of the Institute of Neuroscience here at UO, is probably the world expert on training bats. He showed that bats can be trained to discriminate different pulse-echo delays differing only by 60 μs, which corresponds to distances of 10-15 mm. That's definitely accurate enough to catch a mosquito!

**Size:** The larger the target, the larger the echo amplitude. But amplitude by itself isn't enough information, because the echo amplitude is also larger the closer the target is. So the bat needs to compare echo amplitude to echo delay. A quiet echo at a short delay must be a small, close object. If the same quiet echo has a long delay, it must come from a large object (like a bird) further away.

**Velocity:** The bat is in flight, and so is the insect, so the relative velocity between the two is critical to successful capture. Bats compute relative velocity by taking advantage of the Doppler shift. A constant frequency sound coming toward you sounds higher than if it were stationary, and sounds lower if it's going away from you. When the bat hears an echo at a higher frequency than the call it emitted, it knows it's gaining on its target. Likewise an echo at a lower frequency than the emitted call means the target is outdistancing the bat. Now you can see the advantage of a CF call: the long constant frequency pulse permits a very sensitive analysis of tiny shifts in that frequency.

**Doppler shift compensation**

As we will see below, the auditory system of the bat is highly specialized for echolocation. One of these specializations is an extreme sensitivity to a narrow range of frequencies around the call frequency (more about the neural mechanisms for this later). This presents a

![Doppler shift compensation](image)
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problem when the bat is gaining on the target, and the echo is doppler-shifted up in frequency: the echo is now outside of the sensitive region of the auditory system. To compensate for this, the bat lowers its call frequency, such that the returning echo is always at the frequency of maximum sensitivity. Thus the bat is constantly adjusting its call frequency, as shown by the experiment in the figure.

Doppler shift and flutter
The bat’s amazing sensitivity to tiny frequency deviations allows it to use Doppler shifts for more than simply estimating the relative velocity of the insect target. Incredibly, it can detect the wingbeats of a flying insect. As the wings are moving forwards or backwards, they will impart tiny Doppler shifts on the echo. Thus the wingbeats will produce a frequency modulation (FM) of the echo. In addition, the wings alternate between pointing directly towards the bat (where they produce the strongest echo) and being pointed in some other direction (producing weak echoes). Thus the wingbeats also produce an amplitude modulation (AM) of the echo. These subtle AM and FM fluctuations allow the bat to distinguish one kind of insect from another (sort of like an acoustic texture), so they can pursue only the tastiest ones. Which component (FM or CF) would be more useful for this?

Limits of delay sensitivity
Recall that Jim Simmons showed that bats can distinguish pulse-echo delays as close as 60 μs (i.e. distances of ~10 mm). Later he came up with a variation on this experiment, and “jittered” the delay back and forth to simulate wingbeats. He found that bats could distinguish jitter as small as 10-12 ns! This corresponds to distances of about 2 μm. This suggests that bats can perceive extremely fine-grained distance differences, which could allow it to recognize the “acoustic texture” of a winged insect in as much detail as we could see under a microscope.

![Graph showing performance of bats discriminating echoes that jitter by very small amounts. Average acuity of the bats for jitter is about 10 ns. Two different delay-generating techniques were used - electronic delay lines and cables of calibrated lengths. Each data point is 40-60 trials.](image)
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How does the bat accomplish this incredible behavior? The auditory system is specialized at every level, from the auditory receptors all the way up to the auditory cortex.

The basilar membrane
Hair cells (auditory receptor neurons) are embedded in the basilar membrane in the cochlea. The stiffness of the basilar membrane varies along its length, so that its resonant frequency is tuned, endowing the hair cells with place coding for frequency. In bats, the region of the basilar membrane that is tuned to call frequency is (1) thicker and (2) longer. The increased thickness makes it more sharply tuned, and the increased length means that more hair cells represent that frequency. This increase in representational density is analogous to the higher photoreceptor density seen in the fovea in the primate retina. This feature is therefore often called the “acoustic fovea.” Partly as a result of these two features at the sensory surface, there are more neurons representing call frequency, which are more sharply tuned, all the way up the auditory hierarchy from receptor to cortex.

Call suppression
In addition to the acoustic fovea, there is another specialization that begins at the ear and is repeated up the hierarchy. The problem is that the call is very loud (100 dB) and the echo is very quiet... but the echo is the signal the bat wants to hear. How does the bat avoid swamping its very sensitive auditory system with its own call? The answer is that bats dramatically reduce their auditory sensitivity just during the emission of the call. FM bats, which have very brief calls, contract their middle ear muscles during a call (decoupling the eardrum from the basilar membrane). The processing of the signal is also suppressed in the lateral lemniscus, one of the upstream structures. In CF bats, the call is long and therefore overlaps in time with the echo, so reducing sensitivity just during the call wouldn’t work. CF bats solve this problem by being relatively deaf at the call frequency, and they rely on the Doppler shift to raise the echo up into the sensitive frequency. FM-CF bats use a combination of these two strategies.

Inferior colliculus
Neurons in the IC are exquisitely sensitive to pulse-echo delays. Some kinds of IC neurons respond to both pulse and echo, with precise timing, even when they are only milliseconds apart. This is surprising for at least two reasons. First, neurons (and synapses) usually have a refractory period and are suppressed after firing. Second, auditory neurons usually have a shorter latency the louder the sound is. The echo is much quieter than the call, but IC neurons have a similar latency for both, so they accurately encode the pulse-echo delay. IC neurons have solved these two problems by (1) having a very low spiking threshold, and (2) being sharply tuned to a single frequency in an FM sweep.
Other kinds of IC neurons respond once to a pulse-echo pair, and are tuned to a particular delay. This delay selectivity is probably constructed out of inputs from the kind of IC neurons described above, that respond to both pulse and echo. Delay tuning is not

An IC neuron that responds precisely to both pulse (p) and echo (e) across a wide range of delays and amplitudes. Pollock, 1977.
organized topographically in the IC, but in auditory cortical neurons it is topographically organized (as we saw in the article by Suga and O'Neil). This suggests that delay tuning might be first constructed in IC, and then becomes organized in auditory cortex.

**Auditory Cortex**

Over the last several decades, Nobuo Suga’s laboratory has established that different echolocation tasks are processed in distinct regions of the auditory cortex. This is reminiscent of the distinct areas in visual cortex that process motion, form, etc. The article we read described a topographic map for target range in what is called the FM-FM area. There is also a CF-CF area that encodes relative velocity, and (by far the largest region) the DSCF area that performs Doppler shift analysis.

**FM-FM:**

The call of the mustached bat contains a long CF followed by a short FM component. Recall that the FM component is the best cue for pulse-echo delay (what was the CF best for?). In the FM-FM region, neurons respond poorly to a call or an echo by itself, but respond vigorously to a pulse-echo combination at a particular delay. The best delay is organized in a columnar fashion, such that there is a topographic map of distance (range) across this cortical area. Each call has four harmonics. There are 3 types of neurons, that respond to the combination of pulse-FM1 with either echo-FM2, echo-FM3, or echo-FM4. Each of these types of neurons has its own subregion of the FM-FM area. Not only that, but these neurons are also selective for amplitude, such that each neuron responds best to a particular combination of delay and amplitude. This explains how delay and amplitude are combined to compute the absolute size of a target. Thus these neurons represent a target of a particular size at a particular distance from the bat.

How is the delay selectivity computed? The mechanism is very similar to the Jeffress model for sound localization, which is studied in the barn owl by Terry Takahashi here at the Institute for Neuroscience at UO. The source of the signal is different groups of neurons in the IC that respond to either the pulse or to the echo. The signals from the pulse-responding neurons are passed through a delay line, so that they converge on downstream neurons at exactly the same time as the echo signal. These downstream neurons (probably in the medial geniculate nucleus of the thalamus) are highly selective coincidence detectors, which will only fire when the two inputs arrive together and bring the neuron across threshold. This only happens when the pulse-echo delay exactly
matches the neuronal delay line. Neurons with different delay lines then project topographically to the FM-FM region in the cortex.

**CF-CF:**
The CF component of the call is used for Doppler shift analysis to compute relative velocity. Neurons in the CF-CF region of auditory cortex are specialized for this computation. These neurons don’t respond to the CF component of the call or echo presented alone, but they respond extremely well to the combination of a call-CF with an echo-CF. The topographic arrangement is very interesting: Along the surface of the cortex, the CF1 frequency increases along one axis, whereas the CF2 and CF3 frequencies increase at right angles to that axis. Thus there is a coordinate system in which each point along the cortex represents a particular relative velocity.
DSCF:
The Doppler-shifted CF area is the largest subregion and occupies almost 30% of the entire primary auditory cortex. These neurons respond only to echo CF2 and nothing else, and they are extremely selective, responding only to frequencies in a very narrow range around the resting CF2. For example, CF2 is 61 kHz in mustache bats, and the entire DSCF encodes only the range 60.6-62.2 kHz. This region is essentially the cortical version of the acoustic fovea. These neurons allow the bat to perform very sensitive frequency discrimination, which may be how the bat performs the amazing feats of acoustic texture and wingbeat discrimination. To prove this, Suga pharmacologically blocked DSCF, and showed that bats could no longer perform frequency discrimination (but could still discriminate delays). Conversely, inactivating FM-FM disrupted delay discrimination without affecting frequency discrimination.

Summary:

Bats are capable of incredible behavior, which has allowed them to be extremely successful evolutionarily. Here we have seen how their auditory system is highly adapted for the job of echolocation. We identified the relevant sensory parameters underlying the behavior (such as delay, amplitude, and Doppler shift) and saw that these are first computed and then directly represented topographically in the bat auditory system. Thus what underlies the amazing capability of the bat is the sensory world that they perceive. They must be able to “see” the ranges and relative velocities of targets in their acoustic environment, as effortlessly as we can look out the window and see a visual scene. Being able to fly probably helps too.