Chapter 11

**THE AUDITORY BRAIN AND SOUND LOCALIZATION**

The localization of objects in space via the auditory system is a very complex process. Inner hair cells in the cochlea send signals to the auditory nerve, which then provides input to the cochlear nucleus in the brain stem. The signal then goes to the superior olive and on to the inferior colliculus. Next, the signal goes to the medial geniculate nucleus in the thalamus, which then projects to and receives feedback from the auditory cortex in the temporal lobe. Surrounded by the belt and parabelt regions, the primary auditory cortex (A1) is the first area that receives input from the medial geniculate nucleus. Cells in A1 show a tonotopic organization, meaning that they are organized by frequency.

Sound localization is based on the comparison of sound in the two ears. The azimuth refers to the left-right aspect of sound localization. Elevation refers to the up-down aspect of sound localization. Distance refers to how far away a sound is and whether it is in front of or behind the hearer. The interaural time difference is the time interval between when a sound enters one ear and when it enters the other ear. The interaural level difference is the difference in loudness and frequency distribution between the two ears. The head casts an acoustic shadow, which changes the loudness and frequency distribution of sound going to each ear. The cone of confusion is a region of positions in space in which sounds create the same interaural time and interaural level differences. The folds in the pinnae cause slight reverberations that amplify some frequencies and dampen others, which affects elevation perception. Internal knowledge of the loudness of familiar sounds is a primary method of inferring distance of sounds. The ability to distinguish different sounds in the ambient environment is called auditory scene analysis, which can further be categorized into temporal segregation, spatial segregation, and spectral segregation. Auditory development occurs very early, with a functional auditory system developed by about the 25th week of gestation.

Introduction

* The localization of objects in space via the auditory system is a very complex process.
* At the perceptual level, we use loudness to home in on the spatial location of a sound—the louder the sound, the closer you are to its source.
* Sounds can also be localized when standing still—the auditory system calculates differences in loudness and timing between the two ears.
  + The calyx of Held is a super-giant synapse that connects two neurons in the auditory primary cortex and is responsible for spatial location.
  + Because these synapses are so big, it allows the extremely rapid transfer of information from one cell in the network to the next.

Brain Anatomy and the Pathway of Hearing

Auditory Nerve Fibers

* Inner hair cells in the cochlea form synapses with auditory nerve fibers which are bundled together in the eighth cranial nerve to be sent to the brain.
  + Any particular nerve fiber has a characteristic frequency to which it is most sensitive, consistent with place code theory
  + Each nerve fiber also responds to sets of frequencies both higher and lower than the characteristic frequency, referred to as their tuning curve.
* In the brain stem, the auditory tract goes through the **cochlear nucleus** and then the **trapezoid body**.
  + The cochlear nucleus contains subnuclei with specific functions such as sensitivity to the onset and offset of tones at particular frequencies and lateral inhibition.
  + The trapezoid body is important in determining the direction of sound.
* Then, the sound signal goes to the **superior olive**, which receives input from both ears.
  + This early crossover is crucial for sound localization.
* The next synapse is in the **inferior colliculus** which projects to the **medial geniculate nucleus** of the thalamus.
* The medial geniculate nucleus projects to and receives feedback from the auditory cortex in the temporal lobe.
* Auditory nerve fibers from each ear go to each side of the temporal lobe, but more from the right ear go to the left temporal lobe, and vice versa.

Auditory Cortex

* The **auditory cortex** is a large area located in the temporal lobe.
* The first area that receives input from the medial geniculate nucleus is the **primary auditory cortex (**also known as **A1).**
  + Cells in the primary auditory cortex show a **tonotopic organization**, i.e., cells show a maximal response to specific frequencies and these cells are organized in map-like patterns.
* A1 is one of three areas that make up the **auditory core region**, with the other two being the **rostral core** and the **rostrotemporal core**.
  + The core region appears to serve the same function as V1 does for vision, allowing for the primary analysis of frequencies.
* The **belt** and **parabelt** regions essentially wrap around the primary auditory cortex and they seem analogous to the extrastriate cortex, doing more complex analyses of the auditory signal.
* “What” and “where” information are separated in the auditory system in a way similar to the visual system.
  + The “what” system forms the basis of speech and music perception (see chapters 12 and 13).
  + The “where” system is responsible for localizing sound in space.

Localizing Sound

* In the auditory system, sound localization is based on the comparison of sound in the two ears and is thus analogous to stereoscopic vision.
* The **azimuth** refers to the left-right aspect of sound localization.
* **Elevation** refers to the up-down aspect of sound localization.
* **Distance** refers to how far a sound is from us and whether it is in front of or behind us.

Interaural Time Difference

* The **interaural time difference** is the time interval between when a sound enters one ear and when it enters the other ear.
* Sound coming from the right will enter the right ear a split-second before entering the left ear, and vice versa.
* Because our auditory system can detect this difference in timing, we can use the interaural time difference to determine location along the azimuth.

Interaural Level Difference

* The **interaural level difference** is the difference in loudness and frequency distribution between the two ears.
* The head casts an **acoustic shadow**, which changes the loudness and frequency distribution of sound going to each ear.
  + The acoustic shadow is much more prominent for high-frequency sounds than for low-frequency sounds.
  + High-frequency sounds will be louder in the closer ear, but low-frequency sounds will have approximately the same loudness in both ears.

The Cone of Confusion

* The **cone of confusion** is a region of positions in space in which sounds create the same interaural time and interaural level differences.

Elevation Perception

* Our auditory system detects elevation as a function of changes in sound frequency created by the folds of the pinnae.
* The folds in the pinnae cause slight reverberations that amplify some frequencies and dampen others.
* The **spectral shape cue** is the change in a sound’s frequency envelope created by the pinnae.

Detecting Distance

* One of the main methods for inferring distance of sounds relies on our internal knowledge of the loudness of familiar sounds.
* For instance, human voices can be judged as being closer or nearer based on their loudness, but this may lead to errors.
* Frequency also plays a role in distance perception.
  + High-frequency sounds show a greater decrease in loudness as a function of distance than do low-frequency sounds.
* The proportion of direct sound to reflected sound is another cue for distance.

Auditory Scene Analysis

* The ability to distinguish different sounds in the ambient environment has been called **auditory scene analysis**.
* Bregman’s (1990, 2005) view of auditory scene analysis is analogous to the principles of gestalt psychology.
  + The auditory system uses heuristic rules to determine which frequencies go with other frequencies and which sounds are associated with which objects.
* Auditory scene analysis rules fall into three basic types: timing, space, and frequency.

Temporal Segregation

* **Temporal segregation** is the process whereby sounds that are linked in time are grouped together, whereas sounds that are not correlated with each other are not grouped together.

Spatial Segregation

* **Spatial segregation** is the process whereby sounds that are coming from the same location are grouped together, whereas sounds that are coming from different locations are not grouped together.

Spectral Segregation

* **Spatial segregation** is the process whereby sounds that overlap in harmonic structure are grouped together, whereas sounds that do not overlap in harmonic structure are not grouped together.
* A key aspect of spectral segregation is grouping by **harmonic coherence**, which is a strong predictor of what sounds our auditory system will group together.
* Harmonic coherence takes precedence over spatial segregation.

Auditory Development

* The auditory system develops early.
* Shortly after birth, infants respond differently to sounds they heard in utero and sounds they did not.
* The auditory system is functional at about the 25th week of gestation.
* At two days old, infants can recognize the voice of their mother.
* However, hair cells and the auditory nerve continue to develop throughout the first few years of life.

***In Depth: Biosonar in Bats and Dolphins***

* Both bats and dolphins use an active biosonar system.
* Similar to electric sonar systems, **biosonar** is a process whereby animals emit sounds and then use comparisons of these emitted sounds and their returning echoes to sense the world around them.
* Bats hear sounds at much higher frequencies than humans do; most species hear sounds over 100,000 Hz.
* Bats can also produce very high-frequency sounds.
* Together, hearing and producing very high-frequency sounds allows bats to use biosonar.
* Because there is such a short wavelength, high-frequency sounds are influenced by small objects that obstruct the wave pattern (like flying insects).
  + A high-frequency wave will hit the insect and cause an echo to return to the bat, allowing the bat to detect small prey.
  + Dolphins use the same system to hunt for fish.
* A drawback of high frequencies is that they lose energy rapidly, meaning that their loudness declines rapidly as the sound moves away from the source.
  + Therefore, the initial sound must be very loud.
  + Bat calls are often as loud as 140 dB and dolphin calls may be 200 dB.
  + Because the frequencies are outside our range of hearing, humans luckily cannot hear these loud sounds.
* Bats that live in the forest need to avoid obstacles and hunt whereas bats that live in the desert only need to hunt. Thus, the different kinds of bats have developed different types of biosonar.
  + The forest bats tend to use a CF-FM call, which has a constant high frequency (CF component) which sweeps down in frequency when it detects potential prey (frequency modulated, or FM).
  + Desert bats may not have a CF component.
* Distance from an object is determined by a calculation of how long it takes for an echo to return to the bat.
  + The **target range** is the distance of a predator from its potential target, determined by timing an echo’s return.
* Size of an object is also determined by returning echoes.
  + Larger objects produce bigger echoes.
* A bat must know how fast it is approaching its target so that it can initiate catching behaviors at just the right time.
  + Bats determine their **rate of approach** by measuring the Doppler shift in their calls.
  + Doppler shifts are apparent changes in frequency that occur when there is relative motion between the source of a sound and a detector.
  + If the returning echo appears to be slightly higher than the frequency of the call, the bat knows that it is gaining on its target.
* A bat also needs to know if its target is moving left or right and up or down.
  + Left-right determination is done by a comparison of the returning echo to the two ears, similar to humans.
  + Up-down determination involves comparing sound inputs distributed across its complexly shaped pinnae. Bats can move their pinnae, giving them much better elevation determination than humans.
* Altogether, bats use this auditory information to “see” objects in the environment.
* Dolphin sonar is physiologically different but functionally similar.
  + One of the main differences is that dolphins use neither the sustained CF nor the FM call.
  + Instead, dolphins make pulse calls at a constant frequency.