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1 March 1982; revised 24 May 1982

Localization of an Elevated Sound Source by the Green Tree Frog

Abstract. *Female green tree frogs readily localized an elevated sound source. Prior to hopping on sticks that formed a three-dimensional grid, females usually scanned laterally with their heads elevated after first scanning in the normal, nonelevated fashion. Unlike mammals and owls, frogs lack external anatomical features specialized for resolving vertical and horizontal components of source direction.*

Although acoustic orientation has been studied in many animals, the vast majority of this research has considered only the problem of sound source localization in the horizontal plane. The ability of animals to resolve the elevation of a sound source has been established only in owls, bats, monkeys, and humans (*1*). This is surprising since so many species with elaborate acoustic communication systems are arboreal or semiarboreal. Not only is sound localization in the vertical plane important for social interactions, but also it may be crucial for prey location and predator avoidance. The detection of source elevation is thought to depend on special anatomical features: pinnae in mammals and the asymmetrical (vertical) placement of the ears in owls. In this report we demonstrate that green tree frogs (*Hyla cinerea*), which lack external anatomical features specialized for acoustic orientation, readily localize an elevated sound source.

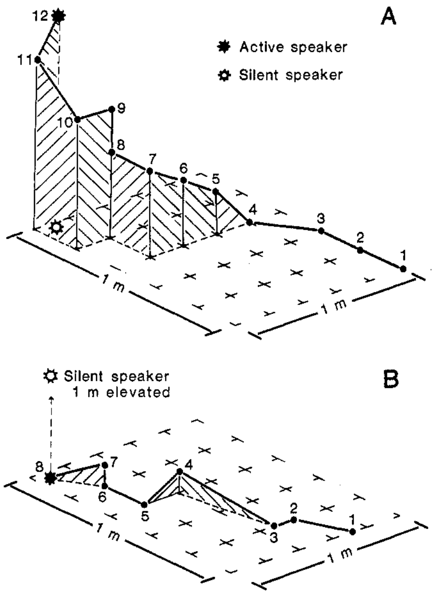

Fig. 1. Diagrams of the grid over which female tree frogs move during approaches to a speaker broadcasting synthetic mating calls. To provide for vertical movements of the animals, thin aluminum stakes (diameter, 10 mm; height, 1 m) were arranged on the grid area (1 m by 1 m); each stake position is indicated by a fine cross or other junction of fine lines in the figure. The grid of vertical 1-m stakes was stabilized by a series of crossbars at 25, 50, and 75 cm. These crossbars also served as reference points for estimating the vertical positions of the animals. Thus a spatial arrangement of many possible positions within 1 m^3 was provided. The speaker suspension plane (vertical) is indicated by the dashed line. The speaker and its support system were physically isolated from the grid so that there were no vibrational cues. (A) Diagram of a typical approach when the elevated speaker was active. The course of the frog is indicated by the heavy line, the numbers representing the frog's positions (1 to 12). The lengths of vertical lines below a number indicate the elevations to which the frog jumped or climbed at each position. (B) Diagram of a typical approach when the ground-level speaker was active, the numbers representing the frog's positions (1 to 8).

Gravid female tree frogs were collected near Savannah, Georgia, and tested within 24 hours. A three-dimensional grid of small aluminum sticks (Fig. 1) was constructed outdoors at the Oatland Island Educational Center. We suspended two identical speakers (Arso 2-inch) immediately behind the grid and isolated from contact with the grid and aluminum sticks. One speaker was about 5 cm above the ground and the second speaker about 1 m above the ground, directly over the other speaker. We broadcast synthetic mating calls [0.9 + 2.7 + 3.0 kHz (*2*)] from one or the other of the speakers, and we released females individually from a point on the ground about 1 m from the side of the grid opposite the speaker suspension plane. Experiments took place at night, and we used a dim flashlight to observe the positions and orientation movements of the frogs during phonotactic approaches to within 15 cm of a speaker.

Even before starting its approach, a frog typically made lateral scanning movements with its jaw parallel to the ground or slightly elevated. These scanning movements were observed throughout an animal's phonotactic approach to the speaker (*2*). Especially when the active speaker was elevated, the frog often repeated these lateral scanning movements after lifting its head. During a few approaches, an animal elevated and lowered its head without lateral scanning. These movements usually occurred when the animal was perched on

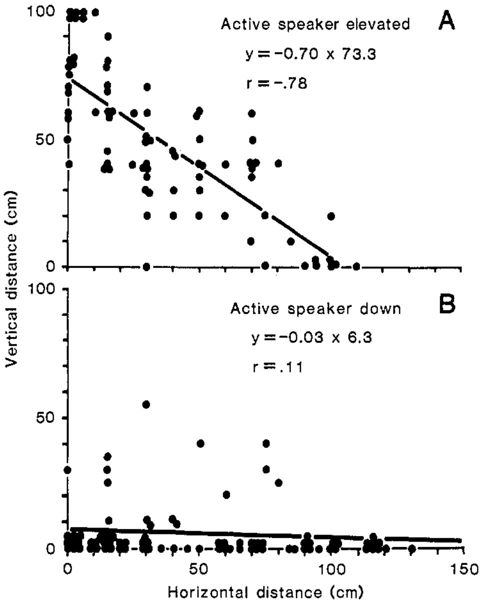

Fig. 2. Vertical distance (elevation) above the grid as a function of horizontal distance to the speaker suspension plane (A) when the active speaker was elevated, and (B) when the active speaker was near ground level. All of the data from 19 approaches are included: nine approaches were made when calls were broadcast from the elevated speaker and ten approaches were made when calls were emitted by the ground-level speaker.

one of the horizontal crossbars that stabilized the grid. In nearly every approach, the frog jumped onto one or more sticks, even when the speaker was not elevated. When on a stick, the animal's initial lateral scanning movements were usually similar to those made when on the ground; that is, it aligned its jaw parallel to the ground even if it had to twist its head to do so. However, sometimes the head was tilted slightly (< 45°) from the horizontal plane. Scanning movements of the tree frog, which occurred in every approach we observed, were one of the most prominent features of its sound localization behavior. By contrast, the barn owl can ascertain both the azimuth and elevation of a sound source even without scanning (*3*).

When the elevated speaker was active, the frog always continued to approach the elevated speaker by hopping from stick to stick, and it often climbed upward on one or more sticks. When the ground-level speaker was active, the frog usually hopped back to the ground before touching the speaker. Typical approaches are diagramed in Fig. 1, and the vertical positions of eight animals during 19 approaches are plotted as a function of horizontal distance from the speaker suspension plane in Fig. 2. Nine approaches took place when the sound came from the elevated speaker, and ten approaches when the sound came from the ground-level speaker. The slope of the linear regression of vertical position on horizontal distance was −0.70 when the elevated speaker was active; the slope was −0.03 when the ground-level speaker was active. When the sound was emitted from the elevated speaker, the animals had usually (eight of nine approaches) already begun to climb on a stick (vertical position > 0) at a horizontal distance of 75 to 90 cm from the speaker suspension plane. The elevation of the speaker at these distances was about 45° to 54°. Sometimes a frog hopped close (within about 20 cm) to the position (plane) from which the elevated speaker was suspended but found itself still 30 to 60 cm below the speaker. The animal almost invariably hopped to a position farther away (horizontally) and then reoriented and began another approach.

Our study is the first to provide behavioral evidence concerning the localization of an elevated sound source in an animal lacking specialized external anatomical features. As we show in detail (*2*, *4*), this ability may be based on a variable sound pressure gradient system. It is well established that insects use a pressure gradient system for sound localization, and it has recently been suggested that small birds also use such a mechanism (*5*). We believe that these animals should also have the ability to localize elevated sounds. As in the tree frog, these soniferous animals must often face the task of distinguishing between elevated and nonelevated mates and reproductive competitors.

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28 August 1981; revised 19 March 1982