inary versions of the manuscript and for most productive discussions of our results. The figures are due to the skill of F. Buchstäber and S. Marcinowski.

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Sound Localization in the Barking Treefrog

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Quantitative behavioral studies on sound localization in frogs have focused on the observation of frogs' phonotactic approaches towards artificial sound sources both in the field (*Colostethus nubicula* [1], *Hyperolius marmoratus* [2]) and under more controlled acoustical conditions in laboratory setups (*Hyla cinerea* [3]). As Rheinlaender and Klump [4] point out, these measurements of the accuracy of sound localization were made in a closed-loop situation. That is, the frogs were able to correct their orientation- or jump-angle during an ongoing presentation of the sounds. Thus, these experiments cannot provide conclusive evidence regarding the ability of frogs to discriminate between different angles of sound incidence, as opposed to merely being able to lateralize the sound source. In this study we present data on open-loop sound localization in the barking treefrog (*Hyla gratiosa*).

Female barking treefrogs were collected in amplexus from a pond at Skidaway Island near Savannah, Georgia. Each was placed at the center of a circular arena with a diameter of 2 m and a measuring grid (30° sectors) drawn onto the floor. The arena was located in a room with sound-absorbing wedges on the walls (cutoff 300 Hz) and was lit by a dim red light. A speaker (Analog-Digital Systems 200) that was covered by a thin layer of acoustic foam, which matched the color of the background of acoustic wedges, was placed at the edge of the arena at a distance of 1 m from the frog. Phonotactic movements were elicited by a playback of a digitized natural advertisement call – an analog recording of a typical call was digitized (12-bit A/D 50000 samples/s) into the memory of an AT&T 6300 personal computer and then recorded onto tape (TEAC A2340SX) through a 8-bit D/A converter and low-pass filter (Krohn-Hite 3200) set to 12500 Hz; this tape was used in the playback with a TEAC A2340SX recorder and a Quad 303 amplifier. The playback level was adjusted to 85 dB SPL (re 0.00002 Pa) at the release point of the female (General Radio 1900A sound level meter, C-weighting, fast RMS).

Females of *Hyla gratiosa* were especially suitable for an open-loop measurement of sound localization because they do not readily move before the playback of an attractive sound. Prior to playback, the long axis of the body of each female was aligned along the 0° reference line on the arena, and the speaker was placed at a randomly prechosen position that resulted in sound incidence angles of between −45° and +45° (15° steps; negative angles left from body axis). A single call was then played back to the frog, and two observers recorded its movements. If the frog did not move after the playback of the first call, then as many as nine additional calls were played back at a rate of 1 s^{-1}. As soon as the frog oriented or jumped after the playback of a call, the playback was terminated and the new angle between the body axis and the reference line was measured in 7.5° increments. Another test with the same frog was then conducted with a new speaker position after the frog had been replaced in the center of the arena. A trial was excluded from the analysis if the female moved prior to or during the playback of a call. Thus, the results of the experiments represent open-loop measurements of the ability of frogs to localize a sound source.

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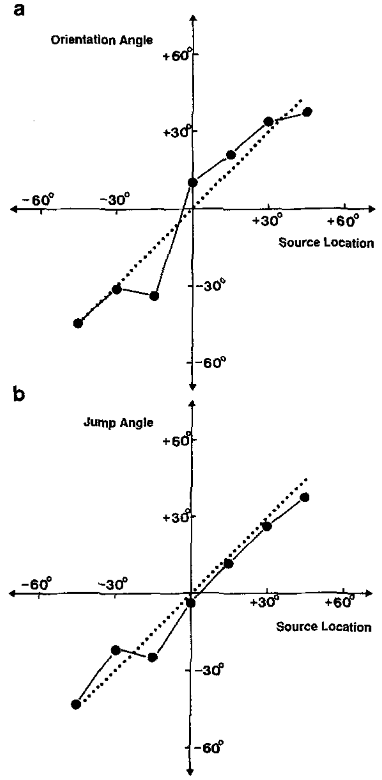

Fig. 1. a) Mean orientation angle in relation to angle of sound incidence; b) mean jump angle in relation to angle of sound incidence

In Fig. 1a we show the mean orientation angle in relation to the angle of sound incidence. The straight dotted line represents the angles expected if the frogs' body axis were perfectly aligned towards the sound source. The distribution of orientation angles at all speaker positions except + 15° differed significantly from the distribution of orientation angles at 0° sound source position (paired Mann-Whitney U-tests, $p_2 < 0.05$, after significant Kruskal-Wallis H-test). Furthermore, orientation angles were significantly larger at + 45° than they were at + 15° (Mann-Whitney U-test, $p_2 < 0,05$), and were significantly more negative at − 45° than they were at − 15° and − 30°. Distributions of orientation angles did not differ significantly between speaker locations at 15° and 30° in either direction (Mann-Whitney U-test). The mean direction of jump angles in relation to the angle of sound incidence (Fig. 1b) was very similar to the plot of the mean orientation angles. However, only at − 45°, + 30°, and + 45° angle of sound incidence were the distributions of jump angles significantly different from the distribution of jumps at 0° (paired Mann-Whitney U-tests, $p_2 < 0.05$, after significant Kruskal-Wallis H-test). Jumps were less accurate than the corresponding orientation responses ($p_2 < 0.02$, Sign test). In 87 cases we were able to record both the jump angle and the preceding orientation angle. In 48 % of the observations there was no difference between the accuracy of jump and orienting response; in 36 % of the observations the orienting response was more precise than the jump response, and in 16 % the opposite was found. The accuracy was especially different when the female frog responded after only one call; in 13 cases the orienting response was more accurate than the jump whereas in only 2 cases the opposite was true.

The variances in the distributions of orienting and jump angles for the various angles of sound incidence were large; the average standard deviations of orienting and jump angles were 21.2° and 24.6°, respectively. Furthermore, the largest variances were in the frontal range at 0° and + 15° sound incidence angles. Figure 2 shows the mean deviation from the expected direction for orienting responses and jumps (i.e., the absolute values of orienting and jump errors). In the frontal range (− 15° to + 15°) the orientation error was significantly larger than at more lateral angles (− 30° to − 45°, and 30° to 45°, $p_2 < 0.05$, paired Mann-Whitney U-tests after significant Kruskal-Wallis H-test). There were no significant differences between jump errors at the different angles of sound incidence ($p_2 < 0.1$, Kruskal-Wallis H-test).

Our data suggest that the barking treefrog has the ability to discriminate between different angles of sound incidence. Only with this ability could the frogs discriminate 45° from 15° and 30°. If barking treefrogs were only lateralizing the sound source, then the size of the orientation and jump angle should be independent of the angle of sound incidence once a critical threshold that allows left-right discriminations is reached. Left-right errors rarely occurred if the sound source was not in front of the frog at between − 15° and + 15°. For all angles of sound incidence, the results show average orienting and jump angles that come close to those expected if the frogs oriented precisely towards the speaker.

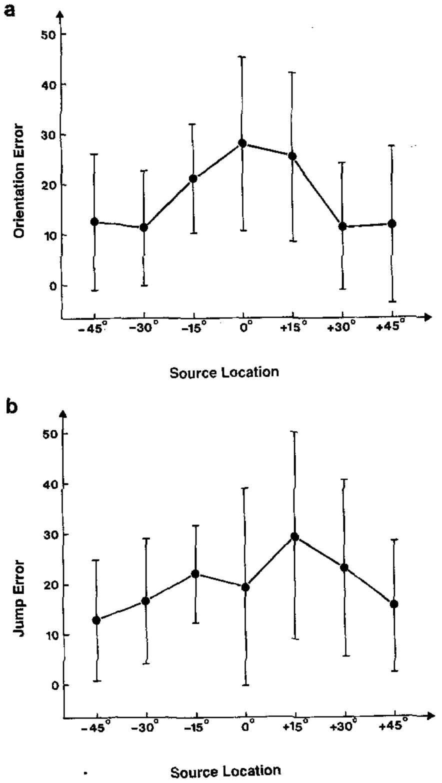

Fig. 2. a) Mean absolute orientation error (in degrees) and its standard deviation in relation to angle of sound incidence; b) mean absolute jump error (in degrees) and its standard deviation in relation to angle of sound incidence

Our measurements of orientation errors also suggest that the frogs have a tendency to turn if the sounds are coming from the frontal range (− 15° to + 15°). Thus, when the frog turns the resulting error will of course be large. The turning patterns are possibly a strategy to enhance binaural disparities if they are low.

Michelsen et al. [5] described directional patterns in the vibration velocity and amplitude of the tympanic membrane of a close relative of the barking treefrog, the green treefrog (*Hyla cinerea*). They tested awake, unrestrained treefrogs, and found that there were no binaural disparities at sound incidence angles of 0° and 180°, and the largest binaural amplitude difference of about 9 dB occurred between the ears ipsilateral and contralateral to the sound source at 90° and 270°. Between 0° and 90° sound incidence angle the binaural disparity increased monotonically and evenly. If there were a similar pattern in the barking treefrog, we would expect it to be able to differentiate between different angles of sound incidence provided that binaural disparities in intensity were sufficiently different. If the frogs are able to detect changes in binaural intensity differences of 1 to 2 dB, then this would account for their ability to discriminate between angles that differ by 30°. Furthermore, the pattern described in the green treefrog predicts that this ability is not limited to the frontal range, i.e., to lateralization of the sound source. Our results suggest that barking treefrogs can also discriminate between lateral angles, e.g., between $-30°$ and $-45°$. Thus our results on open-loop sound localization in the barking treefrog, which suggest the ability of true angle discrimination, are consistent with the measurements of the physical behavior of the pressure-gradient system described in frogs (see also the review in [6]). Further experiments with barking treefrogs are required in order to show where the relevant ports of entry of the airborne sound lie, i.e., whether only the tympana play a major role in the generation of binaural signal disparities or whether additional surfaces (e.g., the skin over the lungs [7]) play an important role. Moreover, we cannot exclude alternative mechanisms, such as the coding of the binaural time disparities in the envelope of the signal, since frogs may code the phase of a signal up to frequencies of 900 Hz [8]. Timing information extracted from binaural phase differences could also explain true angle discrimination in the directional hearing of barking treefrogs.

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Effects of Moving Textured Background on Neuronal Responses in the Toad's Optic Tectum

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The background is important for visual motion processing in both humans and lower animals. Cues derived from the movements of the background and the object are essential for the segregation of the object images, the discrimination between the real object motion and the self-induced object motion, and the reconstruction of the three-dimensional world [1]. In anurans, behavioral experiments have shown that the existence of the background is also essential for the animal's ability to discriminate between the real and self-induced object motion [2]. In motion-processing areas of higher vertebrates, such as the pigeon [3], the monkey [4], and the cat [5], neurons involved in relative motion processing between the background and the object have been reported. In the central nervous system of anurans, however, few experiments have been attempted to elucidate neural bases underlying visual processes such as mentioned above (see [6]). Aiming at this goal, we have designed a perimeter device for this specific purpose, in which an object and a textured background could be moved independently. Here, we will report the results of experiments using this device, in which the textured background was moved and its effects on neuronal responses in the toad's optic tectum were examined. A part of this study has appeared elsewhere in abstract form [7].

Single units were recorded extracellularly from the optic tectum of paralyzed Japanese toads using glass micropipettes filled with 2 % pontamine sky blue 6BX in 0.5 *M* Na-acetate. Recordings were made after the recovery from anesthesia under which the surgery for exposing the optic tectum had been performed. As visual stimuli an 8° × 8° black square (luminance: 1 cd m^{-2}) attached to a transparent plastic sheet and a sheet of Julesz's visual noise pattern [picture element: 0.46° × 0.46°; probability of being white or black: 50 %; luminance: 1 cd m^{-2} (black part), 11 cd m^{-2} (white part)] positioned just behind the transparent sheet were used. The former served as the object, whereas the latter served as the textured background. They were presented at a distance of 25 cm from the toad through a circular window (diameter 83°). The two sheets of stimuli comprised two endless belt systems, which moved independently in horizontal directions, and of which speed and direction were controlled, using two DC reversible motors.

A total of 28 tectal neurons having receptive field size of 8° – 35°, which seemed to belong to the class T5 neurons [8], were analyzed in this study.

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