Research Articles

Electrophysiological study of interaural sound intensity difference in the dolphin *Inia geoffrensis*

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Abstract. A wave observed in the auditory brainstem responses (ABR), sensitive to the side of sound presentation, is described in a dolphin (*Inia geoffrensis*). Dependence of the wave threshold on location of the sound source showed that the interaural intensity difference was more than 20 dB.

Key words. Auditory brainstem response (ABR); dolphins; binaural hearing.

Mechanisms of binaural hearing in aquatic mammals may be characterized by some specific features associated with peculiarities of sound transmission in water. The sound characteristics important for binaural hearing[1,2] are interaural delay and interaural intensity differences. However, the velocity of sound spreading in water, which is 5 times higher than in air, results in a corresponding shortening of the interaural delay. Furthermore, the acoustic impedance of head tissues is closer to that of water than of air. So the question arises whether in water the shading by the head is great enough to create any significant interaural intensity difference. Although air cavities in the head might be supposed to enhance the shadowing effect, the resulting interaural intensity difference has been little investigated.

The present study was undertaken to measure the interaural intensity difference in a dolphin using an electrophysiological method: recording of the responses evoked by auditory stimuli. Specifically, the auditory brainstem responses (ABR) have proved to be particularly valuable for investigations of hearing in dolphins. Using the ABR recording method, some important characteristics of hearing in dolphins have been assessed[3-5], including the directivity of hearing[6].

The experiments described here were carried out on an adult female Amazon river dolphin *Inia geoffrensis*, 215 cm long. The animal was kept in a round pool 6.5 m in diameter, 1 m deep. During the experiments, the animal was supported by a stretcher in such a way that the main part of its body was submersed except for the back and the dorsal part of the head with the blowhole. The stretcher was made of a sound-transparent material (fine network). The head of the dolphin was positioned in the center of the pool. Throughout the experiments the water column was only 40 cm high, to minimize the echo from both the pool bottom and the water surface, i.e. the sound transmission occurred as if in a plane layer.

Sound clicks emitted through a spherical piezoceramic transducer were used as acoustic stimuli. The stimulus rate was 10/s, the spectral band-width of clicks was 10–120 kHz at the -20 dB level, and the maximum spectral density was at 30–50 kHz. Sound intensities from 0 to 110 dB were used for stimulation (the relative level for sound intensity indication used in this work was 1 mPa). The transducer was situated 20 cm below the water surface, at a distance of 1 m from the melon tip, at azimuth angles of $0 \pm 135°$ relative to the longitudinal axis. The sound intensity was monitored by a hydrophone with a pass band of up to 150 kHz located near the animal's head.

ABRs induced by sound clicks were recorded from the head surface using thin needle-shaped electrodes inserted into the skin 3–5 mm deep. This procedure required neither curarization nor anesthesia of the dolphin. The active electrodes were placed on the dorsal or lateral head surface, and the reference one was on the back. The potentials were amplified in a frequency range of 50–

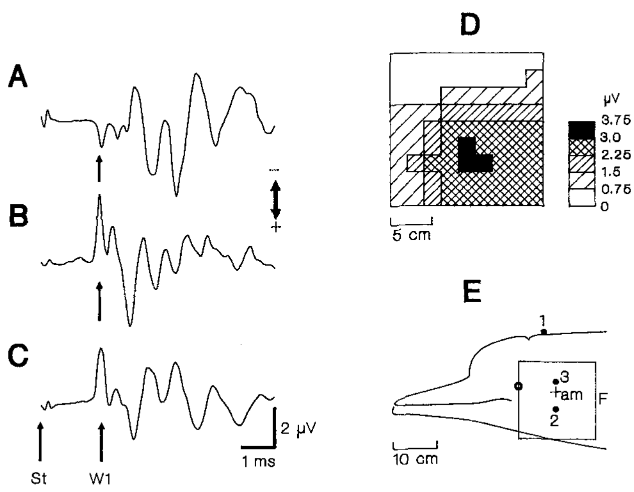

Figure 1. *A* An ABR recorded monopolarly from the vertex (point 1 in scheme E). *B* Monopolar record from lateral surface of the head (point 2). *C* Bipolar record from the lateral surface (points 2–3). Stimulus (St) and W1 wave are indicated by arrows. *D* Spatial distribution of W1-wave amplitude within the 18 × 18 cm region of the lateral head surface; the amplitude is designated by shading density according to the scale on the right. *E* Side-view of the dolphin's head showing the location of recording sites for *A–C* (points 1–3) and of mapping field for *D* (square F); am (cross): auditory meatus.

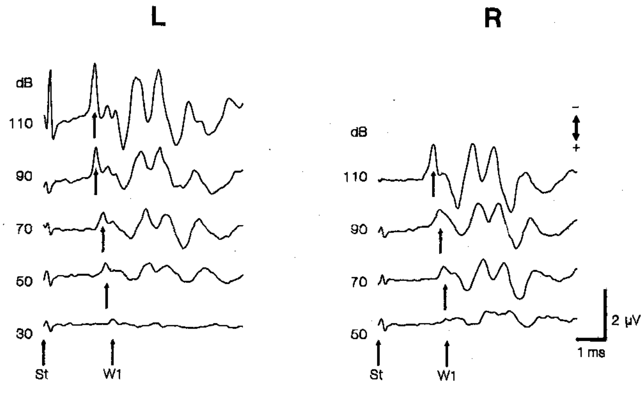

Figure 2. Dependence of amplitude of W1-wave on click intensity. The response was recorded bipolarly from the left side. *L* Sound-source position 45° to the left of the longitudinal axis, *R* 45° to the right. Threshold of W1 wave was estimated as 25 dB for *L* and 50 dB for *R*.

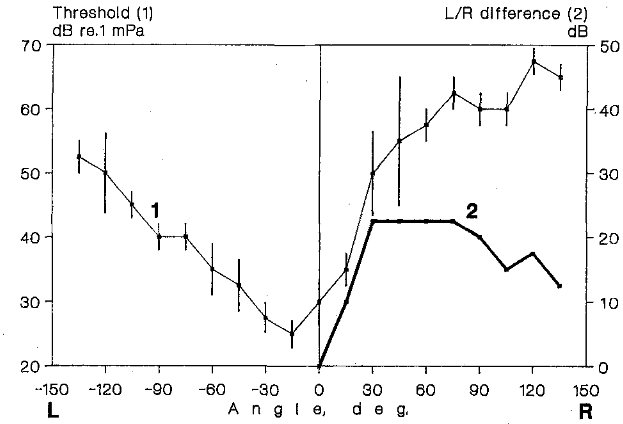

Figure 3. Dependence of the W1-wave threshold on sound-source position (1, left scale) and threshold difference between symmetrical left and right positions (2, right scale).

5000 Hz and then averaged using a routine technique within the time window 10 ms.

An ABR recorded with the standard electrode position on the vertex is shown in figure 1 A. According to earlier data, it consisted of a sequence of waves, each lasting less than 1 ms. The characteristic feature of the ABR of the Amazon dolphin was the presence of the clearly defined earliest wave W1.

Shifting the active electrode from the vertex to a lateral head surface resulted in a significant increase of the W1 wave and a change in its polarity from positive to negative (fig. 1 B). Bipolar recording from the lateral head surface resulted in a greater amplitude of the W1 wave as well (fig. 1 C).

The W1 wave was of maximum amplitude when recorded near the auditory meatus, a few cm below it (fig. 1 D). When the electrodes were moved away from this region, the W1-wave amplitude decreased significantly.

The W1 wave, when recorded laterally, was sensitive to the side from which the sound was presented. When the location of the sound source was ipsilateral to the recording side, the W1 wave had a greater amplitude and a lower threshold as compared to those observed with contralateral source location (fig. 2). W1 waves of nearly equal amplitudes were elicited when the contralateral stimulus was about 20 dB louder that the ipsilateral one (comp. fig. 2; L and R).

Both the lateral position of the focus of the W1 wave and the sensitivity of the wave to the side of sound presentation suggest that this wave originates from some monaural part of the auditory system, peripheral to the first crossing.

The sensitivity of the W1 wave to the side of sound presentation allowed us to measure the directivity characteristics of one ear. In these experiments a sound source was moved around the head in 15° steps, and the threshold of the laterally recorded W1 wave was measured at each source position. A total of 55 threshold measurements were carried out, with 2–5 measurements for each sound source position.

The dependence of the W1-wave threshold on the sound source position is shown in figure 3 (plot 1). The minimal threshold (as low as 25 dB re. 1 mPa) was observed when the sound source was located at 15° ipsilaterally to the recording side. When the source was shifted from this position, the threshold rose markedly. Thresholds for contralateral source positions were significantly higher than those for symmetrical ipsilateral positions.

Plot 2 in figure 3 shows a difference between the left and the right shoulders of plot 1, i.e. the threshold difference between symmetrical left-hand and right-hand source positions. This difference was 10 dB when sources were at an angle of 15° to the longitudinal axis, and more than 20 dB for source locations at an angle of 30° and more. If source positions were more than 90° from the longitudinal axis, the threshold difference was slightly diminished.

We have to bear in mind that there is no conclusive evidence for the unilateral nature of the laterally recorded W1-wave. However, a bilateral component, if it exists in the W1-wave, would diminish, not enhance the sensitivity of the response to interaural intensity differences. So the true interaural intensity difference was at least that shown by the measurements.

Thus the data presented here suggest that acoustical properties of the dolphin's head do create a significant interaural intensity difference up to 20 dB or more. This interaural difference already appeared when the deviation of a sound source from the longitudinal axis was quite small.

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