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Investigating the Dolphin's Peripheral Hearing System: Acoustic Sensitivity About the Head and Lower Jaw

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EXECUTIVE SUMMARY

It is a widely accepted hypothesis that echolocating dolphins (*Tursiops truncatus*) best receive returning acoustic signals over the panbones of the lower jaw. It is also widely assumed that those areas function as the dolphin's peripheral hearing system. Previous research, however, does not exclude the possibility of other sound reception sites and suggests that additional areas of the head may be acoustically sensitive and frequency-dependent. For this report, jawphones were used to behaviorally measure the relative hearing thresholds at four frequencies (10, 30, 60, and 90 kHz) on more than 40 sites of a dolphin's head, from the tip of the rostrum to the base of the pectoral fins. Measurements were converted into iso-sensitivity curves projected onto a two-dimensional, heuristic representation of the head area investigated. The results suggest high-frequency sensitivity along the lower jaw with greater sensitivity forward of the panbone area, sensitivity to low frequency in the area of the external auditory meatus, and an asymmetry in sensitivity favoring the left side of the head. These results may have correlates in the underlying anatomy and suggest that the dolphin's peripheral hearing system is more complex than has previously been assumed.

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INTRODUCTION

Norris' (1968, 1969) model of echolocation started a paradigm shift regarding sound production and reception in bottlenose dolphins. It was previously assumed that dolphins and their cetacean relatives, like other mammals, relied on the larynx and the external auditory meatus (EAM) (Fraser and Purves, 1954, 1959, 1960). While several details are still to be investigated, the accumulated evidence warrants the general acceptance of Norris' theory: Echolocation signals are produced in the area of the nasal complexes of the dolphin's forehead, and returning echoes are best received along the lateral sides of the lower jaw (see Au, 1993). While sound reception at the periphery is no longer seen as best occurring at the dolphin's EAM, it is still assumed to occur at two locations on the animal's head, namely Norris' (1968) "acoustic windows" over the panbones of the lower jaw. The existing evidence, however, does not obviate functional reception at the EAM. Rather, it provides some interesting clues that suggest that the dolphin's peripheral hearing system could be more complex than is generally assumed.

Bullock et al. (1968) measured evoked potentials from the midbrain auditory structure in four dolphin species to investigate hearing sensitivity. Using airborne, waterborne, and vibratory stimuli, they reported that the best pathway for sound to the cochlea was via the lower jaw, particularly for stimuli of 30 kHz and higher. For stimuli lower than 30 kHz, they reported that sensitivity was greater at the side of the head including the area around the EAM. Sensitivity on the melon was also reported.

McCormick et al. (1970, 1980) measured cochlear potentials in the bottlenose dolphin (*Tursiops truncatus*) to investigate sensitivity along the lower jaw. Like Bullock et al. (1968), they reported best sensitivity for frequencies of 30 kHz and above at the panbone and at the EAM for frequencies below 30 kHz. They also reported the tip of the lower jaw and the base of the pectoral fin to be acoustically sensitive.

Renaud and Popper (1975) behaviorally measured the minimal auditory angle (MAA) for a bottlenose dolphin. During testing, they observed an apparent preference in orientation by the dolphin that was a function of the stimulus frequency being presented. For frequencies above 20 kHz, the dolphin appeared to favor reception along its lower jaw. Below 20 kHz, it oriented to apparently favor reception at the EAM.

Brill et al. (1988) used an actively echolocating dolphin to investigate sound reception at the lower jaw. The dolphin was trained to do an echolocation discrimination task under three conditions: (1) no covering over the lower jaw, (2) covering the lower jaw with a hood made of an acoustically opaque material, and (3) covering the lower jaw with a hood made with material that significantly attenuated the dolphin's own returning signals. The results clearly demonstrated that the attenuation of the echoes at the lower jaw significantly impaired the dolphin's ability to perform the task. Recordings made during the experiment revealed that the dolphin had relied on outgoing signals in the range of 30 to 50 kHz (Brill and Harder, 1991). Brill et al. (1988) noted that the hoods used in the experiment did not cover the EAM and that its exposure appeared to provide no advantage to the dolphin's performance. They suggested that the EAM could not be eliminated as a reception site for frequencies below 30 kHz and that there may be frequency-dependent sites of reception on the dolphin's head and lower jaw.

Such evidence suggests that the dolphin relies on more than two sites of sound reception and that there is a sensitivity threshold somewhere between 20 to 30 kHz that determines which sites are best.

It could be hypothesized, therefore, that the dolphin's peripheral hearing system comprises discrete frequency-dependent, sound reception sites in the areas of the panbones and the EAM. In the least, the system could be described as "dual-channel." Other investigators have previously proposed similar hypotheses based on anatomical and physiological evidence. For example, Ayrapet'yants et al. (1973) and Ayrapet'yants and Konstantinov (1974) reported better acoustic sensitivity above 30 kHz at the dolphin's lower jaw and below 30 kHz at the EAM. Lipatov and Solntseva (1974) described a hypodermal fat layer between the EAM and the lower jaw. Bel'kovich and Dubrovsky (1976) suggested that the EAM and lower jaw provided two channels of sound reception that may interact.

More recent evidence continues to support the notion of frequency-sensitive reception sites. Ketten (1992) concluded that there were possible parallel but separate systems for the reception of ultrasonics and low-frequency signals used by the dolphin. She has described three discrete fat bodies in the lower jaw that connect to the tympanoperiotic bone at different locations and may act as discrete channels (Ketten, 1994). Møhl et al. (1999) measured auditory brainstem responses to the placement of a contact sound source along the right side of a dolphin's head and lower jaw. They used a piezoelectric transducer embedded in a soft rubber suction cup, similar to the "jawphones" first used by Moore and Pawloski (1991), that was applied directly to a dolphin resting out of water. The test stimulus was a dolphin click with peak energy at 53 kHz. They reported best sensitivity along the front half of the lower jaw forward of the panbone.

Moore et al. (1995) have described binaural capabilities in a bottlenose dolphin that rival, if not supercede, those described for terrestrial mammals. Dolphins demonstrate impressive capabilities for sound localization (see Au, 1993). The evidence suggests, however, that we cannot assume that the dolphin accomplishes those capabilities in a manner or with systems identical to those of terrestrial mammals. To understand just how the bottlenose dolphin perceives its acoustic world, we must better understand how it receives acoustic signals. Does the dolphin's peripheral hearing system consist of multiple reception sites that are frequency-dependent—a system perhaps similar to a multi-transducer receiver array? To investigate that possibility, we began a pilot study in 1997 (see Brill et al., 1998) in which we set out to behaviorally map acoustic sensitivity on a dolphin's head and lower jaws. Pure tone stimuli of 10, 30, 60, and 90 kHz were presented via jawphones attached to the skin at 43 sites on the animal over the area between the base of the pectoral fins and the tip of the rostrum. A total of 164 relative thresholds were estimated.

METHODS

SUBJECT AND FACILITIES

Our subject was a 14-year-old female bottlenose dolphin (*Tursiops truncatus*), “CAS,” housed in a floating pen complex at the Space and Naval Warfare Systems Center, San Diego (SSC San Diego). CAS had previously participated in several tests of auditory sensitivity. Audiograms measured for CAS indicated normal hearing capabilities (Brill et al., 2001).

EQUIPMENT AND PROCEDURES

Jawphones were first used by Moore and Pawloski (1991, 1993, 1995) to test binaural capabilities in a dolphin. Figure 1 shows the typical construction of a jawphone. A small individual transducer is embedded in a soft, degassed, silicone rubber suction cup that can be safely and directly applied to the surface of a dolphin. In our experiment, the stem of the jawphone was wrapped in closed-cell neoprene to limit ensonification to the area of attachment to the skin. The dolphin could, at any time, dislodge the jawphone.



Figure 1. Cutaway views of a typical jawphone. Transducer is embedded in a suction cup made of degassed rubber. The internal void is filled to avoid air spaces. The stems of the jawphones used in this experiment were wrapped in closed-cell neoprene.

Two separate jawphones, each containing a different transducer, were used in this study. For the test frequency of 10 kHz, a small subminiature earphone element encapsulated in an air-filled chamber was used. For test frequencies of 30, 60, and 90 kHz, a jawphone containing an Edo Western 6600, 10-mm, spherical transducer was used. Each of the jawphones was calibrated for the test frequency(s) for which it would be used. The jawphone being calibrated and a measuring hydrophone (ITC-6069) were secured to a special calibration armature to hold them at a fixed separation distance between their acoustic axes. The two were directly in line with both the long axis of the jawphone being calibrated and the transmitting element. The 10-kHz test frequency was calibrated with the hydrophones set 3-mm apart. The 30-, 60-, and 90-kHz test frequencies were calibrated with the

hydrophones 13-cm apart. The armature was submerged in a tank of water. Measured levels were then used to calculate the animal's thresholds.

A BK Precision 5-MHz, Model 4011 Function Generator produced pure tone stimuli. The stimuli were then fed through an RLC Electronics Model AT201 attenuator and custom equipment built at our laboratory to control a stimulus duration of 1-second and a rise/fall time of 20 ms to eliminate onset/offset transients. The shaped output was then directly fed to either a Hewlett-Packard Model 350D or a Pasternack Enterprises PER 7008-2 attenuator before finally reaching a jawphone. Depending on the dolphin's sensitivity as a function of frequency and location, a Hafler DH-2200 stereo amplifier was used for test frequencies of 60 kHz and sometimes for frequencies of 30 and 90 kHz.

Locations at which a jawphone was placed on the dolphin to measure thresholds were determined by the use of an imaginary grid. The grid can be visualized as a series of truncated cones covering the dolphin's head from the base of the pectoral fins to the tip of the rostrum, with eight longitudinal and eight latitudinal axes (Figure 2). Consistent placement was accomplished through the use of a biteplate with a metered disk and a metered cord attached. The disk was marked to represent latitudinal axes and affixed to the front of the biteplate. The cord, attached to the center of the disk, was marked in equal intervals to represent longitudinal axes. As the dolphin held the biteplate in its mouth, a trainer would extend the cord along the dolphin's head from the appropriate mark on the disk and would place the jawphone at the appropriate coordinate (Figure 3). There was one coordinate on the ventral side at which the jawphone could not be attached due to natural creases in the skin that prevented adequate suction. Figure 4 shows the locations of the 41 coordinates illustrated by markers attached to the fiberglass model of a dolphin. The locations of the panbones were not represented on the grid but were tested at each frequency.

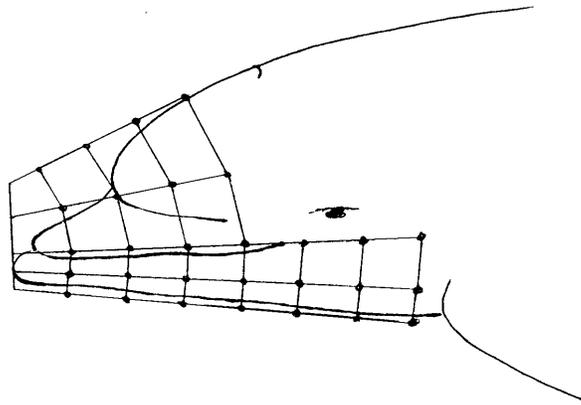


Figure 2. Test locations on the dolphin's head were determined by an imaginary grid with eight longitudinal and eight latitudinal axes.

Behavioral thresholds were estimated using a derivation of an up/down staircase method and a "go/no-go" response paradigm. To begin a trial, the dolphin wearing a jawphone took position in front of an inter-trial station (ITS). When cued by its trainer, the dolphin moved to an underwater test station (TS) 90-cm below the surface of the water and remained there for up to 4 seconds. If a test stimulus was presented after 1.5 seconds (the "go" condition), the dolphin left the TS immediately to touch a nearby response paddle just above the surface. If no stimulus was presented (the "no-go"

condition), the dolphin stayed at the TS until a bridging stimulus was sounded after 4 seconds, cueing the dolphin to return to the ITS. All correct responses were reinforced with an equal fish reward. A Gellerman series (Gellerman, 1933) adjusted to produce a 0.5-first-order conditional probability of a “go” following a “no-go,” or the reverse, was used to determine the trial type.



Figure 3. Consistent placement of the jawphone was determined by having the dolphin hold a biteplate with a metered cord and disk attached.

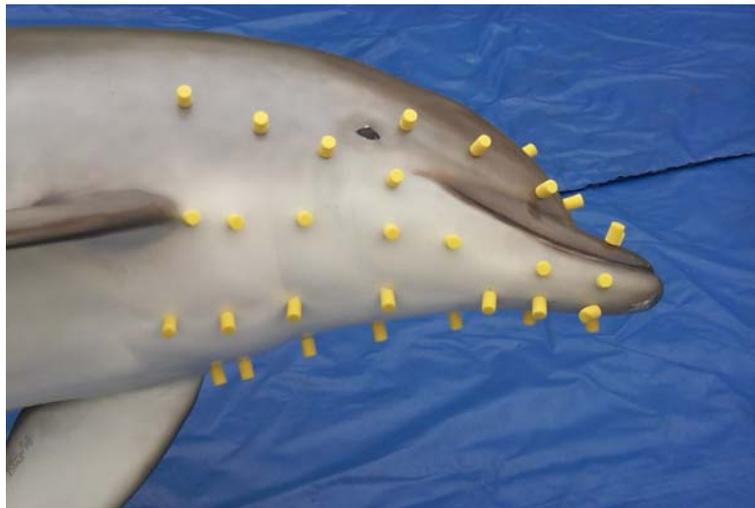


Figure 4. Locations tested with a jawphone are represented on the fiberglass model of a dolphin.

A Gellerman series was also used to determine the frequency to be tested, and a random number table was used to determine the coordinate to be tested prior to the beginning of each session. A session consisted of 10 warm-up trials followed by enough trials to produce 10 reversals, which defined a threshold. Calibrated stimuli were first presented at levels known to be easily audible to the dolphin. The test stimulus was then attenuated from the warm-up level in 2-dB increments until the dolphin failed to respond correctly. The first miss initiated a run, and the sound pressure level (SPL) was increased in 1-dB steps until the dolphin made a correct response on a “go” trial. A run was defined

as a series of attenuator changes in one direction, contingent on the dolphin's response to signal trials. Stimulus levels were not modified as a function of false alarms and correct rejections. Increments of 1 dB were used in both ascending and descending runs for the remainder of the session. Thresholds were estimated by subtracting the average attenuator value of the 10 reversal points from the calibrated stimulus level yielding an estimated 50-percent threshold value.

RESULTS

Table 1 shows the estimated threshold values in peak-to-peak voltages (V_{pp}). The average V_{pp} value at each panbone for each of the four frequencies tested was used as the reference unit to convert these voltages into decibels. The resulting values defined a range from -15 dB (best sensitivity) to 30 dB and above (least sensitivity). For each test frequency, the estimated thresholds were then cast into color-coded iso-sensitivity curves in increments of 5 dB (Figure 5). These curves are a heuristic depiction of the data since the resulting displays do not faithfully conform to the dolphin's actual anatomy. Each panel in Figure 5 represents a dorsal view of the dolphin's head in which the lower edge of a panel corresponds to the tip of the snout, the upper edge to the base of the pectoral fins, and the sides to the ventral midline. Heuristically, the surface of the dolphin's head from the tip of the snout to the base of the pectoral fins is represented as a bounded two-dimensional plane. The approximate locations of the EAMs, eyes, and panbones are indicated.

Three salient features are evident in Figure 5: (1) the area of best acoustic sensitivity is forward of the panbone along the lower jaw; (2) sensitivity appears to improve as a function of frequency; and (3) there appears to be an asymmetry in sensitivity favoring the left side of the head across frequencies, suggesting that the physical areas of sensitivity are larger on that side of the head. To aid in interpreting Figure 5 with respect to the dolphin's actual anatomy, views of the fiberglass dolphin model (Figure 4) with superimposed circles colored to match the iso-sensitivity curves over the test coordinates were produced. Figure 6 shows the iso-sensitivity curves and corresponding views of the dolphin model's head for the estimated thresholds at 10 kHz. At this relatively low frequency for a bottlenose dolphin, best sensitivity occurs below the panbone on the dolphin's left side and around the EAM, eye, and panbone on the right side. At 30 kHz, sensitivity increases by -15 dB along the lower jaw and ventral surface. Sensitivity improves by an additional -10 dB across 30 , 60 , and 90 kHz (Figure 5). At 90 kHz, the views of the dolphin model reveal a contrast in the size of the areas of sensitivity on the left side of the head as opposed to the right (Figure 7). Better sensitivity is apparent along more of the length of the lower jaw on the left side, while the area of sensitivity on the right side appears to be limited to the area between the panbone and the front half of the lower jaw.

Table 1. Threshold values are expressed in peak-to-peak voltage (V_{pp}). The average V_{pp} at each panbone for each of the four frequencies tested was used as the reference unit to convert the voltages to decibels. Letters indicate the area of the head (R = right, L = left, D = dorsal, M = mid, V = ventral, PB = panbone), and numbers indicate the position in that area moving from the tip of the snout to the base of the dorsal fin. Corresponding positions are represented in Figure 4.

	10 kHz	30 kHz	60 kHz	90 kHz			10 kHz	30 kHz	60 kHz	90 kHz			10 kHz	30 kHz	60 kHz	90 kHz
RPB	0.032	0.326	0.07	0.018								LPB	0.023	0.194	0.063	0.014
RD						CD						LD				
1	0.715	0.58	0.176	0.03		1	No Data	1.94	1.765	0.05		1	0.18	0.97	0.056	0.013
2	No Data	0.52	0.07	0.02		2	0.506	3.65	2.222	0.042		2	0.506	0.97	0.497	0.024
3	0.18	3.65	1.249	0.034		3	0.358	2.05	2.493	0.15		3	0.226	5.79	0.884	0.03
4	0.16	2.05	1.573	0.04		4	0.802	2.587	2.797	0.19		4	0.226	4.101	0.992	0.3
RM												LM				
1	0.051	0.77	0.125	0.06								1	0.319	0.27	0.14	0.006
2	0.285	0.52	0.125	0.06								2	0.285	0.729	0.249	0.04
3	0.064	1.37	0.314	0.03								3	0.254	1.45	0.314	0.05
4	0.113	0.65	1.98	0.07								4	0.715	1.156	0.558	0.5
RV						CV						LV				
1	0.802	0.21	0.088	0.01		1	0.226	0.27	0.125	0.01		1	No Data	0.29	0.063	0.005
2	0.802	0.15	0.07	0.01		2	0.254	0.19	0.02	0.008		2	0.201	No Data	0.025	0.003
3	0.358	0.18	0.044	0.003		3	Jawphone could not be applied at this pos.					3	0.319	0.13	0.14	0.003
4	0.319	0.19	0.157	0.008		4	0.715	0.77	0.176	0.03		4	0.113	0.43	0.28	0.03
5	0.018	0.27	0.222	0.008		5	0.358	1.156	0.788	0.05		5	0.127	0.24	0.198	0.02
6	0.16	2.59	0.395	0.03		6	0.802	1.45	0.992	0.14		6	0.451	0.92	0.14	0.02
7	0.568	0.69	0.497	0.038		7	0.506	1.73	0.626	0.11		7	0.16	0.41	0.099	0.05

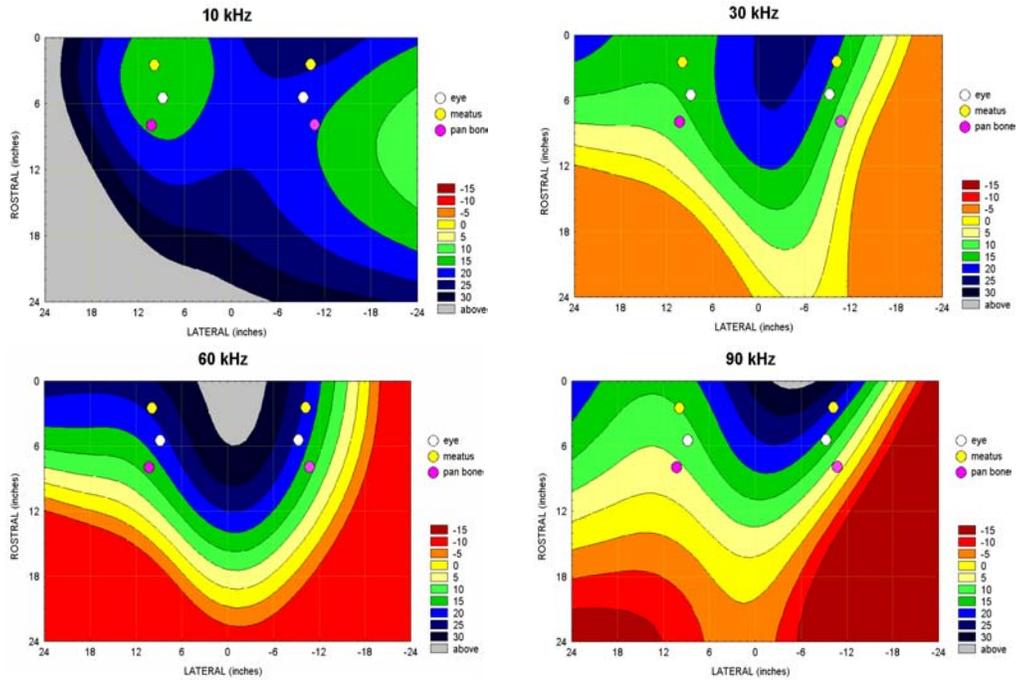


Figure 5. Estimated thresholds measured at 10, 30, 60, and 90 kHz represented in iso-sensitivity curves. Approximate positions of the eye, meatus, and panbone are indicated. They do not faithfully represent the dolphin's morphology. The lower edge of each panel corresponds to the tip of the dolphin's rostrum, the upper edge to the base of the pectoral fins, and the sides to the ventral midline.

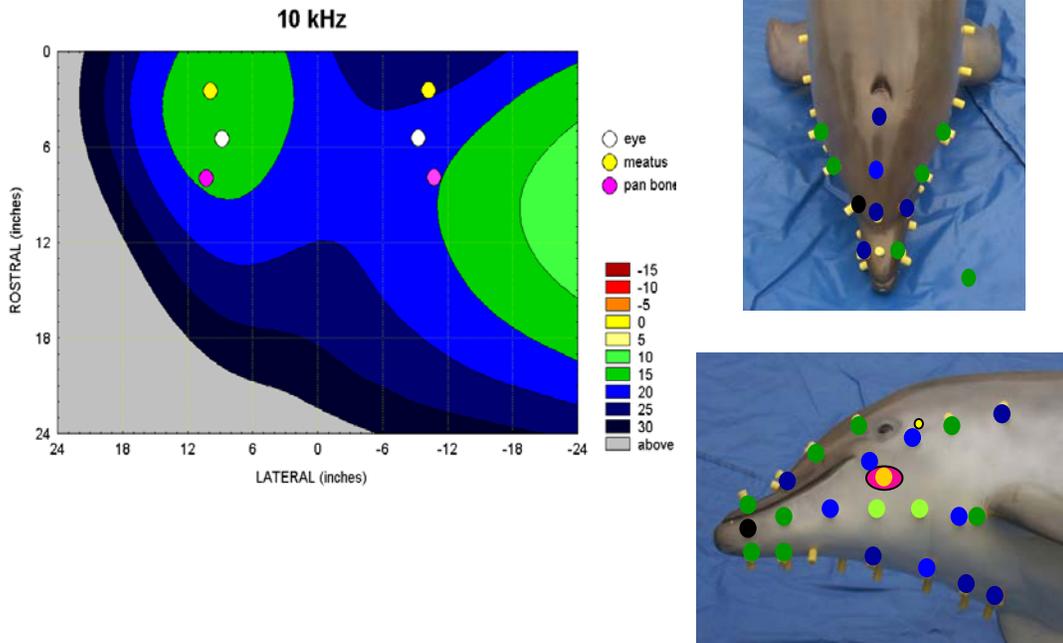


Figure 6. Results at 10 kHz indicate a low level of sensitivity best below the panbone on the dolphin's left side and around the EAM, eye, and panbone on the right side.

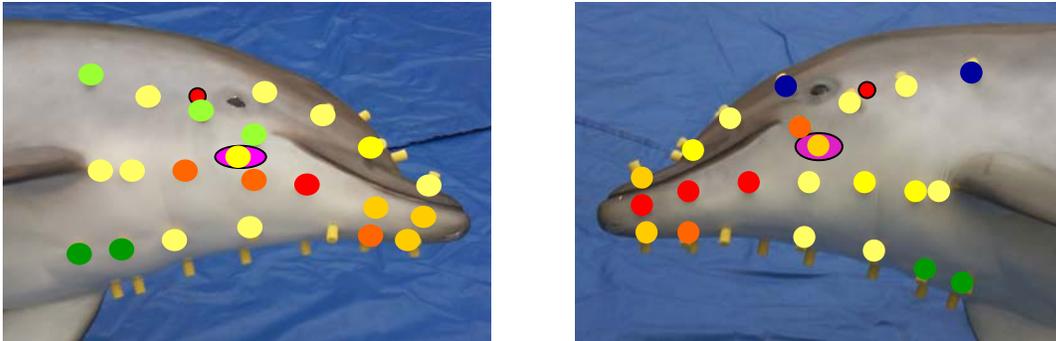
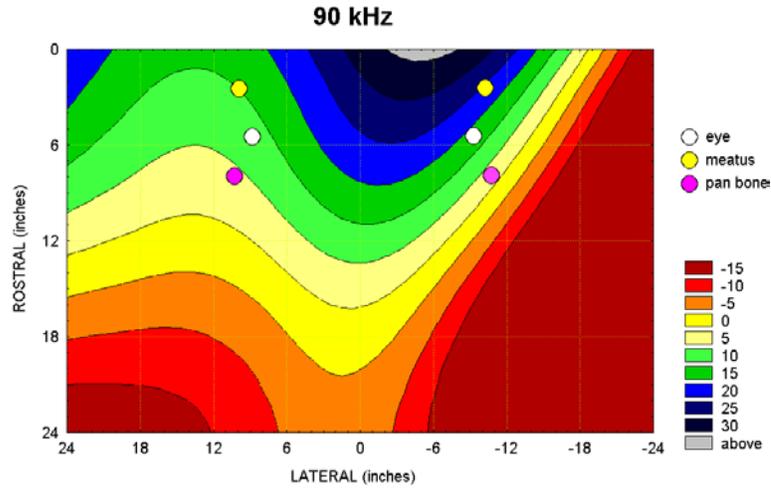


Figure 7. Results at 90 kHz indicate best sensitivity along the lower jaw forward of the panbone and the area of sensitivity as being larger on the left side of the head as opposed to the right.

DISCUSSION

Where Bullock et al. (1968) used electrophysiological techniques, we produced a behavioral mapping of acoustic sensitivity by using jawphones to present calibrated stimuli to specific locations on a dolphin's head and lower jaw. Other than Norris' (1964, 1968, 1969) model of sound reception during echolocation, there are no quantified auditory pathways from the surface of the dolphin's head to the inner ear. The evidence supporting Norris' model provides indications that reception is not occurring solely at the panbone or "acoustic window" of the lower jaw as discussed above. Given that, we anticipated that our data would reveal discretely bounded, frequency-sensitive sites of reception, or "hot spots," that would be evident at the panbones and the EAMs. Instead, we observed areas of sensitivity on the head in an asymmetric pattern with best sensitivity occurring along the lower jaw as a function of frequency.

Similar to the findings of Bullock et al. (1968) and Møhl et al. (1999), we found that acoustic sensitivity was best along the front half of the lower jaw, forward of the panbone areas, on both sides of the head. Norris' (1968) proposed "acoustic window," therefore, may not be the best site of sound reception. Our data do not clearly support the notion of a dual-channel system. The distinct difference in sensitivity patterns that occurs from 10 kHz to 30 kHz indicates that testing sensitivity at one or more frequencies in between would be necessary to fully evaluate the existence of a system in which the panbones and the EAMs are discrete reception sites. The increase in sensitivity as a function of frequency from 30 kHz to 90 kHz does suggest that there are areas of the dolphin's head that are more suited for acoustic sensitivity at higher frequencies—a condition that may indicate that low-frequency sensitivity is not critical to the dolphin's peripheral hearing system.

Our data suggest that a dolphin's area of acoustic sensitivity is larger on the left side of the head than on the right. If acoustic sensitivity in the dolphin's peripheral hearing system is truly asymmetric, we may be able to improve our understanding of the dolphin's demonstrated binaural capabilities. Moore and Pawloski (1993) reported interaural time and intensity discrimination values that surpass those measured for any other mammals. While the dolphin's auditory anatomy is mammalian, it is adapted to function underwater and to be exposed to high-frequency signals and rapid pressure changes. In that medium, the physics of sound are different and flesh and bone do not provide the effective sound shadows that affect time and intensity cues in air. An asymmetry in the dolphin's peripheral hearing system may well compensate for those differences in a manner similar to that reported for such creatures as the barn owl (Knudsen, 1981; Konishi, 1973). The bird's facial ruff is assumed to provide an acoustic collector for high frequencies that are funneled to its EAMs, which are offset, higher on the left than on the right. The owl's capacity to localize using time and intensity differences is thought to rely on the peripheral hearing system, as it is, causing high-frequency components of natural sounds to be perceived as louder in the right ear than in the left.

Given the limitations of our data and the subject pool, we can only speculate at this point. Further investigation is required for several points of interest. Would the results of this experiment be consistent across individuals of the same species and/or other small cetacean species known to echolocate? What correlations are there between the areas and patterns of sensitivity that may be observed and the known underlying anatomical structures? And finally, to what degree does the apparent asymmetry in acoustic sensitivity contribute to the dolphin's known binaural capabilities?

In summary, estimated relative behavioral auditory thresholds measured across four frequencies at a number of locations on a dolphin's head suggest that (1) best acoustic sensitivity occurs along the

lower jaw forward of the panbone, (2) sensitivity over the lower jaw and much of the head improves as a function of frequency, and (3) sensitivity is asymmetric with the area of sensitivity being larger on the left side of the head than the right. To verify these findings and improve our understanding of the dolphin's peripheral hearing system, further investigation is needed.

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