

SOUND LOCALIZATION BY THE BOTTLENOSE PORPOISE *TURSIOPS TRUNCATUS**

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SUMMARY

1. Sound localization was measured behaviourally for the Atlantic bottle-nose porpoise (*Tursiops truncatus*) using a wide range of pure tone pulses as well as clicks simulating the species echolocation click.

2. Measurements of the minimum audible angle (MAA) on the horizontal plane give localization discrimination thresholds of between 2 and 3° for sounds from 20 to 90 kHz and thresholds from 2.8 to 4° at 6, 10 and 100 kHz. With the azimuth of the animal changed relative to the speakers the MAAs were 1.3-1.5° at an azimuth of 15° and about 5° for an azimuth of 30°.

3. MAAs to clicks were 0.7-0.8°.

4. The animal was able to do almost as well in determining the position of vertical sound sources as it could for horizontal localization.

5. The data indicate that at low frequencies the animal may have been localizing by using the region around the external auditory meatus as a detector, but at frequencies about 20 kHz it is likely that the animal was detecting sounds through the lateral sides of the lower jaw.

6. Above 20 kHz, it is likely that the animal was localizing using binaural intensity cues.

7. Our data support evidence that the lower jaw is an important channel for sound detection in *Tursiops*.

INTRODUCTION

Sound localization, the ability to determine passively the position of a sound source in space, is an integral component of audition of many vertebrates. This capability, as well as the physiological and behavioural mechanisms for making position determinations, has been investigated in a wide range of terrestrial organisms (see Erulkar, 1972). However, while it is clear from a few behavioural studies that fish, elasmobranchs and marine mammals can localize sounds (see Popper & Fay, 1973; Popper, Salmon & Parvulescu, 1973; McDonald-Renaud, 1974 for reviews), only limited data exist on the localization mechanisms and capabilities of these groups.

Investigations on humans in air have indicated that sounds are localized differently

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as a function of frequency (see Howard & Templeton, 1966; Mills, 1958, 1972). Sound below 1.5 kHz is localized using interaural differences in time of arrival of the sound (especially signal onset) or by binaural phase differences due to each ear being at a different point in the phase angle. Interaural intensity differences are minimal at these frequencies since the wavelength is larger than the head; and consequently, the head does not cast a useful acoustic shadow or sufficiently attenuate the signal. Above 3 kHz the wavelength is less than half the interaural distance, and the major information is gained from binaural intensity differences since the head serves to shadow the sound at the ear further from the sound source.

These factors, important for localization in air, must be reconsidered for an aquatic environment. The speed of sound in water is five times faster than in air, and as a result the wavelength of sound is five times longer in water. As a result, differences in the time of arrival and in sound intensity at the two ears of any but the very largest marine organism would be very small. Phase differences also are not likely to be significant for the higher frequencies important to the porpoise. Due to the high velocity of sound the only frequencies at which phase determination is likely to be possible would be of long wavelengths. This would not include echolocation frequencies (see Albers, 1965 and Kinsler & Frey, 1962 for reviews of underwater acoustics).

The auditory capabilities of odontocete cetaceans (toothed whales) are as acute and sensitive as in any mammal previously studied. The bottlenose porpoise *Tursiops truncatus* (Montagu) can hear sounds from 75 Hz to 150 kHz with maximum sensitivity in a wide-band centred around 50 kHz (-60 dB re $1 \mu\text{bar}$; Johnson, 1966). In addition, Johnson (1968) determined critical bandwidths using acoustic masking, and a number of workers have shown that *Tursiops* can discriminate frequency differences of 0.3–0.4% (Herman & Arbeit, 1972; Jacobs, 1972) and intensity differences as small as 1 dB (Evans, 1973). Studies of the inner ear and the central auditory system have also demonstrated a high degree of adaptation for analysis of acoustic information (e.g. Bullock *et al.* 1968; Bullock & Ridgway, 1972; McCormick *et al.* 1970; Wever *et al.* 1971a, b).

Odontocetes are also known to produce sound in a variety of behavioural situations. Relatively pure tones below 15 kHz are used in social communications, and short broad-band pulses (20–250 μsec ; 0.1–150 kHz; e.g. Au *et al.* 1974; Diercks *et al.* 1971; Evans, 1973) are used for echolocation. Since sound plays an integral role in odontocete (and all marine mammal) behaviour we would predict good localization acuity. However, studies of sound localization have been limited to one odontocete species. In addition there are comparable data for two pinniped species (Gentry, 1967; Møhl, 1964; Moore, 1975).

In all marine mammal studies, and in many studies of localization of terrestrial vertebrates, localization acuity is defined in terms of the minimum audible angle (MAA). The MAA is generally defined as the angle subtended at the subject by the two speakers, one speaker being set at the reference azimuth, when the subject is just able to discriminate the speakers as two discrete sound sources (see Mills, 1958). Dudok van Heel (1959, 1962) studied sound localization in the harbour porpoise *Phocoena phocoena* at two frequencies and reported MAAs of 11° at 3.5 kHz and 8° at 6 kHz. Andersen (1970a) reported a MAA of 3° at 2 kHz for the same species. Møhl

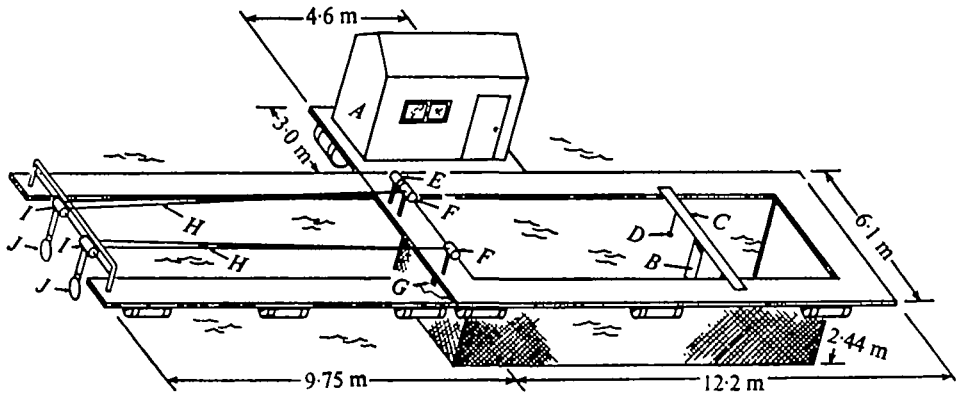


Fig. 1. Experimental Pen for localization experiments. *A.* Equipment Shack. *B.* Bite Bar, positioned 18 m from the midpoint between the two transducers. *C.* Wooden Crossbeam. *D.* Right Response Paddle. *E.* Winch, moved the transducers in and out on the horizontal plane (cable and pulley system is not shown in the diagram). *F.* Winches, used for raising and lowering the right and left transducers. *G.* Buzzer. *H.* Transducer Support Cable. *I.* Metal Pipes, these were moved back and forth on a cable by using winch. *E.* Attached to the pipes were pulleys which fed the support cables to the transducers. *J.* Left and Right Transducers.

(1964) determined an underwater MAA of 3° at 2 kHz in the harbour seal *Phoca vitulina*, and Gentry (1967) found MAAs of 10° at 6 kHz and 15° at 3.5 kHz in the California sea lion *Zalophus californianus*. More recently, Moore (1975) found the MAA of *Zalophus* to be 8.8° for click trains centred at 1 kHz. However, these pinniped data shed little light on the precision of auditory localization by porpoises, since there are significant morphological differences in the ears of the two groups; for example, the pinniped inner ear is not acoustically isolated from the skull as it is in cetaceans (Repenning, 1972).

While the two earlier experiments on odontocete sound localization indicate a good discrimination capability, the studies were incomplete because they were conducted only at a limited number of frequencies (pure tones) below the region of maximum auditory sensitivity for *Phocoena* (see Andersen, 1970*b*) and at the frequencies found in the echolocation click (Diercks, Trochta & Evans 1973). In the present paper, we report on a series of experiments to determine the localization acuity in terms of minimum audible angle for an Atlantic bottlenose porpoise *T. truncatus*. Our experiments, done in a relatively open acoustic situation, provide data for pure tones from 6–100 kHz and for transients resembling echolocation clicks of *Tursiops*.

METHODS AND MATERIALS

Localization acuity was determined by training a sub-adult male *Tursiops* to indicate the position of a sound source relative to a small speaker midway between the two signal sources used in the experiments. During sound presentation the animal maintained station by biting an acoustically 'transparent' bar in order to prevent head movement. When the sound was terminated the animal swam to one of two response paddles indicating from which side the sound was emitted.

Experiments

A series of experiments was conducted to determine various aspects of localization to pure tones and clicks. A description of the general procedure is indicated below and specific points relevant to the individual experiments are included in the section on Results.

The experiments were conducted at the Sag Harbor test facility of the Naval Undersea Center (NUC), Hawaii Laboratory, which has experimental pens in Kaneohe Bay, Oahu, Hawaii. Since the facility is part of a large body of water, few if any of the problems associated with working in confined areas were encountered (see Parvulescu 1964; Popper *et al.* 1973; Popper & Fay, 1973). Ambient sound energy at specific frequencies was not sufficient to mask test signals (see Au *et al.* 1974 for a description of ambient sound in Kaneohe Bay).

The experiments were conducted in a floating pen (Fig. 1) anchored so it could rise and fall with the tide in water that was 6.1 m deep at low tide. The enclosure fencing for the sides and bottom of the pen was standard 11 gauge, 6 × 6 inch (15.2 × 15.2 cm) galvanized steel reinforcing wire. The wire was attached to the inside of 61 cm wide, barrel-supported, wooden walkways. An additional two walkways without fencing were hinged to the front of the pen. This extension supported the transducer suspension system, and a platform, 4.6 m × 3 m, attached to the right side of the pen supported the air-conditioned equipment shack. The extensions enabled the experimental animal to be positioned 18 m from the transducers so it was possible to use small angles in the study.

Prior to localization experiments, we tested auditory sensitivity and found that our animal could detect pure tones from 1 to 140 kHz, the same range as determined for other animals by Johnson (1966) and Bullock *et al.* (1968). The porpoise was trained by operant conditioning techniques to indicate behaviourally whether a sound came from a transducer to the right or left of a buzzer reference point (*G* in Fig. 1), which corresponded to the midpoint of the spatial separation of the transducers. The buzzer signal also functioned as a warning signal to indicate the time of occurrence of the observation interval. Before each trial the porpoise took up position behind the acoustically 'transparent' stationary bite bar. At the sound of the buzzer it bit the bar and continued biting for the duration of the observation interval. The test sound (20 dB re: 1 μ bar at the bite bar) was then presented randomly from either of two underwater transducers submerged at a depth of 122 cm.

At the termination of the test signal the animal indicated the source of the signal (i.e. right or left relative to the buzzer) by swimming to the right or left of the pen and hitting a paddle with his rostrum. A correct response was rewarded with the sound of a whistle followed by a fish. An incorrect response was followed by silence and no fish reward. Immediately after each trial the animal repositioned itself and the next trial began. The trial time averaged 10 s and the intertrial interval averaged 20 s. Silent observation trials were randomly presented on 11% of the trials as a check on responding to the sound stimulus and not to ambient sound. Failure to indicate right or left in these trials was rewarded with a whistle followed by a fish.

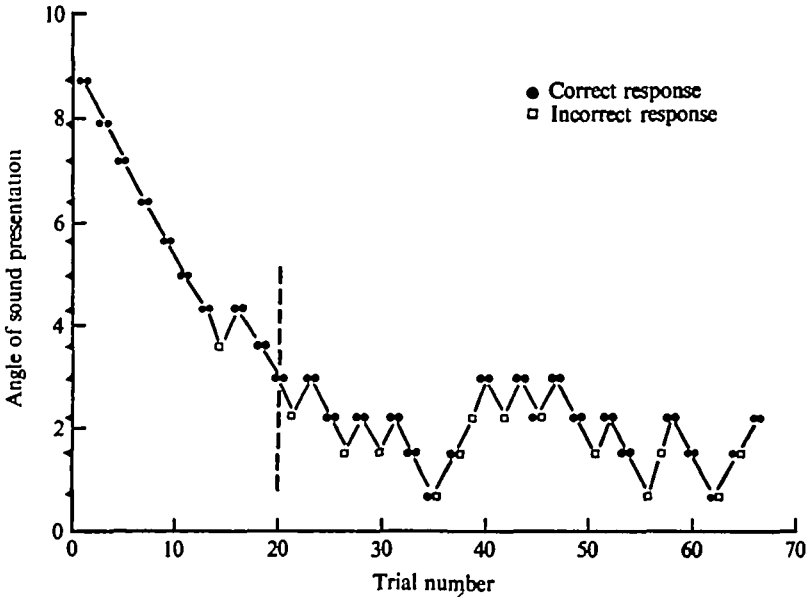


Fig. 2. Graphical representation of correct and incorrect responses in one session at 30 kHz with the animal facing a point between the two speakers (0° azimuth). The session mean ($\bar{x} = 2.0^\circ$) is the average of the 18 reversals which occur after trial number 19.

Stimulus presentation

Stimulus presentation was by a modified up-down staircase which allowed threshold determination at the 70% level rather than the more typical 50% level (Békésy 1960; Dixon & Massey 1969; Levitt 1971). A series of uniformly spaced separation distances was presented to the animal by moving the transducers in and out using a winch and pulley system. The animal was allowed two responses, right and left (two alternative, forced choice). The initial stimulus angle was at least 6° for all horizontal and vertical sessions, and randomly selected from 0.7° , 1.5° and 2.2° settings for click train sessions. Subsequent angles for stimulus presentation, except those with click trains, were determined by the animal's previous response. For the trial following two consecutive correct responses each transducer was moved inward one step. Following one incorrect response each transducer was moved outward one step (see Fig. 2). This step was size 0.5° for sessions testing frequency and stimulus parameters, and for azimuths 0° , 15° and 345° ; and 0.7° for azimuths 30° and 330° .

The MAA (70% level) was calculated as the average value between discrimination (correct response) and failure to discriminate (incorrect response) for 16 or more changes per session (see Fig. 2). Each data point (mean and standard deviations) represents at least 7 replicates on different days.

In one series of experiments using a click train stimulus (see below) the porpoise made a high percentage of correct responses at the smallest angular setting available and so it was impossible to decrease the angular presentation any further. Consequently, the method of constant stimuli (Plutchick, 1968) was selected for determining angular presentations of the signal. The transducers were positioned at three angular

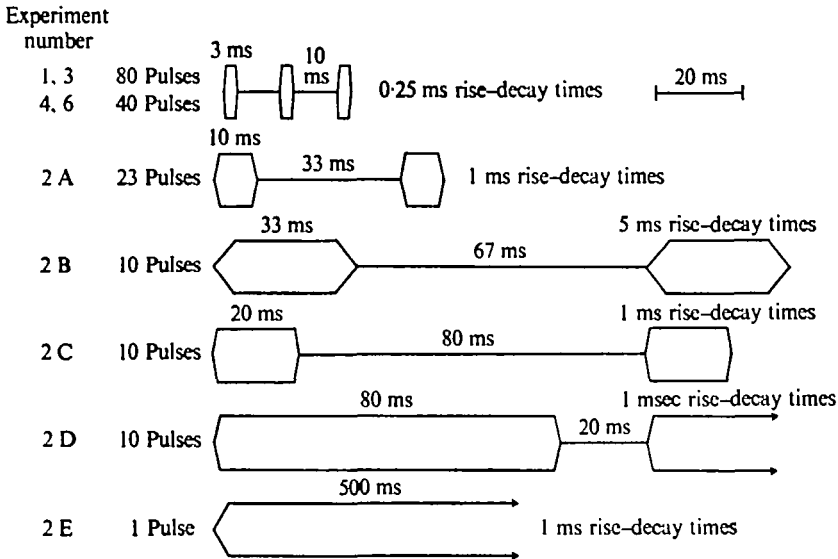


Fig. 3. Parameters of pulse train stimuli tested in Expt 1-4, and 6 showing pulse number, rise-decay time, duration, and interpulse interval.

settings (0.7° , 1.5° , and 2.2°) to the right and left of the 0° reference point. These angles were tested in blocks of 15 trials each. A Gellerman series of random numbers was used to determine the sequence of block presentation and left-right sound presentation within each block. Each session consisted of 90 trials with a total of 30 trials per angular setting. The percentage correct for each angle per session was calculated and then the average percentage for each angle was determined for all seven sessions.

Sound generation and measurement

Pure tones and clicks were used in the experiments; each specific sound is shown in Fig. 3 and described in the results section. Pulsed pure tones were produced with a Wavetek (Model 136) voltage controlled oscillator (VCO) and a Hewlett-Packard (Model 8002A) variable pulse generator. The pulse generator controlled the pulse duration, interpulse interval, and pulse rise and decay times. The actual number of pulses in each trial was controlled by triggering the pulse generator with a logic control system. The signal from the VCO was amplified by a Khron-Hite power amplifier (Model DCA 50) which was flat from 1 Hz to 500 kHz, selectively attenuated for each transducer with a Hewlett-Packard attenuator (Model 350D) and transmitted into the water by either the left or right transducers. From 6 to 20 kHz the transducers were J-9's loaned from the Naval Research Laboratory (NRL), Orlando, Florida. From 20 to 100 kHz the transducers were NRL F-33's. Control experiments at 20 kHz showed that the animal did equally well in localization with both sets of transducers, thereby indicating that the transducers did not affect localization above and below 20 kHz.

The electronics for production of click trains were identical to those for sine waves except that a Wavetek sweep generator (Model 144) was substituted for the VCO. When triggered by the pulse generator, the sweep generator produced on

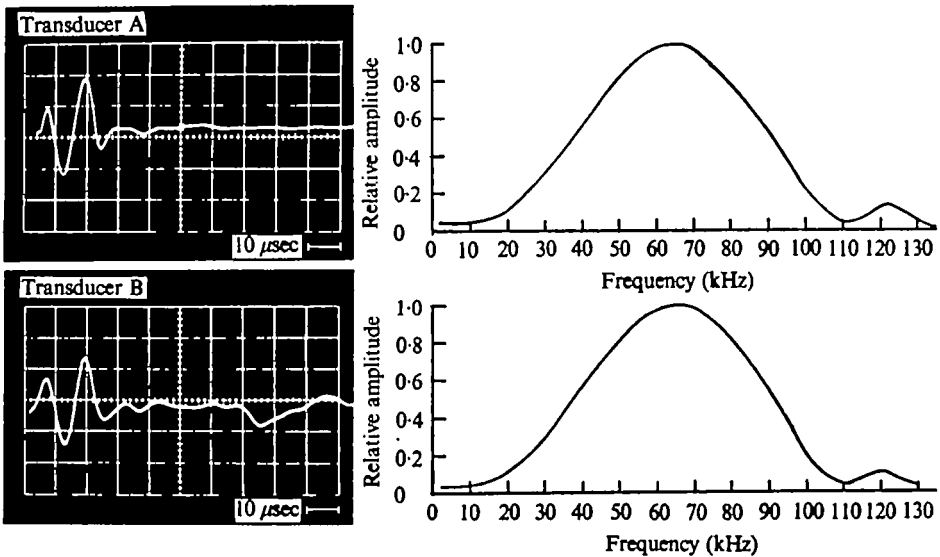


Fig. 4. Example of the waveform and power spectrum of clicks produced by each F-33 transducer used in the experiments. The clicks were recorded by a hydrophone placed 1 m from the transducers.

complete 100 kHz sine wave starting at 0° phase angle and this caused the F-33 transducer to ring, giving a 35 μ sec transient centred at 64.35 kHz (Fig. 4).

Bite bars

Separate bite bars were used in both horizontal and vertical localization experiments. In the horizontal case the bite bar consisted of a Plexiglas (= Perspex) sheet (15.2 cm long, 3.8 cm wide and 0.6 cm deep) held rigidly 76.2 cm below the surface of the water and suspended from a crossbar over the test pen (*C* and *D* in Fig. 1). The bite bar could be rotated to the left or right on the horizontal plane to predetermined positions, where it was locked into place until the next change.

The vertical bite bar was a Plexiglas sheet suspended vertically in the water from the wooden cross beam. A raised section of the Plexiglass guided the animal to a set position of the bite surface. Again, the bite bar could be rotated to different angles in order to change the angle of the porpoise relative to the two speakers.

Both bite bars presented minimum surface area to the direction of the sound field. The acoustic impedance of Plexiglas is close to that of water (Kinsler & Frey, 1962). Consequently, it is unlikely that the bite bar significantly altered the sound field. Careful observations demonstrated that the bite bar moved less than 0.5 degrees when the animal was in position, indicating that the animal was held rigidly in place during all experiments. McDonald-Renaud (1974) gives a more detailed description of the bite bars.

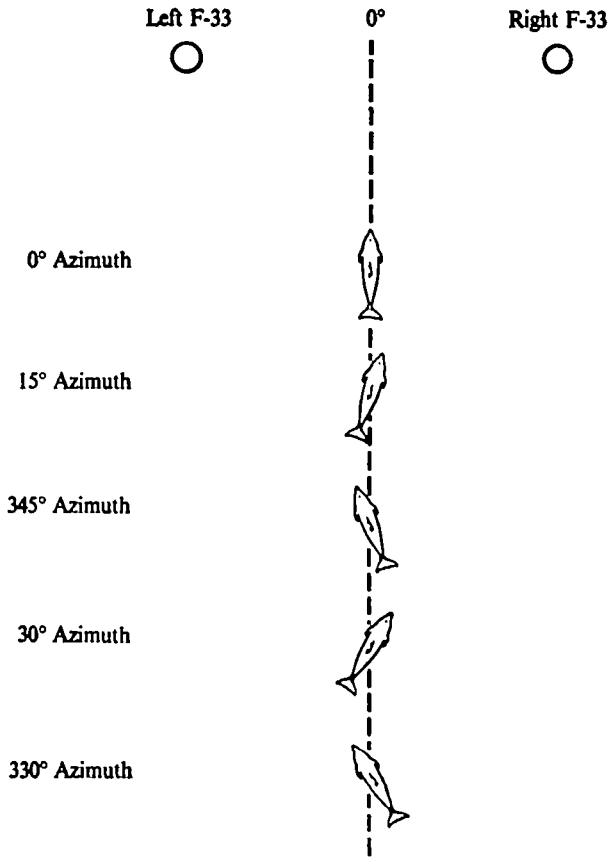


Fig. 5. Porpoise orientation for signals presented at azimuths of 0° , 15° , 30° , 330° and 345° in the horizontal plane. Positioning was the same for the vertical experiments, except the animal was on its side.

RESULTS

(1) *Horizontal localization: frequency*

Horizontal localization thresholds were determined at selected frequencies of 6–100 kHz to ascertain if capability varied as a function of frequency within the major frequency range in the animal's echolocation click (e.g., Au *et al.* 1974; Diercks *et al.* 1971). The sine waves were presented in pulse trains simulating the pulse mode of the porpoise's echolocation signal, although this was not intended to simulate the frequency components of the click. Relatively long rise and decay times of the pulse (0.25 ms) were necessary to prevent introduction of transients caused by ringing of the transducers. All sound stimuli were presented at least 40 dB above threshold level as determined by Johnson (1966). The 1.03 s sound which consisted of 80 pure tone pulses of 3 ms duration, 0.25 ms rise–decay times, and 10 ms interpulse intervals (Fig. 3) gave ample time for discrimination. The animal was positioned at 0° azimuth during the experimental series (Fig. 5).

The results show horizontal localization ability to be somewhat frequency dependent (Fig. 6). The MAAs for 6 kHz (3.6°), 90 kHz (3.2°) and 100 kHz (3.8°) were

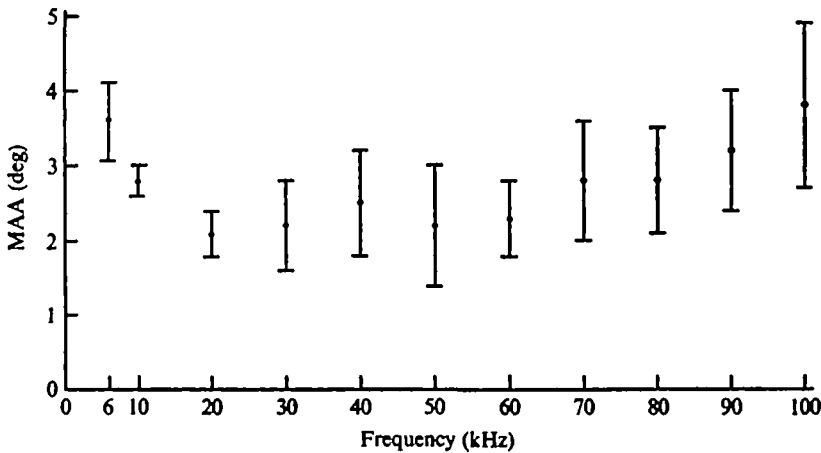


Fig. 6. Localization thresholds determined on the horizontal plane as a function of frequency. Shown are the mean \pm one standard deviation, for 7 determinations per frequency. Azimuth of animal was 0° .

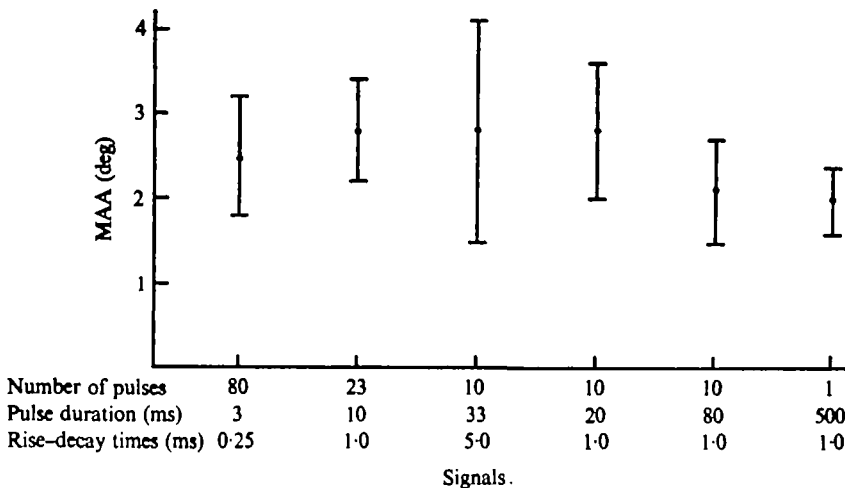


Fig. 7. Localization thresholds determined on the horizontal plane as a function of signal parameters. Mean \pm one standard deviation for seven determinations per frequency. Animal at 0° azimuth.

significantly different from the MAAs for 10–80 kHz ($P > 0.05$; Duncan's new multiple range test, Steel & Torrie, 1960). There were no significant differences between thresholds from 10 to 80 kHz ($P > 0.05$; Duncan's new multiple range test).

(2) *Horizontal localization: signal parameters*

Horizontal localization thresholds with the animal at 0° azimuth were measured at 40 kHz for various combinations of signal parameters to determine if localization capability is altered by changes in pulse duration, number of pulses, rise-decay times or total signal duration. Five different signals were tested (2A–2E in Fig. 3).

MAAs for the five sound stimuli tested (Fig. 7) were not significantly different

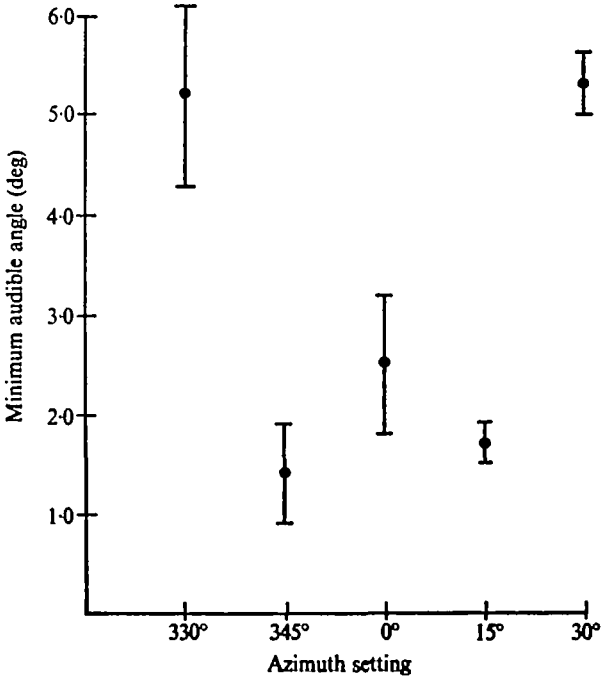


Fig. 8. Localization thresholds determined on the horizontal plane as a function of azimuth. MAAs \pm one standard deviation for 7 determinations per position.

from each other or from the MAA of 2.5° for the 40 kHz signal in the first experiment (Duncan's new multiple range test). MAAs ranged from 2.0 to 2.8° . Therefore within the limits of these sound parameters, localization capability was not altered.

(3) Horizontal localization: azimuth

MAAs for humans increase as the azimuth position of the sound source deviates from 0° (Mills 1958, 1972). To determine if this also occurs in the porpoise, horizontal localization thresholds were measured with the animal turned to four azimuths other than 0° (15° , 30° , 330° , and 345°) as shown in Fig. 5. The animal had no trouble learning to shift its body position and the bite bar was rotated accordingly. The 40 kHz signal had the same parameters as in the first experiment (Sound 1, Fig. 3).

Data (Fig. 8) indicate that localization capability was azimuth dependent. MAAs for the azimuths of 15° and 345° (1.7° and 1.4° respectively) were significantly different ($P = 0.05$) from the MAAs for 0° (MAA = 2.5°), 30° (MAA = 5.3°), and 330° (MAA = 5.2°) ($P = 0.05$ Duncan's new multiple range test). This increase in localization acuity at azimuths of 15° and 345° is contrary to that found in other terrestrial animals, including humans (Erulkar 1972; Mills 1958), where the best angular resolution occurs when the head is oriented at 0° azimuth.

(4) Vertical localization: frequency

Sound localization in the vertical plane has received little attention although it is likely that aquatic mammals should be able to localize well in 3-dimensional space. Since porpoises attend to sound coming from above and below them as well as on the

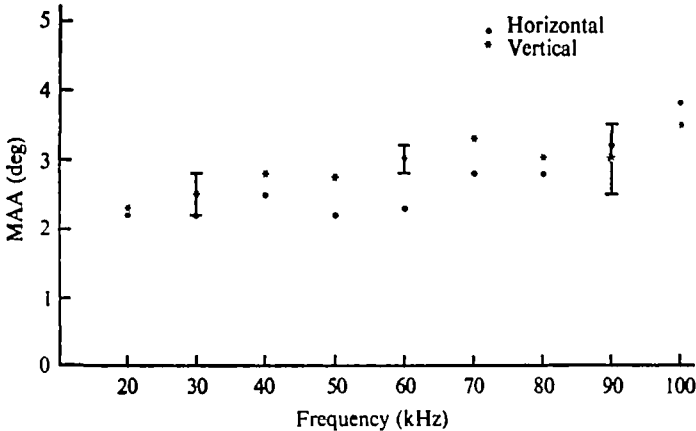


Fig. 9. Comparison of horizontal and vertical localization thresholds as a function of frequency. Standard deviation are indicated for 30, 60 and 90 kHz vertical data (seven sessions each). Reference azimuth = 0°.

same plane, vertical localization thresholds were determined at selected frequencies from 20 to 100 kHz.

It was impossible to place the transducers above and below the animal and still get reliable data since the area in which we worked was relatively shallow. One transducer would have been close to the surface and the other close to the bottom resulting in the two speakers sounding different to our animal due to different reverberation characteristics at the surface and the bottom. Consequently, we left the speakers in the horizontal position and trained the animal, using the vertical bite bar, to turn on its side for brief periods and perform the localization task.

The total duration of the signal was halved to 0.52 s since the animal tended to back off from the vertical bar if signals were as long as 1 s. However, no deterioration of threshold response was detected in comparing the horizontal sessions to the shorter signal. A survey of localization as a function of frequency was conducted with seven sessions each at 30, 60 and 90 kHz and two sessions at the other frequencies using the same sound as used in experiment 1 at 0° azimuth (Sound 1, Fig. 3).

There were no significant differences in localization acuity, as measured by MAAs, in the vertical and horizontal planes ($P = 0.05$, Student's *t*-test, Dixon & Massey, 1969) (Fig. 9). The MAAs calculated for each of the seven sessions conducted at 30, 60 and 90 kHz (MAAs: 2.5°, 3.0°, and 3.0°, respectively) were not significantly different from the horizontal thresholds at these frequencies ($P = 0.05$, Student's *t*-test) or from each other ($P = 0.05$; Duncan's new multiple range test). When the animal was positioned at a 15° azimuth position, the mean MAA for 7 sessions was 2.7° ($\pm 0.3^\circ$).

(5) Horizontal and vertical localization: clicks

Localization acuity in relation to simulated echolocation click trains was tested in both the horizontal and vertical planes at 0° azimuth. The signal consisted of 166 clicks centred at 64.35 kHz (Fig. 3). One 35 μ s click was presented every 3 ms for a total duration of 498 ms. MAAs of 0.7° and 0.9° were determined for click trains in the vertical and horizontal planes respectively (Fig. 10).

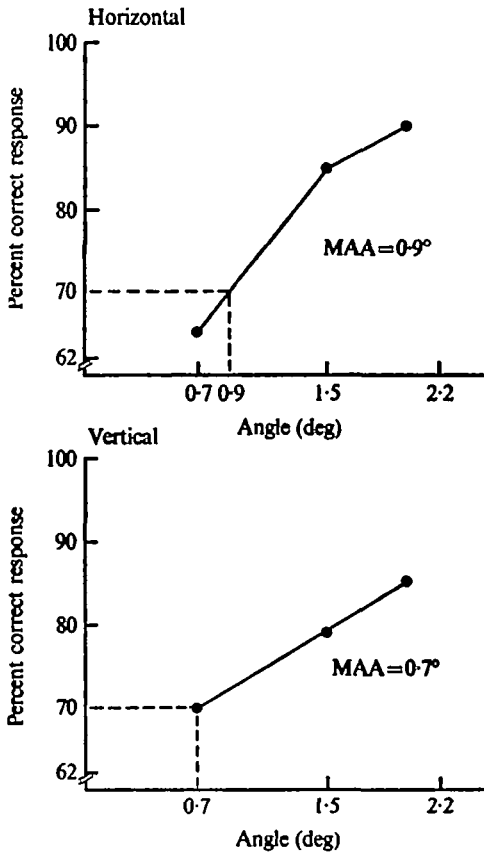


Fig. 10. Graphical determination of localization thresholds for click trains in both the horizontal and vertical planes.

DISCUSSION

These experiments clearly demonstrate that the bottlenose porpoise *T. truncatus* is well adapted for underwater sound localization. Measurements of horizontal minimum audible angles (MAAs) for humans show that their best localization is on the horizontal plane and at 0° azimuth. At 1 kHz, the MAA is about 0.8° , but at higher and lower frequencies, man's localization capability falls off significantly. However, the data for *Tursiops* show that this species is capable of acute localization over a wide range of frequencies on the horizontal plane both when the speakers are on either side of the midline of the animal (Fig. 6) and when the sounds are off to the side (Fig. 8). The horizontal data also suggest a sound localization mechanism that makes use of different binaural cues at different frequencies.

A frequently considered factor in human sound localization is the relationship between the wavelength of sound and the distance between the two outer ears. However, this distance for *Tursiops* (24 cm in our animal) may not be fully appropriate since it is not clear that this species uses the external ear region for sound detection. Reysenbach de Haan (1957) and Dudok van Heel (1962) argue that the external ear canal is non-functional in *Tursiops*, and physiological data show that the lateral surfaces of the lower jaw (14 cm apart) are involved in sound detection, a

least above 20 kHz (Bullock *et al.* 1968; McCormick *et al.* 1970). These same experiments also indicate that there are regions of auditory sensitivity at frequencies below 20 kHz in the general vicinity of the external ear canal.

Our horizontal data suggest that the region around the external ear canal may be functional in sound localization below about 20 kHz, while at and above 20 kHz there is good reason to suggest that the lateral mandibular regions are involved in detection (also see Bullock *et al.* 1968; Norris & Harvey, 1974). Mills (1958, 1972) shows that in humans localization is best when the wavelength of sound is more than the distance between the interaural detectors (binaural phase and time used as cues) and when it is less than half the interaural distance (binaural intensity cues). Between half and one times the interaural distance, localization acuity is relatively poor. If the external ear regions are used as low frequency detectors, wavelengths above 12.8 kHz would be less than half the interaural distance (speed of sound at the experimental site was 1527 m/s (Au *et al.* 1974)), while sounds below about 6.2 kHz would be more than 1 interaural distance in wavelength. As a result, we would expect poor acuity from 12 to at least 6 kHz. However, if the mandibular regions were the receiving area regions, the wavelengths from 12 to 24 kHz would be poorest for detectability and there would be improvement in acuity below 12 kHz. It is clear that our data most closely fit a hypothesis involving the external ear canals in low frequency sound detection or at least in localization.

These data themselves do not support a hypothesis that the lower jaw functions at higher frequencies, but azimuth data indicating best localization when the animal is turned 15° in azimuth agrees with the suggestion, first made by Norris (1968, 1969), that the fat-filled lower jaw is involved in sound detection. Norris (1968) suggested that the impinging sound enters the mandibular channel through an exceptionally thin region (1.0 mm) of the lateral mandible known as the 'pan bone' that lies about midway between the tip of the rostrum and the eye. The impedance of the fat-filled channel closely resembles that of water (Norris, 1968; Norris & Harvey, 1974), and so there is little loss due to impedance mismatch such as between blubber and muscle (Reysenbach de Haan, 1957). A highly significant additional point is the angle of incidence between the 'pan bone' and the water. As a result of the slight impedance differences between the fat in the mandibular channel and the water, the percent transmission between the two fluids deviates from 90°, and the sound transmission coefficient is 0.953 (Norris, 1968; Norris & Harvey, 1974). Norris (1968) pointed out that the 'pan bone' is not parallel to the long axis of the animal and as a result, the angle of incidence between the water and the mandibular fat channel is not minimal when the sound is in front of the animal (also see Norris & Harvey, 1974). Bullock *et al.* (1968) recorded potentials from the inferior colliculus that were evoked by sound stimulation from different directions and determined that the maximum response is when the sound is in a cone 5–30° forward and downward. In addition, they found that as the frequency increased, the cone of best receptivity moves closer to the midline of the animal. Recent experiments by Norris & Harvey (1974) further support the hypothesis; maximum hydrophone response in the region of the auditory bulla occurred when sound came from 20° off the midline.

The results of the horizontal azimuth study show that localization is relatively poor (MAAs of 5.3 and 5.2°) when the animal is turned 30°, compared to an azimuth

of 0° . However, the best pure tone localization occurred when the azimuth was 15° (MAAs of 1.3 and 1.5°), an angle which closely approximates to the best angle of receptivity and suggests that our animal was using the mandibular fat channel for sound detection. The improved localization acuity is readily explained by considering that when the animal is turned 15° , the sounds impinging upon one 'pan bone' are at the best incident angle thus giving a maximum sound level at the inner ear. At the same time, the other 'pan bone' is in an acoustic shadow of the head which would lower the sound level. In addition, and perhaps more importantly, the 'pan bone' away from the sound is at a poor angle of incidence to the sound and this would result in considerable transmission loss for sound to this ear. Since *Tursiops* has a good intensity discrimination ability (1 db; Evans, 1973) it is likely that intensity differences at the ears could provide localization cues.

Vertical localization

Experiments with the animal turned on its side and the speakers 'up and down' relative to the head of the animal suggest an acute vertical localization ability in three dimensional space. This is significantly different from the few data available for man, the only terrestrial mammal studied, which indicate that humans have great difficulty determining the position of a sound source on the median plane (0° azimuth) when the sound is above or below the horizontal plane (e.g., Butler, 1969; Roffler & Butler 1968*a, b*). Roffler & Butler (1968*a*) concluded that binaural cues were not necessary for accurate localization in the vertical plane, but that vertical localization depended on frequencies above 7 kHz and upon the pinna. They postulated that the series of ridges and folds of the pinna impose a pattern of organization on the noise stimulus; the intensities of the high frequencies may be differentially modified by the pinna with the pattern of modification dependent upon the signal angle.

Our data suggest that *Tursiops* has little difficulty in discriminating vertical cues. However, it is unlikely that our animal used binaural information since in both 0° and 15° azimuth vertical experiments the lower jaw was towards one transducer while the upper jaw was towards the other. Consequently, both 'binaural detectors', whether they be the lower jaw or the external meatal regions, were receiving the same cues in all circumstances. The probable mode of 'localization' then can be postulated to be through detection and memory of intensity information. Bullock *et al.* (1968) demonstrated that sounds presented via the lower jaw produce larger responses in the inferior colliculus than do sounds presented to the dorsal portion of the rostrum. Consequently sounds from the transducer facing the lower jaw in our experiments would be more intense than sounds to the dorsal rostrum. Since *Tursiops* has a good intensity discrimination system (Evans, 1973) as well as the ability to remember sounds for at least as long as 120 s (Thompson & Herman, personal communication, 1974), it is possible that the animal learned that the louder sounds came from one speaker and that the less intense sound came from the speaker facing the upper jaw. This suggests that our vertical data do not represent localization in the same sense that the horizontal data indicate localization. The data do support a hypothesis that a normal animal, free to move its head in horizontal and vertical directions, as has been demonstrated during echolocation (Norris *et al.* 1961; an

others), could detect sounds on the vertical plane, remember them for short periods of time, and compare them to the same sound detected when the head was in another position. Thus, the animal could 'scan' for the regions where the sound was most intense and infer the vertical position of the emitter.

Clearly, the pure tone pulses in these experiments do not simulate the normal sounds used by cetaceans in any aspect of their normal behaviour. However, the pure tones have permitted us to determine the frequency response characteristics of the localization system. Considerable changes in the pulse length, interpulse interval, rise and decay time, etc. of the pure tone signals did not alter the localization ability of our animal, at least at 40 kHz. Although Bullock & Ridgway (1972) have shown that certain signals with characteristics of the echolocation clicks can differentially affect the neural response in the brain, it is clear that longer signals, as well as pure tones, do not change the localization response of the animal. However, our experiments using clicks with similar energy spectra to those of the porpoise echolocation click resulted in a marked improvement in sound localization. Bullock & Ridgway (1972) found that rapid rise and decay times alter the firing of units in the inferior colliculus, and while it is not possible to say that cetacean localization depends upon the inferior colliculus, clearly there is an improvement in localization ability when these units respond.

It should also be remembered that our animal was restrained when listening to the test signals and that normal animals move their heads during echolocation behaviour (Norris *et al.* 1961). Consequently, our animal was probably doing relatively 'poorly' in localization compared to a free animal which, besides receiving binaural cues for localization, also can scan the head and seek maximum sound levels and transpose this information into directional information.

Comparisons with other odontocetes are not possible beyond stating that our low frequency data (at 6 and 10 kHz) indicates somewhat better localization acuity than reported for *P. phocoena* by Andersen (1970a) and Dudok van Heel (1959, 1962) using different techniques and with unrestrained animals. It is clearly not possible to extrapolate to other marine mammals, since recent data by Moore (1975) and others have shown that the restrained California Sea Lion (*Z. californianus*) has a best MAA of about 7° to clicks. It is tempting, however, although not fully valid, to extrapolate our data for a single sub-adult male *Tursiops* to other members of the same species and even more so to other odontocetes. Due to the expense and difficulties of working with a marine mammal, it was impossible to repeat our experiments with another individual and so we do not suggest that our data represent the capabilities of all members of the genus *Tursiops*. Rather, this data suggests an acute and well adapted localization system that enhances the auditory ability of the species. It would be of great interest and value to replicate and extend our data (and in fact, all auditory data available for *Tursiops*) to additional individuals in order to determine the intra-specific range of variation. However, it should be pointed out that in the one replication of data for frequency discrimination using two different animals it was found that the variation in discrimination capabilities was more probably ascribable to differences in method than to significant differences in the capabilities of the experimental animals (see Herman & Arbeit, 1972; Jacobs, 1972). Furthermore, it would be of great value to extend our own work with *Tursiops* to more detailed experiments

on the vertical plane as well as an examination of localization using techniques with shorter signal rise-times than our equipment was able to produce.

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