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Frequency-dependent variation in the two-dimensional beam pattern of an echolocating dolphin

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Recent recordings of dolphin echolocation using a dense array of hydrophones suggest that the echolocation beam is dynamic and can at times consist of a single dominant peak, while at other times it consists of forward projected primary and secondary peaks with similar energy, partially overlapping in space and frequency bandwidth. The spatial separation of the peaks provides an area in front of the dolphin, where the spectral magnitude slopes drop off quickly for certain frequency bands. This region is potentially used to optimize prey localization by directing the maximum pressure slope of the echolocation beam at the target, rather than the maximum pressure peak. The dolphin was able to steer the beam horizontally to a greater extent than previously described. The complex and dynamic sound field generated by the echolocating dolphin may be due to the use of two sets of phonic lips as sound sources, or an unknown complexity in the sound propagation paths or acoustic properties of the forehead tissues of the dolphin.

Keywords: dolphin; echolocation; phonic lips; beam steering

1. INTRODUCTION

Dolphin echolocation signals, or clicks, are forward-projected impulsive sounds that originate from structures known as the phonic lips [1]. Of late, the debate about whether one or both of the two phonic lips present in small odontocetes (toothed whales) are used in the production of clicks has been invigorated [2]. One hypothesis states that, although two sets of phonic lips are present in nearly all odontocetes, only one set is predominantly used in click production [2,3]. This argument suggests that physical manipulations of the melon (the fat-filled forehead of the dolphin) and air-filled acoustically reflective structures (e.g. vestibular air sacs) are used to control beam steering and beamwidth variation observed in dolphin click production [4]. On the other hand, evolutionary arguments and some experimental measurements are the basis of the hypothesis that both sets of phonic lips can be used during echolocation, potentially providing the ability to exploit a variable and larger signal bandwidth while also affecting beam control [1,4,5].

The dolphin echolocation beam is described by the spatial distribution of the click amplitude at a known distance from the dolphin. However, little attention has been given to spatial variations in the frequency-dependent click energy, even though the frequency spectrum of the echolocation click is dynamic within a bandwidth potentially exceeding 85 kHz [6]. In this study, a dense hydrophone array was used to record clicks produced by a dolphin performing a target detection task. A frequency band-limited analysis of the beam was performed to quantify variation in the beam as a function of frequency. The results suggest that the echolocation beam potentially originates from two sources. It is argued that the interaction of two active sources could contribute to target localization by providing a forward looking region with a maximum gradient in the beam's amplitude contour (slope edge), which can be used to improve target localization.

2. MATERIAL AND METHODS

A 23 year-old male bottlenose dolphin participated in the study. The dolphin was housed in a floating pen complex in San Diego Bay at the Space and Naval Warfare Systems Center Pacific. The dolphin was trained to bite and hold on to a neoprene-covered vinyl plate (biteplate) while using echolocation to detect targets (figure 1*b*). Testing was conducted from a netted pen enclosure (9.1 × 18.3 m; approx. 10.5 m deep) using a 3.8 cm diameter water-filled stainless steel sphere (target strength = −32 dB re 1 μPa) as a target.

An array of 29 omni-directional hydrophones (Reson TC4013) was attached to a monofilament mesh placed 0.9 m from the dolphin's rostrum, equating to 1.2 m from the source of the echolocation clicks. The mesh was attached to a 1 m high stainless steel frame, with an arc and chord length of 1.6 m and 1.4 m, respectively. The hydrophones were arranged in the shape of a diamond with irregular spacing (figure 1*a*) and each hydrophone was equidistant (1.2 m) from the echolocation click source. Except for the target used in the detection task, and the arrangement of the hydrophone array, all other aspects of data collection were as previously reported [4]. The reader is referred to this paper for a description of the behavioural procedures and the quality controls implemented to ensure that the dolphin could not see the targets and that he remained stationary during detection trials.

Each trial produced a 5 s long sequence of continuously sampled data. Clicks were detected and extracted from the sequences with custom algorithms developed in MATLAB (MathWorks, Inc., Natick, MA, USA). A click was detected if the signal of the hydrophone with the maximum recorded amplitude exceeded a threshold peak pressure of 163 dB re 1 μPa. A 128-sample rectangular window was applied to the clicks and extracted so that each data snippet contained an individual click with a 50 data point buffer prior to the first sample exceeding threshold. The extraction procedure was performed on all hydrophone channels based on the detection time determined from the hydrophone with the maximum recorded amplitude.

Clicks were transformed to the frequency domain using a discrete Fourier transform, resulting in frequency spectra with a 1.0 kHz bin size. The frequency band-limited plots presented in figure 2 were created by integrating the spectral magnitude across 10 kHz frequency bands (i.e. the band magnitude (BM)), ranging from 20 to 140 kHz, for all channels. The BM of each band was then represented as a surface plot covering an area corresponding to the dimensions of the hydrophone array. Data points between hydrophones were interpolated with the nearest-neighbour method using a data point spacing $\Delta h'$, set to $\Delta h/3$, where Δh is the hydrophone spacing. Each contour level of the surface plot represents a 10 per cent decrement from the maximum BM as measured across all frequency bands (see the colour bar of figure 2).

3. RESULTS

Clicks produced during the echo-detection task had a persistent energy peak constrained between 20 and

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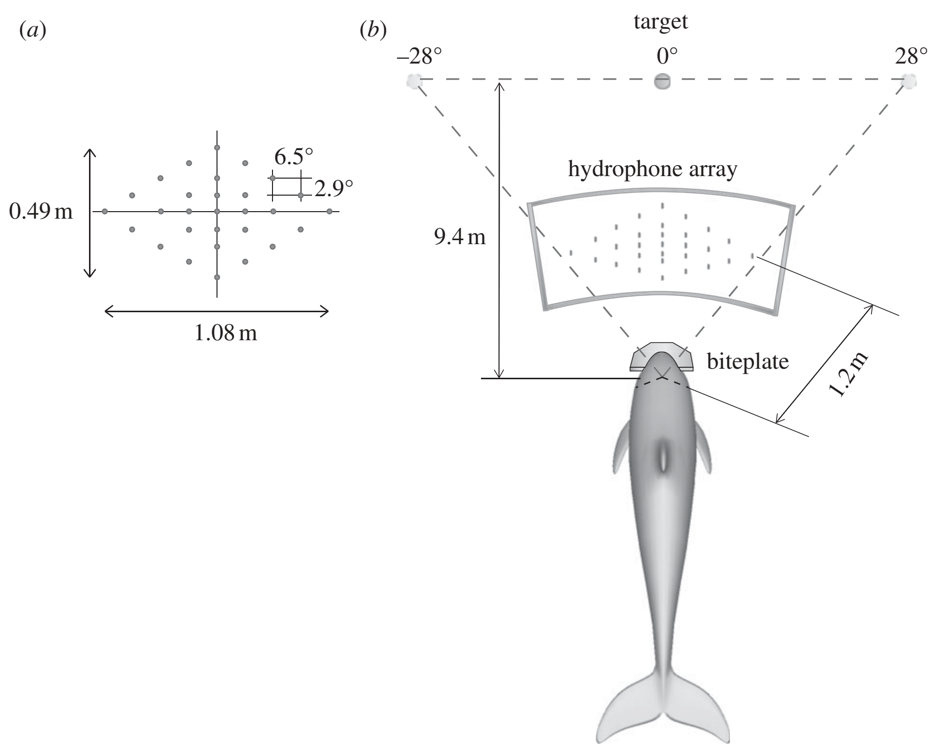

Figure 1. (*a*) Dimensions of the hydrophone array placed in front of the dolphin during the echolocation task. (*b*) The arrangement of the array relative to the dolphin and the potential locations of the target.

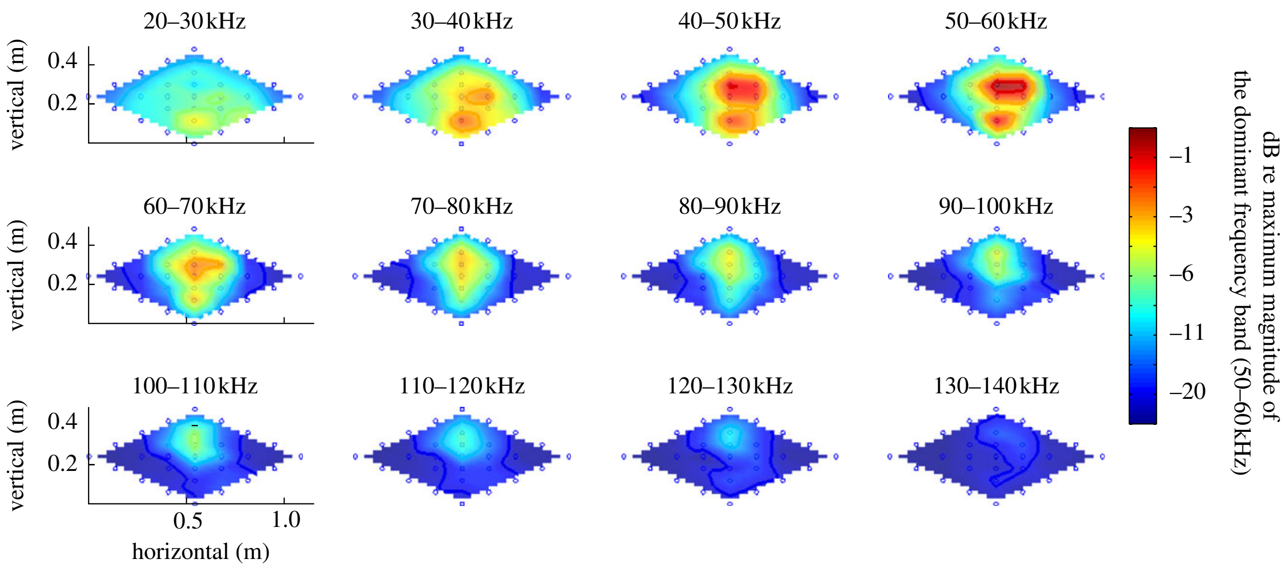

Figure 2. Frequency band-limited distribution of the spectral magnitude of a single dolphin echolocation click. The spatial distribution of the spectral magnitude is plotted against the arrangement of hydrophones (shown in the first column). The location of individual hydrophones is designated by small blue circles. Although the colour projection is on a linear scale, the decibel level relative to the maximum spectral magnitude of the dominant frequency band is provided next to the colour bar for reference. The spatial separation of spectral magnitude peaks is most noticeable between 50 and 60 kHz. The -3 dB magnitude of the lower frequency projection spans 20–70 kHz, whereas that of the higher frequency projection spans 30–80 kHz, but has notable signal components up to 120 kHz.

70 kHz that was typically projected downward by approximately 6° (figure 2). (Figure 2 demonstrates only one click; videos of click sequences may be found in the electronic supplementary material.) Little energy was found in the peak above 80 kHz. However, another peak often appeared with the energy typically focused approximately 3° upward and slightly to the right of the longitudinal axis of the dolphin. The energy of this peak was typically, but not always, between 30 and 80 kHz. Energy up to 120 kHz was observed. The higher-frequency content of the click, as measured on the maximum response axis (MRA) of the beam, disappeared coincident with the disappearance of this higher frequency peak. Ninety-seven trials were conducted with the target presented on-axis and all trials had at least one click with

the two peaks described above. Overall, 41 per cent of the clicks observed from these trials contained the two peaks and there was an average of 7.7 such clicks per trial. The higher frequency peak contained the dominant energy 41 per cent of the time that two peaks were observed.

Angular detection thresholds for the target were unable to be determined as the dolphin was able to detect the target at better than chance for the farthest target displacements. Beams produced by the dolphin were regularly steered off the array, indicating that beam steering exceeded 28° in the horizontal plane and obviating the calculation of a beam steering limit. When beam steering was observed, the respective peaks shifted together. Although it appeared that the spatial relationship of the peaks varied somewhat with beam steering, this could not be quantified because of the loss of recording ability once the beam was off the array. For this reason, only trials with the target presented on-axis were used in determining the prevalence of beams with two peaks.

4. DISCUSSION

The frequency band-limited beam patterns of this echolocating dolphin performing a target-detection task suggest that the echolocation beam may originate from two sources. The beam appears as a dynamic two-source 'optional' system in which a persistent lower frequency beam can be augmented with a higher frequency peak partially overlapping in space, time and frequency. The lower frequency peak energy was regularly in the lower portion of the array, regardless of signal amplitude. The higher frequency peak was not dominant at lower amplitudes and was not observed during the first several clicks in a click sequence across which amplitudes increase. This finding is consistent with the prior discovery of a positive relationship between the amplitude and frequency of dolphin clicks [7].

The spatial and frequency distribution of the echolocation beam produced sloping regions in the beam's magnitude contour between 40 and 70 kHz that typically occurred approximately 3° below the longitudinal axis of the dolphin when the beam was not steered. The sloping regions create a 'valley' with an approximately 6 dB reduction in the spectral magnitude from peaks located above and below it. This magnitude gradient may be exploited to optimize target localization; as observed in Egyptian fruit bats [8], pointing the maximum slope of the beam towards a target maximizes changes in the reflected energy of the target as it moves relative to the echolocating animal. This comes at a cost to the signal-to-noise ratio of the returning echo, which is optimal when the target is contained within the maximum amplitude region of the beam. In the dolphin, the costs of this trade-off may be minimized by bounding the steep sloping region within the higher amplitude ensonification peaks. Studies of click production during target localization need to be conducted with targets having variable target strengths and aspect dependence to assess whether dolphins capitalize on the change in the magnitude slope of the echolocation beam for target localization.

In this paper, it is proposed that the dynamic sound field generated by the echolocating dolphin may be due to the use of two sets of phonic lips as sound sources; however, it may also arise from an unknown complexity of the acoustic propagation path in the forehead of the dolphin (e.g. contributions from reflective structures). The former explanation is more appealing for two reasons. First, the higher frequency peak often encompassed the highest amplitude recording; however, the lower frequency peak was present in nearly every click, whereas the higher frequency peak was not. Second, the appearance of two peaks is consistent with slight differences in the temporal onset of separable down-chirps observed in bimodal dolphin clicks [9]. The phonic lips of the bottlenose dolphin are asymmetric, which may relate to the different bandwidths of the two peaks. Asymmetry of the premaxillary bones and dynamic changes in the air volume of the premaxillary sacs may contribute to the spatial variation of the peaks. The two sets of phonic lips may, therefore, work together in this species to provide plasticity in frequency bandwidth and beam pattern.

Recent work on harbour porpoises suggested that only one set of phonic lips, preferentially the right, produces clicks. Harbour porpoise phonic lips are symmetric and their clicks are higher in frequency, narrower in bandwidth, and generally longer in duration than those of bottlenose dolphins [10]. It is plausible that species-specific anatomic variation contributes to differences in click production across odontocete species. Functional biases may also exist; preferential utilization of one set of phonic lips may be typical for species with symmetric pairs of phonic lips. It must also be remembered that much of the characterization of odontocete echolocation occurs in the laboratory. Laboratory experiments often rely on contrived scenarios to study a particular aspect of echolocation. Under such circumstances, odontocetes probably have no need to exercise the full range of their capability.

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