Biosonar behaviour of free-ranging porpoises

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Detecting objects in their paths is a fundamental perceptional function of moving organisms. Potential risks and rewards, such as prey, predators, conspecifics or non-biological obstacles, must be detected so that an animal can modify its behaviour accordingly. However, to date few studies have considered how animals in the wild focus their attention. Dolphins and porpoises are known to actively use sonar or echolocation. A newly developed miniature data logger attached to a porpoise allows for individual recording of acoustical search efforts and inspection distance based on echolocation. In this study, we analysed the biosonar behaviour of eight free-ranging finless porpoises (*Neophocaena phocaenoides*) and demonstrated that these animals inspect the area ahead of them before swimming silently into it. The porpoises inspected distances up to 77 m, whereas their swimming distance without using sonar was less than 20 m. The inspection distance was long enough to ensure a wide safety margin before facing real risks or rewards. Once a potential prey item was detected, porpoises adjusted their inspection distance from the remote target throughout their approach.

Keywords: echolocation; cetacean; finless porpoise; sonar; dolphin

1. INTRODUCTION

Sonar abilities of dolphins and porpoises have been extensively studied (Au 1993). Not only can these animals detect a remote target using sonar, but they can also precisely discriminate its size, thickness and material composition (Au 1993). In addition to controlled captive experiments, sonar signals of wild dolphins and porpoises have been examined (Akamatsu *et al.* 1998; Au & Benoit-Bird 2003; Lammers *et al.* 2003). Sonar signals of dolphins and porpoises consist of high-intensity and high-frequency ultrasonic pulse trains that stand out well against ambient noises even in the wild (Richardson *et al.* 1995). The number of ultrasonic pulses emitted is considered an appropriate indicator of the search effort made by an animal. Moreover, the target range of the sonar used by dolphins can be estimated by the inter-click interval (Thomas & Turl 1990; Au 1993). These signals can easily be recorded and can provide information about the timing and the distance over which the echolocating animal uses its biosonar. This makes dolphins and porpoises some of the most appropriate model organisms in which to observe biosonar behaviour in the wild.

However, the problem of recording the sonar signals of free-ranging dolphins and porpoises simultaneously with underwater behaviour has remained largely unsolved. Hydrophone systems can observe individual vocalizing cetaceans for only a limited time and they record little behavioural information (Janik *et al.* 2000; Au & Benoit-Bird 2003; Clark & Clapham 2004). A mobile video camera carried by a human diver can record behaviour and vocalizations only during brief encounters with the animals (Herzing 1996). Although underwater sound recording systems have recently been attached to

large marine mammals (Burgess *et al.* 1998; Madsen *et al.* 2002; Nowacek *et al.* 2004; Tyack *et al.* 2004), few studies have succeeded at recording ultrasonic sonar signals concurrently with underwater behaviour of individual dolphins and porpoises (Tyack & Recchia 1991; Akamatsu *et al.* 2000; Thomas *et al.* 2002). Furthermore, none of the data logger systems attached to these animals can exclude vocalizations from other nearby individuals. These data logger systems that are used to record vocalizations are therefore inappropriate for studies of animals that swim in groups, such as dolphins and porpoises.

To investigate the biosonar behaviour of aquatic animals, we developed a miniature stereo acoustic data logger and used it on eight free-ranging porpoises in an oxbow of the Yangtze River, China. Time-sequence data of sonar events and underwater behaviour were recorded for individuals. In addition, the direction of the sound source was stored in the data logger to exclude sonar signals from other individuals. Here, we examine the acoustic activity and behaviour of free-ranging echo-locating finless porpoises in a large open water system.

2. METHODS

Until 1972, the experimental site was a tributary of the Yangtze River, and water still enters from the main stream during every flood season (Wei *et al.* 2002). This oxbow lake, part of Tian-e-Zhou Baiji National Natural Reserve of the Yangtze River, Hubei, China (29.30′–29.37′ N, 112.13′–112.48′ E), is approximately 21 km long and 1–2 km wide. It was established by the Chinese government in 1992 as a reserve for baiji (*Lipotes vexillifer*) and finless porpoises. Since 1990, 49 finless porpoises have been introduced from the main population in the river. Finless porpoises in the lake survive without supplemental food and are observed to reproduce annually. The environment of the lake is considered to be similar to the natural habitat of this species (Zhang *et al.* 1995).

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A miniature stereo pulse event recorder (W20-AS, Little Leonardo, Tokyo, Japan; diameter, 22 mm; length, 122 mm; weight, 77 g) was developed for this research. The data logger consisted of two hydrophones (System Giken Co. Ltd, -210 dB/V sensitivity), an analogue–digital converter, a band pass filter (70–300 kHz) to eliminate noise, 256 MB flash memory and a central processing unit (PIC18F6620, Microchip, USA) inside a pressure-resistant aluminium cylinder. The storage capacity of this system allows recording of the intensity, timing and source direction of ultrasonic pulses for up to 60 h with a sampling rate of 2000 events s^{-1}. The two miniature hydrophones were situated at the front and the back ends of the device. The sound source direction is calculated from inter-hydrophone differences in sound arrival time stored in the data logger. The source direction was used to exclude vocalizations coming from nearby individuals. The dynamic range was between 129 dB peak-to-peak (reference pressure 1 μPa at 1 m) and 157 dB. The resolution of time difference was 542 ns. Simultaneously, swim speed, dive depth, heaving and surging body acceleration were recorded by a behaviour data logger (diameter, 21 mm; length, 114 mm; weight, 60 g; PD2GT, Little Leonardo, Tokyo, Japan). Swimming speed was essential for calculating the swimming distance of the animals; the acceleration parameters were not used in analyses thereafter.

Nine finless porpoises were captured in the reserve in October 2003. Eighteen fishing boats drove finless porpoises from the upper end of the oxbow to the lower end. A net approximately 1 km long was used to divide the oxbow transversely. A round, fine-mesh net was used to encircle the animals. In the final stage, fishermen wearing life jackets dived into the water and captured the animals individually. In the meantime, 18 boats surrounded the seine net and more than 50 fishermen carefully watched each section of the net to avoid entanglement of the animals. The water was less than 1 m in depth, allowing the fishermen to handle the animals safely. All animals inside the net were captured and were temporarily released into a net enclosure for 24 h to calm down. The enclosure was established close to shore and measured approximately 30×60 m^2 with a maximum depth of 3.5 m. All animals were safely captured and released with data loggers after this period. One animal carried two acoustic data loggers on both sides for calibration purposes to compare the received sound pressure levels on each side. The data obtained from this individual were not used for this paper.

Each data logger was equipped with a suction cup (Canadian Tire Corporation), a VHF transmitter (MM130, Advanced Telemetry Systems, USA) and floatation material (expanded polyvinyl chloride, Klegecell #55, Kaneka Company Ltd, Japan) to ensure positive buoyancy for easier retrieval after spontaneous release from the animals. The antenna of the transmitter was designed to be out of the water after detachment and to remain approximately perpendicular to the surface to detect strong radio transmission. The drag force of the whole data logger system was measured in a fluid dynamical experiment tank at the National Research Institute of Fisheries Engineering, Japan, and was found to be less than 60 g at the animals' average 0.89 m s^{-1} cruising speed. The weights of the complete acoustic and behaviour data logger systems in air were 216 and 197 g, respectively. The weights of the data logger systems were adjusted to 20 g positive buoyancy in water. The data logger was fixed to the side of the body in the upper posterior direction from the pectoral fin; this area was the least affected by body movements and

therefore ensured a long attachment time. Recording the sonar signals of finless porpoises was possible at this position even for off-axis sound detection (Akamatsu *et al.* 2000).

To retrieve the data logger systems, the radio signals were monitored by two antennae (RX-155M7/W, Radix, Japan) from the top of the three-storey field station building beside the oxbow. When a continuous radio signal was received, a data logger was considered to be floating. Retrieval operations were started six or more hours after release to avoid any disturbance to the animals. This experiment was conducted under a permit issued by the Fisheries Management Department of Hubei Province.

The time-sequence data from the acoustic and behaviour data loggers were synchronized by the time stamp of the data file. Low-intensity signals below 136 dB, such as surface reflection, were excluded by off-line analyses using new custom software on MATLAB (The MathWorks, MA, USA) and IGOR (WaveMetrics, OR, USA). Splash noises during respiration were easily identified and excluded at dive depths less than 0.3 m, which is six times the resolution of the depth metre (5 cm) on the behaviour data logger. The sonar signals of dolphins and porpoises have a pulse train structure (Au 1993). Inter-click train interval was defined as 200 ms or longer. We calculated the swimming speed in metres per second from the rotation of the propeller deployed in the behaviour data logger using the methods of Fletcher *et al.* (1996).

3. RESULTS

We recorded the biosonar behaviour as well as the underwater body movements of eight finless porpoises. The simultaneous recording time of the acoustic and behavioural parameters varied from 1 to 35 h for each individual (average 8.75 h). In total, we identified 2 425 095 pulses; 49 470 pulse trains and 5113 dive events. The porpoises produced pulse trains on average every 5.1 s.

Many periods of silence between pulse trains were recorded (figure 1). Silent periods sometimes lasted more than 10 s, whereas the swim speed during these periods ranged up to 3 m s^{-1} with an average cruising speed of 0.89 m s^{-1}. Because the underwater visibility in the lake was less than 1 m owing to turbidity, the porpoises could not detect any remote obstacles in front of them without using sonar. The distance over which an animal travelled silently was calculated by multiplying the duration of every period of silence by the simultaneously recorded swimming speed.

We also calculated the distance inspected acoustically by the animals just prior to a period of silence. The acoustically inspected distance is given by the two-way distance travelled by sound within an inter-click interval. However, in cetacean biosonar systems, an additional lag time is required within each inter-click interval for the animal to process returning echoes (Au 1993). This lag time should be less than the shortest inter-click interval. The minimum accumulated distribution of the inter-click interval in a pulse train was 1 ms (figure 2a). The lag time in our study was conservatively assumed to be no more than 5 ms, since frequency of occurrence dropped sharply below this interval. The upper inset of figure 2a shows the scale of the calculated distance inspected acoustically. The distance inspected acoustically in advance was far greater
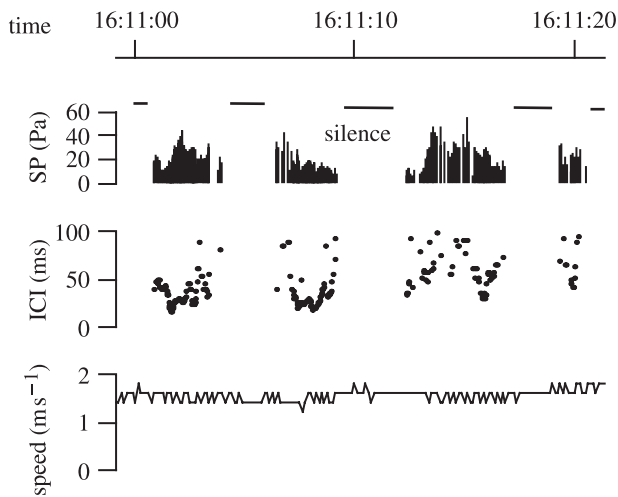
Figure 1. Periods of silence in sonar signal records for a finless porpoise. The time-series of the sound pressure (SP) shows periods of silence between pulse trains indicated by horizontal bars. The distance inspected acoustically was calculated by the inter-click interval (ICI) of a train prior to the silence.

than the distance travelled silently (figure 2b, accumulated data from all monitored individuals). This relationship was consistently observed for all individuals. In 90% of all cases, the acoustically inspected distance was less than 77 m and the modal focal distance was 24 m.

Once a porpoise detected a potential target and approached it, the animal often emitted clicks with a linearly decreasing inter-click interval, hereafter termed the 'approach phase' (figure 3a). Changes in the inspected distance from the beginning to the end of the approach phase were calculated from changes in inter-click interval. Additionally, the distance travelled during the approach phase was calculated by multiplying the duration of the approach phase by swim speed (figure 3b). Finless porpoises changed the inspected distance by 11.0 m on average (maximum 42.7 of the 117 approach phases analysed) and swam 8.6 m on average (maximum 43.0) during the approach phase. These two independent measures—the distance travelled and the distance inspected during the approach phase—were well correlated (figure 3b; $r = 0.80$, $p < 0.005$).

At the end of the approach phase, the minimum inter-click interval was near the assumed lag time (5 ms). A few seconds after the end of the approach phase, the swim speed frequently dropped to zero (see swimming speed profile in figure 3a).

4. DISCUSSION

The finless porpoises observed in this study produced sonar signal trains frequently, on average every 5.1 s. This result suggests that the finless porpoises strongly rely on their acoustic sensory systems for navigation, travelling and capturing prey.

When moving through an environment in which vision is limited, prior acoustic inspection of the area ahead is essential for these animals. This strategy offers substantial advantages both in terms of risk avoidance and prey capture. In particular, animals must detect potentially lethal risks as early as possible. For example, harbour seals have been shown to avoid the long-range vocalizations of killer whales, their primary natural predators (Deecke
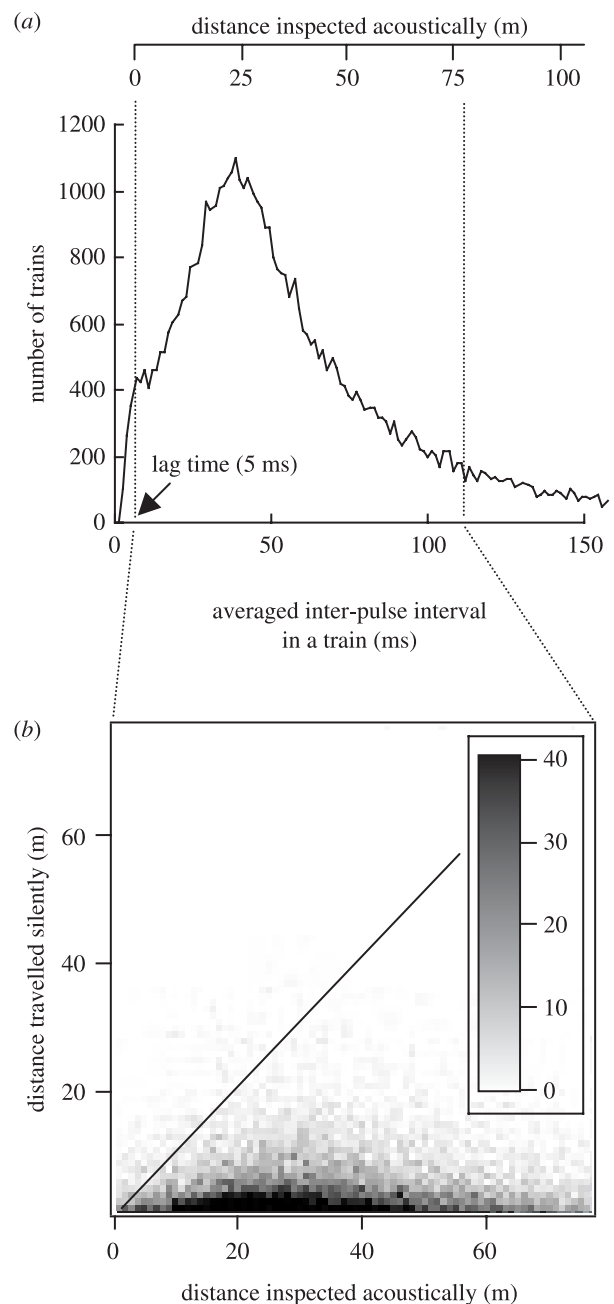

Figure 2. Comparison of the distance travelled in silence and the distance previously inspected acoustically. (a) Distribution of the average inter-click intervals in pulse trains of eight finless porpoises. The lag time (echo signal processing duration) was assumed to be 5 ms. In 90% of cases, the acoustically inspected distance was less than 77 m. (b) The distance inspected acoustically was far greater than the distance subsequently travelled in silence. The grey scale shows the number of observed pulse trains in each bin. Most click trains fell under the diagonal line, indicating that porpoises inspected an area ahead for long enough before silently swimming into it.

et al. 2002). Potential risks for finless porpoises in a freshwater habitat include injuries from or entanglement in underwater debris and entrapment in shallow waters, as well as rough water surfaces or floating materials that prevent safe respiration. Taking such risks can be costly; thus, the porpoises must detect risks in time to avoid them by changing behaviour. As shown in figure 2b, finless porpoises almost always inspect upcoming areas for long
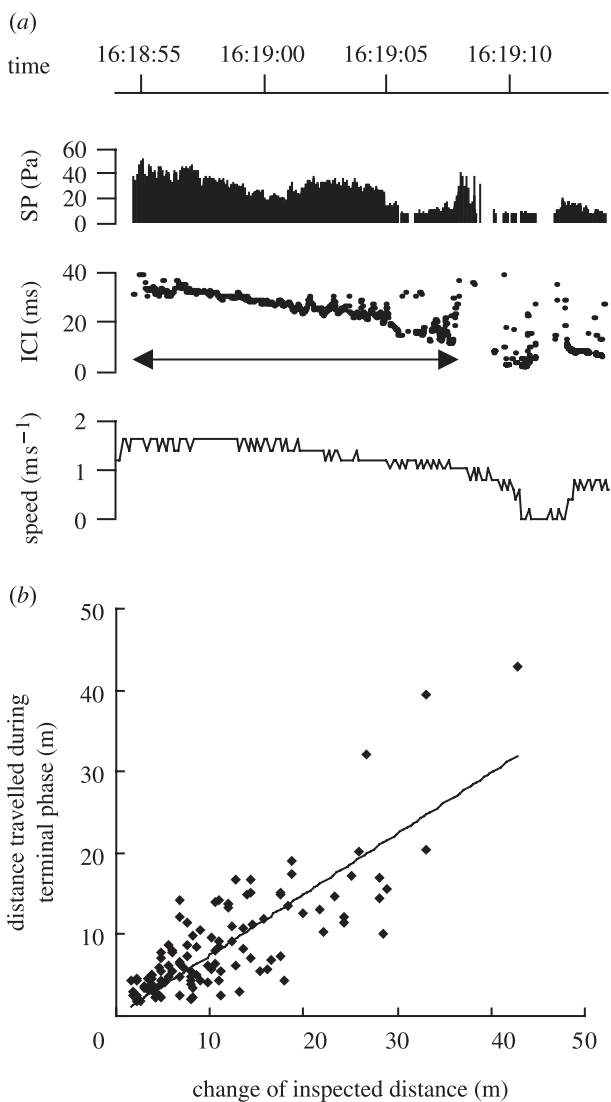
(a)

time

(b)

Figure 3. Comparison of the distance travelled during the approach phase and the change in the distance inspected acoustically. (a) The approach phase (arrow) is characterized by a linear decrease in the inter-click intervals (ICI) of the sonar signals. The swimming speed dropped to nearly zero after the approach phase. SP, sound pressure. (b) The distance travelled during the approach phase was closely correlated with the estimated change in the distance inspected.

enough before swimming into them silently. The porpoises seemed to employ a large safety margin in their sonar range when inspecting the area ahead relative to the distance they swam silently.

The inspection distance of the porpoises was as high as 77 m (figure 2a). This long-range sonar ability in dolphins and porpoises has also been reported in previous studies. In one study, the detection distance of a metal sphere target by a trained bottlenose dolphin (*Tursiops truncatus*) was up to 113 m (Au 1993). Estimated inspection distances of three different odontocetes in the wild reached tens of metres, which was significantly greater than the distances inspected by captive individuals (Akamatsu *et al.* 1998). This suggests that the large safety margins observed in this study may be used by other odontocetes as well. The inter-click interval fluctuated and mean interval was larger than the two-way sound travel time to the target range in the target-detection experiment by a

harbour porpoise (*Phocoena phocoena*; Teilmann *et al.* 2002). The inter-click intervals may be an index for maximum target range, otherwise the harbour porpoise might scan the longer distance behind the target and adjust the inter-click interval before the certain detection of the target.

On the other hand, for the detection of prey, the porpoises are acutely aware of the relative distances to a target that is still out of the visible range. The distance travelled during the approach phase and the change in the distance that was inspected acoustically were similar, suggesting that the porpoises recognized a remote target and focused their sonar on it at a distance sometimes exceeding 30 m (figure 3b). A harbour porpoise, which is of the same family of a finless porpoise, is known to detect a water-filled stainless steel sphere with outer diameter 5.08 cm from up to 14 m by its sonar (Teilmann *et al.* 2002). In the case above, the present finless porpoise might detect a larger target such as a school of fish from long distance.

During the approach phase, the porpoises seemed to employ smaller safety margins since the inspection distance was adjusted to the distance from a potential prey item second by second. Once a porpoise detects an available resource ahead, it focuses the inspection distance on this target. In exchange for the small safety margin, a predator gains the advantage of locating the position of the moving remote prey well in advance.

The increasing repetition rate of sonar signals during the approach to a target has been previously described in bat sonar (Tian & Schnitzler 1997; Moss & Surlykke 2001) before the capture of an insect. At the end of the approach phase in porpoises, the swimming speed dropped. This speed profile is considered the turning behaviour of the animal (Akamatsu *et al.* 2002). The precise adjustment of sonar during the approach phase and the quick body movement strongly suggest that prey capture occurred.

On average, the approach phase of the animals in this study lasted over 11 m in swimming distance, whereas the sonar vocalizations at a higher repetition rate of a bat (*Eptesicus fuscus*) started 1–2 m from a target in a large flight room (Moss & Surlykke 2001). The body lengths of these two species also differ by approximately 10 times (140 cm for finless porpoises, 12 cm for big brown bats). Therefore, both species locked their sonar on a target at a distance of eight times their body length.

Because animals face limitations in detection ability and because their search effort is time constrained, they must use their sensory systems appropriately. The finless porpoises in this study usually searched no more than 77 m ahead, a distance that could be reached within a couple of minutes at their typical cruising speed. Objects farther away are not important to the animal, regardless of whether they are lethal or beneficial. Inspecting the immediate area through which a porpoise is going to travel allows time for decision-making before the animal faces real risks or rewards.

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