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Echolocation by two foraging harbour porpoises (*Phocoena phocoena*)

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SUMMARY

Synchronized video and high-frequency audio recordings of two trained harbour porpoises searching for and capturing live fish were used to study swimming and echolocation behaviour. One animal repeated the tasks blindfolded. A splash generated by the fish being thrown into the pool or – in controls – by a boat hook indicated prey and stimulated search behaviour. The echolocation sequences were divided into search and approach phases. In the search phase the porpoises displayed a clear range-locking behaviour on landmarks, indicated by a distance-dependent decrease in click interval. Only in trials with fish was the search phase followed by an approach phase. In the initial part of the approach phase the porpoises used a rather constant click interval of around 50 ms. The terminal part started with a sudden drop in click interval at distances around 2–4 m. Close to the prey the terminal part ended with a buzz, characterized by constant click intervals around 1.5 ms. The lag time in the search and the initial part of the approach phase seems to be long enough for the porpoise to process echo information before emitting the next click (pulse mode). However, we assume that during the buzz lag times are too short for pulse mode processing and that distance information is perceived as a 'pitch' with a 'frequency' corresponding to the inverse of the two-way transit time (pitch mode). The swimming speed of the animal was halved when it was blindfolded, while the click intervals hardly changed, resulting in more clicks emitted per metre swum.

Key words: harbour porpoise, *Phocoena phocoena*, biosonar, echolocation, foraging behaviour, signal pattern.

INTRODUCTION

Biosonar or echolocation is an active sensory system that evolved independently in mammals at least twice: in bats and in toothed whales. Both echolocators emit high-frequency sounds and process the returning echoes from objects in the surroundings. They use echolocation primarily for orientation and for finding prey. Bats produce echolocation pulses with their larynx, emit them through their mouth or nose, and capture the echoes with the pinnae (for review, see Griffin, 1958; Popper and Fay, 1995; Schnitzler et al., 2003; Thomas et al., 2004). In contrast to this, the biosonar system of toothed whales (odontocetes) is different in many aspects probably as an adaptation to aquatic life (for review, see Au, 1993; Thomas et al., 2004). The sound source is located within their nasal passages where the phonic lips produce echolocation clicks (Amundin and Andersen, 1983; Cranford and Amundin, 2004). These are transmitted through the fatty melon and emerge as a beam of sound from the forehead (Cranford et al., 1996; Goodson et al., 2004). Echoes are received through the lower jaw where special acoustic fats conduct the sound to the middle ear (Brill et al., 1988; Ketten, 2004).

Harbour porpoises (*Phocoena phocoena*) are mainly found in coastal and near-shore environments. For them, as for probably all other toothed whales (odontoceti), echolocation is an important sensory modality. They use it almost constantly (Akamatsu et al., 2007) in orientation tasks (Verfuß et al., 2005), allowing the perception of objects and landmarks based on acoustical images. They also pursue prey with the help of echolocation (Beedholm and Miller, 2007; Busnel and Dziedzic, 1967; Verfuß and Schnitzler, 2002).

The use of echolocation during prey capture has been well studied in insectivorous bats (reviewed by Kalko and Schnitzler, 1998; Miller and Surlykke, 2001; Schnitzler and Kalko, 1998; Schnitzler et al., 2003). Although various bat species use different types of echolocation pulses, the pattern of echolocation pulse sequences emitted by insectivorous bats is surprisingly similar. It can be divided into a search phase and an approach phase (Griffin et al., 1960). The search phase contains the longest pulse durations and intervals, both of which decrease during the approach phase. The approach phase can be divided into an initial and a terminal part (Melcón et al., 2007). The terminal part, which is often called the buzz, can sometimes be further divided into a buzz I and a buzz II (Kalko and Schnitzler, 1989; Surlykke et al., 1993). In buzz I the pulse intervals continue to reduce and in buzz II the intervals are minimal and remain constant at about 6 ms.

The biosonar of odontocetes has mainly been investigated in the context of target detection (reviewed by Au, 1993; Kastelein et al., 1999) and discrimination (reviewed by Au, 1993; Kastelein et al., 1997), and not in the context of prey capture. Nevertheless, a few studies deal with the echolocation behaviour of odontocetes during foraging. Click sequences resembling the pattern of signals used by bats hawking insects have been reported from odontocetes. Slow clicking with long intervals was attributed to searching for prey and rapid sequences of clicks, coined bursts or buzzes, were assumed to indicate the final stage of prey capture (e.g. Akamatsu et al., 2005; Goodson et al., 1988; Goodson et al., 1994; Johnson et al., 2004; Johnson et al., 2006; Johnson et al., 2008; Jones et al., 2008; Madsen et al., 2002; Madsen et al., 2005; Miller et al., 1995; Miller et al., 2004). Johnson and colleagues correlated the echolocation behaviour of beaked whales with prey capture by recording the click sounds of the whale together with the echoes from the prey on a data logger attached to the back of the whale (Johnson et al., 2008). They thus confirmed the correlation of buzzes with prey capture attempts.

Through geological time predator–prey interactions evolved between bats and insects (reviewed by Miller and Surlykke, 2001). Some insects acquired selective audition and evasive behaviours to escape predation by bats. Insects like green lacewings and moths can detect ultrasound in the frequency range of the bats' echolocation calls. Tympanate insects can respond to bat sound by turning away (negative phonotaxis) or by diving passively or with power. Improved bat sonar capabilities presumably evolved to counter avoidance responses by tympanate insects (Miller and Surlykke, 2001).

Such evolutionary predator–prey interactions have barely been investigated for odontocetes. Mammal-eating orcas (*Orcinus orca*) in the northeast pacific use their echolocation strikingly less than their fish-eating relatives, probably so as not to warn their acoustically sensitive marine mammalian prey (Barrett-Lennard et al., 1996). Also, northeast atlantic killer whales use less intense clicks than do their northeast pacific cousins, perhaps to detect echoes from herring before the herring senses the predator (Simon et al., 2007). The extremely high frequency echolocation click sounds of harbour porpoises, on the other hand, may have evolved so as not to be heard by killer whales (Andersen and Amundin, 1976). Morisaka and Connor (Morisaka and Connor, 2007) hypothesize that killer whale predation is the reason why this acoustic feature also evolved in other odontocete species using high frequency, narrow bandwidth clicks, like small dolphins (*Cephalorhynchus*), the pygmy sperm whale (*Kogia breviceps*) and the franciscana (*Pontoporia blainvillei*).

Many fish species can hear sound and some show a flight response to sound stimuli (Canfield and Eaton, 1990; Eaton et al., 1995). A few fish species, like American shad (*Alosa sapidissima*) (Mann et al., 1998; Mann et al., 2001; Plachta and Popper, 2003) detect and respond to ultrasound stimuli. Cod (*Gadus morhua*) can be conditioned to detect ultrasound stimuli (Astrup and Møhl, 1993) and to discriminate between long and short pulse intervals (Astrup and Møhl, 1998). However, a recent study of unconditioned cod showed that they did not respond behaviourally to intense ultrasonic stimuli (Schack et al., 2008). Whether behaviours of fish to ultrasound evolved in response to odontocete predation has been discussed (Astrup, 1999), but still remains unknown.

This paper describes and compares the echolocation and swimming behaviour of two captive harbour porpoises during prey capture experiments that were repeated with one of them being blindfolded. We present for the first time a detailed analysis of the echolocation foraging sequence using synchronized video and high-frequency sound recordings. With these results and those of recent literature we propose phases for the echolocation behaviour of odontocetes during foraging and consider a possible evolutionary predator–prey scenario.

MATERIALS AND METHODS

The experiments were conducted from 1999 to 2000 with the same harbour porpoises and at the same study site as in the spatial orientation experiments presented previously (Verfuß et al., 2005), the 36 m×15 m semi-natural outdoor enclosure of the Fjord and Bælt in Kerteminde, Denmark [see figure 1 in Verfuß et al., 2005 (Verfuß et al., 2005)]. The long sides of the pool are constructed of a corrugated iron wall and an underwater observation tunnel. The ends of the enclosure are restricted by nets (10 cm^2 mesh size), allowing a natural flow of seawater from the Great Belt and Kerteminde Fjord into the study area. The nets were covered with sea grass and algae. The depth of the enclosure varied between 3 and 5 m depending on the tide and the location in the pool. A 4.5 m×4.5 m floating holding pool with a depth of 1.2 m was permanently present within the enclosure and was used for separating the animals when necessary or holding them for medical treatment.

Two harbour porpoises (*Phocoena phocoena* L.), a female (Freja) and a male (Eigil), were involved in this study. The animals were rescued from a pound net near Kerteminde, Denmark, in April 1997 and had then an estimated age of 1–2 years. During the study period, the animals' ages were between 3 and 5 years. The body length of the female was 1.49 m and her weight was 46 kg. The body length of the male was 1.37 m and his weight was 39 kg.

For investigating the echolocation and swimming behaviour of harbour porpoises during fish catches, both animals were trained to remain stationary at one end of the pool. During trials, one animal stayed with the trainer while the other animal was sent to the opposite end of the pool. Two types of trial were conducted: fish trials and no fish trials. In fish trials, as soon as the porpoise headed for the opposite end, a live brook trout (*Salmon trutta f. fario*) weighing between 20 and 85 g was thrown into the release area 1–5 m in front of a hydrophone array, causing a splash. No fish trials were run as controls. In no fish trials, a similar splash was generated with a boat hook – a wooden stick with a plastic hook end – simulating the splash from a fish. At most only one no fish trial per session was placed randomly in fish trials so as not to decrease motivation.

Both types of trial were conducted with Eigil and Freja being able to see. Trials were repeated with Freja while she was blindfolded with digestible gelatine suction cups covering her eyes. Sessions with Freja blindfolded were done shortly after she had finished eyecup training.

Experimental set up and trials

Synchronized video and high frequency sound recordings were taken from the porpoises during experimental sessions. The experiments were done on days with good water clarity and calm weather with no or little rain fall to ensure good visibility and recording conditions. The set up used in this experiment was the same as that used previously [see figures 1 and 2 in Verfuß et al., 2005 (Verfuß et al., 2005)]. Two in-air cameras and two underwater cameras were used. One camera (cam1) was fixed on wires 5.3 m above the mean water surface level giving a top view of part of the west end of the pool, the end where prey capture occurred. The second camera (cam2) was fixed 9.4 m above the mean water surface level on the Fjord & Bælt exhibition centre wall and was used to analyse the porpoises' behaviour at the east end of the pool.

Two video cameras in underwater housings (Evamarine, Geretsried, Germany; cam3+cam4) were mounted 2 m apart on a horizontal steel rod and fixed to a vertical steel pole in the harbour side corner of the west end of the pool. Both cameras were placed 0.25 m under the water surface.

Three HS150 hydrophones (Sonar Research and Development, Beverley, East Yorkshire, UK) with a frequency response up to 180 kHz (±6 dB) were used for recording echolocation behaviour. These were mounted in an array with 1 m spacing, submerged to a depth of 1 m, about 2 m in front of the pontoon at the receiving end of the pool. The array holding the hydrophones was built from PVC tubing to avoid strong echoes.

Signals from the hydrophones were amplified by 52 dB and high-pass filtered at 100 Hz using etec amplifiers (etec, Frederiksværk, Denmark). The sound was recorded on three channels of a RACAL Store 4D high-speed magnetic tape recorder (Racal Instruments GmbH, Bergisch Gladbach, Germany) at a speed of 60 in s^{-1} (=152.4 cm s^{-1}), giving a bandwidth of about 300 kHz. Two of the three RACAL channels were set to 2 V, while the third channel was set to 0.5 V to increase amplification of weak echolocation signals.

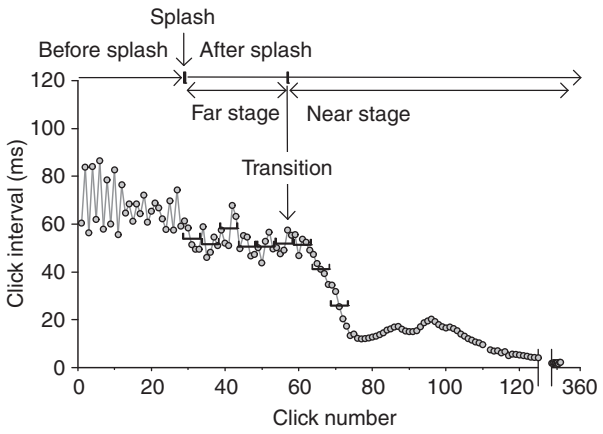

Fig. 1. The sections of a click train in a fish capture trial. The before-splash section ends with the splash, which is produced when a fish hits the water (fish trials) or by a boat hook (no fish trials). In fish trials, the after-splash section is divided into a far stage and a near stage, which begins with the transition to progressively shorter click intervals. Horizontal brackets in the after-splash section indicate the mean click interval over five consecutive clicks. The transition point is defined as being the longest click interval in the first mean of the series of continuously decreasing mean click intervals to a value below 20 ms in the near stage.

The synchronization of all video and sound recordings was done with a custom-built VITC/LTC time code generator (Universität Tübingen, Tierphysiologie, Tübingen, Germany). The LTC time code was recorded on the fourth channel of the RACAL Store 4D tape recorder and the sound channels of the in-air cameras. The VITC time code was integrated in the underwater camera recordings.

Experiments were run on 34 days over the 2 years with 60 experimental sessions totalling 304 trials: 98 fish trials for Freja and 127 fish trials for Eigil, 18 no fish trials for Freja and 19 no fish trials for Eigil, as well as 38 fish trials and 4 no fish trials for Freja when blindfolded.

Video and sound analysis

All video and sound recordings were visually scanned for good quality, defined as reasonably good images of the porpoise on both video cameras (cam1 and cam2), of the fish (if used) and of the catch or attempted catch in the recordings of video camera 2. Catch attempts were defined as the porpoise approaching the fish to a distance of less than 0.1 m, with the porpoise being in the final stage of the echolocation foraging sequence (see Results), and the fish having been able to escape in the last moment by a sudden movement away from the porpoise. Catches/catch attempts recorded on the underwater video cameras (cam3 and cam4) were preferred for analysis. The data of the swim paths shown here are from cameras cam1 and cam2. The sound recordings were selected for a reasonable signal to noise ratio of echolocation clicks.

A total of 29 trials were chosen for detailed analysis of the echolocation behaviour, including 15 fish trials (five for Freja, five for Eigil, five for Freja when blindfolded), and 14 no fish trials (five for Freja, five for Eigil, four for Freja when blindfolded).

For video analysis, selected sequences were digitized with a frame grabber card (HASOTEK frame grabber FG42, Rostock, Germany). The video sampling rate was 25 images s^{-1}, giving a 40 ms time interval between frames. Motion analysis was done frame by frame.

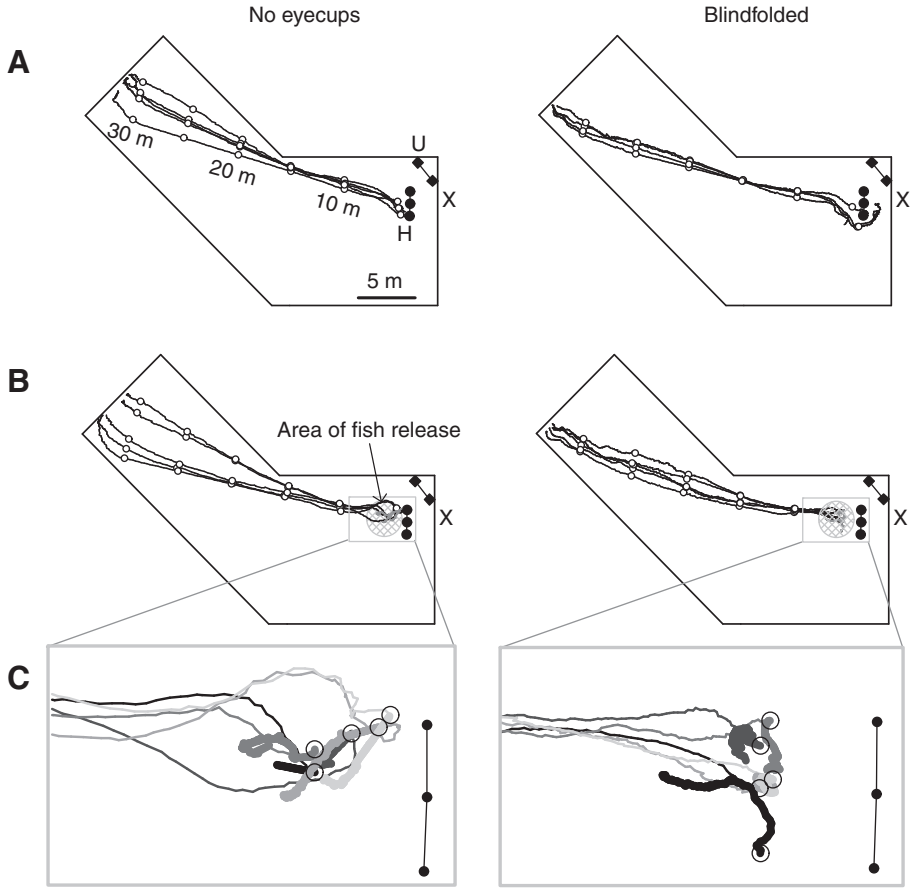

Fig. 2. Swimming paths of Freja in no fish (A) and fish trials (B) with no eyecups and when blindfolded (with eyecups). The hatched circle is the area of fish release. The three black dots show the hydrophone array (H), and the two black squares represent the two underwater video cameras (U). The arbitrary reference point (X) is 1.5 m behind the front edge of the pontoon. White dots on the swimming paths indicate 5 m intervals and the 30 m, 20 m and 10 m points show distance to the reference. The content of the grey frame in B is shown enlarged in C with the swimming paths of Freja (thin lines) and the fish prey (thick lines). Swimming paths of Freja and prey from the same trial are marked with the same grey shade. Black circles indicate the position of the fish catch or catch attempt.

Table 1. Parameters analysed during trials in two tasks (fish and no fish) for the two harbour porpoises, Eigil and Freja, as well as for Freja blindfolded (Freja bf)

	Fish			No fish		
Parameter	Eigil	Freja	Freja bf	Eigil	Freja	Freja bf
Mean time per trial (s)	6.0±0.6	5.6±0.8	12.2±2.0	5.8±1.0	4.5±0.7	9.9±0.6
Mean distance per trial (m)	22.8±0.8	25.2±1.7	25.4±0.6	23.8±1.4	21.5±2.1	24.3±1.0
Mean number of clicks recorded per trial	339.4±44.8	328.2±119.5	630.8±64.4	89.0±12.8	71.2±14.7	195.0±12.0
Mean distance to fish at transition point (m)	4.4±2.6	1.9±0.8	3.9±1.7	n.a.	n.a.	n.a.
Mean click interval at transition point (ms)	57.5±14.4	48.3±16.0	41.5±14.4	n.a.	n.a.	n.a.
Minimum click interval in near stage (ms)	1.4±0.2	1.6±0.1	1.6±0.1	n.a.	n.a.	n.a.
Mean click interval in far stage (ms)*	47.0±6.3	54.7±4.8	47.1±4.0	n.a.	n.a.	n.a.
Mean lag $time_F$ in far stage (ms)*	34.8±5.0	42.8±4.8	35.0±3.0	n.a.	n.a.	n.a.
Mean lag $time_R$ (ms)*	n.a.	n.a.	n.a.	40.2±2.8	34.8±1.7	31.7±0.7
Mean click density (clicks m^{-1})* (excl. near stage)	4.1±1.0	3.2±0.2	7.4±0.7	2.7±0.2	3.1±0.3	6.2±0.8
Mean speed (m s^{-1})	5.4±0.5	5.9±0.5	3.0±0.4	6.3±0.4	5.9±0.5	3.3±0.4
Slope (±95% CI) (ms m^{-1}) before splash for $D_R \leq 26$ m	0.23±1.45	**2.34±1.59**	**0.96±0.63**	–	–	–
Slope (±95% CI) (ms m^{-1}) after splash*	–0.50±0.96	–0.17±0.93	0.02±0.94	**1.80±0.37**	**1.41±0.55**	**1.71±0.90**
Slope (±95% CI) (ms m^{-1}) for D_F (far stage)*	0.19±1.24	–0.03±0.62	0.59±0.76	n.a.	n.a.	n.a.
Slope (±95% CI) (ms m^{-1}) for D_F (near stage)	**10.91±3.90**	–	**9.72±7.15**	n.a.	n.a.	n.a.

The duration of a trial was determined by the first and last click analysed from an echolocation sequence (see Materials and methods). The values for regression slopes (±95% confidence interval, CI) for mean click intervals are shown over distance to reference (D_R; before splash D_R<=26 m; after splash D_R=18–12m excluding the near stage in fish), and over the distance to fish (D_F) in the far stage as well as in the near stage. Regression slope values with a ±95% confidence range that include the value 1.3 are not significantly different from the slope of the two-way transit time. Those ranges including zeros do not show a significant regression, those excluding zero are slopes significantly different from zero. Significant positive regression slopes (marked in bold) show a positive correlation between click interval and distance to reference or distance to fish, respectively. The dashes indicate insufficient data. n.a., not applicable/not available. Number of trials included for Eigil/Freja/Freja bf are: fish=5/5/5, no fish=5/5/4. *Calculated for D_R=18–12 m.

The relative position of the tip of the porpoise's rostrum within each successive frame was determined from the video recordings of cam1 and cam2. For frames in which the porpoise was not visible, its position was interpolated. The same analysis was done with the fish in fish trials, using the central point of the fish's body to determine its position. The distance between the calculated positions of the porpoise and the fish was determined and defined as distance to fish (D_F).

In navigational tasks (Verfuß et al., 2005) with the same set up, both porpoises showed range-locking behaviour on landmarks near the west end of the pool. The time interval between successive clicks decreased linearly with decreasing distance to the end of the pool. In that study an arbitrary reference point was defined at the west end of the pool to establish the use of landmarks. We used the same reference point in this study to examine the influence of landmarks during fish catch. This reference point was midway between the front edge of the pontoon and the net, a point 1.5 m between these. The distance between the calculated position of the porpoise and the reference point is defined as the distance to reference (D_R).

Absolute metric values for the animals' positions were obtained with the help of custom-written software (3D and 3Drek, D. Menne©, Tübingen, Germany) using the method of photogrammetry (see Finsterwalder and Hofmann, 1968; Schwidefsky and Ackermann, 1976). The method of photogrammetry allows the determination of absolute positions of objects in a 3D environment. For the surveillance cameras (cam1 and cam2), the 2D-horizontal movement of the porpoise and the fish, respectively, was reconstructed. The third dimension, swimming depth, was estimated from 0.2 m to 0.7 m below the water surface for most of the traverse, or taken from the 3D motion analysis of the two underwater cameras (cam3 and cam4) if suitable. Marked positions on the pontoons enabled the software to calculate relative positions and distances in the video images into absolute positions. Reconstruction of the porpoise's swimming path was considered successful when the track from each camera overlapped at the middle of the pool, which was common to both surveillance camera views. Tidal differences that changed the distance between the cameras and water surface were taken into account for each session. With this method, distances could be calculated with a maximum error of 5%.

For sound analysis, sequences from chosen trials were played back at 16-fold reduced speed and digitized with a sampling rate of 51.2 kHz, resulting in an effective sampling rate of 819.2 kHz. The click interval, which is the time between two successive clicks as measured from the onset, was measured with custom-made software (Sona-PC, B. Waldmann©, Tübingen, Germany) at an accuracy of 156 µs. The software also showed the onset of each video frame and its specific frame number, which were used to correlate sound and video recordings. It was thus possible to correlate a particular click or click interval with a distance from the porpoise to the fish or to our arbitrary reference point, respectively. Analysis began from the first click recorded in a trial and stopped after the fish was caught, or the porpoise reached the hydrophone array in no fish trials, ~5 m in front of the reference point. The first and last click analysed therefore determined the trial duration, the travelled distance and the total number of analysed clicks within a trial as given in Table 1.

Not all clicks of a click train were captured by the hydrophones. Harbour porpoises have a directional sound beam pattern (Au et al., 1999) and pauses in recordings occur not necessarily because of a lack of click production, but because of the porpoise moving its beam away from the recording hydrophone. Recordings from the three hydrophones confirmed beam scanning by our porpoises. Therefore all click intervals longer than 120 ms, indicating that the animal directed its sonar beam away from the hydrophone, were excluded from the analyses.

Click trains, swim speed and statistical analysis

Click trains were divided into two sections, a before-splash section and an after-splash section (Fig. 1). In fish trials, the porpoises showed a clear reaction to the fish when closing in on their prey (see Results) by suddenly shortening the click interval. Thus each fish click train was further divided into far stage and near stage (Fig. 1). In the after-splash section, averages over five successive click intervals were calculated. The transition from far stage to near stage was defined to be in the first such group of five clicks, where the mean click interval values start to continuously decrease over time to a value below 20 ms. The transition point was defined as being at the longest click interval in the first mean.

The orientation tasks conducted previously (Verfuß et al., 2005), performed with the same porpoises and the same set up, showed that the median click interval decreased linearly with decreasing distance to reference from 26 to 12 m, revealing a range locking on a landmark near the reference point. A comparable decrease of click interval was observed in the no fish trials of the present study (see Results). As in Verfuß et al. (Verfuß et al., 2005), the click interval/distance to reference data pairs were grouped into distance to reference bins 1 m in length. The median click interval was determined for each 1 m bin. Then the mean of the trial medians for each distance bin was calculated separately for each animal, type of trial and click train section. All mean values comprise the medians of at least three trials. As the near stage was clearly a response to the fish, the assessment of a relationship between the click interval and the reference point was omitted for this stage.

For each porpoise, trial type and click train section, a regression analysis was performed on the mean click interval of the D_R bins from 26 to 12 m. The slope of the regression plus 95% confidence interval were determined using SYSTAT (V10, SPSS, Chicago, IL, USA). For the after-splash data, the regression analysis was repeated for D_R=18–12 m as only those distances were obtained for Eigil in fish trials. For the far stage, regression analyses on the mean click interval of the D_F bins were also performed.

For the after-splash section of no fish trials, the mean ± s.d. of the trial median lag $time_R$ for D_R=18–12 m was determined for Eigil, Freja and Freja blindfolded. The lag $time_R$ is defined as the time difference between the click interval and the corresponding two-way transit time to the focal object (here the reference point R). We calculated the two-way transit time between the outgoing click and the returning echo from the reference point by assuming the speed of sound in water to be 1.5 m ms^{-1}, giving a slope of 1.3 ms m^{-1}. For the far stage of fish trials, the regression analysis revealed no significant decrease in the click interval with decreasing distance to fish (or reference; see Results). Therefore, the mean ± s.d. of trial median click intervals for D_R=18–12 m was determined for Eigil, Freja and Freja blindfolded. For the transition from far stage to near stage, the mean ± s.d. for the distance to fish and the click interval at the transition point were determined. The mean ± s.d. of the median lag $time_F$, the lag time calculated with reference to the fish as focal object, for D_R=18–12 m was determined for Eigil, Freja and Freja blindfolded for the far stage of fish trials.

The swim speed was calculated as the running mean of 10 video frames (0.4 s) from the frame-by-frame speed. The mean ± s.d. of swim speeds within D_R=26–12 m was determined for each porpoise and each task so they could be compared with swim speeds obtained previously (Verfuß et al., 2005).

The click density is defined according to Schnitzler (Schnitzler, 1967) as the number of clicks produced per metre travelled. It was calculated with the formula click $interval^{-1} \times speed^{-1}$, giving clicks per metre. The mean ± s.d. click density was determined for D_R=18–12 m for comparison with lag $time_R$ and click interval.

Mean swim speeds and click densities were tested for individual differences and differences between Freja with and without eyecups using a mixed effect model with 'task' being a random variable, calculated with the programme R 2.5 (R Development Core Team, 2007; Pinheiro and Bates, 2000; Zuur et al., 2007). Differences between Freja with and without eyecups as well as individual differences between mean lag $time_R$ and mean click interval were tested using a general linear model adopting a quasi-poisson distribution (McCullagh and Nelder, 1991). Task-specific differences in mean speed and mean click density were also tested using a general linear model.

Multiple testing of a single null hypothesis required an alpha-level adjustment for the general linear model results. We did this by correcting P-values for the number of tests: two tests for lag $time_R$ and click interval (comparison between the two animals and between Freja with/without eyecups), three tests for speed and click density (comparison between the two tasks for Eigil, Freja and Freja blindfolded). We calculated corrected P-values (P_{corr}) using the equation $P_{corr}=1-(1-P_{orig})^k$ (Sokal and Rohlf, 1995) where P_{orig} is the originally derived P-value and k is the number of tests conducted.

RESULTS

Swimming behaviour

After being sent by the trainer, Freja and Eigil swam directly towards the opposite end of the pool (Fig. 2). In no fish trials the animals went straight through the area of fish release and sometimes also around the hydrophone array, apparently searching for fish (Fig. 2A). When blindfolded, Freja showed clear scanning movements by turning her head left and right while approaching the catch area. This was obvious in trials with and without fish. In fish trials the fish often stayed where it hit the water. After a few seconds, the fish mostly swam downwards towards the bottom of the pool. Near the release area the porpoises began to pursue the prey (Fig. 2B,C). Close to the fish the porpoises often turned upside down (belly up) with a rotation around the long body axis and caught it from underneath. This rotation was not seen in recorded trials of Freja when blindfolded with eyecups, but she performed the belly up behaviour when being trained for wearing eyecups.

The average swim speed was higher for both porpoises in foraging trials (with and without fish) than in trials where the animals swam the same track to perform a navigational task (Fig. 3A) (Verfuß et al., 2005). The porpoises increased their speed to a maximum near the middle of the pool, after which the swim speed declined as they approached the catch area (Fig. 3B).

Eigil often increased his speed just after the splash was generated (Fig. 3B). In fish trials the splash occurred at shorter distances to the reference point than in no fish trials (fish: 20.1±2.8 m; no fish 24.7±1.5 m). The acceleration in fish trials therefore started closer to the middle of the pool. This resulted in a lower top speed compared with that for no fish trials (Fig. 3B), and thus gave a significantly lower mean speed (P_{corr}=0.039; explained variance, expl. σ^2: 0.56; Fig. 3A). Freja's average swim speed did not differ between fish and no fish trials ($P_{corr}\geq$0.633; expl. $\sigma^2\leq$0.17) and she swam about half as fast with eyecups on (Fig. 3A; Table 1). The difference in swim speed was highly significant [P=0.005; random effect (task): variance=2.1×10^{-11}; residual=4.1×10^{-2}]. There was no significant difference between Freja and Eigil in swim speed [P=0.928; random effect (task): variance=2.3×10^{-11}; residual=4.7×10^{-2}].

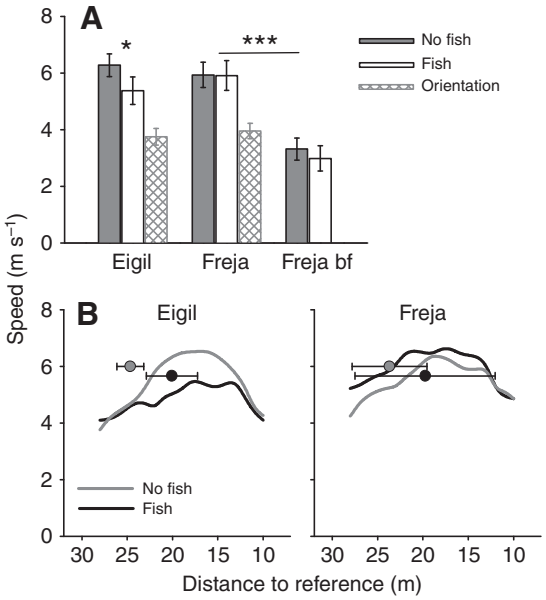

Fig. 3. (A) Mean swim speed (±s.d.) of the two porpoises, Eigil and Freja, and of Freja blindfolded (Freja bf) in no fish trials (grey bars) and fish trials (white bars). *Significant difference in swim speed between fish and no fish trials for Eigil (P<0.05). ***Significant difference in swim speed between Freja with and without eyecups (P<0.001). The speed of the same individuals in the orientation task described previously (Verfuß et al., 2005) is shown for comparison (hatched bars). (B) Swim speed of the porpoises Eigil and Freja in fish trials (black line) and no fish trials (grey line). The swim speed is given as the running mean averaged over 10 video frames (0.4 s). The circles and horizontal bars give the mean distance to the reference (±s.d.) of the porpoise at the time the splash occurred in fish (black) as well as in no fish trials (grey). Number of trials for Eigil/Freja/Freja bf are: no fish=5/5/4 and fish=5/5/5.

Echolocation behaviour

The porpoises continuously emitted echolocation signals in all trials (Figs 4 and 5). In no fish trials click interval decreased with decreasing distance to the reference point for most of the track (Fig. 4, Fig. 5A). When blindfolded, Freja decreased click interval until she was about 19 m from the reference. Here the click interval rose slightly and then decreased parallel to the two-way transit time (Fig. 4B left, arrow; Fig. 5A right).

In fish trials the echolocation behaviour changed after the splash. Before the splash, click interval mostly decreased with decreasing distance to the reference, similar to no fish trials (Fig. 4 right; Fig. 5B). Shortly after the fish was thrown into the pool, the porpoises switched to click intervals around a constant mean of about 50 ms. This part ended with a transition to progressively decreasing click intervals to a minimum of about 1.5 ms (Fig. 4 right; Fig. 5B,C). The minimum values were produced at distances of less than 1 m to the fish and were independent of the distance to the reference (Fig. 5B,C). In individual sound sequences the variability of the click interval was rather high. To demonstrate the general trends in echolocation behaviour we determined the average click interval for distance classes and investigated how they change in relation to distance to the reference point and distance to the fish (Fig. 6). With this approach it was possible to conduct a regression analysis for the different parts of the echolocation sequences described above and to compare data from the different animals and tasks.

In no fish trials not enough data points were obtained before the splash to perform a regression analysis. After the splashes, Eigil and Freja reduced their average click interval significantly in correlation with decreasing distance to the reference (Fig. 6; Table 1; distance to reference, D_R=24–12 m/18–12 m: Eigil, R^2=0.886/0.969, P<0.001/<0.001; Freia, R^2=0.808/0.896, P=<0.010/0.001) thus indicating range locking. When blindfolded, Freja's click interval decreased, but suddenly increased at about 19 m (Fig. 4B left, arrow; Fig. 5A; Fig. 6A) indicating a switch of range locking to a different landmark. When Freja (blindfolded) was closer than 19 m to the reference point she reduced the click interval significantly in correlation with decreasing distance to the reference (D_R=22–12 m/18–12 m: R^2=0.096/0.828, P=0.353/0.004; Fig. 6A; Table 1). The slope of the regression for the click interval decrease was not significantly different from that of the two-way transit time (1.3 ms m^{-1}) for Freja and Freja blindfolded, but was to some extent steeper for Eigil (Table 1). The mean lag time$_R$ was significantly different for Eigil *versus* Freja (P_{corr}=0.012, expl. σ^2=0.63), and for Freja *versus* Freja blindfolded (P_{corr}=0.024, expl. σ^2=0.62; Table 1).

In fish trials we also investigated separately the sections of the echolocation sequences before and after the splash. Before the splash, Freja blindfolded or not decreased click interval significantly with decreasing distance to the reference point (D_R=26–22 m/26–19 m without/with eyecups: R^2=0.974/0.830, P=0.002/0.002) thus indicating range locking (Table 1). This is not obvious for Eigil (D_R=26–21 m: R^2=0.455, P=0.142), perhaps because the distance covered before the splash is too short to show this effect. After the splash we discriminated two different sections in the echolocation sequences. The far stages of fish trials began with the splash and ended with the transition to the near stage, which was characterized by a sudden change to shorter intervals (Fig. 1). In the far stage, Eigil and Freja blindfolded or not kept the mean click interval fairly constant (Fig. 6B), independent of testing over the distance to reference (Eigil, D_R=18–12 m: R^2=0.262, P=0.240; Freia, D_R=21–12 m/18–12 m: R^2=0.106/0.041, P=0.358/0.662; Freia bf, D_R=18–12 m: R^2=0.001, P=0.956) or distance to fish (Table 1; D_F measured within the corresponding D_R range given above: Eigil, D_F=12–6 m: R^2=0.031, P=0.706; Freia, D_F=16–6 m/11–6 m: R^2=0.001/0.129, P=0.931/0.484; Freia bf, D_F=13–6 m: R^2=0.368, P=0.111). The slope of the regression was not significantly different from zero in all cases (Table 1). There were no significant differences between the mean click interval of Eigil *versus* Freja (P_{corr}=0.168, expl. σ^2=0.35), and of Freja *versus* Freja blindfolded (P_{corr}=0.070, expl. σ^2=0.49; Table 1). With the beginning of the near stage the click intervals decreased significantly with a steep slope much greater than the slope of the two-way transit time (Eigil/Freja bf: R^2=0.959/0.959, P<0.001/=0.021; the D_F for Freja between 1 and 0 m was too short to conduct a regression analysis; Fig. 6B; Table 1). The click interval reached minimum values of about 1.5 ms when the porpoises were less than 1 m from the fish (Fig. 4; Fig. 5B,C; Fig. 6B; Table 1). Nevertheless the click interval was greater than the two-way transit time to the fish. The transition from far to near stage was at D_F=4.4±2.6 m for Eigil, at D_F=1.9±0.8 m for Freja, and at D_F=3.9±1.7 m for Freja blindfolded. The click interval at the transition of far to near stage was 57.5±14.4 ms for Eigil, 48.3±16.0 ms for Freja and 41.5±14.4 ms for Freja blindfolded (Table 1). The porpoises continued echolocation after the fish was caught or had been able to escape. The length of the click interval commonly increased again after the capture or capture attempt (Fig. 4; Fig. 5B,C).

We did not systematically determine the click amplitude of the recorded sound sequences. However, the signal amplitude of clicks within near stage was at least 12 dB lower than in the far stage. The low amplitude of the final buzz made it difficult to record this part of a catch sequence entirely or sometimes even partly.

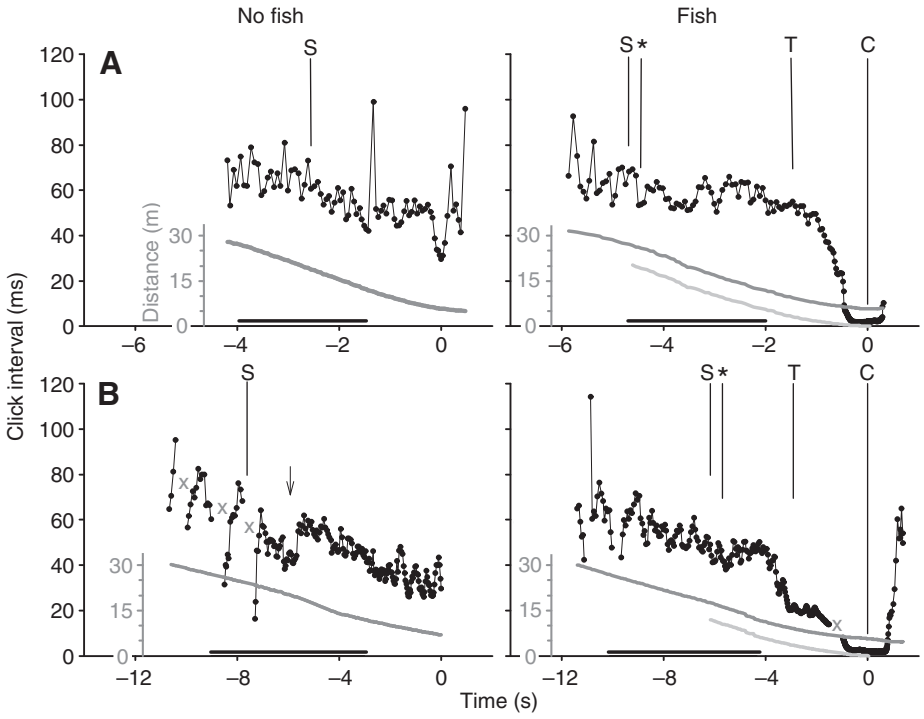

Fig. 4. Click interval of typical click trains emitted by Freja (A) and Freja blindfolded (B) during no fish trials and fish trials. The click interval is plotted against time relative to the arrival of the porpoise in front of the hydrophone array in no fish trials (distance to reference, 5 m), and relative to the time of fish catch in fish trials (distance to fish, 0 m). As additional information, the corresponding distance is given (second *y*-axis in grey) to the reference (dark grey line) and to the fish (light grey line). The time of splash (S), the presumed time of prey detection (*), the time at the transition from far to near stage (T) and fish capture (C) are also shown. The black bars on the *x*-axes mark the time stretch D_R=26–12 m, from which data were included in further analyses. Clicks with intervals >120 ms were not plotted (marked by X in B). The sudden increase in click interval shown by the arrow at about –6 s (19 m) for Freja (blindfolded) in the no fish trial (B left) indicates a shift to another landmark (see Results).

Click density

The click density arising from the inverse product of swim speed and click interval describes how many clicks are emitted per distance travelled and was determined for the after-splash section in no fish trials and the far stage section of fish trials (Table 1). The two porpoises used a similar click density in the different tasks [P=0.720; random effect (task): variance=7.8×10^{-11}; residual=15.5×10^{-2}]. Eigil had a significantly lower click density in no fish trials compared with fish trials (P_{corr}=0.039, expl. σ^2=0.55), but for Freja the click density did not differ ($P_{corr}\geq$0.139, expl. $\sigma^2\leq$0.45). Blindfolding produced a highly significant effect; click density was at least twice as high with as without eyecups [P<0.001; random effect (task): variance=3.0×10^{-11}; residual=6.1×10^{-2}; Table 1].

DISCUSSION

The echolocation behaviour of foraging harbour porpoises can be divided into different phases, similar to those of bats although the echolocation signal structure of bats is different from that of odontocetes. This interpretation is supported by studies on bottlenose dolphins (Goodson et al., 1988; Goodson et al., 1994; Morozov et al., 1972), narwhals (Miller et al., 1995), beaked whales (Johnson et al., 2004; Johnson et al., 2008), sperm whales (Miller et al., 2004), finless porpoises (Akamatsu et al., 2005) and Atlantic spotted dolphins (Herzing, 2004). According to the changes in click interval we can identify a search phase and an approach phase (Fig. 7). The latter can be divided into two parts, an initial part with more or less constant click intervals and a terminal part beginning with a sharp reduction in click interval and ending with the shortest click intervals (1.5 ms). The terminal part is rather similar to the terminal buzz of insectivorous bats during prey capture.

Based on ours and other studies, we propose that echolocation by foraging odontocetes can be influenced by environmental conditions similar to those reported for insectivorous bats. Bats hunting far away from the vegetation and the ground in more open spaces tend to use long search signals at long intervals, which allows for long distance detection of prey. Bats hunting in a more cluttered environment near vegetation and the ground use shorter search signals with shorter intervals (Neuweiler, 1983; Kalko and Schnitzler, 1993; Jensen and Miller, 1999; Schnitzler et al., 2003). Odontocetes also change the click interval depending on the distance to background targets as shown by others and by us here for the harbour porpoise. Thus for an odontocete hunting for prey in coastal waters where the background is at relatively close range one could expect shorter click intervals compared with animals foraging in open water. Harbour porpoises in captivity and in the wild show a dependence of click interval on distance to background objects as seen in Fig. 4, Fig. 6A and Fig. 7A, and as reported by Akamatsu and colleagues and Verfuß and colleagues (Akamatsu et al., 2007; Verfuß et al., 2005; Verfuß et al., 2008) and for finless porpoises by Akamatsu and colleagues (Akamatsu et al., 2005) (Fig. 7B). However, after detection of the prey the click interval becomes relatively constant in the initial part of the approach before the start of the terminal phase (Fig. 6B; Fig. 7A,B). In contrast we would expect a pelagic odontocete hunting for prey in deep and open waters to use longer click intervals when searching for prey. The perceptual range of the animal's echolocation system and not the distance to background targets might be expected to set the upper limit for click intervals. Beaked whales are open water predators of mainly squid and the click intervals they use when searching for prey are nearly 10 times those of our harbour porpoises. They may react to prey by shortening the click interval, but the interval can also be kept constant before going into the terminal phase (Johnson et al., 2008; Madsen et al., 2005) (Fig. 7Cb,a). In the latter situation (Fig. 7Ca) the whale may still be able to search for distant prey while approaching the closer targeted prey. Consequently, both environmental and perceptual situations can dictate an odontocete's echolocation behaviour.

Search phase

In the search phase odontocetes are expecting echoes from prey within the perceptual range of their biosonar system. We assume that the click pattern in this phase is determined by environmental

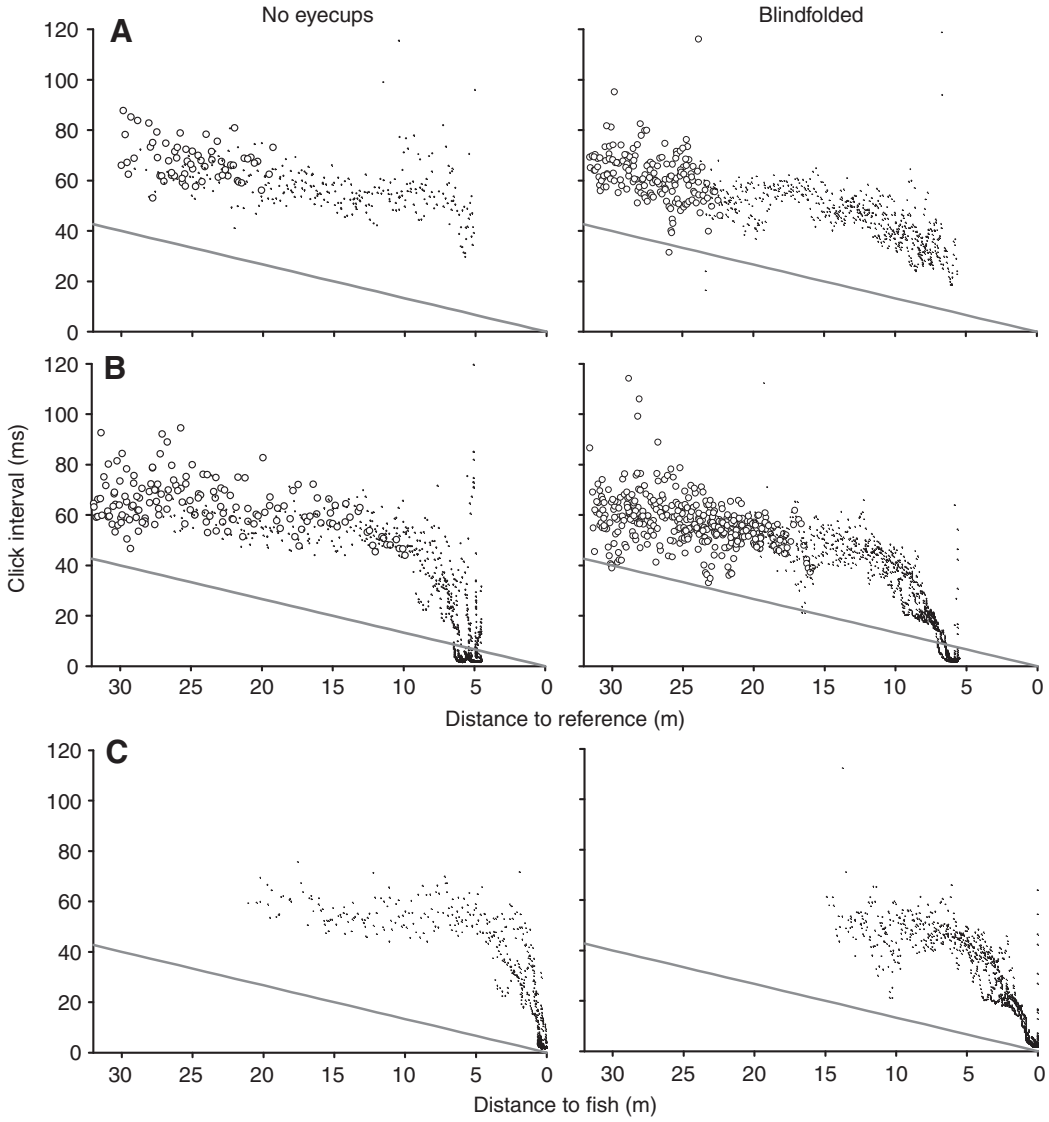

Fig. 5. Click interval plotted against distance to reference (D_R) for Freja with no eyecups and when blindfolded during no fish trials (A) and fish trials (B). White circles indicate click intervals before and black dots click intervals after the splash. The grey line marks the two-way transit time to the reference point (A,B) or to the fish (C). Data after the splash in B are displayed in C against distance to fish (D_F). Number of trials for Freja/Freja bf are: no fish=5/4 and fish=5/5.

conditions if background targets are within the perceptual range. This is the case in the present study where the click pattern of the search phase is determined by range locking onto a landmark. This is indicated by a reduction of click interval according to a decrease of the two-way transit time between the landmark and the animal. The data from no fish trials show that Eigil and Freja use a landmark close to the reference point at the capture end of the pool (Fig. 4; Fig. 5A; Fig. 6A; Table 1) as in the orientation tasks described previously (Verfuß et al., 2005).

Our studies of the acoustic behaviour of captive harbour porpoises during orientation and prey capture might help explain recordings from free-ranging porpoises equipped with acoustic tags. One such study was described by Akamatsu et al. (Akamatsu et al., 2005) for a finless porpoise (*Neophocoena phocaenoides*). This animal showed clear range-locking behaviour while swimming in an isolated waterway (Fig. 7B, Search), which started at about 40 m from a presumed prey capture (Fig. 7B, Terminal). The authors interpreted this behaviour as range locking on a potential prey target after detection at the instant where the click intervals begin to decrease. A similar behaviour was also described for a harbour porpoise in Danish waters (Akamatsu et al., 2007). We interpret these recordings differently. We assume that during the reduction of click intervals the animals are still in search phase and are range locked to landmarks in the background. We think that the finless porpoise switches from one landmark to another at the beginning of the echolocation sequence shown in Fig. 7B marked S, as indicated by the sudden rise in click interval as seen in the no fish trials of Freja when blindfolded (Fig. 4B; Fig. 5A; Fig. 6A). Furthermore we feel that prey detection is indicated by the switch to variable click intervals around a mean (Fig. 7B, marked D), as we will discuss later.

There are hardly any prominent landmarks within the perceptual range of the odontocetes inhabiting open waters. We hypothesize that odontocetes in open space situations will adjust their click interval in the search phase to a specific search range, which may be the maximum perceptual range. This would result in click intervals around a constant mean. Madsen et al. (Madsen et al., 2005) recorded the echolocation behaviour of deep-diving beaked whales (*Mesoplodon densirostris*) while foraging in open water with an acoustic data logger attached to the animals. They report a stable click interval with values of 300–400 ms for the search phase. The authors calculated that these values indicate a maximum search range of 275 m assuming a lag time of 20 ms (Madsen et al., 2005).

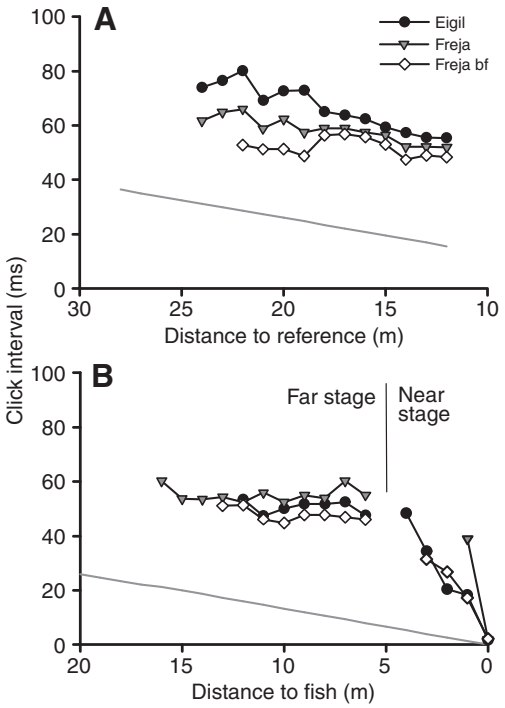

Fig. 6. Mean click interval after the splash for Eigil (black circles), Freja (grey triangles) and Freja blindfolded (Freja bf; white diamonds). The grey line indicates the two-way transit time to the reference point (A) or to the fish (B). A shows mean click interval with no fish present. B gives mean click interval of far stage and near stage over the distance to the fish. Note that the click intervals are rather constant around about 50 ms in the far stage for fish trials. See text for further explanations. Number of trials for Eigil/Freja/Freja bf are: no fish=5/5/4 and fish=5/5/5.

Approach phase

The approach phase starts after the detection of echoes from suitable prey. These echoes contain information about the location and the nature of the prey. According to the click pattern, the approach phase can be separated into two parts. In the initial part the click intervals are distinctly longer than in the terminal part. The rather fast transition from long intervals to shorter intervals in the terminal part occurs at quite short distances to the prey (on average between 1.9 and 4.4 m in the present study). The change in click interval also causes a distinct shortening in lag time (click interval minus two-way transit time between predator and prey), which may indicate that the returning echoes are processed differently during the two parts of the approach phase.

Initial part of the approach phase

In the present experiments, the porpoises were conditioned to perceive the splash as a cue for fish. The splash occurred at distances of about 15–20 m between porpoise and fish. After detection they started to emit clicks at intervals around a mean of between 47 and 55 ms in what we describe as the initial part of the approach phase. In some sequences this switch from decreasing intervals (typical for the search phase) to constant click interval is clearly visible (Figs 1 and 4) thus indicating detection shortly after the splash. We therefore conclude that in most trials the porpoises detected the fish shortly after the fish was thrown into the pool.

In the echolocation sequence of a foraging finless porpoise presented in Fig. 7B (Akamatsu et al., 2005) we can also identify a section with click interval oscillating around a constant mean that we interpret as the initial part of the approach phase.

Morozov and colleagues (Morozov et al., 1972) describe the echolocation behaviour of free ranging bottlenose dolphins while approaching and capturing a dead mackerel at distances as far as 40 m. They measured the mean click interval and saw range-locked behaviour during the approach up to target distances of about 4 m, with a 20 ms mean lag time. However, the distribution of click intervals is right skewed, thus the median is shorter than the examined mean. The calculation of the median also indicates that the reduction of click intervals from 16 to 4 m is distinctly less steep as predicted from the curve of the two-way transit time. Therefore we believe that at distances from 16 to 4 m the dolphin is in the initial part of an approach phase with approximately constant click intervals. We also believe that at distances greater than 16 m the dolphins are range locked to the end of the pool and not to the fish (see also Verfuß et al., 2005), again similar to the behaviour of our harbour porpoises in the search phase.

In fish catch trials similar to the ones presented here, the same porpoises as used in our study showed a change of emission level of the outgoing signal with distance (Beedholm and Miller, 2007). The porpoises decreased the source level with decreasing distance (R) to their prey by a value close to 20 log$R$ meaning that the signal level at the fish would be fairly constant. Possible consequences of this for the echolocator, the harbour porpoise, are discussed by Beedholm and Miller (Beedholm and Miller, 2007). The nearly constant incident sound levels and click intervals during the approach to the prey could be advantageous. By keeping both click interval and sound pressure at the prey nearly constant the predator could conceal its approach while closing in on the prey. This only makes sense if the prey is able to hear and to react to the echolocation signals of the predator. Mann and colleagues (Mann et al., 1998) showed that the American shad, *Alosa sapidissima*, responded to echolocation-like clicks over long distances. They speculated that ultrasonic hearing in some fish prey could have evolved in response to selection pressure by echolocating predators like dolphins and porpoises. However, interactions between fish and echolocating odontocete predators remain to be discovered.

The echolocation behaviour of foraging beaked whales that feed mainly on squid (Santos et al., 2007) has been described by Madsen and colleagues (Madsen et al., 2005). We have already mentioned that these toothed whales – living in open waters – are not range locked during the search phase. Their data show that these odontocetes use about the same constant click intervals in the search phase and the initial part of the approach (Fig. 7Ca). They could not find a distance-dependent reduction in emission level in this initial part of the approach phase. This does not contradict our assumptions, as it has been shown that squid do not react to sound sequences similar to those emitted by beaked whales even if exposed to high amplitude clicks with short interval (Wilson et al., 2007). We therefore assume that the prey of beaked whales will not notice the approaching danger so that there is no selective advantage in adjusting the emission level. By using a similar source level and click interval in the initial part of the approach phase as in the search phase the animals have the advantage of a large perceptual range that allows them to search for their next prey item while approaching the current one. However, beaked whales adapt their click interval during the initial part of the approach if the echo scenery is complex (Johnson et al., 2008). The shortening of click intervals may indicate clutter echoes within the perceptual range, e.g. like those caused by schooling prey. This would eliminate the need to search for other prey at longer distances (Fig. 7Cb).

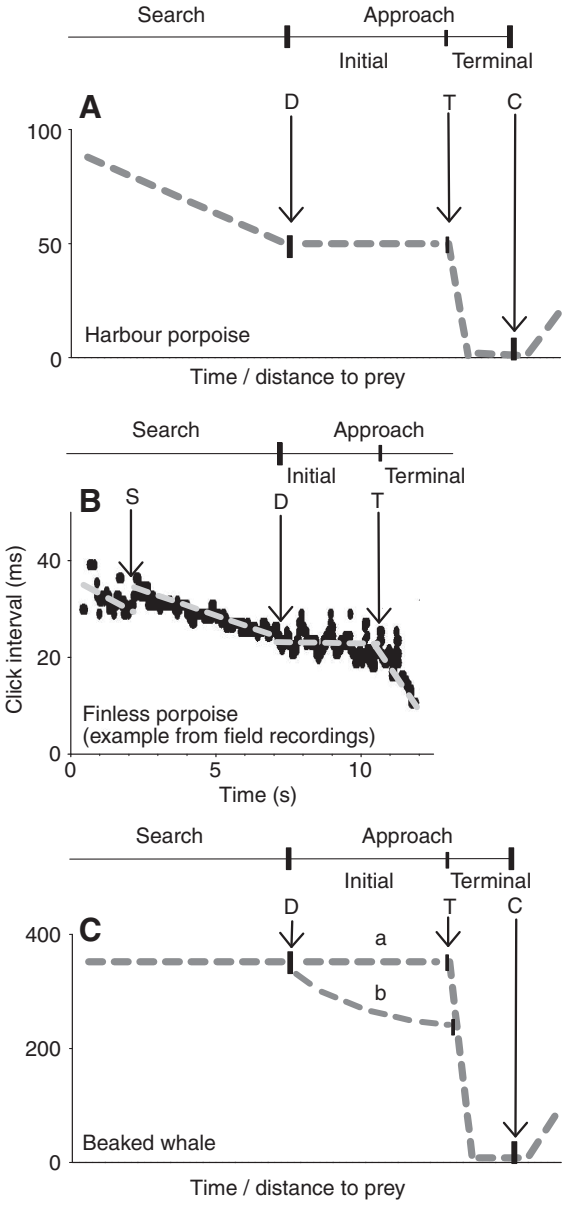

Fig. 7. The phases of the echolocation behaviour of odontocetes during foraging according to the change of click interval over time or distance to prey. When harbour porpoises search for prey in a confined space or at shallow depths (A), the click interval may indicate range locking to obstacles. This is also seen in the echolocation sequence of a finless porpoise [adapted with permission from Akamatsu et al. (Akamatsu et al., 2005); B] where a sudden rise in click interval suggests a switch, S, from one landmark to another positioned further away. (Black dots show the click intervals, the grey dashed lines indicate the estimated regression line of the click interval within different parts of the echolocation sequence.) Beaked whales in a pelagic open environment (C) may use click intervals adapted to maximum perceptual ranges. After detecting a prey, D, the approach phase begins and the whale closes in on the prey. In the initial part of the approach phase, different signal patterns have been observed. In porpoises the mean click interval remains rather constant, maybe as an adaptation to prey with ultrasound hearing (A,B). Beaked whales either continue to emit clicks with long intervals when they have detected a single prey item, presumably for keeping a large perceptual range (Ca), or shorten the click interval perhaps for adapting their perceptual range to schooling prey patches (Cb). At a certain distance to the prey the click interval progressively decreases indicating a transition, T, to the terminal part of the approach phase with rapidly decreasing click intervals. At close distances to the prey the terminal part ends with the buzz that is characterized by constant and very short click intervals (absent in B). The buzz ends with the capture of the prey, C, which is followed by an increase in click interval. For further explanation see text. Please note the difference of ordinate scale in A to C.

Terminal part of the approach phase

The terminal part of the approach phase starts with the sudden and rapid shortening of click intervals (Fig. 1; Fig. 4; Fig. 5B,C; Fig. 6B). In analogy to echolocating bats the terminal part may also be called the 'buzz' (Kalko and Schnitzler, 1998). In the present study, the buzz consists of two sections that differ in click pattern. In the first section the click interval is reduced from about 50 ms, sometimes in an oscillating manner, to intervals below 10 ms (Fig. 4). In the second section the click interval is short and kept quite constant at values between 1.4 and 1.6 ms. The transition from the initial part to the terminal part occurs at a mean distance between 1.9 and 4.4 m. At the beginning of the second section of the terminal part the animals are close to the prey, below about 1 m. Although click interval shortens rapidly in the terminal part of the approach phase, it is at no time shorter than the two-way transit time to the fish. The terminal part ends shortly after the catch with a rapid increase of the click interval (Fig. 4B). Naturally the animal can continue to produce clicks after the catch as sound is generated in the nasal air passages and emitted through the melon (Cranford et al., 1996; Cranford and Amundin, 2004; Goodson et al., 2004).

Buzzes have been recorded in the field from several odontocetes species (e.g. Akamatsu et al., 2005; Goodson et al., 1994; Herzing, 2004; Madsen et al., 2005; Miller et al., 1995). The authors assumed that buzzes were associated with prey capture or attempted prey capture. Our experiments, and other studies, demonstrate that the buzz is connected with the final approach to a target (Busnel and Dziedzic, 1967; Evans and Powell, 1967; Johnson, 1967; Madsen et al., 2005; Morozov et al., 1972). Goodson and colleagues (Goodson et al., 1994) investigated the echolocation behaviour of a solitary bottlenose dolphin during foraging. They recorded a rapid increase in repetition rate (the inverse of the click interval) preceding the final and nearly constant high repetition rate of the buzz and interpreted this as range-locking behaviour on the prey during the approach. According to this assumption one can calculate a swim speed of 12.6 m s^{-1} or 45 km h^{-1} from the change in click interval. This speed is unlikely during prey capture. Therefore we assume that the shortening of the click interval corresponds to the beginning of the terminal part of the approach phase and does not indicate range locking on the prey.

Two possible processing modes in the approach phase

The lag time, corresponding to the available time to process a click-echo pair before emitting the next click, is calculated as the difference between click interval and the two-way transit time. The distinct shortening of the lag time at the transition from the initial part to the terminal part of the approach phase may indicate a change in information processing mechanisms for the estimation of range. In the initial part of the approach phase where the porpoise is in the far stage (see Fig. 5C; Fig 6B) the lag time is sufficiently long for the porpoise to process the range information in each click–echo pair. With each new click the porpoise gets new distance information. This type of information processing is termed the pulse-mode by Au and Nachtigall (Au and Nachtigall, 1997).

The constant mean click interval during the initial part of the approach (Fig. 6B; Fig. 7A) inevitably results in an increase of lag time. In our experiments the lag time doubles on average from about 24 to 48 ms if we assume an initial part to begin at 20 m and end at 1 m. This increase in lag time provides more time for information processing of click–echo pairs.

The terminal part of the approach begins with an abrupt and continued shortening of the click interval. The fast reduction of click interval during the final approach to the prey causes a continuous decrease of the lag time down to values below 1.5 ms at click intervals of 1.5 ms when the prey is reached. This strong reduction probably does not leave enough time for pulse-mode echo processing. Therefore we assume that odontocetes use another processing mode at these short lag times. Nordmark (Nordmark, 1960) suggested that bats perceive pulse–echo trains with a changing time delay as a kind of tone changing in pitch corresponding to the inverse of the delay between pulse and echo. Thus this pitch would encode the two-way transit time. For our porpoises the terminal phase began at distances to the fish of between 4.4 and 1.9 m. This would give average two-way transit times of 5.9–2.5 ms, which would correspond to a pitch frequency of 170–395 Hz. Close to the prey at a distance of 37.5 cm and a two-way transit time of 0.5 ms the corresponding pitch would be at 2000 Hz. We assume that dolphins can estimate range by evaluating this increase in pitch with decreasing distance to the target. We call this possible processing mode at short lag times the pitch-mode. In this mode the sound pressure level of the clicks in the buzz is low, therefore only a close object will return echoes strong enough for processing. Whether porpoises perceive echo information during the terminal phase as a two-way transit time pitch is not known and future investigations are necessary to test this hypothesis.

Swim speed

Our data also reveal that the swim speed is task dependent. The porpoises swam much faster when looking for fish. During no fish trials ($6\,m\,s^{-1}$) the speed was double that during navigational tasks ($3\,m\,s^{-1}$). A high swim speed was also used during fish trials. Eigil clearly raised his swim speed after the splash in trials with and without fish (Fig. 3B), which suggests that Eigil connects the splash with a fish thrown into the water. Another indication that the porpoises anticipate a fish in connection with the splash is the clear scanning movements of Freja when blindfolded that start near the release area, presumably a sign of searching for the fish. Eigil increased his swim speed in fish trials later than in no fish trials perhaps due to the delayed production of the splashes in fish trials compared with no fish trials. This would explain the significantly lower mean speed ($5.4\,m\,s^{-1}$) of Eigil in fish trials (Fig. 3A; Table 1). A swim speed of $6.2\,m\,s^{-1}$ was recorded from a wild harbour porpoise that was presumed to be foraging (Lucke et al., 2000).

The influence of blindfolding

Freja uses the same echolocation pattern during foraging when blindfolded with eyecups. She keeps similar click intervals and lag times during the search and the initial and the final part of the approach compared with trials with no eyecups (Fig. 4; Fig. 5; Fig. 6B; Table 1). However, she swims about half as fast with eyecups on than she does without (Fig. 3A), which results in a longer foraging sequence. Thus the click density doubles, increasing the information gained per metre covered (Table 1). These results suggest that Freja uses multi-modal sensory information, vision and echolocation, when possible during searching and the initial part of the approach. In trials with Freja being blindfolded, we saw a rapid increase in click interval near the middle of the pool (Fig. 4B; Fig. 5A; Fig. 6A) and significantly shorter lag times (calculated in relation to the reference point) during no fish trials compared with no fish trials where she was not wearing eyecups (Table 1). This suggests that when blindfolded Freja is using landmarks that are closer to her for orientation than the arbitrary reference point during search. She also seems to use more landmarks when blindfolded. Perhaps she 'feels her way' acoustically through the pool when vision is lacking. Then again the eyecups might just make Freja feel more insecure, resulting in a slower swim speed. We have not done prey capture experiments in total darkness to test this.

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