Spatial orientation in echolocating harbour porpoises (*Phocoena phocoena*)

Ursula K. Verfuß[1,2,*], Lee A. Miller[3] and Hans-Ulrich Schnitzler[2]

[1]*Fjord & Bælt, Margretes Plads 1, DK-5300 Kerteminde, Denmark,* [2]*Tierphysiologie, Zoologisches Institut, Universität Tübingen, Auf der Morgenstelle 28, D-72076 Tübingen, Germany* and [3]*Institute of Biology, University of Southern Denmark, DK-5230 Odense M, Denmark*

*Author for correspondence at present address: German Oceanographic Museum, Katharinenberg 14/20, 18439 Stralsund, Germany
(e-mail: ursula.verfuss@meeresmuseum.de)

Summary

Studies concerning the echolocation behaviour of odontocetes focus mainly on target detection and discrimination, either in stationary animals or in animals approaching a specific target. We present the first data on the use of echolocation for spatial orientation or navigation. Synchronised video and high-frequency recordings were made of two harbour porpoises trained to swim from one position to another across an outdoor pool in order to correlate swimming and echolocation behaviour. Both porpoises showed a clear range-locking behaviour on specific positions near the end of the pool, as indicated by a decrease in click interval with decreasing distance. The decrease in click interval followed the two-way-transit time, which is the time interval between the outgoing click and the received echo from the focal object.

This suggests that the porpoises used focal objects as landmarks. The lag time, defined as the time between the arrival of an echo from a landmark and the emission of the next click, was task specific. The lag time was longer for difficult tasks (26–36 ms) and shorter for simpler tasks (14–19 ms), with some individual differences between the two animals. Our results suggest that echolocation by odontocetes is used not only for target detection, localisation and classification but also for spatial orientation.

Key words: harbour porpoise, *Phocoena phocoena*, biosonar, echolocation, echolocation behaviour, signal pattern, spatial orientation, landmark.

Introduction

Not long after the discovery of biosonar in the bottlenose dolphin (*Tursiops truncatus*) in the early 1950s (see Au, 1993), the harbour porpoise (*Phocoena phocoena*) was also shown to echolocate (Busnel and Dziedzic, 1967). Since then, the high-frequency click sounds used by harbour porpoises for echolocation were described (Møhl and Andersen, 1973; Amundin, 1991; Verboom and Kastelein, 1995; Goodson and Sturtivant, 1996; Kamminga et al., 1996), their hearing abilities investigated (Andersen, 1970; Popov et al., 1986; Bibikov, 1992; Kastelein et al., 2002), their sound production studied (Amundin and Andersen, 1983; Amundin et al., 1988; Cranford et al., 1996) and the transmission beam pattern mapped (Au et al., 1999). In addition, Kastelein et al. (1997, 1999) studied their abilities to detect and discriminate targets hanging freely in the water column or buried in sand.

Teilmann et al. (2002) and Verfuß and Schnitzler (http://www.uni-tuebingen.de/tierphys/Fledermaeuse/Delfine.htm or http://www.uni-tuebingen.de/tierphys/Fledermaeuse/final_report.pdf) showed that harbour porpoises wait for the echo of an outgoing signal before sending out the next signal. This echolocation behaviour is also used by bottlenose dolphins (e.g. Morozov et al., 1972) and false killer whales (*Pseudorca crassidens*; Thomas and Turl, 1990). The time between receiving an echo and emitting the next click is called the lag time (Au, 1993) and is considered to be relatively constant during specific echolocation tasks, as shown for bottlenose dolphins (e.g. Au et al., 1981; Morozov et al., 1972) and the false killer whale (Thomas and Turl, 1990). A beluga whale (*Delphinapterus leucas*), however, used three different click patterns. In one of these, the beluga produced clicks before receiving echoes from preceding emissions, making the intervals between clicks shorter than the two-way-transit time, the time interval between the emission of a click and the reception of an echo from the target (Au et at., 1987; Turl and Penner, 1989).

In bats, echolocation is used for spatial orientation and prey capture (Schnitzler et al., 2003). We assume that odontocetes use echolocation in a similar way. However, the biosonar of odontocetes has mainly been investigated in the context of target detection (reviewed in Au, 1993; Kastelein et al., 1999) and discrimination (reviewed in Au, 1993; Kastelein et al., 1997) and not in the context of spatial orientation. Schnitzler et al. (2003) postulate that echolocation in bats evolved primarily for orientation in space or navigation and that the

transition to prey acquisition followed later. The term navigation is used according to Trullier et al. (1997), who defined navigation as the ability of animals to find, learn and return to specific places. Schnitzler et al. (2003) define three categories of navigation: small-, middle- and large-scale navigation. Small-scale navigation is the process of moving around in the immediate environment, with the animal's goals being within its range of perception. Middle-scale navigation comprises the ability to follow routes to goals beyond the perceptual range but within the home range of an animal. Routes are characterized by sequences of places to which animals react with recognition-triggered responses (Trullier et al., 1997). Each place is defined by a certain landmark or constellation of landmarks, prominent or conspicuous objects that serve as guides. Large-scale navigation encompasses movements in unfamiliar areas, for example during migration or homing, which is defined as guided or directed movements homeward or to a destination.

Nothing is known about how harbour porpoises use their echolocation abilities for spatial orientation. The present paper investigates and compares the echolocation behaviour of two harbour porpoises during orientation tasks in a semi-natural outdoor pool by using the concept of small- and middle-scale navigation. We show that echolocation plays an important role for spatial orientation and that it is used for navigation.

Materials and methods

Study site

The experiments were conducted from 1998 to 2000 in a 36 m×15 m semi-natural outdoor enclosure of the Fjord & Bælt in Kerteminde, Denmark (Fig. 1). 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
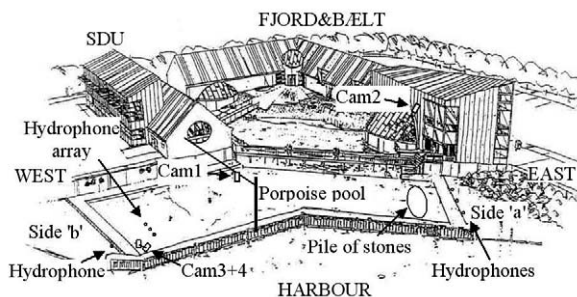

Fig. 1. Experimental set-up in the Fjord & Bælt porpoise pool. Shown are the positions of the two in-air cameras (cam1 and cam2), the two underwater cameras (cam3+4), the hydrophones and the hydrophone array, as well as the position of a pile of stones. Three hydrophones at the east end and one hydrophone at the west end of the enclosure were used to record echolocation clicks from the porpoises during navigational trials atb and bta. Cam3+4 and the hydrophone array were set up for the navigational task atb+. For descriptions of the navigational tasks, see the text. The holding pool is not shown. Equipment and positions are not drawn to scale. SDU, University of Southern Denmark, Marine Biological Research Center.

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 varies between 3 m 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 within the enclosure served for separating the animals or holding them for medical treatment.

Animals

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

Experimental procedure

The animals performed three tasks: (1) they were sent from side 'a' to side 'b' ('atb'), (2) they were sent from side b to side a ('bta'), and (3) they were sent from side a to side b, with equipment – two underwater cameras (cam3+4) and a hydrophone array – placed in the water near side b (atb + equipment = 'atb+') (Fig. 1).

For these tasks, both animals were trained to station at one end of the pool (Fig. 1, side a or side b). During trials, one animal stayed with a trainer while the other animal was sent to the opposite side of the pool (side b or side a, respectively), where a second trainer splashed at the water surface to attract the animal's attention. When the porpoise headed towards the 'destination point', which is approximately 0.5 m in front of the second trainer, the trainer lifted her hand ~30 cm above the water surface. The porpoise had to touch the trainer's hand to end the behavioural trial. No target was submerged into the water during a trial. The holding pool was positioned in a corner of the enclosure at the starting end to minimize disturbing the experimental procedure.

Experimental set-up and trials

Synchronised video and high-frequency sound recordings were made from the porpoises during all orientation tasks. Experimental sessions were done on days with good water clarity and calm weather with no or little rainfall to assure good visibility and recording conditions. Two surveillance cameras were used for the video recordings. One camera (Fig. 1, cam1) was fixed on wires approximately 5.3 m above the water surface, giving a top view of part of the west end of the pool. The second camera (Fig. 1, cam2) was fixed ~9.4 m above the water surface on the Fjord & Bælt exhibition centre wall and was used to analyse the porpoises' behaviour at the east end of the pool. No recordings were made for the atb+ trials with cam2. On days with atb+ trials, two video cameras in underwater housings (Evamarine, Geretsried, Germany) were mounted 2 m apart on a horizontal steel rod and fixed to a vertical steel pole in the harbour-side corner of side b (Fig. 1).
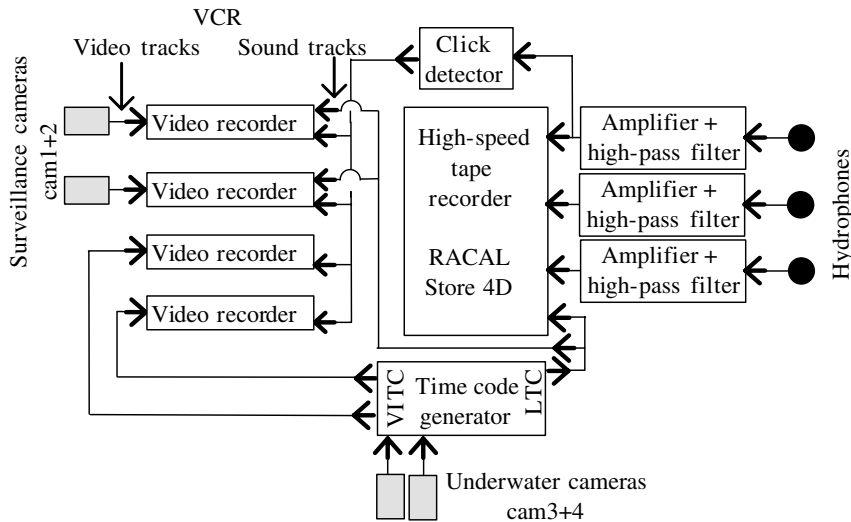
Fig. 2. Schematic drawing of the recording set-up. Depending on the navigational task, up to three hydrophones were used, connected to three amplifiers and high-pass filter units. The sound was recorded on a broad band (300 kHz) tape recorder. The sound of one hydrophone was connected to a click detector, the output of which was recorded on one sound channel of each of the four video recorders. The VCRs recorded images from the two in-air cameras (cam1+2) and the two underwater cameras (cam3+4 – not operating in this study). The video and audio recordings were synchronized using a custom-built time code generator (LTC, longitudinal time code; VITC, video time code).

Both cameras were placed 0.25 m under the water surface. This equipment was not operational in these studies and served as temporarily introduced objects during atb+ trials.

Up to three HS150 hydrophones (Sonar Research & Development Ltd, Beverley, UK), with a frequency response up to 180 kHz (±6 dB), were used for all tasks. For atb trials, one hydrophone was attached to a plastic rod and submerged 1 m below the surface at the back edge of the pontoon at side b. In bta trials, three hydrophones were attached to the back side of the pontoon on side a, approximately 2.5 m apart and 0.5 m deep, to increase the chances of recording clicks that could be blocked by a pile of large stones on the bottom of the enclosure (Fig. 1). For the atb+ trials, an array consisting of three hydrophones with 1 m spacing was submerged to a depth of 1 m approximately 2 m in front of the pontoon at side b (Fig. 1). The array holding the hydrophones was built out of plastic rods to avoid strong echoes.

Signals from the hydrophones were amplified by 52 dB and high-pass filtered at 100 Hz using Etec amplifiers (Etec, Copenhagen, Denmark; Fig. 2). 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 inches s^{-1}, giving a bandwidth of ~300 kHz.

The synchronization of all video and sound recordings was done with a custom-built VITC/LTC time code generator (Universität Tübingen, Tierphysiologie, Tübingen, Germany; Fig. 2).

The atb+ trials were recorded on seven days in October and November 1998 with 25 experimental sessions, totalling 117 trials (56 trials with Freja and 61 trials with Eigil). The atb and bta trials were recorded on six days in May and June 2000 with 12 experimental sessions, totalling 65 trials (16 atb and 15 bta trials with Freja, and 18 atb and 16 bta trials with Eigil).

All video and sound recordings were visually scanned for quality, defined as reasonably good sighting of the involved porpoise on the recordings of both video cameras (cam1 and cam2) and a reasonable signal-to-noise ratio for the emitted echolocation click series on the sound recordings. A total of 43 out of 182 trials were chosen for detailed analysis of the echolocation behaviour, including 16 trials for atb (eight for Freja, eight for Eigil), 17 trials for bta (nine for Freja, eight for Eigil) and 10 trials for atb+ (five for Freja, five for Eigil).

Video analysis

Selected video 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. The relative position of the tip of the animal'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.

For analysing the distance from the porpoise to its destination, we defined an arbitrary 'reference point'. We did this by examining the porpoises' echolocation behaviour, which showed a clear decrease in click interval during the approach (see the Results). The decreasing click interval indicated that the animal had locked its sonar on to a landmark somewhere near the end of the pool. This landmark might have been the front edge of the pontoon where the trainer sat (~0.5 m behind the destination point) or the net at the end of the pool (~3.5 m behind the destination point). We therefore chose the 'reference point' to be midway between the front edge of the pontoon and the net, a point 1.5 m between these (Fig. 3). The distance between the calculated position of the porpoise and the reference point was defined as 'distance to reference'.

Absolute metric values 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 3-D environment. For the surveillance cameras (cam1 and cam2),

the 2-D-horizontal movement of the porpoise 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. Marked positions on the pontoons enabled the software to calculate relative positions and distances in the video images into absolute positions.

Reconstruction of the swimming path was considered successful when the track from each camera overlapped at the middle of the pool, which was common to both camera views. Tidal differences that changed the distance between cameras and water surface were taken into account for each session. With this method, distances could be calculated with a maximum error of 5%.

In atb+ tasks, only one surveillance camera (cam1) was used (Fig. 1). Distances to reference beyond the view of cam1 were interpolated by using a polynomial fitting formula of the swim speed obtained for each porpoise in atb trials. With the assumption of a similar swim speed in atb trials and atb+ trials, the missing distances in atb+ trials could be calculated.

Sound analysis and correlation with video recordings

The sound sequences of the chosen trials were played back at 16-fold reduced speed and digitised 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, was analysed by saving the onset time of each click into a text file. This was done with custom-made software (Sona-PC; B. Waldmann$^©$, Tübingen, Germany) with 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 of the porpoise to our arbitrary reference point. Analysis began from the first click recorded in a trial and stopped with the clicks emitted when reaching the destination point, which was ~0.5 m in front of the pontoon. This is called a 'navigational trial' for atb and bta. For atb+, the navigational trial ended when the porpoise reached the hydrophone array, ~2 m in front of the pontoon. The first click and last click of a navigational trial were used to determine the time and distance navigated. Also, the total number of clicks recorded during the navigational trial was determined (see Table 1).

Click exclusion criteria

Not all clicks of a click train were captured by the hydrophones. Harbour porpoises possess a very directional transmission beam pattern (Au et al., 1999), and pauses occur in the echolocation train as the animals move the beam away from the recording hydrophone. Recordings from the three hydrophones used in the bta trials 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.

During the experimental trials, the porpoises locked their sonar onto spots near the end of the pool, indicated by a decrease in the click interval during the traverses. In the beginning and near the end of each trial, the porpoises did not swim straight towards the destination point (see Results, Swimming behaviour). To assure inclusion of those parts of the traverses during which the porpoises swam directly towards the end of the pool, and therefore most likely focus on the same spot, only a middle range from 26 m to 12 m was chosen for analysing click intervals and lag times for all tasks (see Fig. 3).

Relationship between click interval and distance to reference

For assessing the relationship between click interval and the distance to the reference point, the click interval and corresponding distance data pairs of all analysed click trains (echolocation click sequences) were pooled separately by animal and task. The data pairs were then grouped into distance-to-reference classes using a bin of 1 m. Median click intervals and the 25% and 75% quartiles of each class were determined because the data were not normally distributed. The same procedure was done with the corresponding lag time and distance-to-reference data pairs. The 'lag time' is the time difference between the click interval and the corresponding two-way-transit time to the reference point. We calculated the two-way-transit time of the porpoises' click–echo pairs to the reference point assuming the speed of sound in water to be 1.5 m ms^{-1}, giving a slope of 1.3 ms m^{-1}.

A regression analysis was performed on the 1 m bin median click interval values from 26 m to 12 m (Fig. 4) for each porpoise and task. Median values comprised at least three click intervals in each bin and results from at least three trials. The slope of regression with 95% confidence interval was determined (Table 1; Fig. 5).

For each click train, the mean and standard error of the median lag times were determined for distances between 26 m and 12 m for each porpoise and task. These data were compared using a *t*-test for individual or task-specific differences in the lag time (Table 1; Fig. 6). Multiple testing of a single null hypothesis required an alpha-level adjustment. We did this by correcting *P*-values for the number of tests (three in comparison between the two animals and four in comparison between the three tasks). We calculated corrected *P*-values (P_{corr}) using the equation $P_{corr}=1-(1-P_{orig})^k$, which we derived through conversion of the Dunn–Šidák equation (Sokal and Rohlf, 1995), where P_{orig} is the originally derived *P*-value and k is the number of tests conducted.

Determination of swim speed

The swim speed was calculated during each trial of the atb and bta tasks in the following manner. The running mean of the porpoises' speed over 10 frames (0.4 s) was calculated frame by frame, resulting in smoothed speed data. The mean ± standard error of the mean swimming speed for each trial between distances from 26 m to 12 m were determined for each porpoise and each task. These data were compared with a *t*-test for testing individual or task-specific differences in swim speed (Table 1).
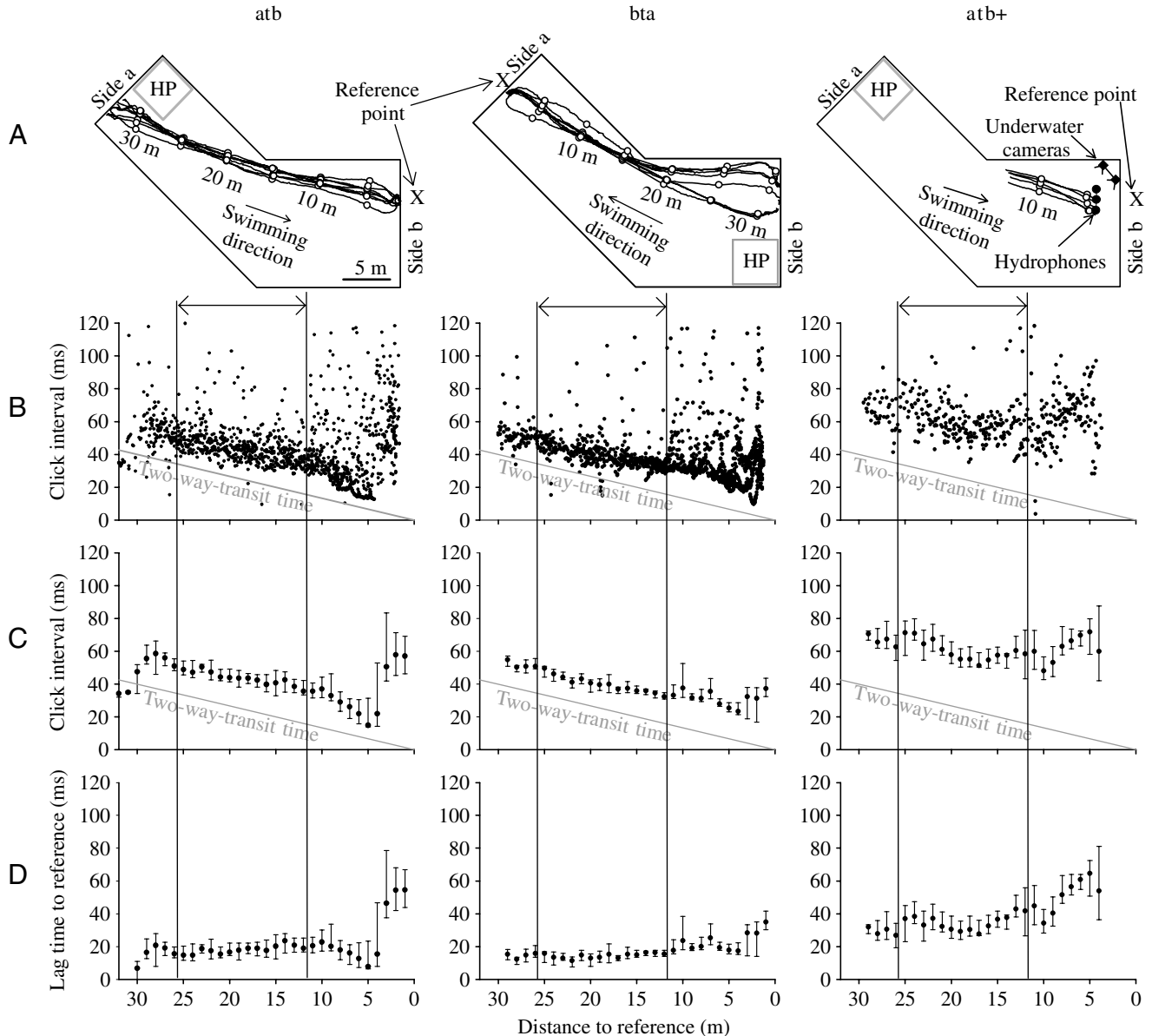
Fig. 3. Swimming paths, click intervals and lag time of the female porpoise, Freja, for all three tasks. (A) Swimming paths for each task: side a to side b (atb; *N*=9), side b to side a (bta; *N*=8) and side a to side b + additional equipment (atb+; filled circles show the hydrophone array, and the squares represent the two underwater video cameras). Only the last portion of the navigational path is shown in the atb+ trials (*N*=5), as no recordings were made with cam2. The arbitrary reference point (X) is 1.5 m behind the front edge of the pontoon at each end of the enclosure. Open circles on the swimming paths indicate 5 m intervals, and the 30 m, 20 m and 10 m points show distance to the reference. The grey boxes show the position of the holding pool (HP). (B) Click interval over distance to reference, plotted for the three tasks. The two-way-transit time line of the click–echo pair is indicated (grey line). (C) The median click interval (75% and 25% quartile) for each 1 m bin distance to reference for each task is shown. The two-way-transit time line of the click–echo pair is indicated. (D) The median lag time (75% and 25% quartile) relative to the reference point is shown for each task. The vertical lines and horizontal arrows in B–D indicate the 26 m to 12 m portion of the trial used for statistical calculations in the atb, bta and atb+ tasks. Note the large deviations in click interval near the beginning and end of atb trials.

Results

Swimming behaviour

After being sent by the trainer from the far end of the pool, the porpoise turned around and swam nearly directly to the destination point approximately 0.5 m in front of the pontoon (Fig. 3). Both porpoises increased their speed to a maximum near the middle of the pool, after which the swim speed declined while approaching the destination point. The animals swam in a slight curve a few metres before reaching the second trainer. The mean swim speeds during the 26 m to 12 m stretch for Freja and Eigil are shown in Table 1. Swim speed and distance travelled could not be calculated for atb+, as no video

Table 1. *Parameters analysed during navigational trials in three tasks for two harbour porpoises*

	Task/porpoise					
	atb		bta		atb+	
Parameter	Freja	Eigil	Freja	Eigil	Freja	Eigil
Mean navigational time per trial (s)	9.1±1.7	9.0±0.7	8.4±1.1	8.9±1.1	6.9±1.6	6.7±1.6
Mean navigational distance per trial (m)	27.1±3.1	26.4±1.5	25.1±3.4	27.1±1.7	–	–
Mean no. of clicks recorded per trial	163.8±76.4	191.0±47.2	185.3±50.0	208.5±17.4	95.8±19.2	88.0±18.9
Mean speed (m s^{-1})	4.0±0.1	3.8±0.1	4.0±0.1	3.8±0.2	–	–
Mean lag time (ms)	19.2±1.2	17.6±1.1	14.4±0.6	16.8±0.5	35.7±2.9	26.4±1.7
Slope (±95% confidence interval) (ms m^{-1})	0.91±0.23	1.32±0.29	1.12±0.18	1.21±0.13	1.03±0.66	1.86±0.36

A navigational trial is the distance travelled during the time frame where echolocation clicks could be analysed (see Materials and methods). The table gives mean time and mean distance values (± S.D.) of the duration of click trains and the number of recorded clicks, as well as mean speed, mean lag time (± standard error) and the slope of regression (±95% confidence interval) of the median click interval over distance to reference point.

Number of trials included for Freja/Eigil are: atb=9/8, bta=8/8 and atb+=5/5. In atb+, the navigational trials were shorter than in atb and bta (see Materials and methods). This causes a shorter navigational time as well as a lower number of recorded clicks for atb+ compared with the other tasks. For atb+, no navigational distance and no speed could be determined, as no recordings were taken with cam2 (see text).

recordings were obtained with cam2 for this task. There was no significant difference in swim speed between porpoises for the same task (for atb, P_{orig}=0.162, d.f.=15; for bta, P_{orig}=0.611, d.f.=14) or between tasks for the same porpoise (for Eigil, P_{orig}=0.611, d.f.=14; for Freja, P_{orig}=0.996, d.f.=15), therefore no alpha-level adjustment for multiple testing of a single null hypothesis was required.

Echolocation behaviour

The porpoises continuously emitted echolocation signals in all trials. The mean number of clicks recorded during

navigational trials and the corresponding mean time and distance covered are given in Table 1. The click interval decreased with decreasing distance [26 m to 12 m of the total distance navigated (32 m)] to our arbitrary reference point approximately 1.5 m behind the front edge of the pontoon (Fig. 3). The decrease in median click interval (Fig. 4) is significant for both porpoises and for all tasks (Freja atb, r^2=0.863; Eigil atb, r^2=0.893; Freja bta, r^2=0.938; Eigil bta, r^2=0.973; Freja atb+, r^2=0.486; Eigil atb+, r^2=0.913; $P \leqslant 0.006$). However, the slopes of the regressions for click intervals are not significantly different from that of the two-way-transit time (1.3 ms m^{-1}), except for Freja during atb (slope 0.908±0.228, 95% confidence interval) and for Eigil during atb+ (slope 1.861±0.361, 95% confidence interval) (Fig. 5).

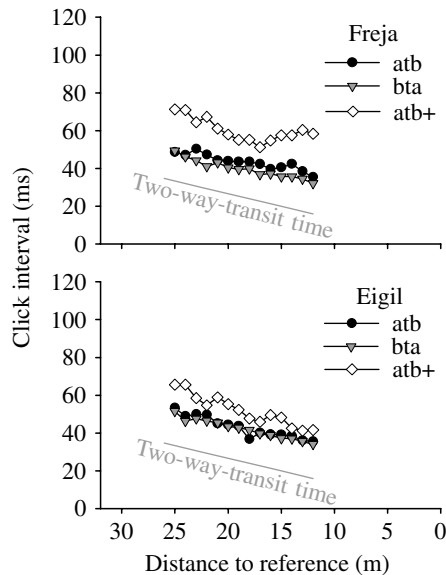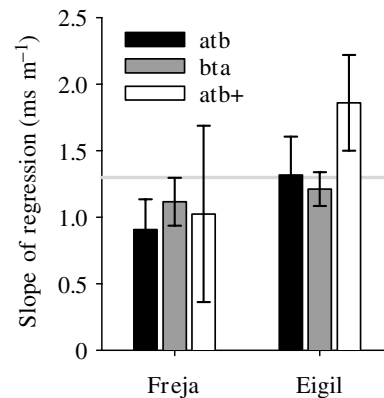The mean lag time, as indicated by the difference between

Fig. 4. Median click interval over the 26 m to 12 m portion of all trials for the two porpoises and the three tasks: atb trials (black circles), bta trials (grey triangles) and atb+ trials (open diamonds). The two-way-transit time line of the click–echo pair is indicated. 1 bin=1 m. Note the longer click intervals for the atb+ trials.

Fig. 5. Slope of regression (±95% confidence interval) of the median click intervals shown in Fig. 4 for the two porpoises and the three tasks: atb trials (black bars), bta trials (grey bars) and atb+ trials (open bars). The grey horizontal line indicates the 1.3 ms m^{-1} slope of the two-way-transit time line of the click–echo pair over distance to reference point. Confidence intervals that do not touch or cross the 1.3 ms m^{-1} line are significantly different from it.
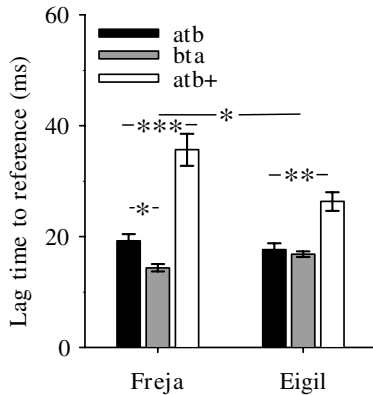
Fig. 6. Mean lag time of the medians (± standard error) to the reference point for the two porpoises and the three tasks: atb trials (black bars), bta trials (grey bars) and atb+ trials (open bars). The horizontal lines indicate significant differences in lag times: $*P_{corr}<0.05$, $**P_{corr}<0.01$, $***P_{corr}<0.001$, where P_{corr} is the corrected P-value (Sokal and Rohlf, 1995). The upper horizontal line indicates a significant difference between Eigil and Freja for task bta. Number of trials for Freja/Eigil are: atb=9/8, bta=8/8 and atb+=5/5.

the two-way-transit time to the assumed reference point and the corresponding click intervals (Fig. 4), is depicted in Fig. 6 and the values are given in Table 1. There are no significant differences between the lag time calculated for Eigil in atb and bta trials ($P_{corr}=0.952$, d.f.=14) and between Eigil and Freja in atb trials ($P_{corr}=0.738$, d.f.=15) and in atb+ trials ($P_{corr}=0.070$, d.f.=8). There are significant differences for the other combinations shown in Fig. 6, ranging from $P_{corr}=0.024$, d.f.=14 (Eigil and Freja, bta) to $P_{corr}=0.000197$, d.f.=12 (Freja atb+ and atb). Both animals show significantly longer lag times for atb+ trials compared with atb trials.

There are two reasons for the lower mean number of clicks recorded from the animals in atb+ trials. First, the lag times are longer in atb+ trials. Second, the atb+ navigational trials are shorter, since these ended when the porpoises reached the hydrophone array approximately 2 m in front of the destination (the pontoon) where the navigational trials for atb ended.

Discussion

The importance of echolocation

Our major finding is that the harbour porpoises used their echolocation abilities to lock on to local places or landmarks while navigating from one point to another in this enclosure. The porpoises had been in the enclosure from one to three years prior to our experiments and one can assume that they were familiar with the surroundings. Despite this, they always produced echolocation signals during the sessions, as well as between sessions, when monitoring with a click detector. To obtain useful video recordings of the porpoises' behaviour, we only performed experiments when the water was fairly clear. Harbour porpoises have good vision (Kastelein et al., 1990), and therefore we assume that the porpoises could use their vision for spatial orientation. Nevertheless, both animals used

active echolocation to conduct the tasks given to them. Consequently, we conclude that echolocation plays a major role for the porpoises while orientating and navigating in the pool.

Our conclusion supports the findings of Kastelein et al. (1995) that harbour porpoises in a pool used the same amount of echolocation in light as well as darkness. Nevertheless, echolocation is complemented by visual information. The female porpoise, Freja, was trained to catch live fish with and without opaque eyecups (U. K. Verfuß, L. A. Miller, P. Pilz and H.-U. Schnitzler, unpublished). Click intervals were hardly affected, but a significantly slower swim speed when wearing eyecups gave an increased number of click–echo pairs per metre travelled. This behaviour increased the received information flow per distance travelled, which was assumed to compensate for the lack of vision. Also 'resident' killer whales (*Orcinus orca*) in Canadian waters showed no change in echolocation activity with water clarity (Barrett-Lennard et al., 1996).

Range-locking behaviour and lag time

Thus far, range-locking behaviour has been tested either with swimming odontocetes approaching a target (Morozov et al., 1972) or with stationary odontocetes locating single targets offered at different distances (reviewed in Au, 1993). Range locking means that the next click is emitted after reception of an echo and a specific lag time. In bottlenose dolphins, lag times between ~15 ms and 45 ms have been reported (Morozov et al., 1972; Au, 1993).

In our investigations, the porpoises were not asked to detect any target. Nevertheless, both animals demonstrated an obvious range-locking behaviour when moving from the starting to the destination point. Lag times were approximately 14 ms to 19 ms if they approached the destination point without equipment in the water (atb and bta) and were distinctly longer, approximately 26–36 ms, with equipment in the water (atb+) (Table 1). The continuous decrease of click interval combined with a nearly constant lag time at distances from 26 m to 12 m suggest that the porpoises acoustically locked on to a distant reference point somewhere near the destination. We cannot determine whether the reference point was the front edge of the pontoon on which the trainer was positioned (~0.5 m behind the destination point) or the net at the end of the pool (~3.5 m behind the destination point). We therefore calculated the lag times to an arbitrary reference point that was about midway between the front edge of the pontoon and the net.

The demonstrated range-locking behaviour indicates that the porpoises use information from a specific object in the background, a landmark, when approaching the destination point. This clearly shows that the porpoises use echolocation for spatial orientation even when swimming along stereotyped routes. If the landmark is picked up immediately after leaving the starting point, the echolocation task constitutes small-scale navigation, since the goal is within the perceptual range of the animal. In this case, the lag time should be about constant throughout the whole route from the start to the destination point, but this only occurred in the central portion of the traverses (Fig. 3).

In middle-scale navigation, where the goal is beyond the perceptual range (see Introduction), an animal follows a route along several landmarks. In so doing, the porpoises should switch with their lock-in behaviour from one landmark to the next. We think that such behaviour explains the differences in the means of the lag times shown by Freja in experiments atb and bta and the individual differences between Freja and Eigil in bta (Fig. 6). We assume that while the animals used the same landmark in atb, in bta Freja locked onto a pile of stones (see Fig. 1) representing a landmark positioned ~3 m in front of the reference point at side a whereas Eigil mostly used a landmark near our reference point. Therefore, our calculated two-way-transit time for Freja bta was too long by approximately 4 ms. If we add this value to the calculated lag time of 14.4 ms shown in Table 1, we get a new lag time of 18.4 ms. This is very close to the value of 19.2 ms determined for Freja in the atb trials and is also closer to the value of 16.8 ms for Eigil in bta. Another example for the switching from one landmark to another is the change from very short lag times at the beginning of a trial to the more constant values later in the trial then to long lag times at the end of the trial in the atb experiments for both porpoises (see Fig. 3D, atb). These changes are explained if the porpoises first used the nearby holding pool as a landmark, then switched to the landmark at the opposite side of the pool and finally used the corner of the enclosure as a landmark when turning just before reaching the destination point, as they often did. An earlier release of the landmark at the opposite end of the pool by Freja in atb+ trials, where obstacles are a few metres in front of the destination point, could explain why click interval increases at shorter distances to reference (Fig. 4); thus, the lag time is overestimated in this case. Eigil seems not to be disturbed by introduced obstacles since the click intervals decrease monotonically in the atb+ experiment (Fig. 4). In conclusion, these harbour porpoises lock their biosonar on to landmarks during spatial orientation tasks.

Our experiments atb and bta are rather similar to those of Morozov et al. (1972), where five dolphins (*Tursiops truncatus*) had to swim in a netted aquarium over a distance of 25–30 m to get a dead fish. In the 24 m to 4 m section of the traverse, the lag times were ~20 ms, or similar to what we found with harbour porpoises. They assumed the dolphins were range locking on to the prey but it seems more likely that the animals locked on to some object in the background in the range of 24 m to 4 m and on to the target thereafter. Range locking has also been demonstrated in stationary *Tursiops truncatus* that had to detect or discriminate targets offered at different distances (for a review, see Au, 2000). In such experiments, lag time values between 19 ms and 45 ms have been measured. Au (2000) points out that in these experiments targets have been used that are totally alien to the animals, and the environments in which the experiments were made may also have been rather unnatural. Additionally, the animals were tested after long training periods. We therefore suggest caution when stating that echolocating odontocetes will lock onto every natural target, including prey. If distant large targets that can serve as landmarks and small targets such as swimming fish are present at the same time, we assume that range locking is mainly connected to spatial orientation and not to prey detection. Madsen et al. (2005) recorded the biosonar performance of deep-diving beaked whales (*Mesoplodon densirostris*) while foraging in open water and found no range locking during prey capture. The lack of landmarks on which to lock in deep waters might explain this behaviour. On the other hand, finless porpoises (*Neophocoena phocaenoides*) in an isolated waterway showed a clear range-lock behaviour during foraging, starting up to 42 m from the presumed prey capture (Akamatsu et al., 2005). The authors interpreted this behaviour as detection and approach of a potential prey target. Accepting the use of landmarks for orientation in odontocetes, it might be more likely that at such distances the finless porpoises lock on to larger objects in potential foraging areas and that prey detection occurs after arrival at the foraging site.

Read and Westgate (1997) describe orientation behaviour by wild harbour porpoises. They concluded from their satellite tracking studies that porpoises moving out of the Bay of Fundy into the Gulf of Maine did so by following the 92 m isobath, which probably represents an important movement corridor. To keep acoustic contact with a bottom contour is a typical small-scale navigational task, whereas the migration to the Gulf of Maine can be attributed to middle- or large-scale navigation, depending on the familiarity of the destination.

The described spatial orientation behaviour of our harbour porpoises and that reported by Read and Westgate (1997) is similar to the spatial orienting behaviour of bats, which also use echolocation to follow routes along a sequence of landmarks and contours such as tree lines, forest lanes and edges (Verboom et al., 1999; Schnitzler et al., 2003). Both animal groups show a kind of guidance behaviour for maintaining a certain spatial relationship to landmarks (O'Keefe and Nadel, 1978; Trullier et al., 1997; Mallot, 1999).

Lag time versus *processing time*

It is assumed that lag time is necessary to process the information of the preceding pulse–echo pair (Morozov et al., 1972). We found that lag time is task dependent. In the experiments atb and bta (no equipment near the destination point), we measured lag times between 14 ms and 19 ms. In the experiment atb+, with a more complex spatial situation (equipment in the water), the lag times were longer, with means around 36 ms for Freja and 26 ms for Eigil. This may indicate that the animals now needed more time to process the more complex information in the pulse–echo pairs. This result corroborates the findings of Au et al. (1981). They measured lag times of only 7.0–9.4 ms in a detection experiment with *Tursiops truncatus*. These values are considerably shorter than the lag times of 18–22 ms measured in a discrimination task in an earlier experiment with the same animals (Au, 1980). Thus, different echolocation tasks affect the mean lag time used by these dolphins. The dependence of lag time on the difficulty of an echolocation task reflects the neuronal process that is necessary to extract the task-relevant information from the pulse–echo pairs without being disturbed by the succeeding

pulse. It is plausible that a simple task such as detection (the presence or absence of a target) needs less processing time than a more complex task such as discrimination or categorization of targets.

Spatial orientation

In the present study, the click interval depended on the spatial orientation tasks. The porpoises were locked onto specific places in the background that we call landmarks. From this fact, we derive the general hypothesis that odontocetes use echolocation not only for foraging but also for spatial orientation. This hypothesis is supported by data from other studies also indicating the use of landmarks by odontocetes.

Teilmann et al. (2002) conducted an experiment where a harbour porpoise had to detect a target at distances ranging from 12 m to 20 m. In all trials of this experiment, a constant mean click interval of 59 ms was measured, resulting in mean lag times changing between 32 ms and 43 ms. The porpoise apparently did not lock onto the target. The authors describe the experimental pool as a 34 m×20 m outdoor floating net-enclosure with a small (3.6 m×2.9 m) research pen at one side, where the porpoise stationed for each trial. The net of the enclosure was covered with marine fouling. Assuming that the animal used the end of the enclosure as a landmark and locked onto it, we can calculate the lag time. This landmark was positioned at a distance of 30.4 m from the porpoise (34 m length of pool minus 3.6 m length of research pen), which results in a two-way-transit time of 40.5 ms and a lag time of 18.5 ms. This lag time is comparable with the lag times found in Freja and Eigil during atb and bta tasks.

The findings of Akamatsu et al. (1998) that click intervals of odontocetes in a natural surrounding are longer than those of animals kept in pools reflect, in our opinion, the different distances to the background, which encloses guiding landmarks in both environments. The shorter click intervals used by animals in pools indicate that the landmarks used for spatial orientation were closer, resulting in a shorter two-way-transit time for the distance porpoise to landmark.

An observation of Goodson et al. (1994) also supports our hypothesis that odontocetes use echolocation for spatial orientation. He found shorter click intervals when *Tursiops truncatus* was foraging between pier heads. The nearby piers were potential landmarks, giving a short two-way-transit time for the click–echo pairs, and were therefore allowing the dolphin to shorten the click interval to keep the lag time constant.

Our view that the click interval is chosen in relation to distance to the background is also supported by Goold and Jones (1995), who recorded click intervals from sperm whales (*Physeter macrocephalus*) at the beginning of a dive, which were long enough to receive echoes from the seabed before the production of the next click. They therefore suggested that seabed proximity may have some influence on the click rate in sperm whales.

Also, the observation of Hooker and Whitehead (2002) that the click interval in northern bottlenose whales (*Hyperoodon ampullatus*) is somehow connected either to the distance to the research vessel or to the diving depth points in the same direction.

Our data, but also the findings of other studies, support the postulate by Murchison (1980) that: "…*the adoption of the word 'target' into biosonar terminology may have brought a subtle bit of inappropriate conceptual simplicity with it because it implies that the experimenter knows the one stimulus, among all the stimuli available, that the echolocating animal is attending to. This implies that the stimulus defined as target by the experimenter is, at all times during the experiment, defined as target by the echolocating animal. Analysis of repetition rate/target-to-animal distance relationship might be affected by these assumptions and implications*".

When interpreting experimental and field data, one must remember that the echolocation systems of odontocetes have evolved not only for the detection, localization and classification of single targets (such as prey) but also for spatial orientation. We even assume – similar to the evolution of echolocation in bats (Schnitzler et al., 2003) – that it is more likely that the evolution of echolocation in odontocetes occurred in two steps; first, the evolution of echolocation for spatial orientation and, second, a later transition for prey acquisition. This conceptual framework calls for a new view on field data of odontocetes orienting and foraging in different types of habitats. For instance, animals living near the coast or in rivers (e.g. harbour porpoises or finless porpoises) can use echolocation for spatial orientation in relation to the background and for prey acquisition whereas pelagic animals (such as beaked whales) can use it only for prey acquisition if they have no acoustic contact to the bottom. This may explain differences in the use of echolocation by pelagic and coastal odontocetes, similar to differences found in bats in the two guilds: 'open space aerial foragers' and 'edge space aerial foragers' (Schnitzler et al., 2003).

References

Akamatsu, T., Wang, D., Nakamura, K. and Wang, K. (1998). Echolocation range of captive and free-ranging baiji (*Lipotes vexillifer*), finless porpoise (*Neophocaena phocaenoides*), and bottlenose dolphin (*Tursiops truncatus*). *J. Acoust. Soc. Am.* **104**, 2511-2516.

Akamatsu, T., Wang, D., Wang, K. and Yasuhiko, N. (2005). Biosonar behaviour of free-ranging porpoises. *Proc. R. Soc. Lond. B.* **272**, 797-801.

Amundin, M. (1991). Helium effects on the click frequency spectrum of the harbour porpoise, *Phocoena phocoena*. *J. Acoust. Soc. Am.* **90**, 53-59.

Amundin, M. and Andersen, S. H. (1983). Bony nares air pressure and nasal plug muscle activity during click production in the harbour porpoise, *Phocoena phocoena*, and the bottlenosed dolphin, *Tursiops truncatus*. *J. Exp. Biol.* **165**, 275-282.

Amundin, M., Kallin, E. and Kallin, S. (1988). The study of the sound production apparatus in the harbour porpoise, *Phocoena phocoena*, and the Jacobita, *Cephalorhynchus commersoni* by means of serial cryo-microtome sectioning and 3-D computer graphics. In *Animal Sonar: Processes and Performance* (ed. P. E. Nachtigall and P. W. B. Moore), pp. 61-66. Plenum Press: New York.

Andersen, S. (1970). Auditory sensitivity of the harbour porpoise *Phocoena phocoena*. *Invest. Cetacea* **2**, 255-259.

Au, W. W. L. (1980). Echolocation signals of the Atlantic bottlenose dolphin (*Tursiops truncatus*) in open waters. In *Animal Sonar Systems* (ed. R. G. Busnel and J. F. Fish), pp. 251-282. Plenum Press: New York.

Au, W. W. L. (1993). *The Sonar of Dolphins*. New York, Berlin, Heidelberg: Springer-Verlag.

Au, W. W. L. (2000). Echolocation in dolphins. In *Hearing by Whales and Dolphins* (ed. W. W. L. Au, A. N. Popper and R. R. Fay), pp. 364-408. New York: Springer.

Au, W. W. L., Penner, R. H. and Kadane, J. (1981). Acoustic behavior of echolocating Atlantic bottlenose dolphins. *J. Acoust. Soc. Am.* **71**, 1269-1275.

Au, W. W. L., Penner, R. H. and Turl, C. W. (1987). Propagation of beluga echolocation signals. *J. Acoust. Soc. Am.* **82**, 807-813.

Au, W. W. L., Kastelein, R. A., Rippe, T. and Schooneman, N. M. (1999). Transmission beam pattern and echolocation signals of a harbour porpoise (*Phocoena phocoena*). *J. Acoust. Soc. Am.* **106**, 3699-3705.

Barrett-Lennard, L. G., Ford, J. K. B. and Heise, K. A. (1996). The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. *Anim. Behav.* **51**, 553-565.

Bibikov, N. G. (1992). Auditory brainstem responses in the harbor porpoise (*Phocoena phocoena*). In *Marine Mammal Sensory Systems* (ed. J. A. Thomas, R. A. Kastelein and A. Y. Supin), pp. 197-211. New York: Plenum Press.

Busnel, R.-G. and Dziedzic, A. (1967). Resultants metrologiques experimentaux de l'echolocation chez le *Phocaena phocaena* et leur comparaison avec ceux de certaines chauves-souris. In *Animal Sonar System, Biology and Bionics* (ed. R.-G. Busnel), pp. 307-356. Jouey-en-Josas, France: Laboratoire de Physiologie Acoustique, INRA-CNRZ.

Cranford, T. W., Amundin, M. and Norris, K. S. (1996). Functional morphology and homology in the odontocete nasal complex: implications for sound generation. *J. Morph.* **228**, 223-285.

Finsterwalder, R. and Hofmann, W. (1968). *Photogrammetrie*. Berlin: Walter de Gruyter.

Goodson, A. D. and Sturtivant, C. R. (1996). Sonar characteristics of the harbour porpoise (*Phocoena phocoena*): source levels and spectrum. *ICES J. Mar. Sci.* **53**, 465-472.

Goodson, A. D., Klinowska, M. and Bloom, P. R. S. (1994). Enhancing the acoustic detectability of gillnets. In *Gillnets and Cetaceans* (ed. W. F. Perrin, G. P. Donovan and J. Barlow), pp. 585-595. Cambridge: Black Bear Press Limited.

Goold, J. C. and Jones, S. E. (1995). Time and frequency domain characteristics of sperm whale clicks. *J. Acoust. Soc. Am.* **98**, 1279-1291.

Hooker, S. K. and Whitehead, H. (2002). Click characteristics of northern bottlenose whales (*Hyperoodon ampullatus*). *Mar. Mamm. Sci.* **18**, 69-80.

Kamminga, C., Cohen Stuart, A. and Silber, G. K. (1996). Investigations on cetacean sonar XI: intrinsic comparison of the wave shapes of some members of the *Phocoenidae* family. *Aquat. Mamm.* **22**, 45-55.

Kastelein, R. A., Zweypfennig, R. C. V. J. and Spekreijse, H. (1990). Anatomical and histological characteristics of the eyes of a month-old and adult harbor porpoise (*Phocoena phocoena*). In *Sensory Abilities of Cetaceans* (ed. J. A. Thomas and R. A. Kastelein), pp. 463-480. New York: Plenum Press.

Kastelein, R. A., Nieuwstraten, S. H. and Verboom, W. C. (1995). Echolocation signals of harbour porpoises (*Phocoena phocoena*) in light and complete darkness. In *Harbour Porpoises – Laboratory Studies to Reduce Bycatch* (ed. P. E. Nachtigall, J. Lien, W. W. L. Au and A. J. Read), pp. 55-67. Woerden, The Netherlands: De Spil Publishers.

Kastelein, R. A., Schooneman, N. M., Au, W. W. L., Verboom, W. C. and Vaughan, N. (1997). The ability of a harbour porpoise (*Phocoena phocoena*) to discriminate between objects buried in sand. In *The Biology of the Harbour Porpoise* (ed. A. J. Read, P. R. Wiepkema and P. E. Nachtigall), pp. 329-342. Woerden, The Netherlands: De Spil Publishers.

Kastelein, R. A., Au, W. W. L., Rippe, H. T. and Schooneman, N. M. (1999). Target detection by an echolocating harbour porpoise (*Phocoena phocoena*). *J. Acoust. Soc. Am.* **105**, 2493-2498.

Kastelein, R. A., Bunskoek, P. and Hagedoorn, M. (2002). Audiogram of a harbor porpoise (*Phocoena phocoena*) measured with narrow-band frequency-modulated signals. *J. Acoust. Soc. Am.* **112**, 334-344.

Madsen, P. T., Johnson, M., Aquilar de Soto, N., Zimmer, W. M. X. and Tyack, P. (2005). Biosonar performance of foraging beaked whales (*Mesoplodon densirostris*). *J. Exp. Biol.* **208**, 181-194.

Mallot, H. A. (1999). Spatial cognition: behavioural competences, neural mechanisms, and evolutionary scaling. *Kognitionswissenschaften* **8**, 40-48.

Møhl, B. and Andersen, S. (1973). Echolocation: high frequency component in the click of the harbour porpoise (*Phocoena ph.* L.). *J. Acoust. Soc. Am.* **54**, 1368-1372.

Morozov, V. P., Akopian, A. I., Burdin, V. I., Zaitseva, K. A. and Sokovykh, Y. A. (1972). Tracking frequency of the location signals of dolphins as a function of distance to the target. *Biofizika* **1**, 139-145.

Murchison, A. E. (1980). Detection range and range resolution of echolocating bottlenose porpoise (*Tursiops truncatus*). In *Animal Sonar Systems* (ed. R.-G. Busnel and J. F. Fish), pp. 43-70. New York, London: Plenum Press.

O'Keefe, J. and Nadel, L. (1978). *The Hippocampus as a Cognitive Map*. Oxford: Oxford University Press.

Popov, V. V., Ladygina, T. F. and Supin, A. Y. (1986). Evoked potentials of the auditory cortex of the porpoise, *Phocoena phocoena*. *J. Comp. Physiol. A* **158**, 705-711.

Read, A. J. and Westgate, A. J. (1997). Monitoring the movements of harbour porpoises (*Phocoena phocoena*) with satellite telemetry. *Mar. Biol.* **130**, 315-322.

Schnitzler, H.-U., Moss, C. F. and Denzinger, A. (2003). From spatial orientation to food acquisition in echolocating bats. *Trends Ecol. Evol.* **18**, 386-394.

Schwidefsky, K. and Ackermann, F. (1976). *Photogrammetrie. Grundlagen, Verfahren, Anwendungen*. Stuttgart: Teubner.

Sokal, R. R. and Rohlf, F. J. (1995). *Biometry – The Principles and Practice of Statistics in Biological Research*. New York: Freeman & Co.

Teilmann, J., Miller, L. A., Kirketerp, T., Kastelein, R. A., Madsen, P. T., Nielsen, B. K. and Au, W. W. L. (2002). Characteristics of echolocation signals used by a harbor porpoise (*Phocoena phocoena*) in a target detection experiment. *Aquat. Mamm.* **28**, 275-284.

Thomas, J. A. and Turl, C. W. (1990). Echolocation characteristics and range detection threshold of a false killer whale (*Pseudorca crassidens*). In *Sensory Abilities of Cetaceans* (ed. J. A. Thomas and R. A. Kastelein), pp. 321-334. New York: Plenum Press.

Trullier, O., Wiener, S. I., Berthoz, A. and Meyer, J.-A. (1997). Biologically based artificial navigation systems: review and prospects. *Prog. Neurobiol.* **51**, 483-544.

Turl, C. W. and Penner, R. H. (1989). Differences in echolocation click patterns of the beluga (*Delphinapterus leucas*) and the bottlenose dolphin (*Tursiops truncatus*). *J. Acoust. Soc. Am.* **86**, 497-502.

Verboom, W. C. and Kastelein, R. A. (1995). Acoustic signals by harbour porpoises (*Phocoena phocoena*). In *Harbour Porpoises – Laboratory Studies to Reduce Bycatch* (ed. P. E. Nachtigall, J. Lien, W. W. L. Au and A. J. Read), pp. 1-39. Woerden, The Netherlands: De Spil Publishers.

Verboom, B., Boonman, A. and Limpens, H. J. G. A. (1999). Acoustic perception of landscape elements by the pond bat (*Myotis dasycneme*). *J. Zool.* **248**, 59-66.