

Characteristics of echolocation signals used by a harbour porpoise (*Phocoena phocoena*) in a target detection experiment

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Abstract

The characteristics of echolocation signals used by a harbour porpoise (*Phocoena phocoena*) during a target detection experiment are described. A water-filled steel sphere (either 5.08 or 7.62 cm in diameter) was placed at distances of 12, 14, 16, 18 and 20 m from a harbour porpoise stationed in an underwater hoop. Detection was determined by a go/no-go procedure. Target trials were alternated with no-target trials according to a pseudo-random schedule. The harbour porpoise detected the large sphere at all distances, while the small sphere was detected up to 14 m. It used clicks with less energy when detecting the large sphere at all distances. The porpoise used, on average, 13 clicks to make a decision for the large sphere, which was significantly fewer compared to the small sphere (34 clicks) and to no-target trials (37 clicks). The mean interval between clicks was almost constant (about 59 ms) and independent of distance to target. The individual pulse trains showed two kinds of small-scale variations in click intervals: (1) jittering, which could be a way of avoiding range-ambiguous interference and (2) cyclic modulation. The mean source levels for all targets and all distances ranged from 157 to 169 dB *re* 1 μ Pa (p-p). The clicks were on average 77 μ s in duration and had a peak frequency of 131 kHz. A low amplitude pre-click was seen prior to the majority of the clicks recorded. The pre-click occurred on average about 270 μ s before the main click, regardless of target present or not, and was correlated temporally and spectrally to the subsequent main click. A pre-click has not previously been reported or found in the signals

of three other harbour porpoises and may be an anomaly in this individual.

Key words: harbour porpoise, *Phocoena phocoena*, echolocation, target detection.

Introduction

The harbour porpoise (*Phocoena phocoena*) uses short, high frequency echolocation clicks of narrow bandwidth (Møhl & Andersen, 1973) for orientation and prey capture (Verfuss *et al.*, 1999). Au *et al.* (1999) described some characteristics of the echolocation signals of a harbour porpoise. The 3-dB transmission beam width is 16°, the peak frequency is about 128 kHz with a 3-dB bandwidth of about 16 kHz, and the source level is about 157 dB *re* 1 μ Pa (p-p). Click intervals range from 20 to 35 ms or longer than the two-way transit time.

Active echolocation involves production of sound, as well as detection and processing of echoes. According to Au (1993), echolocating bottlenose dolphins (*Tursiops truncatus*) do not emit a new pulse until they receive the target echo from the preceding pulse. Hence, the click interval is presumed to depend on propagation time of the sound from the animal to the target and back again, defined as the two-way-transit-time, and on the animal's processing time. The time difference between the click interval and the two-way transit time is called the lag-time (Au, 1993), which presumably includes the time necessary to receive and process the echo from the preceding pulse.

Target detection experiments have previously been carried out on bottlenose dolphins (Au *et al.*, 1974), beluga whales (*Delphinapterus leucas*) (Au *et al.*, 1985) and false killer whales (*Pseudorca crassidens*) (Thomas & Turl, 1990). Au (1993)

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concluded that these three odontocetes are able to vary the source level of their echolocation clicks. For bottlenose dolphins, source levels vary from 150 to 230 dB *re* 1 μ Pa (p-p). The lower amplitudes are usually measured in tanks while the higher levels are measured in open water. Within click trains from bottlenose dolphins, Au (1993) found that the source level among clicks vary up to 25 dB.

The main goals of this target detection experiment on the harbour porpoise (*Phocoena phocoena*) were to investigate the ability to detect a well-defined object at different target ranges and to describe the signals used for this task quantitatively. Based on these and similar results the distance at which a harbour porpoise is able to detect an object with known target strength can be extrapolated. This is presently of high importance when trying to understand the reasons for the considerable bycatch in bottom-set gillnets that takes place throughout the Northern Hemisphere (e.g., Lowry & Teilmann, 1994; Perrin *et al.*, 1994). Target detection in this context has been described by Kastelein *et al.* (1999, 2000a).

Materials and Methods

The present study occurred between 16 and 18 August 1997 and was part of a larger investigation concerning the target detection abilities of a harbour porpoise (Kastelein *et al.*, 1999). In the present study, we provide a short overview of the facility and experimental setup; for a detailed description see Kastelein *et al.* (1999). However, the acoustic equipment, sound recordings, and data analysis are unique to the present study.

The study took place in a large floating net-pen measuring 34 x 20 m, with a net floor at a depth of about 2.6 m. The water depth was between 3 and 8 m, depending on the tide. The retaining pontoons were submerged about 10 cm. Nylon net, with a twine 3-mm thick and a stretched-mesh size of 9 cm, formed the bottom and sides of the pen. The net was covered with marine fouling. The pen was placed in an abandoned harbour with a flat sandy silt floor. The water temperature was about 21°C, with a salinity of 3.5‰, giving a speed of sound of about 1520 m/s. The facility was part of the rehabilitation and research centre operated by the Harderwijk Marine Mammal Park and Waterland Neeltje Jans, Holland. The study animal, a male harbour porpoise (PpSH030), stranded as a newborn and was rehabilitated in the Harderwijk Marine Mammal Park for four years. He measured 133 cm in length and weighed 35.6 kg at the time of the experiment.

Experimental setup and procedure

During the experiment, the study animal entered a research pen (3.6 x 2.9 x 1.2 m deep) situated in one end of the large pen. It was trained to station in an underwater hoop (60 cm in diameter). The centre of the hoop was 80 cm below the surface and 40 cm behind an aluminium plate (1.1 x 1.3 m, 3 mm thick), which separated the research pen from the rest of the pool. An opening in the plate (45 x 45 cm) was covered by an aluminium sliding door (3 mm thick), which was operated by the trainer when the target was in place. The opening in the plate also was covered by black plastic to avoid any visual cues of target presence. The acoustic attenuation through the plastic was less than 2 dB, tested using a 120 kHz pulsed signal.

Two water-filled stainless steel spheres with outer diameters of 5.08 and 7.62 cm were used as targets (target strength etc. are given by Kastelein *et al.*, 1999). Thin nylon monofilament lines were used to lower and raise the targets, which were operated by a person in a hut out-of-sight of the porpoise and trainer. The targets were positioned 80 cm below the surface. An underwater video camera above the hoop monitored the position of the porpoise. A trial started when a target was in place (or absent) and the porpoise was in the correct position in the hoop. A voice command was given to the trainer who signaled the animal to go into the hoop after which the sliding door was opened. A double-blind procedure was followed since the trainer was unaware of the presence (or absence) of the target and was told if the animal responded correctly or not. To further reduce the chance that the porpoise was aware of the target entering the water, the target was always lowered very gently into the water and in 'no target' trials it was lifted out of the water again.

Each session had 21 trials, consisting of six trials with the large sphere, five trials with the small sphere, and 10 trials with no target presented in pseudo-random order. There were never more than three present or absent trials in succession and the small sphere was never presented in two successive trials to avoid frustrating the animal when the sphere was offered out of the detection range. The distances (12, 14, 16, 18 and 20 m) were assigned randomly. A go/no-go response procedure was used. If the animal correctly detected a target, it returned to the trainer immediately for a reward. If no target was present and correctly rejected, it was trained to stay in the hoop for 6 s and thereafter return to the trainer to receive a reward. The animal was not rewarded for misses or false alarms.

Acoustic recordings

Acoustic recordings were made during six sessions, one each at 12, 14, 16 and 18 m and two at 20 m, giving 60 trials with no target, 30 trials with the

small target, and 36 trials with the large target (126 trials total). Echolocation signals were monitored with two hydrophones (Brüel & Kjør 8103) at distances of 2 m and 3 m in front of the hoop, where the porpoise stationed at about the level of the blowhole. Each hydrophone was connected to a preamplifier (B&K 2635). The hydrophones were calibrated at 250 Hz and at a known sound level before each session (B&K pistonphone 4223). A third hydrophone (HS 150, Sonar Products Ltd, Rudston, UK) was placed at 27 m from the porpoise. Signals from the three hydrophones were recorded separately on a four-channel Racal Store-4 tape recorder running at 762 mm/s (30 in/s). The whole recording system had a flat frequency response from 100 Hz to 130 kHz (± 3 dB). At frequencies higher than 130 kHz, the hydrophone attenuates at about -12 dB per octave. The level of background noise in the pen, measured with another system, was about 80 dB *re* 1 μ Pa from 100 Hz to 100 kHz (Kastelein *et al.*, 2000b).

Data analysis

The percentage of correct detections was calculated as correct detections/(correct detections+misses) \times 100 for each target size and distance. The percentage of false alarms was calculated as false alarms/(false alarms + correct rejections) \times 100.

When analysing tape recordings, the Racal was connected to a PC equipped with a 12 bit Digital Signal Processing (DSP) board (SPB2, Signal Data, Copenhagen, Denmark) with a sampling rate of 44 kHz. The recorded signals were played back and analysed using custom software. This application measures the time interval between clicks, the number of clicks in a train, and click energy. For the latter, the program uses two amplitude triggers, a pre-history, and a post history time (each 125 μ s) to capture a click. Ninety-seven percent of the energy of the click between the trigger cursors was calculated and referred to one second. The energy in each click was compared to that of the calibrating signal over one second, and expressed in dB *re* 1Pa²s after compensation for amplification factors. The five most intense clicks in each trial were selected for energy analyses, assuming they are among the clicks used the porpoise for detection. These clicks had good signal-to-noise ratios (at least 30 dB), meaning that noise contributed little to the total energy. These clicks were also used to calculate the source levels (click energy at 1 m from the hoop) for each target and for no target at each distance. The energy calculations were accurate to between 1 and 2 dB. The energy measure is the most appropriate to use since the dolphin ear seems to function as an energy detector (Johnson, 1968; Au, 1993). The sound pressure levels can be estimated since our reference of 0 dB *re* 1Pa²s is equivalent

to +160 dB *re* 1 μ Pa root mean square (rms) or +169 dB *re* 1 μ Pa (p-p) assuming a click duration of 100 μ s.

The data obtained from the custom software were converted into Microcal Origin 5.0 or MSEXcel 97 spreadsheets and the number of clicks per trial and the click intervals were extracted. For verification, random selections of trials were also analysed manually in Spectra Plus 3.0a (Pioneer Hill Software, Poulsbo, WA) by counting the number of clicks and measuring clicks intervals within click trains. We excluded clicks separated by more than 200 ms, because they probably represented clicks from different trains. This reduced the variation by avoiding the error caused by large intervals, which occasionally occurred when the porpoise stopped echo-locating and started again.

For comparison with previously reported values, we used Spectra Plus 3.0a to measure click durations (the time where the signal is clearly above noise), peak frequencies (the frequency with maximum amplitude in the spectrum), and -3 dB bandwidths (the frequency range between the -3 dB points to either side of the peak frequency). In addition, we used MathCad 2000 (MathSoft, Inc., Cambridge, MA) to calculate centre frequency (based on rms bandwidth, Au 1993). SYSTAT 7.0 was used for two-way ANOVA tests and linear regressions, and Stat 100 (BioSoft, Cambridge, UK) was used for *t*-tests all at $\alpha=0.05$ level.

Results

The porpoise correctly detected the large sphere (7.62 cm) in all trials at all distances (100%, trials=36). He correctly detected the small sphere (5.08 cm) on all trials at 12 m and 14 m (100%, trials=10), but was not able to detect the small sphere at 16 m (0%, trials=5) and average performance was 20% at 18 and 20 m (trials=15). False alarm rate (go on target absent) for all trials was 5% (trials=60; Table 1).

Table 1 shows that the porpoise used significantly fewer clicks per trial to assess the large sphere (mean=13, trials=36) than to assess the small sphere (mean=34, trials=30, *t*-test, $P<0.001$). This was independent of distance to the target and whether the small sphere was detected or not. Significantly fewer clicks were used to assess the large sphere compared to the no-target trials (mean=37, trials=60; *t*-test, $P<0.001$). There was no difference in the number of clicks used when the small sphere was present or absent (*t*-test, $P>0.05$).

The porpoise used the same mean click interval in all sessions (Table 1). No significant difference was found in the mean click interval with respect to the type of target or the distance to target (*t*-test, $P>0.05$). The overall mean click interval was 59 ms

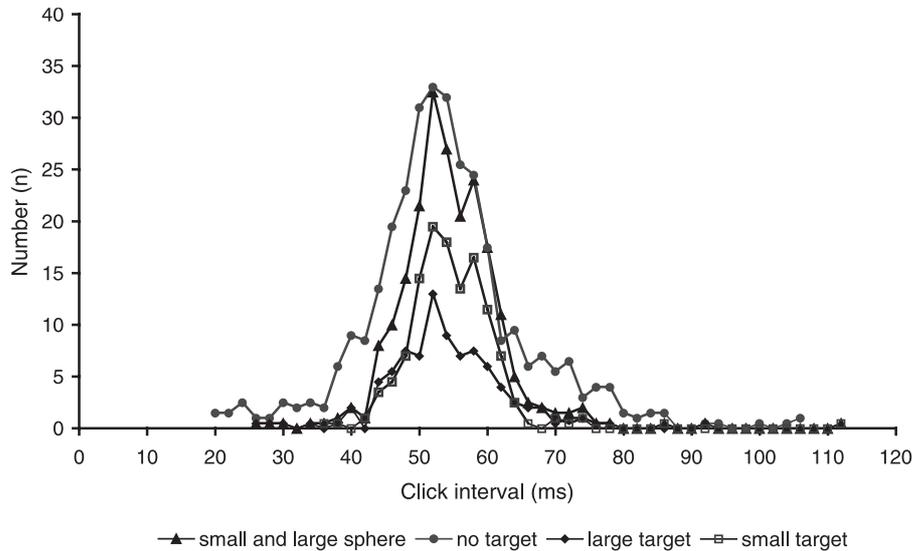


Figure 1. Distribution of click intervals for target and no target trials at a target distance of 14 m. A typical example showing that click intervals are rather uniformly distributed around a mean for all trials irrespective of target present or no target. However, note that the variation of click interval is greater for the small target compared to the large target. The total number of intervals is 1108.

(range=55–64, SD=3, intervals=3431) for all trials and for all situations (Table 1). The variation of click intervals was tested at 14 m. It was identical for the small and large sphere, but a significant difference was found between the target present and target absent trial (F-test, $P<0.001$). A general feature of the trials investigated is that the click intervals show two kinds of pulse-to-pulse variations. First there was a variation around the mean, as seen in Figure 1. Secondly, cyclic variation as well as fluctuations in click intervals were seen in the 60 single trials examined, five from each target for each distance. An example of two such trials is shown in Figure 2.

The mean energy source level varied between 0 and -12 dB *re* $1\text{Pa}^2\text{s}$ for all distances and all situations (Table 1). These values are equivalent to 169 and 157 dB *re* $1\ \mu\text{Pa}$ at 1 m (p-p). For each distance, significantly less intense signals were used to assess the large sphere, while more intense signals were used when the small sphere or no target was presented ($P<0.001$, $F_{2,61}$ two-way ANOVA). There was no significant difference between the energy of clicks used to probe for the small sphere and when no target was present, independent of distance ($P=0.137$, $F_{1,44}$ two-way ANOVA). The porpoise used significantly more intense signals to probe for targets as the distance increased from 16 m to 20 m ($P<0.001$, $F_{1,11}$ for large sphere; $P<0.001$, $F_{1,98}$ for small sphere: linear regression). Figure 3 shows the changes in source level from click to click for the small target at 12 and 20 m. The animal generally

puts more energy into the clicks when the small target was at 20 m, where he could not detect it. We saw an increase in click energy during the first part of the trial in many of the 126 trials analysed, an example of which is shown in Figure 3. In addition, there can be changes of more than 10 dB in energy over three successive clicks.

A typical click is shown in Figure 4. Measured manually, the mean duration of a click was 77 μs (range: 61 μs to 123 μs , SD=17, clicks=26), the mean peak frequency was 131 kHz (range: 125 kHz to 136 kHz, SD=4, clicks=26) and the mean -3 dB bandwidth was 16 kHz (range: 10 kHz to 21 kHz, SD=3, clicks=26). These values are essentially identical to those reported earlier for the same animal (peak frequency: 128 ± 7.0 kHz, -3 dB bandwidth: 16 ± 4 kHz; Au *et al.*, 1999). A majority of clicks were preceded by a weaker 'pre-click' (arrows in Fig. 4), which occurred on average 268 μs (SD=43, clicks=94) before the main click. There was no statistical difference in the time-delay between pre-click and main click whether or not a target was present (*t*-test, $P=0.56$, $df=45$), or when comparing the delay of the same click measured at the 2 m and 3 m hydrophones (*t*-test, $P=0.77$, $df=46$). The centre frequency of the main click (132 kHz, SD=1, clicks=14) and that of the pre-click (132 kHz, SD=6, clicks=14) were not significantly different (*t*-test, $P=0.71$, $df=13$). This suggests that the pre-click is produced by the animal and is not a reflection from an object in the environment. The pre-click was also found in

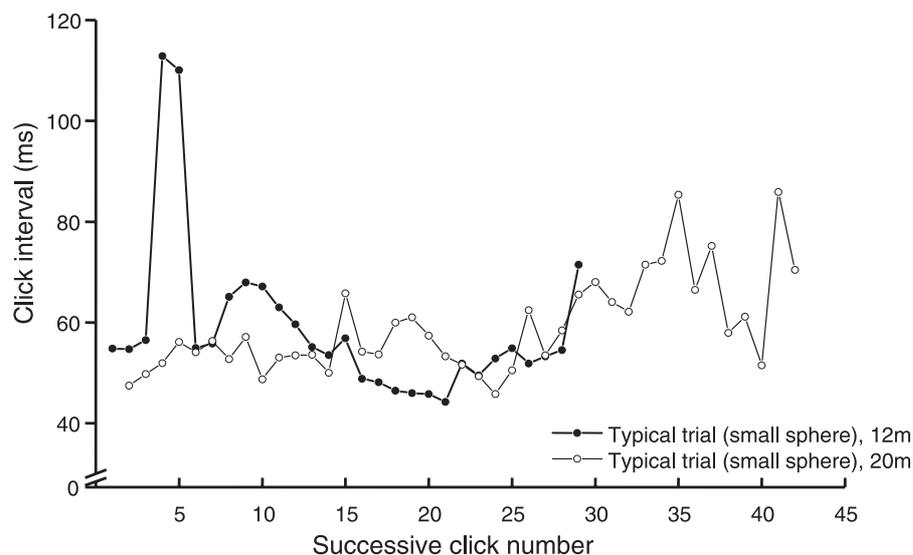


Figure 2. The click interval as a function of click number in two typical trials using the small sphere. Click intervals are rarely constant, but lengthen and shorten in an irregular cyclic pattern. Intervals between most clicks fall within a 50 to 80 ms period irrespective of distance to the target. The two long click intervals at the beginning of the trial with the target at 12 m may result from missing clicks. The animal could not detect the target at 20 m. (Bin width: 2 ms.)

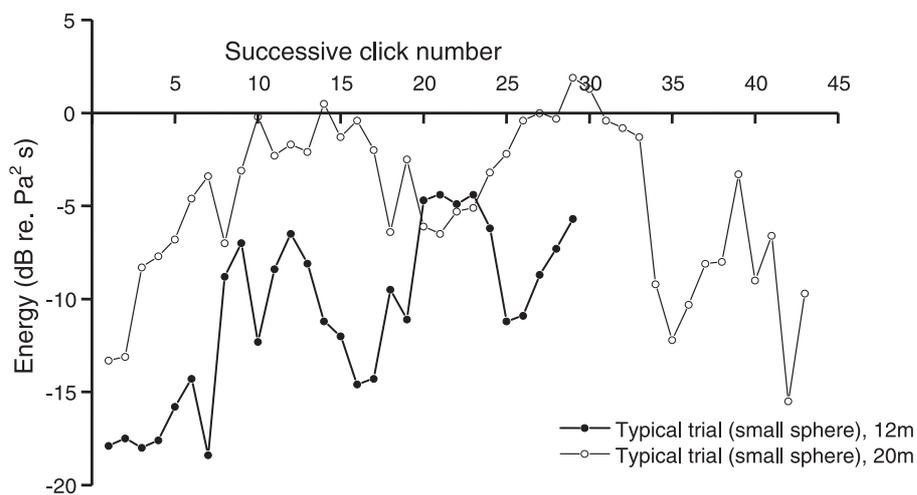


Figure 3. Source levels of clicks as a function of click number in two typical trials with the small sphere. The animal used signals with less energy to detect the small sphere at 12 m than when probing for the same target at 20 m, where he could not detect it. Note that the energy can change by more than 10 dB over a few clicks. Zero dB on the energy scale corresponds to about +169 dB re 1 μ Pa (p-p).

recordings from an earlier study on the same animal at the same location (Au *et al.*, 1999) when the recordings were re-analysed. The centre frequency of the main click (125 kHz, SD=2, clicks=6) and the pre-click (122 kHz, SD=11, clicks=6) from the study by Au *et al.* (1999) were not significantly

different (*t*-test, $P=0.52$, $df=10$), and the delay between the pre-click and the main click was 226 μ s (SD=29, clicks=7). These values are lower than what we found, but this may be due to the one-year time span between measurements where the animal grew in weight by 5.4 kg and in length by 5 cm.

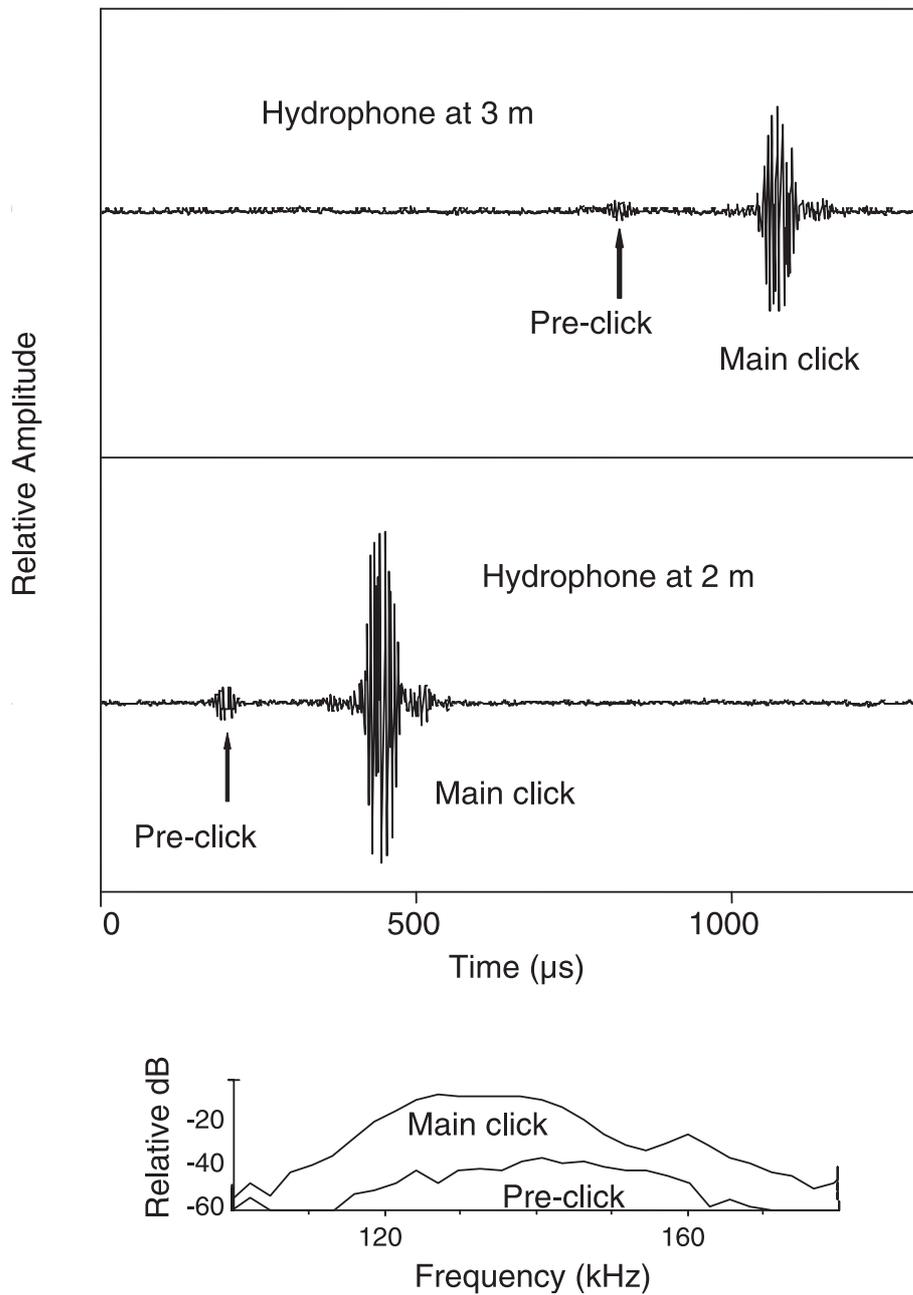


Figure 4. Simultaneous recordings from hydrophones at 2 m and 3 m from the porpoise. A pre-click (arrow) precedes the main click by the same delay (about 270 μs) in each recording. The pre-click has essentially the same spectral characteristics, but is about -20 dB *re* the main click. The frequency resolution is 5.5 kHz.

Table 1. Pertinent data from target detection experiments by a harbour porpoise using 7.62 cm and 5.08 cm diameter spheres or no target present at five different distances.

Distance to target (TWT)	Target type (sphere)	No. of trials	Correct detection %	Mean clicks per trial, (SD;n)	Mean click interval per trial, ms (SD;n)	Mean SL of 5 strongest clicks per trial in dB re 1 Pa ² s (SD;n): dB re 1 μPa(p-p)
12 m (16 ms)	Large	6	100	11.0 (2.8; 6)	58.2 (23.7; 60)	- 10 (2; 30):159
	Small	5	100	31.0 (16.7; 5)	58.8 (13.2; 150)	- 7 (2; 25):162
14 m (18 ms)	No target	10	100	31.6 (8.0; 10)	63.4 (18.0; 300)	- 7 (2; 50):162
	Large	6	100	9.0 (2.2; 6)	58.6 (16.0; 47)	- 6 (3; 30):163
	Small	5	100	22.4 (8.6; 5)	57.4 (13.0; 104)	- 1 (1; 25):168
16 m (21 ms)	No target	10	90	41.6 (12.1; 10)	59.1 (20.4; 393)	- 0 (2; 50):169
	Large	6	100	14.6 (7.0; 5)	59.1 (21.9; 68)	- 12 (5; 25):157
	Small	5	0	30.2 (11.4; 5)	63.9 (22.5; 142)	- 9 (3; 25):161
18 m (24 ms)	No target	10	100	35.9 (12.9; 10)	61.9 (20.1; 343)	- 7 (2; 50):162
	Large	6	100	11.2 (3.6; 6)	63.2 (24.4; 61)	- 7 (2; 30):162
	Small	5	20	37.6 (11.1; 5)	58.2 (10.2; 181)	- 4 (1; 25):165
20 m (26 ms)	No target	10	100	33.1 (8.0; 10)	55.5 (13.2; 310)	- 6 (2; 50):163
	Large	6	100	15.8 (3.8; 6)	56.4 (20.1; 89)	- 4 (2; 30):165
	Small	5	40	35.0 (8.1; 5)	56.8 (14.9; 167)	- 2 (2; 25):167
20 m	No target	10	90	42.3 (10.3; 10)	60.7 (20.5; 399)	- 2 (2; 50):167
	Large	6	100	13.8 (6.9; 6)	60.2 (19.6; 76)	- 6 (4; 30):163
	Small	5	0	45.4 (19.1; 5)	54.8 (17.0; 212)	- 2 (1; 25):167
	No target	10	90	35.0 (14.4; 10)	61.8 (22.9; 329)	- 2 (1; 50):167

SD is the standard deviation and n is the number of trials, number of intervals or number of clicks. $SL_{(energy)}$ (dB re 1 Pa²s) = $SL_{(pressure)}$ (dB re 1 μPa p-p) + 169 dB assuming a click duration of 100 μs. See Methods for energy calculations. TWT is the two-way transit time, the time for the click to reach the target and the echo to return to the animal (speed of sound = 1520 m/s).

Discussion

The porpoise detected the large sphere at all distances (12–20 m) and the small sphere at 12 and 14 m, but performance was much poorer at distances greater than 14 m. This is more or less consistent with the results found by Kastelein *et al.* (1999) in an extensive study on the target detection abilities of the same animal both before and after the present study. Kastelein *et al.* (1999) found 100% (trials=362) correct detection for the large sphere for all distances between 12 and 20 m. The correct detection for the small sphere was 90% (n=60), 80% (n=61), 50% (n=59), 30% (n=65) and 10% (n=58) at 12, 14, 16, 18 and 20 m, respectively. The only distance where the results of the two studies differed was 16 m where the animal made no correct detections of the small sphere in our study. The false alarm rate was 5% in our study compared to about 3% in Kastelein *et al.* (1999). Kastelein *et al.* (1999) calculated the 50%-correct detection threshold for the large and the small sphere to be 26 m and 15.9 m, respectively. This comparison indicate that in general the results obtained in the present study are representative for the target detection ability of this animal.

In the target detection experiment described here, the head of the porpoise was stable; however, not

fixed, and pointed directly towards the target. Thus, we could record all clicks emitted by the porpoise and compare the number of clicks, click intervals and energy for distances between 12 and 20 m. The animal used about the same number of clicks when the small sphere was presented as when a target was absent. He always used fewer clicks to evaluate the large sphere at all ranges (Table 1). This indicates first, that echoes from the small sphere were near the animal's detection threshold and secondly, that the animal apparently abandon any attempt of finding the target if he could not do it within the first 30–40 clicks. An exception may be the 14 m session where fewer clicks were used to detect the small sphere, but with higher source levels. The reason for this is unclear, but may be due to the low sample size.

In target detection experiments with bottlenose dolphins, Au *et al.* (1974) found that during target absent trials the dolphins still echolocate with a click interval corresponding to what would be expected had target been present. We found no difference between the mean click intervals in trials with target present and trials with target absent, but the variation around the mean value was significantly higher when no target was present. This indicates that the study animal expects the echo to arrive at a given time, which could explain the greater

variation in click intervals when the target was absent.

The porpoise used a nearly constant mean interval of around 60 ms between clicks independent of distance to the target and, thus, did not adjust for the two-way transit time or the time from emission of a click to reception of the echo. The mean values could obscure some adjustment of the click intervals within each trial, but this does not seem to be the case because the click intervals within trials do not change according to target distance (Table 1). The click interval was always longer than the two-way transit time, for example by 32.2 ms at 20 m to 42.8 ms at 12 m. This result is inconsistent with results from bottlenose dolphins, in which the lag-time remains relatively constant (Au, 1993). During an investigation of the transmission beam pattern of the same animal used in the present study, Au *et al.* (1999) found click intervals of 30 to 45 ms. These intervals were somewhat shorter than the mean click interval we found (59.3 ms), but the target distances were also shorter, 7 to 9 m (Au *et al.*, 1999).

A recent study shows that harbour porpoises adjust for the two-way transit time while capturing prey (Verfuss *et al.*, 1999). The click interval was always longer than the two-way transit time by about 50 ms when the porpoise approached a fish from a distance greater than about 8 m. The reason why our results do not show an increase in click intervals as a function of target range could be that this experienced animal used a time window that covered all distances tested.

Kadane & Penner (1983) found a slight pulse-to-pulse change in click intervals in bottlenose dolphins, a phenomenon they termed 'jittering', which should reduce range ambiguity and range-ambiguous interference. Even 1 to 2 ms of jittering is sufficient to reduce interference and ambiguity. The harbour porpoise in our study used click intervals distributed around a mean interval (Fig. 1), similar to the results obtained from dolphins (Kadane & Penner, 1983). It appears from Figure 2, that the porpoise exhibits pulse-to-pulse changes in click intervals analogous to jittering. Another variation was observed in which click intervals rise and fall in what seems to be a cyclic pattern (Fig. 2). This is somewhat similar to what Au (1993) found in target detection experiments using bottlenose dolphins. A distinction between the two kinds of variations should be made since it is believed that the cyclic changes are modulations that to some extent are controlled by the animal, while jittering is probably a build in instability of the echolocation system (Kadane & Penner, 1983). Like dolphins, the harbour porpoise may be able to reduce range-ambiguous interference and range ambiguity by the jittering of click intervals.

The ability of a harbour porpoise to adjust the output of its echolocation has not previously been described. The animal in the present study used more energy when searching for the small sphere and when there was no target present compared to when it detected the large sphere. This was the case at each distance (Table 1). The distances were chosen in random order to reduce the animal's expectation of a specific distance and to make each session an independent event, but why the animal used high click energies at 14 m is unclear. Aside from this, the porpoise used clicks with progressively more energy when searching for targets at 16, 18 and 20 m, and clicks with about the same energy for targets at 12 and 16 m. The progression of source level with distance to target is consistent with findings from bottlenose dolphins (Au *et al.*, 1974), beluga whales (Au *et al.*, 1985) and false killer whale (Thomas & Turl, 1990) under similar experimental conditions.

The source levels found in this study are similar to what Au *et al.* (1999) recorded from the same animal one year earlier. The results from our study fall within the range of source levels of harbour porpoises recorded in other studies, which varied from about 130 to 177 dB *re* 1 μ Pa (p-p) (Møhl & Andersen, 1973; Akamatsu *et al.*, 1994; Hatakeyama *et al.*, 1994; Goodson *et al.*, 1995). As mentioned above, our animal increased the energy of clicks with increasing target distance, indicating the possibility for harbour porpoises to make even stronger signals than have been measured to date.

The pre-click seen in Figure 4 originates from the sound producing mechanism of this animal. Since the present study, we made controlled recordings from two porpoises at Harderwijk Marine Mammal Park, The Netherlands, and one porpoise at the Fjord & Bæltcenter, Denmark. We could not measure a pre-click from these animals. The pre-click may just be an anomaly of our study animal, but it does invite some limited speculation on sound production. Assuming the presence of an internal reflector (Amundin, 1991), it seems unlikely that the pre-click arises from a reflection in the melon. We measured the speed of sound (a click) in 4.8 cm of melon tissue at 37°C and found a mean velocity of 1136 m/s. If the pre-click originates from a generator that is separate from a reflector giving the main click, then the generator would be 15.2 cm from the reflector. This seems unrealistic since the melon is only about 10 cm long (Amundin & Cranford, 1990; Kastelein *et al.*, 1997). Another possibility could be the muscular activity in the nasal plug during onset of a click (Amundin & Andersen, 1983) where pressure opens the valve producing the pre-click and then snaps shut when the pressure falls causing the main click. Dubrovsky & Giro (1999) actually constructed a pressurized model

that produced three noticeable acoustic pressure clicks in their attempt to explain a mechanism of click production in the bottlenose dolphin. The spectral characteristics of the pre-click and main click are quite similar (Fig. 4). This would be expected if the sound generating system of the harbour porpoise possessed a resonant or filtering mechanism to produce the characteristic narrow-band clicks. Results of some preliminary studies using the heads of dead porpoises suggest the presence of a filtering mechanism. In any case, detailed studies of sound production in the harbour porpoise are needed to establish mechanisms.

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