



## BRIEF COMMUNICATIONS

### Discrimination between high and low repetition rates of ultrasonic pulses by the cod

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Cod were trained to detect a shift in the repetition rate of intense ultrasonic pulses (approximately 210 dB re 1  $\mu$ Pa). For cod exposed to predation by toothed whales, this ability may provide information to guide evasive manoeuvres. © 1998 The Fisheries Society of the British Isles

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There is increasing evidence that fish are capable of detecting intense ultrasound. In cod, Astrup & Møhl (1993) found psychophysical thresholds to 38 kHz of approximately 195 dB re 1  $\mu$ Pa; in clupeids, Dunning *et al.* (1992) and Nestler *et al.* (1992) found behavioural thresholds for 125 kHz down to 145 dB re 1  $\mu$ Pa. In all cases, the ultrasound sensitivity was conjectured to have survival value for fish by providing them a means of detecting the ultrasonic sonar signals emitted by predatory toothed whales.

In odontocetes, often experiments have shown that the interval between sonar signals is proportional to the distance from whale to target (Morozov *et al.*, 1972; Turl & Penner, 1989; Thomas & Turl, 1990; Au, 1993). Thus, close to targets, high repetition rates are prevalent. In free-swimming narwhals, sound recordings have revealed an almost bat-like pattern of sonar-signal emission (Miller *et al.*, 1995), with long periods of 4–10 pulses  $s^{-1}$  (pps), interrupted by short bursts with predominant repetition rates of 110–400 pps. Although behavioural confirmation is lacking, it seems reasonable that these bursts are the odontocete equivalent of the terminal buzz phase seen in echolocating bats during the final stage of prey capture (Miller *et al.*, 1995).

If fish can evaluate the repetition rate of sonar signals, it may provide them with intensity-independent clues about an odontocete predation threat. Therefore, experiments were performed to determine whether cod *Gadus morhua* L., can discriminate between low and high repetition rates of ultrasonic pulses.

Experimental fish were captured in fish traps in shallow water in the Århus Bay, Denmark. Individuals were labelled GD1 to GD7 and measured 39–45 cm in total length. Animal holding facilities, anaesthesia, ECG technique, anechoic tank, and general set-up were the same as used in Astrup & Møhl (1993) with the exception that the present study used a 50-kHz echo-sounder transducer (XGM 1300) with a sound-radiating surface of  $9 \times 11$  cm (aimed laterally at the front half of the fish) and a different custom-made power amplifier. This combination could deliver pulses of varying durations with available intensities for low duty cycles of up to 214 dB re 1  $\mu$ Pa pe rms (pe rms is peak equivalent root mean square; Stapells *et al.*, 1982). With a repetition rate of 100 pps, it was capable of delivering 1-ms pulses with an intensity of up to 211 dB re 1  $\mu$ Pa. The pulses from the transducer were subjected to an analysis of the inevitable low-frequency, low-level components of pulsed sound. This analysis was identical to the one performed on pulses from the 38-kHz transducer used in Astrup & Møhl (1993); by averaging 256 pulses, energy in the frequency range 25–400 Hz could be detected down to

c. 30 dB below background noise. From the presently used 50-kHz transducer, the low-frequency components were as weak or weaker than those of the previously used 38-kHz transducer, i.e. at least 12 dB below background noise for pulses with an ultrasound level of 200 dB re 1  $\mu$ Pa.

In the experiments, cod were tested with classical cardiac conditioning, where bradycardia is established by coupling a test stimulus with a mild electric shock (Otis *et al.*, 1957; for a detailed description of the technique as applied in this study, see Astrup & Møhl, 1993). As a screening procedure, each animal was tested first for reaction to ultrasound *per se*. For these tests, each trial consisted of 30 s of silence that constituted the period of reference heart-rate monitoring. After this followed a 10–15-s test period during which 3-ms sound pulses at a 1-pps repetition rate (the test stimulus) were applied at intensities of 211–214 dB re 1  $\mu$ Pa. A mild electric shock (4–10 V d.c., 200 ms) terminated the trial. A response was defined as a trial in which any of the heartbeat intervals in the test period exceeded the longest of the intervals in the 30-s reference period by at least a factor of 1.1. A stability criterion caused trials to be reinitiated if more than a 75% difference between any two heart-beat intervals occurred in the reference period; this allowed liberally for variation, but pronounced bradycardia or ECG-signal drop-out caused reinitiation. The trials were separated by 3–5 min. Conditioning was considered established after five consecutive responses.

After conditioning, a threshold for 3-ms pulses (1 pps repetition rate) was established with a staircase method (described in Astrup & Møhl, 1993). From some animals, thresholds for 100-ms pulses (1 pps repetition rate) shaped with linearly rising and falling 50-ms ramps were obtained in addition.

To test for repetition-rate discrimination, the experimental paradigm was changed so as to make the test stimulus a shift in repetition rate from 5 to 100 pps, this shift resembling the shifts observed in nature (Miller *et al.*, 1995). Thus, the animal was exposed to ultrasonic pulses with a 5-pps repetition rate during the 30-s reference period. In blank trials, the 5-pps repetition rate continued throughout the 10–15-s test period, and no electric shock was administered. In contrast, test trials featured stimulation with pulses of 100 pps repetition rate in the test period, and the trial ended with an electric shock. Blank and test trials occurred pseudorandomly in about equal numbers with no more than two consecutive trials of the same kind. The duration of the ultrasonic pulses was 1 ms, and intensities were approximately 10 dB above threshold.

All seven cod tested were conditioned (i.e. responded) to 50-kHz ultrasonic stimulation and thus passed the screening procedure. The threshold mean for 3-ms pulses was 202.2 dB pe rms re 1  $\mu$ Pa (s.d. =  $\pm$  5.3 dB). With conditioning established, five fish were tested with the transducer rotated 90°, i.e. not aiming at the fish. This reduced the ultrasound intensity at the fish's position by 33 dB, and except for one ambiguous case (GD7, described below), responses were eliminated. With this result it could be concluded, as with the 38-kHz transducer used in Astrup & Møhl (1993), that the cod were responding to the ultrasonic component of the stimulus, and not to unintentional cues, including the inevitable low-frequency, low-level components of pulsed sound. These components are radiated omni-directionally and are thus little affected by transducer orientation.

Thresholds to shaped 100-ms pulses were obtained from three, rather sensitive fish, yielding a mean of 197.8 dB re 1  $\mu$ Pa (s.d. =  $\pm$  2.2 dB); an average difference of <1 dB was observed to 3-ms threshold estimates that were obtained immediately before or after the 100-ms threshold sessions. This corroborates the ultrasonic component as being the effective stimulus since the low-frequency energy of the 100-ms pulse was at least 30 dB lower (i.e. not detectable) than background noise and presumably 30–40 dB lower than for unshaped pulses. It also shows that duration-intensity trading, i.e. a lowering of the threshold with increased stimulus duration (Hawkins, 1981; Fay & Coombs, 1983), does not occur for pulses longer than 3 ms, a result that is in agreement with our previous findings (Astrup & Møhl, 1993).

The one ambiguous case (GD7) has a response rate of 23% ( $n=61$ ) with the transducer rotated 90°. This was significantly higher ( $G$ -test,  $P<0.025$ ) lower than in a control test of the false-alarm rate in the absence of stimulation (7%;  $n=70$ ), but the responses were

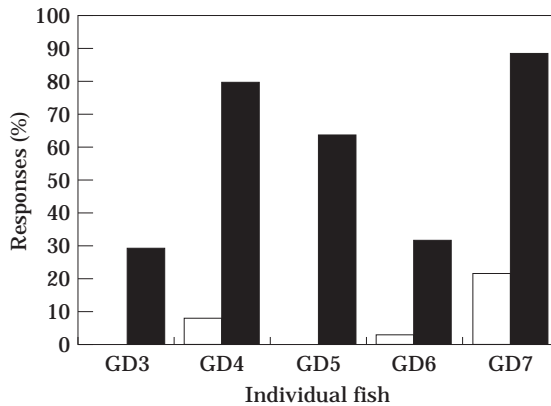


FIG. 1. Responses in blank trials [5 pulses  $s^{-1}$  (pps) repetition rate;  $\square$ ] and test trials (100 pps repetition rate;  $\blacksquare$ ), plotted as percentages to facilitate comparison between individual fish. GD3 and GD5 showed no responses in blank trials. For all fish, the difference in response rates between blank and test trials was statistically significant ( $G$ -test). Significance levels for GD3 ( $n=69$ ):  $P<0.001$ ; GD4 ( $n=27$ ):  $P\leq 0.001$ ; GD5 ( $n=32$ ):  $P\leq 0.001$ ; GD6 ( $n=370$ ):  $P\leq 0.001$ ; GD7 ( $n=18$ ):  $P<0.025$ . Blank and test trials occurred in approximately equal numbers. GD6 was exposed to a further test of method suitability (which proved inconclusive), hence the large number of trials for this animal.

not consistent enough to meet the conditioning criterion. Moreover, the threshold for shaped 100-ms pulses was virtually identical (within 1 dB) to the thresholds for 3-ms pulses. Thus, the responses with the transducer rotated  $90^\circ$  do not appear to have been caused by low-frequency components. The fish was positioned in a PVC chamber (sound transparent) that separated it from the water volume which held the transducer; therefore the responses are unlikely to have been caused by any electrical stimulation deriving from the strong electrical pulses used to drive the transducer. This is similar to a case in [Astrup & Møhl \(1993\)](#), and again we have no explanation for these seemingly aberrant observations. However, they call for caution in generalizing on the effective stimulus for the individual fish.

For the 3-ms pulses, the mean threshold obtained in this study was 7.8 dB higher than the threshold obtained with the 38-kHz transducer in [Astrup & Møhl \(1993\)](#). Although the small number of animals used in this study must be kept in mind, the threshold difference was highly significant ( $t$ -test,  $P\leq 0.001$ ). For the 100-ms pulses too, thresholds in this study were *c.* 8 dB higher than thresholds for long-duration stimuli generated with the 38-kHz transducer. Still, a difference of 8 dB is sufficiently small that a fairly flat threshold curve for ultrasound is assumed ([Astrup & Møhl, 1993](#)).

Five of the screened animals were tested for discrimination of pulse repetition rate (two fish died prematurely). As significant differences in the number of responses in blank (false alarm rate) and test trials were found for all individuals ([Fig. 1](#)), the fish appeared able to discriminate between the different repetition rates employed in blank and test trials.

The data set showed considerable variability among the fish. Although the conditioning technique is known to produce variable results for individual fish ([Otis \*et al.\*, 1957](#)), the conditioning paradigm may be rather demanding since it requires the fish to detect a change in a stimulus instead of the mere presence of a stimulus. This might have accentuated individual differences in learning capability, and it may also be an explanation for the overall low response rates in the discrimination experiments.

It is concluded that cod can discriminate between repetition rates of ultrasonic pulses. Therefore, in addition to detecting the mere presence and the intensity of sonar signals, they may evaluate an odontocete threat by the repetition rate of the signals. Apparently they do not use duration-intensity trading for the task since this is inconsistent with our

finding of almost identical thresholds to long and short pulses. The mechanism of detection and discrimination is unknown.

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