DETECTION OF INTENSE ULTRASOUND BY THE COD
GADUS MORHUA

JENS ASTRUP AND BERTEL MØHL

Department of Zoophysiology, University of Århus, 8000 Århus C, Denmark

Summary

The ability of cod to detect intense 38kHz pulses was studied in an anechoic tank, using a classical cardiac conditioning method. All 15 cod studied reacted to 3ms pulses. The average threshold was 194.4dB re 1 μPa (S.D. 5.4dB, S.E.M. 0.3dB). The data do not reveal the sensory modality involved. A number of additional experiments indicate that the ultrasonic energy *per se* is the effective stimulus. The threshold is too high for most sources of marine ultrasound to be detected, but is low enough to allow the cod to detect echolocating odontocetes at a range of 10–30m. The results also indicate that cod can detect echo-sounders of the fishing fleet at similar ranges.

Introduction

The biosonar signals of odontocete whales are used in prey localization. An ability of the prey to detect these signals constitutes an obvious survival value. An example of such a predator/prey interaction has already been found in the well-known bat/insect interaction, where at least seven insect families have independently developed sensitivity to ultrasound as a warning mechanism against preying bats (e.g. Surlykke, 1988). Being a major group of prey for odontocetes, marine fish would be expected to benefit from an ability to detect ultrasound.

Reports from experienced fishermen have suggested that fish can detect ultrasound. Using echo-sounders in their work, they have repeatedly made observations that convince them that fish react to the sounders (P. Pedersen, personal communication). The sounders operate in the ultrasonic range 25–125kHz, with source levels as high as 230dB re 1 μPa. Moreover, Offutt (1968) reported that goldfish responded to high, but unspecified, levels of 50kHz sound and conjectured that this could be a basis for a warning mechanism against preying odontocete whales. This idea has not had any noticeable impact on marine fish audiometry however, including Offutt's own work on cod (1974).

The reason for this may be a combination of two factors. (1) Lack of acceptance of the idea. A large body of results on the hearing abilities of fish has produced a consensus that this group of animals has its auditory capabilities restricted to the lower audio frequency range and below. Because most species investigated showed markedly declining sensitivity in frequency ranges of (typically) 0.1–2kHz (Hawkins, 1981),

these frequencies have been taken to indicate the upper end of the useful auditory range. The generic auditory range of fish thus established covers the spectrum of acoustic signals from what has been regarded as biologically relevant sources, including other fish (Fish and Mowbray, 1970). (2) The source levels (i.e. sound pressure level in the acoustic axis at 1m distance) of odontocete biosonar signals in nature are much higher than previously thought. Evidence has now accumulated that source levels in nature are 40–50dB above classical values, obtained largely from tank measurements (as compiled by Evans, 1973). Au *et al.* (1974) obtained source levels of 228 dB re 1 μPa pp (peak to peak) from bottlenose dolphins, Thomas and Turl (1990) recorded source levels of 221dB re 1 μPa pp from a false killer whale and Møhl *et al.* (1990) obtained 218dB re 1 μPa pe rms from narwhals (perms is peak equivalent root mean square). Results from the present work follow this convention (Stapells *et al.* 1982). Ultrasonic sensitivity may therefore be expected at levels that have, up till now, been regarded as beyond the physiologically relevant range. These levels are 30–60 dB above the maximum stimulus levels ever used to assess hearing in cod (Offutt, 1974).

The present experiments were undertaken to answer the following questions: are cod sensitive to intense, ultrasonic pulses such as those produced by echo-sounders and toothed whales and, if so, are they sensitive to the ultrasonic component of the spectrum or to the low-intensity, low-frequency component inherent to short pulses? The results obtained under our experimental conditions indicate that cod are indeed sensitive to ultrasonic pulses and that the ultrasonic component is the effective stimulus.

Materials and methods

Experimental animals

Immature cod (*Gadus morhua* L.) 18–36cm in length, labelled G1–G20, were caught in creels at shallow depths (<5m) or by trawling in Århus Bay. The fish were kept in captivity in tanks with recirculated sea water at approximately 12˚C for at least 12 days before experiments.

The experimental procedure used was the classical cardiac conditioning technique, where the conditional response, bradycardia (slowing of the heart rate), is established by coupling of the sound stimulus with a mild electric shock (Otis *et al.* 1957). The fish were anaesthetized in a 1:10000 solution of ethyl-*p*-aminobenzoate (Benzocaine, Sigma) in sea water. 0.8mm silver wire electrodes coated (except for the tip) with polyvinyl chloride (PVC) for electrocardiogram (ECG) recording were inserted ventrally and fastened with a suture. After anaesthesia, the fish were allowed to recover for at least 6h before testing began. Each fish was first tested for sensitivity to sound in the 200–300Hz range (stimulus duration 10–15s). Only fish that could be conditioned to audio frequencies were tested for ultrasonic sensitivity (15 out of 20).

The ECG signal was amplified by Grass P15 preamplifiers and, when required, bandpass filtered at 25Hz by a Krohn-Hite filter (model 3550). The signal was then led to a Gould OS250A oscilloscope, set to be triggered by the QRS-component of the ECG. The time of triggering occurrence was logged by a computer with a resolution of 10ms and was used for heart rate determinations.

Testing was performed in an anechoic tank approximately $1\,m^3$, with a reflection coefficient of less than 0.1 (i.e. reflected signals were $-20\,dB$ relative to incident signals) in the 20–200 kHz range. The tank was built according to principles given by Bjørnø (1972). Inside the tapwater-filled tank was a 37.5 l chamber containing recirculated sea water, aerated and maintained at 11–13°C by equipment outside the anechoic tank. The chamber was made of sound-transparent PVC. The fish was loosely restrained within this inner chamber by a tubular cage of open mesh PVC (Fig. 1).

Psychophysical procedure

A trial was initiated by 30 s of pre-stimulus heart rate monitoring, followed by a stimulus period of 10–15 s ending with an electric shock (4–10 V d.c., 200 ms). The response was considered positive if any of the heartbeat intervals during the stimulus period exceeded by a factor of 1.1 the longest of the heartbeat intervals included in the 30 s pre-stimulus period. The pre-stimulus period usually contained 18–25 heart beats. The procedure and criterion are basically the same as those used by Sand and Karlsen (1986). To avoid temporal conditioning, the trials were initiated at pseudo-random intervals of 3–8 min. Conditioning was considered complete when five consecutive positive responses were obtained.

Thresholds were determined using a staircase technique (e.g. von Békésy, 1947). By decreasing the stimulus level by 3 dB after a positive response but increasing the stimulus level by 3 dB after a negative response, we obtained a series of stimulus level reversals bracketing the threshold. Threshold estimates were calculated as the mean of the midpoints between the negative and the following positive reversals in the series and were usually based on six such midpoints. Because the animals often stopped responding after prolonged testing, these sessions were separated by 20–60 min. For each stimulus type, enough sessions were carried out to obtain a threshold estimate with an s.e.m. (standard error of the mean) of less than 2 dB. Timing, heart rate monitoring, data collection and administration of the electric shock were computer-controlled; in some sessions,
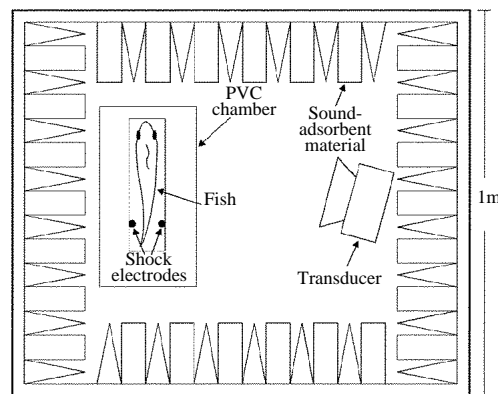

Fig. 1. Diagram of the anechoic tank, with fish, PVC chamber and transducer. All tank surfaces, including the lid, were lined with sound-absorbent material (butyl rubber loaded with aluminium and cork powder).

adjustment of the stimulus levels was carried out by the experimenter, but in most sessions this was also computer-controlled, making unattended testing possible and thereby eliminating the possibility of false clues mediated inadvertently by the experimenter.

When the stimulus level approaches threshold, the response of an animal becomes erratic and variable (e.g. Wodinsky and Tavolga, 1964; Francis, 1975). Because of this, and possibly because of sporadic background noise (the acoustic tank was not isolated from the floor), the fish would sometimes show spontaneous bradycardia in the absence of experimental stimulation. Therefore, a criterion for acceptable stability that caused the computer program to reinitiate trials if the heart-beat intervals varied by more than 75% in a 30s pre-stimulus monitoring period was set up. This empirically obtained value ensured that almost all ordinary variation passed, whereas pronounced bradycardia caused reinitiation. The criterion also served to stop a session in the case of ECG signal dropout and other irregularities. The mean rate of reinitiated trials for all sessions was 6.2%.

Stimulation

Two methods were used for ultrasonic stimulation. The first method was based on a Simrad EK-38/22E scientific echo-sounder unit. The transducer is a ceramic unit with a plane active surface of approximately $25\text{cm}\times15\text{cm}$, tuned to 38kHz ($Q$, i.e. centre frequency, divided by the 3dB bandwidth, was 13). The transducer was mounted 50cm from the fish. This unit provided pulses with durations between 0.3 and 3ms and sound levels at the fish's position of up to 224dB re 1 μPa. The pulses were shaped only by the Q of the transducer. The second method used the same transducer, but the signal was generated by conventional electronics and amplified by a specially built power amplifier. This allowed for control of pulse shape, but the maximum level attainable was only 206dB re 1 μPa for stimulus durations shorter than 3ms and 203dB re 1 μPa for stimulus durations longer than 3ms. Pure-tone stimuli (duration 8s) and pulsed stimuli were generated this way. Shaped stimuli were generated by adding a custom-made shaper to this equipment.

Sound levels as a function of input to the transducer were measured as free-field values (fish absent) with a Brüel & Kjaer (B&K) 8103 hydrophone at a position corresponding to the head of the fish. The hydrophone was calibrated against a B&K 4223 calibrator. Except for 8s stimuli (continuous), the repetition rate for all pulse types within the 10–15s stimulus period was 1Hz.

The homogeneous part of the sound field in the anechoic tank at the position of the fish was restricted (within 3dB at 7cm from the centre of the sound field, and within 9dB at 16.5cm from the centre of the sound field). The transducer cannot be regarded as small because the difference in distance from a point in the sound field at the position of the fish and two widely separated elements in the source is not negligible compared to the wavelength of 3.9cm. Consequently, sound pressure and particle displacement cannot be expected to be exactly in phase at all points. Therefore, the sound field is not quite homogeneous, and estimating the precise intensity is complicated. However, far-field measurements of sound pressure from the transducer, made in a harbour, gave values within 1dB of those obtained in the tank. This legitimizes the use of sound pressure as an estimate of the effective sound intensity for the tank experiments.

To test for a possible near-field effect at the normal transducer-to-fish distance of 50cm, one cod was tested under far-field conditions (250cm between transducer and fish) in a yachting harbour.

Possible stimulus artefacts

A major difficulty in an investigation of this kind is the generation of a powerful, ultrasonic stimulus without accompanying energy below 500Hz, and/or in other modalities, such as vibrational, electric and magnetic ones. With regard to audio components, we are looking for ultrasonic sensitivity at levels roughly 120dB above threshold at best frequency in the audio range. One source of such energy is inherent to the use of pulsed sounds: short-duration pulses with fast rise and fall times will have a broad spectrum extending into the audio range, whereas pulses with gently tapering leading and trailing edges will have their energy confined close to the frequency of the carrier wave. The dynamic span of 120dB between the ultrasonic and possible audio components of interest poses problems for direct measurements of possible off-frequency false clues. Theoretical analysis of 3ms pulses from the sounder indicated that energy could be present at 80dB re 1 μPa, i.e. above known pure-tone thresholds for the cod at audio frequencies (Chapman and Hawkins, 1973; Offutt, 1974). The analysis did not take into consideration possible effects of integration time, for which values considerably longer than 3ms have been found (Hawkins, 1981; Fay and Coombs, 1983).

To verify the analysis, a B&K 8101 hydrophone (calibrated against a B&K 4223 calibrator) was placed at the position of the fish, and the transmitting transducer was turned 90° to weaken the ultrasonic component relative to the audio frequency component that is omnidirectionally radiated. Input to the transducer corresponded to a stimulus 6dB above average threshold with normal transducer orientation. A passive low-pass filter attenuated the 38kHz component of the recorded signal by 80dB, before it was applied to a one-third octave filter (B&K 2112) set at centre frequencies of 25, 40, 80, 160, 250 and 400Hz. The output of the filter for 256 pulses was then averaged by a HP 54600A oscilloscope. In this way, the low-frequency component of unshaped pulses was detectable with the values shown in Fig. 2, whereas shaped pulses with rise times of 10ms and longer had no detectable energy. Also, for six fish, some of the threshold determinations were carried out with a continuous noise masker in the audio range added as background (Fig. 2).

To test for a number of false clues, the transducer was rotated 90° after threshold determination. This lowered the ultrasonic sound pressure at the fish's position by 25dB. One or more sessions were then carried out with the input to the transducer corresponding to at least 6dB above the most recently established threshold estimate. Positive responses would suggest that stimuli other than the ultrasonic one were effective.

Results

Fifteen cod passed the audio frequency screening test and were tested for ultrasonic sensitivity. All showed conditioning to 3ms, 38kHz pulses from the EK38/22E echo-

sounder unit. For five fish, the number of training trials required to reach the criterion (five consecutive, positive responses) was on average 54% fewer for ultrasound than for the initial training at audio frequencies. Threshold estimates were obtained for twelve animals (Fig. 3). The standard procedure was first to test the animals for sensitivity to 3 ms pulses. A total of 52 threshold estimates was obtained at this reference duration, giving a mean value (based on individual midpoint values) of 194.4dB re 1 μPa (s.d. 5.4dB, s.e.m. 0.3dB). For nine fish, comparisons could be made between the first and the second estimate obtained. For seven fish, the first estimate was on average 5.5dB higher than the second, suggesting a learning effect. These seven estimates are included in the grand mean of the 3ms data because removing them changes it by less than 0.5dB. In two fish, the situation was the reverse, with the second estimate being an average of 3.5dB higher than the first.

Twenty-six threshold estimates for five fish (G7, G9, G16, G17, G20) were obtained for shaped sound pulses (rise/fall time 10ms or more) with durations ranging from 10ms to 8s (Fig. 3, triangles). For 22 of these, comparisons could be made with threshold estimates for unshaped 3ms pulses, obtained within the same 24h. The mean difference found was +1.9dB (s.d. 1.9dB) with a maximum difference of +5.1dB (shaped relative to unshaped). The mean value (based on individual midpoint values) of all threshold estimates for pure-tone stimuli (8s) was 190.9dB re 1μPa (s.d. 3.4dB, s.e.m. 0.5dB, four fish, eight sessions), but this value may be an underestimate, because only fish with fairly low thresholds could be tested using stimuli longer than 3ms.

For six fish (G7, G8, G9, G16, G17, G20), some of the threshold determinations were performed with a continuous audio noise masker added as background. Comparisons with unmasked thresholds obtained within 24h for the same stimulus type could be made for seven sessions and showed a mean difference of −0.7dB (s.d. 1.5dB) with a maximum difference of +2.5dB (masked relative to unmasked).

For two fish (G1, G7), considerably higher threshold estimates were obtained for stimulus durations shorter than 3ms, suggesting time integration phenomena (Fig. 4). The slopes of the regression lines fitted to the data for stimuli shorter than 3ms were −2.8 dB and −2.7dB per doubling of duration ($r=-0.89$ and $r=-0.77$, respectively), approaching the expected value of an ideal energy integrator (−3 dB per doubling of
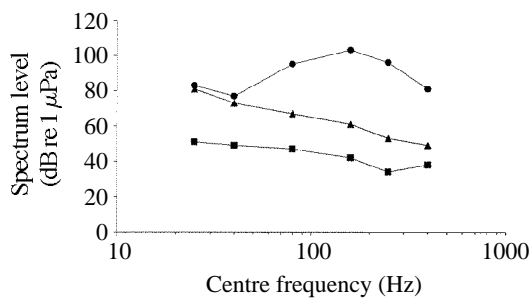

Fig. 2. Background noise (triangles), the low-frequency component of unshaped 38kHz sound pulses (squares) and the audio masking level (circles) plotted against frequency. All values are spectrum levels.
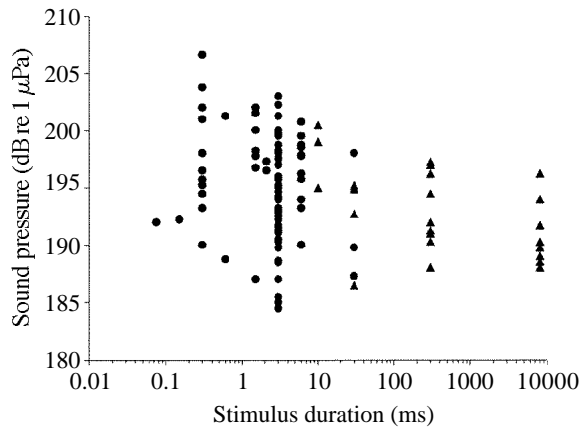
Fig. 3. Threshold estimates plotted as a function of stimulus duration. Circles, threshold estimates for unshaped pulses; triangles, threshold estimates for shaped pulses. Total number of threshold estimates was 122.

duration). Threshold estimates for G7 were obtained in the presence of the noise masker. For the remaining four fish (G9, G16, G17, G20) that were tested for a stimulus duration of 0.3ms, there was a difference of +2.4dB (s.d. 0.8dB) between average estimates for 0.3ms and 3ms stimulus durations.

Seven out of eight cod tested with the transducer rotated by 90° stopped responding. The one dubious case (G6) is dealt with below.

One cod (G20) was also tested in a harbour, using 3ms pulses from the EK38/22E echo-sounder. The fish was 250cm from the transducer and the sound pressure at the fish's position was 202dB re 1 μPa. The cod met the standard criterion for reaction to ultrasound, both in the harbour and in the tank.

Of the 15 fish tested, two fish (G2, G18) died after conditioning, but before any threshold estimates could be made. One fish (G6) showed extreme variability, with
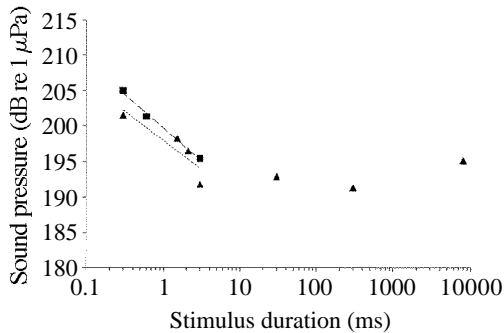
Fig. 4. Data from two fish (G1 and G7) showing time integration phenomena for stimulus durations shorter than 3ms. Squares, G1, mean threshold values; triangles, G7, mean threshold values. Regression lines (on midpoint values): G1 (dashed line), −2.8dB per doubling of duration, $r=-0.89$; G7 (dotted line), −2.7dB per doubling of duration, $r=-0.77$.

responses at 200dB re 1 µPa at times, whereas at other times no responses could be obtained even for sound pressures as high as 224dB re 1 µPa. This made valid threshold estimates impossible. Furthermore, with the transducer rotated 90˚, this fish responded in five consecutive trials of one session, but in a follow-up session of 40 trials no positive responses were recorded. Another fish (G19) showed less stable conditioning when the noise masker was used, and valid threshold estimates for this condition were not obtainable because of equipment limitations. This fish could not meet the conditioning criterion for shaped pulses (five consecutive positive responses), but a response rate of 41% was nevertheless obtained for a stimulus level of 203dB re 1 µPa, considerably above the spontaneous response rate (146 trials, trial re-initiation rate 7%).

A general problem was the limited maximum output level of the conventional electronics equipment relative to the thresholds. For fish with high thresholds, this prevented us from pursuing some problems such as time integration phenomena. Obtaining thresholds to shaped pulses with long rise/fall times and long durations for insensitive fish was also not possible.

Discussion

The main result of this study is the qualitative demonstration of sensitivity to ultrasound. The data show some inter- and intra-individual variation. Several possible sources for this variation exist. (1) *Sound field*. Because the fish was not completely restrained and because the homogeneous part of the sound field was restricted, the sound intensity impinging on the fish would depend on the animal's position inside the cage. However, before placing the fish in the acoustic tank, care was taken to place the front of the fish cage in the centre of the sound field (assuming a rostral receptor position). The fish should not be able to move its head more than a distance corresponding to a variation of 3dB. (2) *Psychophysical method*. The heart rate response is a startle response, illustrated, for example, by the observation that it can already be present in the first trial. Such responses are unstable (Francis, 1975) and there is no simple, reinforceable coupling between perception and response. For the qualitative aspects of the present investigation ('are cod able to detect ultrasound?'), the method is adequate because conditioning to ultrasound was demonstrated in all 15 specimens. (3) *Modality*. This is determined by the 'label' of the neurones carrying the information to the central nervous system. The mechanism by which the cod perceives ultrasound is not obvious. The very intense stimulation required may have stimulated sense organs for modalities other than sound, probably with different thresholds.

Although detection of intense ultrasound by humans is mediated by the cochlea and is perceived as audio sound (Pumphrey, 1950), evidence for a similar mechanism in the cod is ambiguous. Consistent with the sound modality hypothesis is the observation that, for five fish, the number of training trials required to reach the criterion (five consecutive positive responses) was on average 54% fewer for ultrasound than for the initial training at audio frequencies. This can be interpreted as coupling or association. The overall picture, however, is blurred by the inter-individual variation and by the fact that the conditioning method uses a startle response. The observation of a low integration time of

3 ms (when observable at all) is very different from both the cod's and the goldfish's audio frequency integration time of several hundred milliseconds (Hawkins, 1981) and approximately 700 ms (Fay and Coombs, 1983), respectively. Moreover, audio masking had no effect on the ultrasonic thresholds. Both of these observations are inconsistent with the hypothesis that the normal auditory system reacts to ultrasound.

A number of observations suggest that the cod were indeed responding to the primary ultrasonic, acoustic stimulation and not to secondary effects. These observations are: (1) the negligible difference in thresholds for shaped and unshaped stimuli; (2) the negligible difference in thresholds obtained with and without audio masking; and (3) the absence of a response after 90° rotation of the transducer. All three observations suggest that the response was not caused by a possible low-frequency tail of the stimulus spectrum, or by some other unintentional cue(s). Especially for the shaped pulses, a completely different threshold value should have been obtained if the response was caused by a low-frequency tail, because the low-frequency energy of such pulses was 30–40 dB lower than that of unshaped pulses. The aberrant response pattern of one fish (G19, dealt with above) suggests a more complicated picture, but is more likely to be a result of the loose coupling between perception and response.

We, like Offutt (1968), suggest that the observed ultrasound detection ability may have evolved as a means of warning against toothed whale predators, similar to the way that the ultrasound hearing mechanisms seen in several orders of insects protect them from bat predators. Although the demonstrated ultrasound detection ability clearly requires observations in the field before a function (such as a predator warning mechanism) can be considered established, we would like to point out that the low sensitivity is not inconsistent with such a mechanism. In the aerial environment where the bat–moth interactions take place, sound propagation is poor and natural sources of ultrasound other than bats are infrequent. Insects' sensitive, but unsophisticated, ultrasonic detectors therefore have low rates of false alarms. In the sea, sound propagation is very good and sources other than odontocetes (e.g. biological ones, such as snapping shrimps, and geophysical ones, such as cracking ice) also generate ultrasound. Therefore, a simple detector will have to be insensitive to reduce the number of false alarms.

The threshold values obtained, including those with short duration pulses (Fig. 3), indicate that cod can detect echolocating odontocetes at a range of 10–30 m. This appears reasonable for the proposed function as a predator warning mechanism. Because of technical constraints only one frequency, 38 kHz, was tested. Lack of knowledge of sensitivity as a function of frequency somewhat limits the inferences that can be made. The simplest assumption about the sensitivity function, however, is that it is fairly flat, like the one known for human sensitivity to ultrasound (Corso, 1963). The echolocation signals of most odontocete species have broad-band characteristics (Au *et al.* 1974, 1985), which means that the estimated detection range is not markedly affected by the fact that the main energy of odontocete clicks is often at frequencies higher than 38 kHz.

The results also indicate that cod can detect echo-sounders at similar ranges (10–30 m). This may have implications for the use of echo-sounders by the fishing fleet and for acoustic investigations of fish population size.

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