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A Case for Passive Sonar: Analysis of Click Train
Production Patterns by Bottlenose Dolphins
in a Turbid Estuary

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Introduction

The use of a sophisticated echolocation system to navigate and to discriminate prey and other targets has been demonstrated in many odontocetes (for reviews and

comparisons with the bat's systems, see Au 1993, 1997, and the introduction to this volume). This active sonar capability is based on the emission of short, broadband clicks, usually in trains, and on the interpretation of their echoes, providing the echolocating animals, and also

their companions, with detailed information about their environment.

In the best-studied species, the bottlenose dolphin (*Tursiops truncatus*), peak frequencies of clicks are at around 70 kHz (interestingly close to its frequency of best hearing). Detection of the broadband pulses of this species is somewhat facilitated by their energy levels at relatively low frequencies. In four examples of bottlenose dolphin clicks represented in fig. 3 of Au 1997, at 20 kHz the relative amplitude levels were approximately 70%, 50%, 50%, and 20% of the respective peak frequencies.

THE MIXED BLESSING QUESTION

Several researchers have reported instances in which odontocetes did not take advantage of their echolocation ability, either because it simply was not necessary, or because it might have been more adaptive to be quiet. A classical example is that described by Wood and Evans (1980) of Scylla, a bottlenose dolphin being used in the experiments of Diercks et al. (1971). Still blindfolded after the procedures, Scylla was observed following closely and capturing a live fish, several times, surprisingly without the emission of clicks.

Evans and Awbrey (1988) reported an observation of a group of beluga whales (*Delphinapterus leucas*), in turbid waters, feeding on salmon apparently without echolocation. Usually very vocal odontocetes, these belugas were silent throughout the episode. It is likely that the belugas were able to track the fish, like Scylla, using the sounds and pressure changes made by the moving prey.

Another relevant example is that reported by Barrett-Lennard, Ford, and Heise (1996) from killer whales (*Orcinus orca*); these authors compared click train production by groups feeding on fish and by groups feeding on aquatic mammals. It was observed that the latter killer whale groups emit significantly less echolocation signals, preferring apparently to detect and approach their prey with passive audition alone, perhaps because aquatic mammals can hear their clicks.

The serious fact that so many dolphins get trapped in fishing nets they could easily detect using echolocation (Au and Jones 1991) also shows the need for a better understanding of the ecological context of sonar production. In what circumstances will dolphins use the full potential of their specialized sonar system? Under what conditions may they rely on other sensory channels, or on passive audition? Borrowing the phrase used by Fenton (1980) to describe the same problem faced by bats, how do they manage "the mixed blessing of echolocation"? When will they avoid the shortcomings of active sonar and use more stealthy ways of creeping up on their prey?

Other researchers have focused on these partially unanswered questions, as other chapters in this section of the book illustrate. The purpose of this chapter is to contribute to the discussion of these bioacoustical issues by presenting data collected as part of a study of the

acoustic emissions by the bottlenose dolphins resident in the Sado Estuary, Portugal.

Materials and Methods

The Sado Estuary and the adjacent coastal waters, along the western coast of Portugal, sustain a resident population of bottlenose dolphins, of the Eastern Atlantic robust form, who enter the estuary mainly to feed (dos Santos and Lacerda 1987). The population has been declining in the last decades, apparently due to high infant mortality, and now there are about 35 resident animals. Descriptions of the area have been provided by dos Santos and Lacerda (1987) and dos Santos (1998).

Although a busy harbor, a city, many industries, and agriculture generate a great deal of pollution, the dolphins find in the turbid waters of the estuary several species on which they feed. The more important prey species are probably the mullets (*Mugil cephalus*, *Liza ramada*, *Liza aurata*, and *Chelon labrosus*), cuttlefish (*Sepia officinalis*), eels (*Anguilla anguilla*), and shad (*Alosa fallax*). Other locally abundant species that have not yet been identified as dolphin prey include the Lusitanian toadfish (*Halobatrachus didactylus*).

The dolphins were followed in a small boat with an outboard engine, in trips lasting between 30 min and 6 h, during which a nonintrusive distance was maintained (usually >50 m). Behavior sampling was ad libitum, and the recording method was either continuous or with scans every 5 or every 10 min, depending on dolphin movements or position.

Underwater sound recordings were made with a B&K 8101 hydrophone and a Sony TCD-D10 Pro DAT recorder, a setup that is flat up to 22 kHz. Obviously, this equipment will only record the lower frequency component of the sonar clicks. Fortunately, we were able to verify in the field that the bottlenose dolphin clicks really are broadband and that their lower frequency component must be nearly omnidirectional. In fact, our sensitive hydrophone detected clicks up to a few hundred meters from the dolphins, even if they were facing away from it. Note that we only wanted to study the occurrence pattern of the clicks, not their acoustical properties. So we assumed for the purpose of the present analysis that, although our instrumentation was suboptimal, we recorded the lower frequency components of all sonar click trains produced by the dolphins near the boat.

This part of our larger study used samples recorded on 13 different days, in 1992, 1993, and 1995, in five different months. These tape segments were selected because they had good signal-to-noise ratios, complete commentary on the animals' positions and behavior, and samples of the different activity patterns in almost all of the habitat subareas.

Sound analysis was performed initially using the package Hypersignal-Workstation (PC-based), digitizing the signals with a 12-bit Data Translation A/D board,

with a sampling frequency of 44.1 kHz. More recently, Canary 1.2.4 has been used, and the signals have been digitized at the same sampling frequency by the in-built sound board of a PowerMacintosh 7100.

The sound segments selected were arbitrarily divided in one-minute samples. In the 447 one-minute samples obtained, signals were carefully counted by two researchers, using waveforms and sonograms whenever necessary (especially when trains overlapped). Signal occurrence was quantified using the categories “click trains,” “burst pulses,” “bray series,” “bangs,” “whistles,” and “total number of vocalizations” (dos Santos 1998). Analysis of these counts and the other variables (e.g., group size, activity, and zone) included Spearman rank correlations, and simulation statistics using the program ACTUS for contingency tables (Estabrook and Estabrook 1989).

Results

Recordings were made near groups of dolphins engaged in various activities. Using behavioral criteria such as division in subgroups, proximity among animals, directionality and speed of the group’s movement, dive sequences, aerial behaviors, and visibility of prey, five classes of general activity patterns were identified. These were “Travel” (rapid, linear displacement), “Travel/foraging” (zigzag displacement, long dives), “Disperse foraging” (animals quite spread, variable behaviors, some feeding events), “Surface group feeding” (aroused feeding around the same area), and “Social interactions at the surface” (aroused behaviors, with physical contacts and no prey visible).

As to the acoustic production, the average number of signal units (click trains, bray series, etc.) recorded near the groups per minute was 16.6, but in 20.6% of the one-minute samples no signals were detected.

The distribution of the abundance of click trains sample was also different from the expected. Not only did 23% of the samples have zero echolocation clicks, but a considerable 44% contained less than five click trains (fig. 55.1). So we created two nominal categories of train abundance: “Low train occurrence” (to include all samples with less than five click trains in one minute) and “High train occurrence.” We then compared the distribution of these two categories of click train abundance with the occurrence of the various behavioral patterns. Having the data thus organized in a contingency table, the table was tested for independence using simulation statistics. This demonstrated that lines and columns are not independent ($p < 0.001$), specifically because of the results in those cells denoted with asterisks (table 55.1). Low train occurrence was more frequent than expected in Travel and Travel/feeding. High train occurrence was only more frequent than expected in Disperse feeding, where a diversity of behaviors is usu-

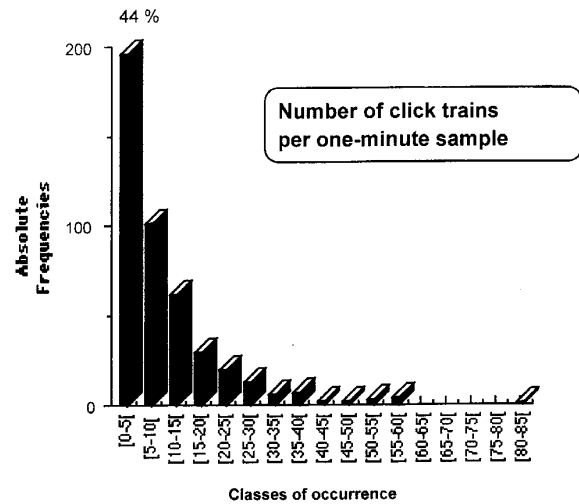


Fig. 55.1. Distribution of the abundance of click trains per sample

TABLE 55.1. Distribution of samples with less than five click trains (Low train occurrence) and more than five click trains (High train occurrence) per one-minute sample, in the various activity patterns, and results of contingency table analysis with simulation statistics (ACTUS). Asterisks denote significant cells.

Activity pattern	Low train occurrence	High train occurrence
Travel	15 ($p = 0.037$)*	5
Travel/feeding	151 ($p < 0.001$)*	110
Disperse feeding	25	107 ($p < 0.001$)*
Surface group foraging	5	23
Social interactions at the surface	0	6

ally observed in various social subunits, including prey capture at the surface and other aroused activities.

In the samples used for this study, dolphin group size ranged from 3 to 25; the class with the highest number of signal counts comprised 8–12 animals. Our data allowed us to examine the relationship between the number of click trains in a sample and the number of dolphins counted in the group whose behavior was being monitored. That is, how does sonar signal abundance correlate with group size? Also, how does the production of all signal categories correlate with group size? From these data, correlations are null and nonsignificant, both between number of trains and group size ($r_s = 0.04$, $p = 0.43$, $n = 447$), and also between total number of signals in each sample (including the lower frequency pulsed signals and the whistles) and group size ($r_s = 0.018$, $p = 0.71$, $n = 447$).

Discussion

These results raise some interesting questions concerning the use of echolocation signals by bottlenose dol-

phins in this population. It is readily admitted, however, that further studies should use broadband recording systems, or at least some kind of an ultrasound detector, and a more detailed sampling and analysis program. Even with the current limitations, a few points can be discussed.

The null correlations between signal production and group size, contrary to what would be expected, suggest that there might be some restriction mechanism that regulates acoustic production in groups. The absence of a positive correlation between number of possible emitters and number of vocalizations, in any situation and in any sound category, suggests that dolphins might follow some communication and echolocation “emission rule.” Such a rule could help the dolphins to avoid the need to process too many signals of different origins (perhaps like in the conversations among humans).

Especially in the case of sounds with a predominant echolocation function, like click trains, there might exist emission rules possibly based on sex or age or a dominance hierarchy, or alternation routines. Johnson and Norris (1994) speculated that in spinner dolphins (*Stenella longirostris*) there might be a “trading of the duty” to allow each individual the opportunity to rest the emission tissues after intense click production. It would be relevant to point out that this sharing of sonar duties would require that dolphins analyze echoes of clicks emitted by conspecifics. The ability to use bistatic sonar was firmly established by the experiments of Xitco and Roitblat (1996) with the natural clicks of bottlenose dolphins, although it had already been strongly suggested by the experiments of Scronce and Johnson (1976) using artificial pulses.

Considering that visibility is very limited inside the Sado Estuary and that the dolphins spend a great deal of time feeding in turbid water, with no risk of predator interception, the production of sonar signals was globally much lower than expected. Table 55.1 suggests that these dolphins travel and try to find their prey mostly in silence. This means that, for orientation and prey detection, they must be using processes other than echolocation. Vision is certainly useful for tracking landmarks and underwater features in the more shallow or clear areas. Also, vision should allow dolphins to follow prey near the surface. However, visibility is very limited at the bottom of their main foraging grounds, such as in the deep south channel of the estuary. An obvious possibility is that audition, or passive listening (or passive sonar as a submariner would call it), is of more primordial importance to these animals’ feeding ecology than one would predict. In that case, one wonders what reasons there could be for these animals to refrain from using their sonar, in a situation where predator interception of signals is not a risk.

One explanation might be that some preferred preys are difficult to find in the substrate through echolocation, because they hide in nests and in thick debris screens. Other prey species might show avoidance behaviors upon detection of sonar signals; in fact, this may be the case for the shad, *Alosa fallax*. Mann, Lu, and Popper (1997) showed that the related species *A. sapidissima* does detect and avoid sources of ultrasonic signals like dolphin clicks (see also Astrup and Møhl 1993 for the case of cod).

Some possible prey species, like the Lusitanian toadfish, are quite sonorous, and might be easier to find by passive sonar tracking. This toadfish’s conspicuous display calls are produced by males from May to September, the nesting period of the species. The frequencies are rather low, mainly below 700 Hz (dos Santos 1998; dos Santos et al. 2000), but dolphins might be able to detect them at a useful distance. The hypothesis that bottlenose dolphins in the Sado Estuary eavesdrop on toadfish sounds requires further research. It is likely that they prey on the toadfish, considering what is known about equivalent fauna in Florida (Barros and Odell 1990). Playback experiments, at the appropriate pressure levels, could tell us whether dolphins do track these sounds, and at what distances would they be able to detect and locate their sources.

In this context, it is relevant to consider the question of the possible effects of anthropogenic underwater noise—which, in this estuary, shows pressure levels and spectra typical of industrial zones (Ferreira, Bento-Coelho, and dos Santos 1996; dos Santos 1998). If dolphins depend on audition to hear some of their prey, and if the ambient noise or the noise produced by some particular sources overlap in frequency with prey calls and masks them, then the indirect effects of underwater noise might be more stressing for the animals than the direct impacts on their auditory system.

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