Acta Astronautica 105 (2014) 534–537

Contents lists available at ScienceDirect

Acta Astronautica

journal homepage: www.elsevier.com/locate/actaastro

Clicks, whistles and pulses: Passive and active signal use in dolphin communication

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ARTICLE INFO

Article history:
Received 28 November 2013
Received in revised form
13 June 2014
Accepted 1 July 2014
Available online 8 July 2014

Keywords:
Animal communication
Dolphins
Signals
Information
SETI
Astrobiology

ABSTRACT

The search for signals out of noise is a problem not only with radio signals from the sky but in the study of animal communication. Dolphins use multiple modalities to communicate including body postures, touch, vision, and most elaborately sound. Like SETI radio signal searches, dolphin sound analysis includes the detection, recognition, analysis, and interpretation of signals. Dolphins use both passive listening and active production to communicate. Dolphins use three main types of acoustic signals: frequency modulated whistles (narrowband with harmonics), echolocation (broadband clicks) and burst pulsed sounds (packets of closely spaced broadband clicks). Dolphin sound analysis has focused on frequency-modulated whistles, yet the most commonly used signals are burst-pulsed sounds which, due to their graded and overlapping nature and bimodal inter-click interval (ICI) rates are hard to categorize. We will look at: 1) the mechanism of sound production and categories of sound types, 2) sound analysis techniques and information content, and 3) examples of lessons learned in the study of dolphin acoustics. The goal of this paper is to provide perspective on how animal communication studies might provide insight to both passive and active SETI in the larger context of searching for life signatures.

1. Introduction

Dolphin communication is both complex and contextual [1]. Dolphins communicate using both vocal and non-vocal signals including visual, tactile, kinesthetic, and chemoreceptive [2] including cross-modal abilities [3]. Because of the highly developed acoustic sense in dolphins, researchers have emphasized the recording and analysis of vocalizations [4]. Dolphin sound production and reception are highly directional in both frequency and intensity [5]. Dolphins produce two sounds simultaneously producing clicks on the right side and whistles on the left side [6]. Dolphins are also capable of internal sound pointing by reshaping their sound focusing organ (the melon) and parameters including frequency, intensity, and duration can all be modulated independently, providing opportunity for detailed encoding of information [7]. The directional nature of dolphin sound adds a complication to many studies and requires triangulation involving multiple hydrophones or separation of individuals during recording.

Dolphin sounds are divided into three primary categories: Whistles, clicks, and burst pulsed sounds. All sounds can be used socially while echolocation is thought to be primarily for navigation and hunting. Spectrally distinct sound types include 1) Whistles – primarily social communication including *frequency-modulated whistles, amplitude modulated whistles and whistle squawks,* 2) Clicks – navigation and orientation including *echolocation click trains*, and *buzzes* and 3) Burst pulsed sounds – primarily social sounds including *squawks, barks and pops*. Recently discovered

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http://dx.doi.org/10.1016/j.actaastro.2014.07.003
0094-5765/

synchronized vocalizations include *squawks, screams,* and *brays*, and show prosodic elements to dolphin communication. Dolphins also make in-air vocalizations including *chuffs, raspberries*, and non-vocal impulse sounds including *jaw-claps, tail cavitation, tail slaps*, and *bubbles* [8].

Dolphins are both predator (on fish, squid) and prey (sharks, orcas) and use both passive and active sonar. Hearing sensitivity is excellent and many species produce signals with a bi-modal frequency bands around 40–50 kHz and 130–140 kHz [9]. But when do dolphins listen passively and when do they actively search? Passive acoustic vigilance and "eavesdropping" on neighbors allows for information sharing from one individual to another without cost, while active vigilance via echolocation is used for final targeting of prey or clarification of information already passively detected. However, the costs of active vigilance may have a cost as it does for other species [10].

The need for stealth is best exemplified by the use of crypticity by killer whales (*Orcinus orca*). *Resident killer whales* in the Pacific Northwest eat fish and use regularly spaced clicks when hunting their prey, primarily fish that do not hear high frequencies. *Transient killer whales,* that eat small dolphins and porpoise who hear high frequencies, use irregularly spaced click patterns that are hidden in the background noise [11].

2. Measurement techniques and information content

Historically, whistles are the most studied dolphin vocalization because of their ease in measurement. The majority of literature on whistles report *qualitative* comparative visual assessments of frequency contours made by human judges while *quantitative* techniques (Discriminant Function Analysis, Principal Component Analysis) have been occasionally attempted [12]. Neural networks (NN) have been used to quantify whistles, although NN analysis requires *a priori* data to train a computer [13]. Since many datasets may have a low N of whistles this is not a practical technique for many studies. NNs have also been primarily developed for tracking whistles contours, which eliminates the measurement of other important social signals such as burst-pulsed sounds.

Recently passive acoustics have become a popular technique in the field, along with some real-time acoustic tools [14]. Although passive acoustics allows the presence or absence of a species to be detected over large periods of time, it does not address the detailed social or cognition questions posed about dolphins and whales. To compensate for this issue, researchers have used information theory to assess the complexity of dolphin whistles [15,16] although other social signals have not been analyzed using this technique. Little work has been done on analyzing sequences of sound types to look for spatial, prosodic, motif, or rhythmic information although newly emerging literature would suggest that this is an important aspect of dolphin communication [17,18].

Increased understanding of mechanistic and perceptual classification is needed to determine the natural boundaries of signal units and classification by delphinids, as it has been for other taxa [19–23]. Recently analysis of dolphin signature whistles using standard techniques indicate that the separation of fundamental units in whistles may help in the identification of caller ID and the process of communication [24].

Both the presence of referential calls or a graded system of communication, or both, is still unspecified for dolphins. Although some researchers argue that the signature whistle meets the criterion for a reference identifying an individual, the identification and isolation of other fundamental units of sound, potentially referential, within the dolphin signal repertoire, has only recently been attempted using cutting-edge computer techniques [25,26].

Complex syntax, semantics and referential signal use has been found in many species. Studies of alarm calls in wild vervet monkeys [27], ground squirrels [28] and prairie dogs [29] have revealed elements of symbolic referential communication and competence. Similarly, laboratory studies of intra and interspecies referential communication and competence have revealed both semantic and syntactic understanding in common and pygmy chimpanzees [30] and bottlenose dolphins [31]. Dolphins, a non-terrestrial and most alien of social mammals, have the second largest encephalization quotient and complex cognitive abilities [32,33] and have a variety of mechanisms of information transfer [34] and teaching mechanisms [35], and would be likely candidates for such complexity.

Information content has also been explored in the context of interspecies interactions of delphinids. What is the mechanism or process by which two disparate species understand each other? Cross-species communication is also both passive and active. Some species take advantage of their neighbors monitoring abilities and learn the meaning of appropriate alarm calls (birds, primates). Two examples in the dolphin world illustrate the creation of shared/mutual calls during interaction. Resident killer whale pods in the Pacific Northwest have pod dialects. However, when interacting with other pods, they have a small repertoire of shared calls for use with the other group [36]. Recently, the complex dynamics of vocalization used between two species of sympatric dolphins in Costa Rica has been reported, suggesting that they also share types of calls when together and revert back to their own species calls when separate [37]. Both these examples suggest that it is more efficient to create a new communication system with another species than to learn the intricacies of the other's communication signals. Ironically this has been the approach of necessity in human/animal cognitive interfaces due to the lack of understanding of nonhuman animal communication systems. In fact this technique has proven successful for bonobo chimpanzees [30], African grey parrots [38] and, to a limited degree, dolphins [39,40,41]. The question of whether there are universal features of communication across all species, as described for birds and mammals [42], or avenues of sensory system overlap, remains largely unexplored.

When studying other species we often learn of our own biases and assumptions regarding the world around us. The following are four specific examples of lessons we have learned through the field of dolphin acoustics and