

# SIGNAL COORDINATION IN MARINE MAMMALS: CUES FROM THE TIME DOMAIN OF VOCAL INTERACTIONS

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## ABSTRACT

Marine mammals are renowned for a precise coordination of social behaviors. To further elucidate these accomplishments, we investigated the time domain of vocal interactions and also relationships between the quality and the coordination mode of signals. Subjects (n=10) were bottlenose dolphins (*Tursiops truncatus*) which produce several structurally diverse vocalizations: e.g. burst-pulse sounds (bursts) and whistles. Our study revealed that bursts were responded to by bursts only, which occurred status-related within a small time window after stimulus end (latency: ~ 0.2 s). Responses to whistles were status-related too, but occurred with a different timing and more flexible and as either other whistles or directed locomotion. These findings document that the coordination mode of dolphin signals is related to both social and signal class-specific properties. As the time of signal transmission is strikingly short in an aquatic medium, we conclude that marine mammals perform a highly sophisticated form of signal processing.

**Keywords:** Vocal Signaling, Time Specific Interaction, Behavior Coordination, Marine Mammals.

## 1. INTRODUCTION

A coordinated performance of behavior is typical for the social life of animals, and this coordination can be remarkably precise. Such has been shown for various kinds of interactions, e.g. courtship displays or territorial contests, and for many communal activities such as foraging, hunting or traveling, too [1]. From an evolutionary perspective, well-coordinated behaviors can be expected if such performance mode allows group members to tackle a given problem in an optimal way, i.e. more economical and better than just individual-wise [2]. There is evidence that the selective power of this simple principle has led to an evolution of many different mechanisms which guarantee a mutual adjustment of behavior. The mechanisms operate, for example, with either a phasic or a tonic characteristic and can involve even individual or social learning [3]. Additional properties of these mechanisms reflect the diversity of species and also the abundance of biological and social problems that individuals have to manage cooperatively.

There are various methodological strategies to investigate forms of behavioral coordination and to uncover the mechanisms underlying them. A non-invasive and additionally well-established method is to first study the time and pattern specific relationships between the behaviors of two or more individuals. In a second line of research, these relationships can serve then to deduce and test hypotheses about the underlying data processing and its respective mechanisms. This procedure allowed already to successfully ascertain the rules of avian counter singing and dueting, and to elucidate thereby mechanisms controlling these vocal interactions [4]. Its application is especially expedient if the code system of a studied society or species is unknown or information about a given social context is difficult to assess.

Both problems are particularly acute in the study of marine mammal communication and have clearly constrained the progress in this field of research. They arise here, for example, as a consequence of the limited visibility or the extraordinary speed of sound transmission in the water what can impede e.g. the localization of a given caller. There is evidence that such information deficits can be compensated, at least partly and initially, by clarifying how a given vocal signal of one individual is responded to by which signal of another individual and how this process continues [5]. With this as a reference, an inquiry into the time and pattern specific relationships between the vocal signals of dolphins or whales would seem promising.

Cetacean vocalizations are subdivided into seven classes: (a) short ultrasonic 'clicks' used for echolocation, (b) loud 'bangs' addressed to specific prey (fish), (c) the 'songs' of whales, (d) 'whistles', (e) 'burst-pulse sounds', (e) low-pitch sounds ('gulps'), and 'noisy sounds'. Whistles and pulsed sounds are widespread across species, play crucial social role and thus should be termed 'calls' [6][7]. According to structure and functional properties, these calls can be specified as follows: Whistles are pure-tone signals with a duration of about one second or more and a frequency envelop that usually ranges between 1.5 kHz and 27 kHz. They reach very far, but are used in close contact too. Pulsed sounds, on the other hand, have a more complex structure, i.e. each pulse consists of a burst of elements that can contain both low-frequency and high-frequency components. They are applied in close

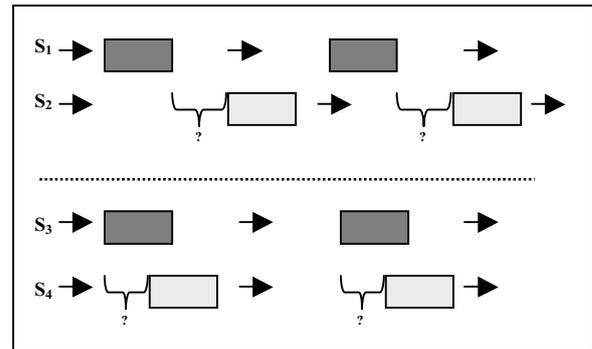
contact and seem to mediate agonistic messages. However, this function is not really clear, yet.

The major body of research published on the vocal communication of marine mammals concerns bottlenose dolphins (*Tursiops truncatus*), and most of it has focused on features and functions of their so-called signature whistles [8]. Additionally, signal parameters of other whistles and their relation to social contexts were studied as well [9]. Since about 15 years, however, a growing number of studies are addressing also the vocalizations of killer whales (*Orcinus orca*). This research concentrated basically on the inter-group function of whistles and pulsed sounds, with a special focus on the development and use of vocal dialects [10]. To supplement these various approaches, we are advertising now a different line of research which can be conducted with bottlenose dolphins and killer whales as well. It is based on results of a long-term study that was performed in a large open-sea enclosure and provided data about both the vocal interactions of group members and vocal responses to specific playback experiments. Here, we describe the design and some crucial results of our study.

Our inquiry into the rules and mechanisms of cetaceans' interactions addressed especially the following three questions. First, which call pattern would individuals use when responding to a group member's vocalization? Would they preferentially vocalize the same type or a different pattern? Second, would individuals respond within specific latency intervals? And, would the latencies of responses to whistles differ from the latencies of responses to pulsed sounds? Finally, would the latencies reflect time specific relationships to the start or the end of a stimulus signal? Studies on vocal interaction of other animals suggested already that answers to these questions can indeed be crucial for a better understanding of the rules of signal coordination in these marine mammals. To give an example: Data documenting an active temporal overlap of signals would point to an agonistic quality of a given vocal interaction [5].

## 2. METHODS

The study was performed with a group of bottlenose dolphins (*Tursiops truncatus*) living in the semi-free confinement of the Dolphin Reef (Eilat) located at the Northern part of the Red Sea. The site provided excellent conditions for a longterm study of social behaviors and also specific playback experiments: First, the dolphins' behavior and all experiments were monitored from a laboratory that provided access to an observation platform 10m above the dolphin area. This allowed us a continuous multi-channel recording of the individuals' activities and signaling. Second, all dolphins (group composition: 1, 3 adults; 2, 2 juvenile; 2,0 calves) had been studied beforehand [11] and were well known individually. Finally, the enclosure was large enough (> 10.000 m<sup>2</sup>) to allow for long distance stimulation, including e. g. a clear assessment of stimulus induced approaches towards a loudspeaker.

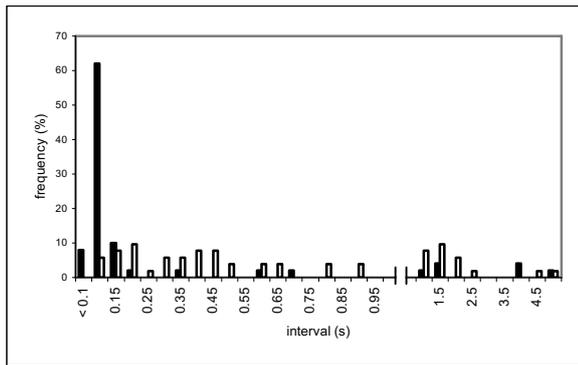


**Figure 1:** Models of two typical interaction processes. Brackets illustrating our measurements of latency intervals (question marks). Bars = symbols of vocal signals. Top: Alternating signal performance. It results if one or both individuals respond to the end of a perceived signal. Bottom: Overlapping signal performance. It results if one individual responds before the end of a perceived signal. Note: Frequency distributions of latency data allow to assess instances of turn-taking or deviations from this rule.

Sampling and analyzing behavioral data followed classical methods [11][12]. The recording device comprised (a) an underwater video camera (H8 Sony CCV 820) located close to the loudspeaker, but inside the dolphin area, (b) a supervision video camera (Hitachi KP-C551 CCD) located at the roof of the observation tower, (c) two hydrophones (Bruel & Kjaer 8103; Magrec HP/30) connected to (d) two multi-channel recorders (VHS Panasonic AG-7350 and NV-SD45). The components of this system operated in parallel during each experiment. All people involved in running the recording system or observing the dolphins by eye were trained and tested beforehand.

During our playback experiments, dolphins were presented with (a) the signature whistle of a dolphin who had left the group some weeks before the experiments or (b) whistle-like sound patterns which we synthesized by Avisoft software and therefore were regarded as 'unknown to the dolphins'. The stimuli belonged to one of the following classes: DH = contour 'down→horizontal', HU = contour 'horizontal→up', HH = contour 'horizontal only'. These signals were given in a random order during different experimental sessions and with a time interval of more than three minutes between consecutive playbacks. Every test contained a playback of only one single signal and was started only when it was certain that all dolphins were far apart from the location of the speaker (> 30m).

In either kind of approach we concentrated especially on measuring and analyzing of time data, i.e. the intervals between a stimulus and the onset of a subsequent signal (Figure 1). Statistical significance of relationships between variables was tested by ANOVA and  $\chi^2$ -methods.



**Figure 2:** Frequency distribution of silent intervals measured between calls (here: burst-pulse sounds) that two dolphins had vocalized alternately (measurement: signal end to start of subsequent signal). Filled columns: latency data of a female. Vacant columns: latency data of a dominant male (see Fig.1, top).

### 3. RESULTS

#### 3.1 Burst-pulse sounds

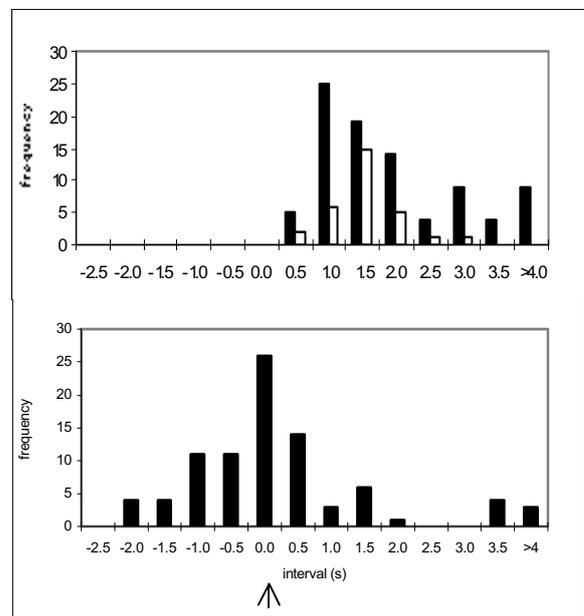
Analyses of ad libitum data showed that performances of bursts were difficult to predict and usually short in duration. We observed, however, that they occurred more frequently if two dolphins encountered each other in a frontal position at a gate. Such a gate seemed to establish a virtual boundary with one individual on either side. As this setting allowed a recording of both the vocal and the non vocal displays of animals by a stationary camera, we analyzed especially material of interactions by pulsed sound recorded at the gate.

Our analyses revealed three results: First, vocal responses to pulsed sounds were always given by bursts of the same pattern quality. Thus there was a kind of vocal matching. In addition, most vocalizations were accompanied by vertical movements known as 'head-jerking' and a release of airbubbles through the blowhole. Second, calls were performed alternating. To further clarify this coordination mode and to test especially whether both individuals contributed equally to this effect, we measured the silent intervals between the end of any given signal and the start of the next signal. Then, the latency data were plotted separately for each individual. Comparison of the resulting frequency distributions revealed a significant difference ( $F_{1,49} = 0.89, p = 0.32$ ), and only the data of one individual allowed to ascertain a clear time specific responding to the end of a perceived signal (Figure 2). This documented that the alternating performance of pulsed sound was predominantly an achievement of one individual, here a female with a dominance status below her counterpart (response latency: 0.2 s).

#### 3.2 Whistles

Analyses of ad libitum data showed that a major part of whistles was performed in a serial manner and such series were usually given by a single individual. In addition, an interactive use of whistles was rare, and many whistles were responded to by nonvocal behaviors, e.g. stimulus directed movements. Therefore, we decided to investigate time and pattern specific stimulus-response relationships by playback experiments (see Methods). Analyses of experimental data, i.e. evaluation of cues extracted from (a) interruptions of behaviors observed before stimulus onset or (b) vocalizations and movements after stimulation revealed the following results:

First, each stimulus category was responded to by at least one dolphin. In none of the trials did any animal show an escape behavior. Rather, dolphins began to approach the area of the speaker (latency: ~ 3s). Categories differed in the proportion of trials that induced a response and also in the quality of responses.



**Figure 3:** Frequency distributions of intervals between stimulus whistles (presented during playback) and the starts of whistles vocalized by a responding dolphin. Top: Measurement between starts of signals. Vacant columns show how many responses overlapped a preceding stimulus. Bottom: Measurement between stimulus end and start of a whistle. Negative time values refer to cases of overlap (Arrow points to interval '0').

Second, responses to a natural whistle (here: signature whistle of a former group member) were extremely strong and performed as whistles and or as rapid approaches to the speaker area. In contrast to such approaches, whistle responses were given by the

dominant male only. The latency of whistle responses was related to stimulus starts and ranged from 1 to 2 s (Figure 3). Additionally, many stimuli were overlapped by responses.

Third, in trials with synthesized stimuli, DH-whistles were more effective (86 %) than HU-whistles (54 %) and HH-whistles (25 %). These effects showed individual- and status related differences. For instance, HU-whistles were preferentially responded to by the dominant male who, without a prior whistle, rapidly approached the speaker area and then remained there for a longer inspection. DH-whistles, in contrast, induced mainly slow approaches of different dolphins, including adult females.

#### 4. CONCLUSIONS

Above all, our study showed that an inquiry into the time domain of vocal interaction provides an expedient methodological tool to elucidate the rules of pattern coordination, even in cetaceans. That is, data representing the time specific relationships between mutually performed signals can indeed allow to better address and eventually uncover the social significance of interactions, including a possible role of nonvocal behaviors. Such can be concluded from our finding that responses to perceived stimuli were preferentially pattern specific and also status-related. As the time of signal transmission is strikingly short in an aquatic medium, latency measurements can be particularly substantial and appropriate for investigating the signal processing of cetaceans. To give an example, the coordination mode of signaling observed in our dolphins reflected a genuine 'turntaking' for burst-pulse sound, but not for whistles that could overlap a given stimulus. As 'overlapping' is a reliable indicator of agonistic responses [4][5], we conclude that only our whistles induced aggressive messages. Interactions by burst-pulse sound, in contrast, did not point to an agonistic motivation of the signaling dolphins. Therefore, an earlier functional interpretation of pulsed sounds has to be revised now.

Our results on the role of whistles merit some additional comments. Signature whistles are regarded as contact calls [8]. However, the whistle that was serving as a natural stimulus had been recorded from a former rival of the responding male. Thus, the frequent overlap of this stimulus was not very surprising. We conclude that the tested male responded to the stimulus as soon as he had recognized the whistle contour, and that he needed about 1 s to manage this task.

The responses to the synthesized whistles point to a different aspect: i.e. they confirmed a hypothesis predicting that the rising shape of a whistle can symbolize an approach (here: encoded in the 'HU' whistle), whereas a falling shape symbolizes a retreat (here: encoded in the 'DH' whistle) [12]. Our results provide the first evidence that cetaceans are able to distinguish such signals and to respond to them like birds and other mammals can do [13]. As signals with an 'up-rising' frequency contour can encode an

agonistic message, it was particularly interesting that only the dominant male approached the source of 'HU'-whistles.

It is clear, that our first inquiry into the time domain of dolphin vocal interactions needs to be complemented by further investigations. However, given the problems that often constrain an elucidation of cetacean communication, we suggest to apply the design also to other species of marine mammals now.

#### 5. ACKNOWLEDGEMENTS

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