eScholarship
International Journal of Comparative Psychology

Title

Exploring Burst Pulses as Indicators of Positive Affect in Bottlenose Dolphins (Tursiops truncatus) During Match-to-Sample Trials

Permalink

https://escholarship.org/uc/item/2zj1r8bf

Journal

International Journal of Comparative Psychology, 38(1)

ISSN

0889-3667

Authors

Royse, Christianna D
Miller, Emma C
Johnson, Christine
et al.

Publication Date

2025-09-26

DOI

10.46867/ijcp.42260

Supplemental Material

https://escholarship.org/uc/item/2zj1r8bf#supplemental

Copyright Information

This work is made available under the terms of a Creative Commons Attribution License, available at https://creativecommons.org/licenses/by/4.0/

Peer reviewed

eScholarship.org Powered by the California Digital Library
University of California

INTERNATIONAL JOURNAL OF COMPARATIVE PSYCHOLOGY

2025, 38
Charles I. Abramson
Editor
Peer-reviewed

Exploring Burst Pulses as Indicators of Positive Affect in Bottlenose Dolphins (*Tursiops truncatus*) During Match-to-Sample Trials

Christianna D. Royse[1], Emma C. Miller[1], Christine M. Johnson[2], & Christine R. Harris[1,3]

[1]Department of Psychology, University of California, San Diego, Gilman Drive, La Jolla, San Diego, California, 92093, U.S.A.

[2]Department of Cognitive Science, University of California, San Diego, Gilman Drive, La Jolla, San Diego 92093, U.S.A.

[3]Center for Academic Research and Training in Anthropogeny, 9500 Gilman Drive, #0060, La Jolla, CA 92093, U.S.A.

The bottlenose dolphin (Tursiops truncatus) vocalizations called “burst pulses” exhibit distinct acoustic properties and can potentially be linked to affective states. This study aimed to determine if dolphins produce burst pulses during match-to-sample with both successful and unsuccessful outcomes and to explore any association with positive affect. We observed that burst pulses occurred in 74% of match-to-sample trials (in which the subject views a sample object and selects the match from a group of alternative objects), with a significantly higher frequency during correct responses. Additionally, there was a notable difference in the proportion of burst pulses occurring before versus after the trainer’s bridge, with more burst pulses occurring before the trainer’s bridge. The timing and characteristics of these burst pulses suggest they may be related to the dolphins’ interest and excitement rather than merely a response to reinforcement. These findings provide new insights into the complexity of dolphin vocalizations and their potential connection to affective states.

Keywords: bottlenose dolphins, burst pulses, match-to-sample, positive affective states, victory squeal, vocalizations

見本合わせ課題におけるバンドウイルカ(*Tursiops truncatus*)のポジティブな感情の指標としてのバーストパルスの探求

バンドウイルカ（*Tursiops truncatus*）の鳴音である「バーストパルス」は、際立った音響特性を示し、感情状態と関連している可能性がある。本研究は、イルカが見本合わせ課題において、成功時と失敗時の両方でバーストパルスを発するかどうかを判断し、バーストパルスのポジティブな感情との関連を探ることを目的とした。我々の観察によると、「バーストパルス」は、見本合わせ課題（被験体が手本となる物体を見て、複数の選択肢の中から一致する物体を選ぶ課題）の 74%で発生し、正解した際の頻度が有意に高かった。さらに、トレーナーのブリッジの前と後でバーストパルスが発生する割合に顕著な違いがあり、ブリッジの前にバーストパルスが発生することの方が多かった。これらのバーストパルスのタイミングと特性は、単なる報酬への反応ではなく、イルカの興味や興奮に関連している可能性を示唆している。これらの発見は、イルカの鳴音の複雑さや、それが感情状態と潜在的に結びついている可能性について、新らたな洞察を提供する。

キーワード：バンドウイルカ、バーストパルス、見本合わせ、ポジティブな感情状態、勝利の雄叫び（victory squeal）、鳴音

Please send correspondence to Christianna D. Royse. Email: cdewind@ucsd.edu

Exploración de las Ráfagas de Pulsos como Indicadores de Afecto Positivo Durante Pruebas de Igualación a la Muestra en Delfines Nariz de Botella (*Tursiops truncatus*)

Las vocalizaciones del delfín nariz de botella (*Tursiops truncatus*), llamadas "ráfagas de pulsos", exhiben propiedades acústicas distintivas y podrían estar relacionadas con estados afectivos. El presente estudio tuvo como objetivo determinar si los delfines producen ráfagas de pulsos durante pruebas de igualación a la muestra, tanto con resultados exitosos como fallidos, así como explorar su asociación con el afecto positivo. Se observó que las ráfagas de pulsos se produjeron en el 74 % de las pruebas de igualación a la muestra (en las que el sujeto observa un objeto de muestra y selecciona el equivalente entre un grupo de objetos alternativos), con una frecuencia significativamente mayor durante las respuestas correctas. Además, se observó una diferencia notable en la proporción de ráfagas de pulsos que se produjeron antes y después del puente de entrenamiento del entrenador, siendo mayor la frecuencia de estos pulsos antes del puente del entrenador. El momento y las características de estas ráfagas de pulsos sugieren que podrían estar relacionados con el interés y estados afectivos positivos de los delfines, más que con solamente una respuesta al refuerzo. Estos hallazgos ofrecen nuevos conocimientos sobre la complejidad de las vocalizaciones de los delfines y su posible conexión con los estados afectivos.

Palabras clave: delfines nariz de botella, pulsos de ráfaga, igualación a la muestra, estados afectivos positivos, chillido de victoria, vocalizaciones

Research has shown that a number of non-human animals convey positive and negative affect through vocalizations (Boissy et al., 2007; Briefer, 2012; de Waal, 2011; Dupjan et al., 2008; Seyfarth & Cheney, 2003; Snowden, 2003; Soltis et al., 2005; Whitham & Miller, 2024). Positive affect broadly refers to an individual's subjective experience of pleasurable states (Ashby et al., 1999; Boissy et al., 2007; Diener et al., 2002; Isen et al., 1988; Mellor, 2015; Mendl et al., 2010; Shiota et al., 2021; Watson et al., 1988). In humans, this affect is often expressed through behaviors that reflect an internal sense of pleasure, a desire to maintain that state of well-being (Diener et al., 2002; Isen et al., 1988; Lyubomirsky et al., 2005), and an increased sense of energy, engagement, and focus (Watson et al., 1988). Research has shown that reward can induce positive affect (Ashby et al., 1999). While positive affect reflects a broad and enduring state, positive emotions, such as joy, are typically brief experiences linked to specific events and are often accompanied by distinct behavioral and physiological changes (Fredrickson, 2001; Shiota et al., 2017). In animals, emotions are commonly defined as presumed internal states that arise in response to environmental stimuli and are expressed through observable behavioral and physiological changes (de Waal, 2011). Our understanding of how bottlenose dolphins (*Tursiops truncatus*), henceforth called dolphins, convey emotions through vocalizations is limited (although, see Clegg et al., 2017; Delfour & Charles, 2021; Herzing, 2015).

Burst pulses are a type of vocalization produced by dolphins and are broadband signals that are irregularly patterned and contain abrupt changes in their frequency/amplitude makeup (Herzing, 1996; Jones et al., 2020; Luis et al., 2016). Previous studies have linked the ‘victory squeal,’ a type of burst pulse that occurs directly after the dolphin successfully completes a task, to positive experiences connected to success and reward (Ridgway et al., 1991; 2014; 2015; 2018; Dribble et al., 2016). However, it remains unclear whether these burst pulses signal positive affect due to task completion or recognition of a correct response. This study aims to fill this knowledge gap by examining whether dolphins produce burst pulses during a match-to-sample task, where the subject views a sample object and selects the matching item from a group of alternatives. We will investigate the occurrence of burst pulses in both successful and unsuccessful outcomes to explore their potential role in signaling positive affect.We will begin with a review of current knowledge on burst pulses and the emotions they might express, followed by an overview of our studies examining the positive emotions conveyed through these vocalizations.

Dolphins possess exceptional communication abilities. The character, timing, and context of vocalizations may reveal the affective state and the function of these sounds in communication (Au & Hastings, 2008; Herman & Tavolga, 1980; Herzing, 1996; Janik & Sayigh, 2013; Ridgway et al., 2014; Tyack, 2000). Dolphins produce three distinct types of vocalizations: whistles, echolocation clicks and burst pulses. Whistles are narrowband, tonal signals used to communicate in social contexts. Interestingly, each dolphin produces an individually distinct 'signature whistle' used for individual identification (Caldwell et al., 1990; Janik et al., 1994, 2006; Macfarlane et al., 2017). One use of these whistles is by mothers and calves during separations, typically indicating stress, distress, or alarm, and potentially other affective states (Cook et al., 2004; Dudzinski, 1996; Kuczaj et al., 2013; Smolker et al., 1993; Tyack, 1986).

In contrast, echolocation click trains are composed of high-intensity broadband repeating clicks and serve primarily for navigation and hunting purposes. However, they may also have communicative aspects through "eavesdropping" (Au et al., 2000; Gotz et al., 2006; Xitco & Roitblat, 1996). That is, other animals listening in to these calls may be able to determine the dolphin's focus of interest (e.g., the presence of target prey).

Burst pulses, which are acoustically similar to echolocation clicks, have an inter-click interval of less than 10 ms and 'sweeping' frequencies—meaning that burst pulses can be irregularly patterned and contain abrupt changes in their frequency/amplitude makeup (Herzing, 1996; Jones et al., 2020; Luis et al., 2016). The functionality of burst pulses differs from echolocation clicks, as these pulses are often associated with high-arousal states ranging from aggression (Branstetter et al., 2012; Herzing, 2015; Overstrom, 1983) to what has been referred to as 'victory squeals,' oftentimes produced after completing a task (Ridgway et al., 2014; 2015; 2018). Previous studies suggest that during social interactions, burst pulses may indicate the behavioral and emotional states of the producer dolphin (Blomqvist & Amundin, 2004; Eskelinen et al., 2016; Herzing et al., 2015; Lammers et al., 2003). It's important to note that burst pulses encompass a wide range of sounds with various functions, with the victory squeals being just one example.

Burst Pulses

Although burst pulses are commonly produced by dolphins and make up the majority of dolphin vocalizations (Herman & Tavolga, 1980; Herzing, 2000; Jones et al., 2020), very few studies have examined these signals (see Au & Hastings, 2008). Burst pulses are among the first vocalizations a dolphin produces. A neonate dolphin produced burst pulses exclusively for the first five days before producing whistles, highlighting the possible significance of these signals in dolphin communication (Killebrew et al., 2001).

Despite their significance, the categorization of burst pulses has historically been influenced by human perception. Burst pulses have been categorized based on how they sound to the researcher, with labels like 'squawk' and 'mew.' Lammers et al. (2015) noted that humans often perceive these calls as continuous sounds because our temporal acuity is limited to distinguishing sounds separated by 3.2 to 22 ms. In contrast, dolphins can resolve clicks separated by as little as 0.26 ms, suggesting they can perceive the individual components of these complex vocalizations (Au, 1993). Unlike most whistles, burst pulses can also reach frequencies extending beyond 150 kHz (Au & Hastings, 2008). Until recently, our understanding of these high-frequency sounds has been limited by the upper threshold of human hearing (approximately 20 kHz) and the low sampling rates of recording equipment, restricting our ability to analyze their full range and function.

A challenge with burst pulses is distinguishing them from echolocation clicks; one type of sound often blends into the other during sound emission (Au & Hastings, 2008). Burst pulses during the terminal phase of an echolocation click train have been suggested to indicate the completion of the echolocation task and may be a means for the individual to convey a sense of satisfaction (Au & Hastings, 2008). These authors further proposed that when burst pulses are not associated with echolocation clicks, these pulses are more likely to be emotionally induced social sounds. Such observational descriptions have yet to be fully explored and may provide an avenue to better understand burst pulses by considering the contexts in which they are produced.

Burst pulses are commonly observed in various affective-laden situations (Kuczaj et al., 2013). When it comes to aggressive encounters, Branstetter et al. (2012) proposed that burst pulses may serve a function similar to facial expressions in aggressive primates and canids. The strong, directional nature of these pulses allows dolphins to convey an aggressive, emotional state to specific conspecifics and enables nearby conspecifics to monitor the progress of aggressive interactions. Moreover, it has been noted that burst pulses may also have a tactile effect on the recipient (Johnson & Herzing, 1991), such as during the joint application of synchronized burst pulses during aggressive interactions (Herzing, 1996; Herzing, 2015).

Burst pulses, typically characterized by high frequencies, tend to dissipate into the environment more rapidly than low-frequency signals. This results in a limited active space, which refers to the distance over which conspecifics can perceive and recognize the sound (Quintana-Rizzo et al., 2006; Au & Hastings, 2008). Given that burst pulses predominantly consist of higher frequencies, they are likely employed for communication with nearby conspecifics, such as in the case of the aggressive burst pulse.

In addition to the aggressive context, another type of burst pulse, identified in the field is a “bray,” is thought to be used as a food call for conspecifics, or even to potentially stun prey (Janik, 2000). During behavioral focal follows, braying was associated with 93% of all feeding events. This burst pulse stands out from other observed pulses due to its lower frequency, with most of its energy concentrated below 2 kHz, resulting in a more extensive active space (since low frequencies tend to travel farther than high frequencies do). This suggests that the signal is intended for a wider audience. Thus, such sound characteristics, should be taken into account to better understand these and other burst pulse functions.

Along with directionality, another important characteristic to consider is the duration of the signal. According to Herman (2010), the duration of dolphin vocalizations could potentially be utilized to convey emotional states, and this association may represent another universal feature of dolphin vocalizations. This appears to be the case, for instance, in the “looping” or rapid repetition of whistles in excited (Norris et al., 1994) or stressed (Esch et al., 2009) animals. While researchers have started to classify burst pulses based on their duration, there is inconsistency in the duration classification of what constitutes a 'short' and 'long' burst pulse across different studies (Jones et al., 2020; Killebrew et al., 2001; Luis et al., 2016; Overstrom, 1983), making comparisons challenging. Similarly, the duration of burst pulses may increase when the producer is in an excited state (Kuczaj et al., 2013). Consequently, duration presents a promising feature for distinguishing various types of burst pulses and/or the contexts of their use.

Victory Squeals

One of the initial studies to look at burst pulses in terms of affective sounds was Ridgway et al. (1991), in which burst pulses that occurred after successful completion of a task, such as turning off a switch, were labeled as a ‘victory squeal’ (VS). Since then, it has been found that this type of burst pulse occurs after fish capture (Ridgway et al., 2015), successful performance (signaled by a trainer) (Ridgway et al., 1991; Ridgway et al., 2014), and during a multipart task in the open ocean (Dibble et al., 2016; Ridgway et al., 2018). Jones et al. (2020) highlight how the behavioral context of the emission can be used to distinguish these burst pulse sounds from other pulse sounds rather than the sound's acoustic parameters.

Ridgway et al. (2014) conducted a study where they trained 12 dolphins and two belugas on behavioral tasks (such as diving and hearing threshold tasks) using four different sound signals (tone, air whistle, underwater buzz, and tone onset) as secondary reinforcers. They measured the timing of when the victory squeal (VS) occurred in relation to the delivery of reinforcement. They observed a shift in the timing of the VS before and after training. Before training, the VS came after the fish (reward), but after training, the VS came after the secondary reinforcer and before the fish. The authors highlight how this may reflect that the animal expects a reward, and propose that the trainer's bridge may stimulate dopamine release in the brain, leading to the VS (although actual dopamine release has not been studied in dolphins). Ridgway et al. (2014) also suggest that the victory squeal is likely an expression of motivation and, as such, represents a basic reward system present in the brains of mammals.

Another study by Ridgway et al. (2015) examined fish capture and VS production with seven individual dolphins. From 606 trials, occurring in both open water and enclosures, the dolphins produced the VS approximately 89% of the time, and the duration of the VS lasted 0.2-20 s after fish capture. This study further supports the idea that VS could be related to reward. To better understand the function of this call, and whether it is related to prey capture, functions as a food call, or is a reflection of emotional pleasure, Dibble et al. (2016) examined VS without the immediate reward and away from the trainer. This study involved three individual dolphins performing various tasks, such as marking buried "practice" mines and disc retrieval. They observed that the dolphins produced a VS after completing the final task 14-53% of the time. As these dolphins were away from the other conspecifics and trainers, Dibble et al. (2016) suggested that this may be an individual expression of satisfaction and indicates that the dolphins "know" when they have completed a trained behavior and succeeded.

Following this, Ridgway et al. (2018) studied two dolphins during a multipart task consisting of searching for and marking mine simulators in different contexts (either buried, resting on the seabed, or moored). They found that VS was produced on 72% of the marks. The two individuals produced VS at different rates; dolphin Y produced a VS 62% of the time, and dolphin Z produced a VS 100% of the time. Ridgway et al. (2018) suggested that perhaps dolphin Y could not confirm the buried simulators when marking the target and may have had lower VS rates due to uncertainty about the successful completion of the task. These studies highlight that VS is probably a vocalization associated with positive feelings related to achievement or perceived success, and it may also be tied to certainty.

In humans, certainty is an important dimension in the cognitive appraisal of emotions1. It shapes how individuals perceive and respond to various emotional situations, influencing both emotional states and behaviors. In a classic study by Smith and Ellsworth (1985) on emotional appraisals, individuals reported feeling less certain when experiencing emotions like surprise, fear, or hope, while they felt more certain during emotions such as happiness, pride, or boredom. Given this link between certainty and emotional responses in humans, a similar pattern may exist for dolphins, where greater certainty could be associated with producing specific vocalizations, such as victory squeals.

[1] In this context, we assume that appraisals elicit emotions, although some theories argue that appraisals themselves constitute the emotion (for discussions on appraisals see Lazarus, 1991; Roseman & Smith, 2001; Ellsworth & Scherer, 2003; Smith & Kirby, 2009)

Beyond victory squeals, dolphins likely experience a range of positive affective states, making considering their vocalizations as affective signals essential. Some of these states may include interest, anticipation, and excitement. For instance, dolphins under human care often display anticipatory behaviors before feeding sessions, reflecting heightened emotional engagement. For example, Clegg and colleagues (2018) observed that dolphins' anticipatory behaviors toward trainers correlated with their participation levels in subsequent events. Since vocalizations were not explicitly analyzed in this study, this remains an area for new research exploring the connection between anticipation and vocal cues. Excitement, like anticipation, might similarly influence vocal behaviors, signaling dolphins' engagement and interest.

Although direct studies on excitement in dolphins are limited, human research indicates that emotions like excitement, curiosity, and interest have distinct vocal profiles (Silvia, 2008). Interest, a 'knowledge emotion' (Silvia, 2008), is considered a highly pleasurable state that drives motivation and engagement and fosters learning and curiosity. Studies by Banse and Scherer (1996) associate human interest with vocal traits such as faster speech rates and broader frequency ranges. Similar vocal signals in dolphins, along with the timing and context of these sounds, may indicate various positive emotions, including interest, certainty, and excitement.

Current Study

The unique sound characteristics and potential emotional significance of burst pulses make them a promising vocalization for exploring affect in dolphins. Although quantitative data on burst pulses is limited, their frequent occurrence in dolphin vocalizations and their likely connections to various affective states highlight the necessity for more research. Building off the research done by Ridgway et al. (1991, 2014, 2015, 2018) on victory squeals and the methods of Jaink (1994), our goal is to determine if burst pulses occur during trials with both successful and unsuccessful outcomes and to further investigate them as indicators of positive affect. Ridgway's studies did not include a condition where the animals could make an incorrect response, which makes it unclear whether the VS signaled positive affect over task completion or knowing that they made a correct response. Our study will analyze the presence of burst pulses in bottlenose dolphins during match-to-sample trials with both success and failure outcomes. Specifically, we will test the following hypotheses:

Hypothesis One

In this study, we explore the presence of burst pulses in tasks with clear success and failure outcomes. Specifically, we investigate whether these burst pulses occur during both correct trials (when the dolphin successfully chooses the correct response) and incorrect trials (when the dolphin does not choose the correct response) and if burst pulses are more commonly linked to correct responses, akin to 'victory squeals' as noted by Ridgway et al. (2014, 2018) and Dibble et al. (2016). Our hypothesis is that burst pulses will mainly manifest during correct trials, reflecting success and the expectation of a reward. However, if they also appear in incorrect trials, this may suggest that they reflect other positive affect.

Hypothesis Two

Building on our initial hypothesis, we seek to investigate the timing of these burst pulses. More specifically, do burst pulses happen only after the trainer's reinforcement? Drawing from Ridgway et al.'s (2014, 2015) work, we propose that burst pulses might occur following the trainer's bridge, suggestive of a "victory." Conversely, if these vocalizations take place immediately before the bridge, they could represent anticipatory responses, showcasing increased motivation, interest, or overall excitement (Clegg et al., 2018). This timing may highlight a unique, positive state distinct from the victory squeals.

Hypothesis Three

Expanding on the idea that burst pulses may convey positive affect beyond celebrating success, we investigate how specific characteristics of these vocalizations—such as their occurrence in bouts, their duration in between contexts, and behavioral correlates like swim time—might further support the hypothesis that these burst pulses reflect other positive emotional states (such as excitement/interest).

a) *Bouts of burst pulses*: Bouts are currently understudied and may indicate elevated excitement or engagement during tasks, similar to how increased repetition in whistles has been linked to heightened arousal in previous research (Dawson, 1991; Norris et al., 1994; Probert et al., 2023). This highlights the potential importance of studying burst pulse bouts as indicators of excitement or heightened affective states.

b) *Swim time*: The time it takes for a dolphin to make a decision may reflect their level of interest or motivation in the task. Faster swim times could correspond with higher excitement or anticipation as the task progresses (Clegg et al., 2018).

c) *Burst pulse duration*: The duration of burst pulses may vary depending on their context, such as at the 'send' location (when released to perform the task) versus the 'choice' location (where the task is completed). Drawing from findings that longer vocalizations are associated with increased activity and arousal (Au & Hastings, 2008; Kuczaj et al., 2013; Jones et al., 2020), we hypothesize that longer burst pulses may indicate higher levels of excitement and interest.

Method

Subjects and Location

Participants in this study were seven Atlantic bottlenose dolphins (*Tursiops truncatus*) from the U.S. Navy's Marine Mammal Program. This includes three males: KNG (9 years old), KDK (10 years old), and CRT (14 years old), as well as four females: PEL (20 years old), MUU (44 years old), SNA (39 years old), and BAI (22 years old). These dolphins are housed in natural seawater enclosures in San Diego, CA. They are rewarded with fish and other secondary reinforcers for their participation, and each dolphin receives their full allotment of fish during the research sessions, regardless of their performance.

Permits

The U.S. Navy Marine Mammal Program (MMP), Naval Informaiton Warfare Center (NIWC) Pacific houses and cares for a population of bottlenose dolphins and California sea lions in San Diego Bay (CA, USA). Secretaty of Navy Instruction 3900.41H directs that Navy marine mammals be provided the highest quality of care. NIWC Pacific is accredited by AAALAC International and adheres to the national standards of the U.S. Public Health Service policy on the Humane Care and Use of Laboratory Animals and the Animal Welfare Act. NIWC Pacific's animal care and use program is routinely reviewed by an institutional animal care and use committee and the U.S. Navy Bureau of Medicine. The animal use and care protocol for Navy dolphins in support of this study was approved by NIWC Pacific's Institutional Animal Care and Use Committee (No. 148-2022), to Co-PIs Dr. Christine M. Johnson and Christianna D. Royse.

Materials

In a match-to-sample (MTS) task, the subject viewed a sample object and selected the match from a group of alternative objects. For the MTS tasks in 2022, objects were either metal, wood, or air-filled plastic, all roughly a foot in diameter. In 2023, objects were air-filled plastic, all roughly a foot in diameter. All recordings were made with omnidirectional hydrophones (Cetacean Research Technology, *model CR3*) with a linear frequency range of 0.0004 to 180 *kHz* 3*dB* and an effective sensitivity of -209.45 re 1V. Power was supplied via the sound card (Cetacean Research Technology*, SpectraDAQ-200*) through the IEPE (integrated electronic piezoelectric), which provided 24 V DC at 4*ma* of constant power to the hydrophone. The sound card (SpectraDAQ-200) had a sampling rate of 192 *kHz* (Nyquist frequency of 96 kHz) with 24 bits of resolution and was calibrated directly to the hydrophone's sensitivity. In 2022, a single hydrophone was placed near where the animal examined the sample object in the task, positioned approximately 1 m in front of the animal's head and 0.3 m from the water's surface. In 2023, two hydrophones were placed on either side of where the animal made a choice in the task, with each hydrophone positioned to the side of the target and 0.3 m from the water's surface.

Data Collection

Data collection took place from February 2022 through June 2023. In both years, the task was delayed MTS, in which the dolphin was first presented with a sample object underwater on one side of the enclosure at the '*send location*.' The dolphin was trained to echolocate on the sample object, and the sample was only removed once echolocation clicks were heard (from the hydrophone located in the enclosure). After the sample was removed, the dolphin swam across the enclosure and was presented with alternative objects at the '*choice location*,' Each alternative was presented against its own underwater backdrop (a 3' × 5' PVC frame covered in white nylon), which were side-by-side on the far wall. A response target—consisting of a 4" × 4" flat surface—was permanently attached to the outer edge (far left or far right) of each backdrop frame. The dolphin was required to touch the target closest to the correct alternative object to indicate its choice. Figure 1 provides a schematic showing the layout of the MTS setup, and Figure 2 shows a screenshot of the actual setup during an MTS trial. Importantly, this setup was identical for both choice and errorless trials.

Figure 1

Schematic showing a bird's eye view of the layout of the MTS setup between 2022 (panel A) and 2023 (panel B). A side view (panel C) shows where the target was located on the PVC backdrop.

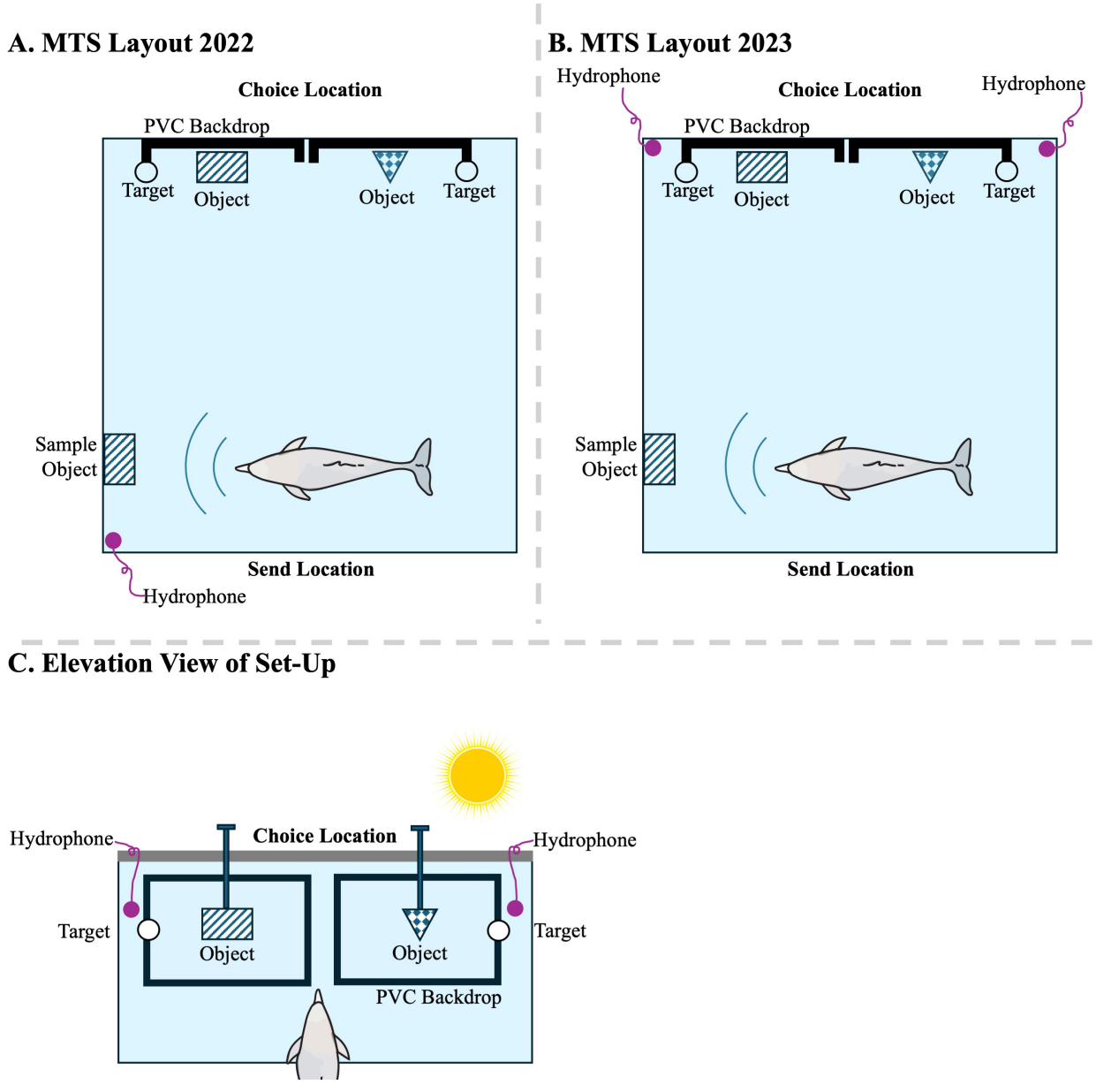
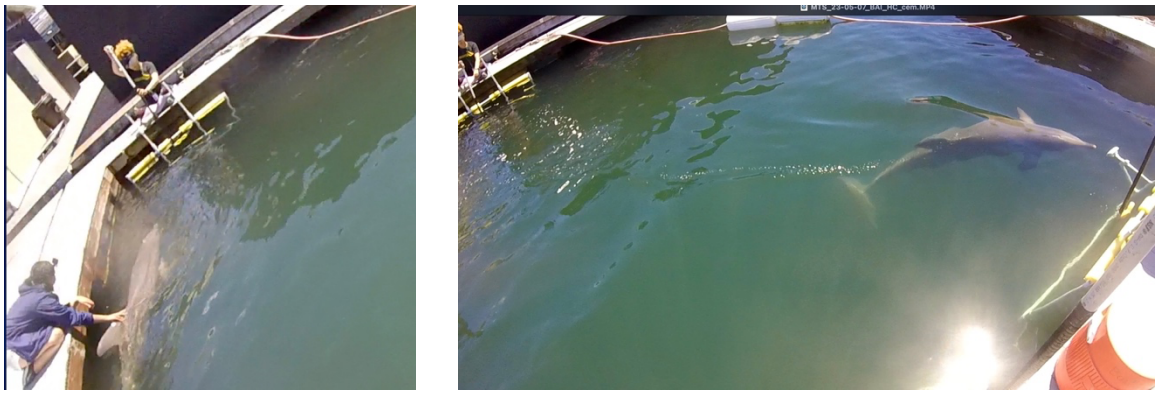


Figure 2

Photos of the Match-to-Sample Setup: Send Location (left) and Choice Location (right)



Note: The MTS trial starts at the 'send location,' as seen on the left, where the trainer stations the dolphin to echolocate on the sample object presented. The dolphin then swims from the 'send location' to the 'choice location.' The 'choice location,' as seen on the right, is where the dolphin touches the target to indicate the choice.

While training and running MTS trials, the dolphin could be presented with a single alternative, which always matched the sample, intended to constitute an "errorless" trial. In the errorless trial, there were still two targets (since they were attached to the PVC backdrop); however, only one matching object was present. The other target was present but did not display an object. In regular trial sessions, the dolphin was presented with two objects: correct (matching the sample) and incorrect. When the animal made a correct choice by touching the associated target, the trainer signaled to the dolphin with a 'bridge' whistle and rewarded the dolphin with part of its food allotment and other secondary reinforcement. If the dolphin made an incorrect choice, the trainer did not reinforce the dolphin, and typically sent it back to its original station to repeat the trial or move on to the subsequent trial. The number of trials within a session varied depending on food availability and dolphin participation. All sessions ended positively (such as using an 'errorless' trial). As part of the protocol, if the dolphin made incorrect choices multiple times in a row, the trainer intervened and provided more errorless trials to encourage continued participation.

2022 MTS. In 2022, the dolphins had already met the criteria for the delayed MTS task, defined as correctly choosing the matching object in 19 out of 24 consecutive choice trials (excluding errorless trials). Each session typically consisted of eight to 23 trials. Sessions usually began with a few errorless trials, to ensure the dolphin's confidence, followed by choice trials. All seven dolphins participated in 2022 with a total of 367 trials (combined across dolphins), with 49 errorless trials, and 318 choice trials.

During these MTS trials, the dolphin was required to select a matching object based on its material or shape. The dolphin's movements within the enclosure were recorded manually through handwritten notes. Each task followed a highly routinized sequence of events and observers documented each transition in real-time (e.g., echolocating on the sample, moving toward the alternatives, making a choice). These observations determined the dolphin's location in the enclosure during each trial, which will play an important role in our analyses.

2023 MTS. In the 2023 MTS trials, the MTS procedure was modified so that all objects were identical, and the match was based on the movement pattern of the sample stimulus. The three males participated in this task and were in the early stages of training, having not yet reached criteria (19 out of 24 consecutive trials). As a result, more errorless trials were given to maintain a high success rate. The number of errorless trials was gradually reduced as the dolphins became successful, and more choice trials were introduced. It is important to note that during this training phase, dolphins could still make an errorless response incorrect by selecting the wrong target. The three males participated in 2023 with a total of 254 trials (combined across dolphins), with 198 errorless trials, and 56 choice trials.

Additionally, synchronized recordings were made using hydrophones and deck cameras, with each research session beginning with a human-made tone to align the audio and video data. This synchronization allowed us to accurately extract the timing of the trainer's bridge from these recordings for analysis. To ensure a conservative approach, we only analyzed burst pulses within 5 s before or after the trainer's bridge at the '*choice location*.' Like in 2022, observers documented each transition in real-time (e.g., echolocating on the sample, moving toward the alternatives, making a choice). These observations, and confirmation from the video data, were used to determine the dolphin's location during each trial. In both datasets, any burst pulse produced at the *'send location'* was analyzed separately from those produced at the '*choice location*.'

Data Auditing

Acoustic analysis was performed in Raven Pro v. 1.6 (Center for Conservation Bioacoustics, 2014) and Audition CC 2024 v.12 (Adobe Systems, Build 13.0.8.43). Spectrograms were viewed in Raven with a time axis of 60 s, a frequency axis of 96 kHz, a discrete Fourier transform (DFT) of 512, a 50% overlap, and a Hann window. All waveforms were checked for overloading and aliasing. Burst pulses were classified based on their characteristic inter-click interval of less than 10 ms and sweeping frequency and amplitude changes (Herzing, 1996; Jones et al., 2020). Only burst pulses at the 'send' and 'choice' locations were used in the analysis. Any burst pulses with a signal-to-noise (SNR) ratio less than 10 dB (Wang et al., 2016) were excluded from the analysis. A single rater manually counted burst pulse vocalizations using timing data from observational sheets as guidance. The rater reviewed and double-checked all counts during two separate sessions to ensure accuracy and consistency.

Statistical Analysis

All statistical analyses were performed using JASP (Version 0.16.3; JASP Team, 2024) and RStudio (Version 1.4.1717; RStudio Team, 2024). We used a generalized linear mixed-effects model framework (GLMM) to account for the data's non-normal distribution and accommodate the experimental design's nested structure. This model accounted for both fixed and random effects. Additionally, a binomial test was performed to determine the timing of burst pulses relative to the trainer's bridge.

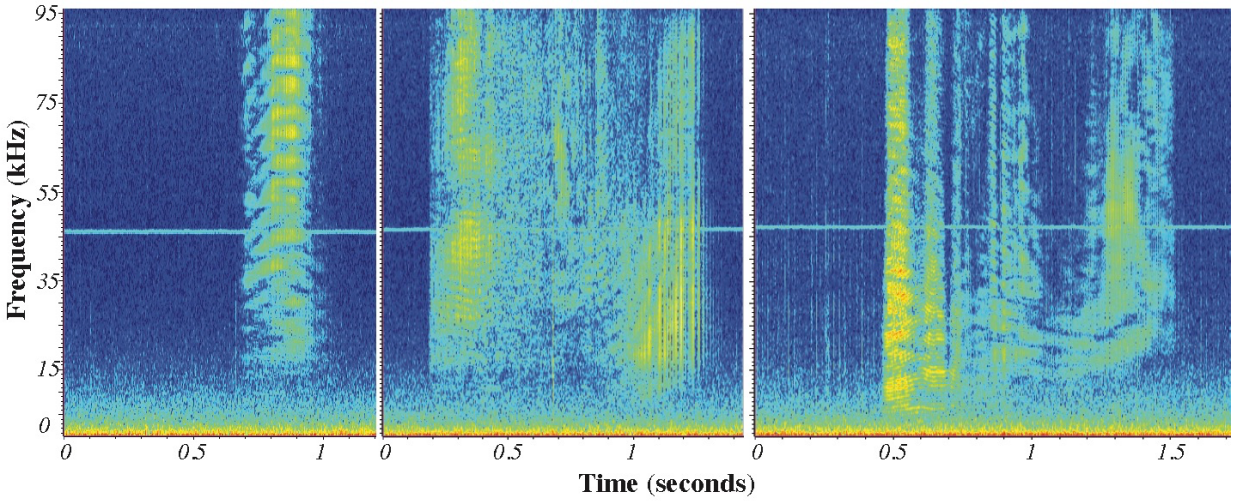
Results

Descriptive Results

Data were analyzed from a total of 621 MTS sessions. Figure 3 shows three examples of the different burst pulses produced at the '*choice location*.' Overall, burst pulses at the '*choice location*' occurred during 74% of the trials. Males produced burst pulses during 87% of their trials, and females produced burst pulses during 67% of their trials. Figure 4 shows the proportion of burst pulses made by the seven dolphins at *both* the send and choice locations for 2022 and 2023 combined. This highlights individual differences among our dolphins, particularly with the burst pulses produced at the '*send location*,' which will be further discussed below. Please refer to Supplementary Tables 1, 2, and 3 in the supplementary section for additional data on individual dolphins.

Figure 3

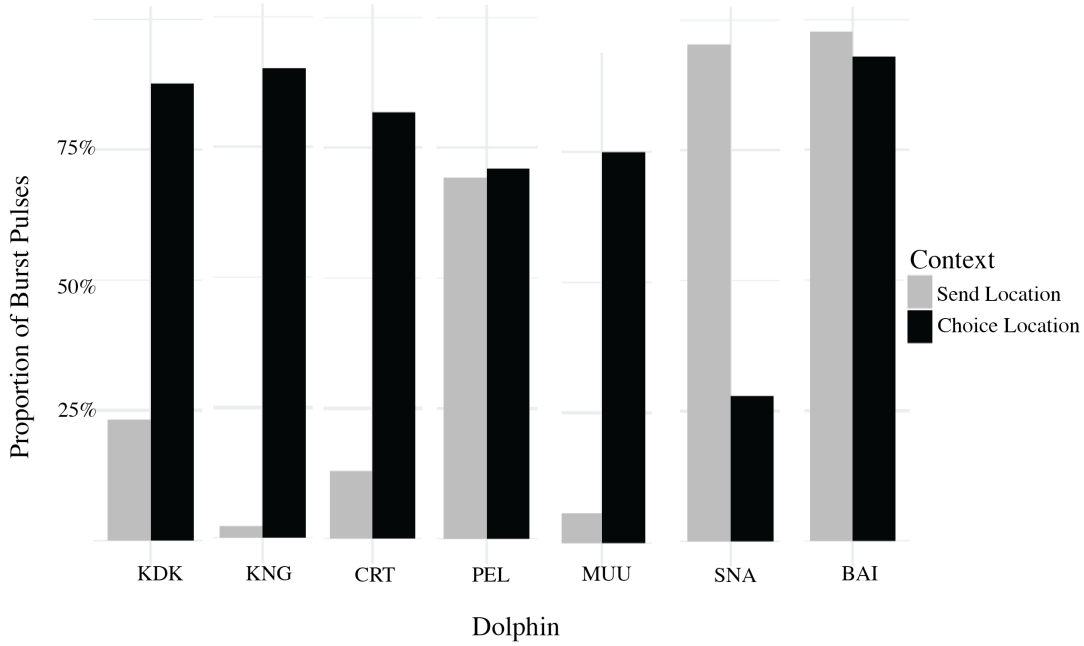
Burst Pulse Spectrograms



Note: Spectrograms displaying various burst pulses generated at the 'choice location' during MTS. The horizontal axis indicates time in seconds, while the vertical axis shows frequency in kHz. The brightness of the colors reflects amplitude, with brighter shades denoting louder sounds.

Figure 4

Proportion of Burst Pulses Produced



Note: Summary of the proportion of burst pulses across the trials by individual dolphins at the send and choice locations. This data is combined from 2022 and 2023. KDK, KNG, and CRT are the three males, and PEL, MUU, SNA, and BAI are the four females.

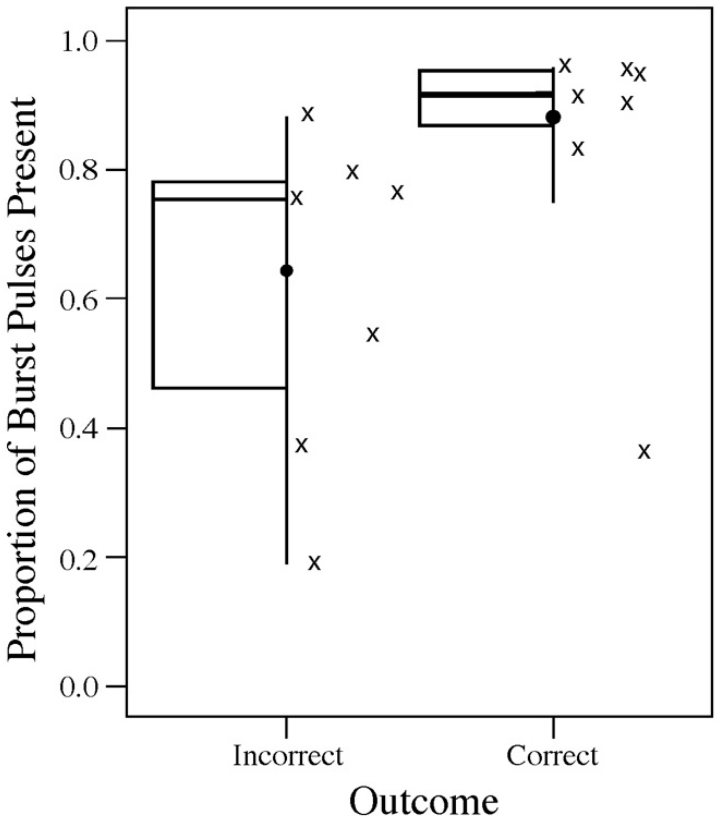
Exploratory analysis revealed no notable difference in burst pulse occurrences at the 'choice location' between choice (M = 0.79, 95% confidence interval (CI) = 0.63 - 0.90) and errorless trials (M = 0.80, CI = 0.59 - 0.63). That is, burst pulses occurred 80% of the time in errorless trials and 79% in choice trials. As a result, we collapsed the data across trial types (errorless and choice) for all subsequent analyses. As mentioned above, the dolphin could still get the "errorless" trials incorrect by touching the wrong target during training periods since both backdrops were still used.

During match-to-sample trials, are burst pulses produced more when the dolphin responds correctly?

To test the hypothesis that burst pulse presence would be more common during correct than incorrect trials, we employed a GLMM to examine the relationship between burst pulse occurrence and the trial outcome (correct or incorrect), while accounting for individual differences among dolphins (variance = 1.012, SD = 1.006). This analysis included only burst pulses produced at the '*choice location*' and included data from 2022 and 2023. The analysis demonstrated that burst pulses were significantly more likely to be present during correct trials (M = 0.88, 95% CI [0.75-0.95]) compared to incorrect trials (M = 0.64, 95% CI [0.44 – 0.81]): Estimate = 1.35, SE = 0.23, z = 5.79, $p < .001$, (Figure 5). In the correct trials, burst pulses were observed 88% of the time, whereas they were present in 64% of the incorrect trials. This suggests a strong association with task success, but does not exclude their presence during incorrect trials, implying a broader range of affective states.

Figure 5

Distribution of Burst Pulses on Correct and Incorrect Outcomes



Note: This box plot shows the distribution of the proportion of burst pulses present across two outcomes: "Incorrect" and "Correct." The black lines within the boxes represent the median values, while the edges of the boxes indicate the interquartile range (IQR), encompassing the middle 50% of the data. Whiskers extend from the quartiles to 1.5 times the IQR or the most extreme data points within that range. X represents individual dolphins as a random effect. The central dot in each box represents the mean proportion of burst pulses for each outcome category, i.e. each incorrect (M = 0.64) and correct (M = 0.88).

Are bouts of burst pulses present?

We next turn to the relatively understudied occurrence of "bouts" of burst pulses, which we defined as two or more burst pulses occurring within 1 s of one another, and explore whether an increase in bout production might be indicative of excitement. To do so, we focus on the 2023 data (males only) since these data include both video and audio recordings. Across all 181 trials—correct and incorrect combined—we identified 105 bouts and 71 single burst pulses. Bouts were present 62% of the time on correct trials (90/146) and 43% on incorrect trials (15/35). Single burst pulses were present 38% of the time on correct trials (55/146) and 46% on incorrect trials (16/35). Most bouts of burst pulses occurred during correct trials. On correct trials, the number of burst pulses per bout ranged from two to five, with the majority consisting of two burst pulses (n = 77). Bouts of three burst pulses were less common (n = 12), and there was only one instance of a bout with five burst pulses (n =1).

Do burst pulses happen only after the trainer's reinforcement, signaling success, or before, potentially signaling excitement?

We posit that if burst pulses occur more frequently after the trainer's reinforcement, they likely reflect a response to success. However, if burst pulses occur more frequently before reinforcement, then they more likely reflect other positive affective states such as excitement/interest. To examine this, we looked at burst pulses occurring at the '*choice location*,' on correct trials only. Using video/audio footage of the 5 s before and after the trainer's bridge, we were able to determine the timing of bouts and single burst pulses in relation to reinforcement. Of the 55 single burst pulses, 42 occurred before the bridge, and 13 occurred after (see Table 1). Of the 90 bouts during correct trials, 56 occurred entirely before the bridge, six occurred entirely after, and 28 spanned the bridge (i.e., at least one burst pulse in the bout happened before and one after the bridge). Bouts that spanned the bridge were excluded from subsequent analyses. A binomial test revealed a statistically significant difference in the proportion of bursts occurring before the bridge (77.4%) compared to after the bridge (22.6%), $p < .001$ (proportion = 0.77, 95% CI [0.724 - 01.00]; (see Figure 6). This is consistent regardless of if looking at exclusively bouts or individual burst pulses (see Table 1.). These findings differ from Ridgway's findings, raising questions as to whether burst pulses that occur before the bridge truly function as 'victory squeals' tied to reinforcement. It seems more likely that the great prevalence of burst pulses prior to the bridge may indicate excitement/interest rather than victory.

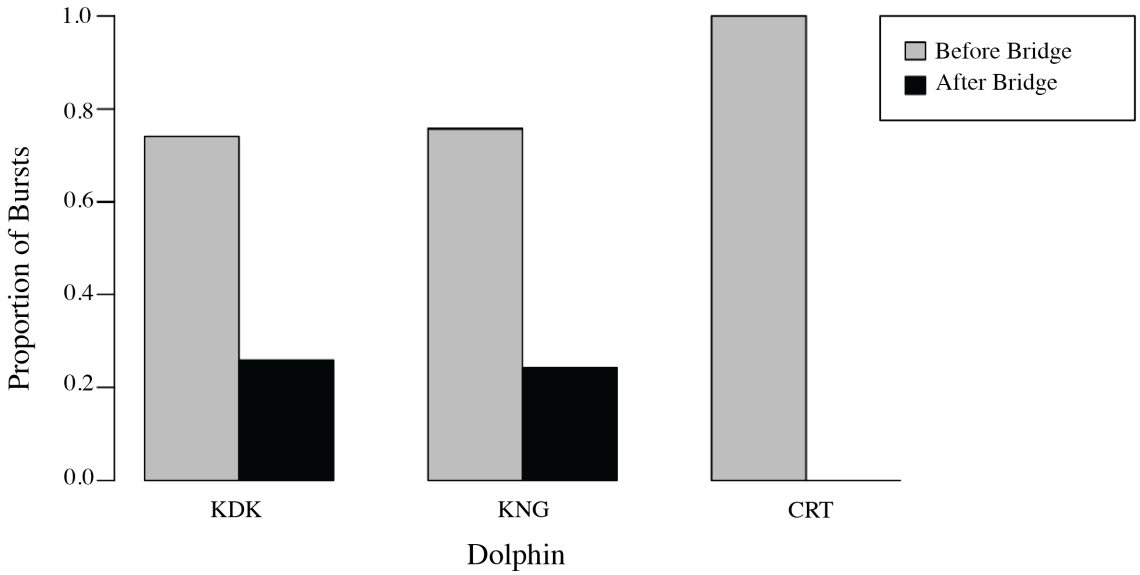
Table 1

Descriptive results of burst pulses occurring in 'bouts' and burst pulses occurring individually on correct trials only.

	Individual Burst Pulses	***Burst Pulse Bouts***	***Single Burst Pulses***
Before Reinforcement	176	56	42
After Reinforcement	59	6	13
Spanning Reinforcement	N.A.	28	N.A.
Total	235	90	55

Figure 6

Proportion of burst pulse occurrence before the trainer's bridge and after the trainer's bridge.



Note. Figure contains 2023 data only.

Does faster Swim Time, as a possible measure of excitement, correspond to increased levels of burst pulses?

To further investigate the possibility that excitement and interest drive the production of burst pulses before the trainer's reinforcement, we tentatively hypothesized that such states might also manifest in faster swim times. To investigate this, we examined whether the dolphins' swim time—a potential indicator of interest—was associated with the timing and type of burst pulses produced during correct trials. Swim time was measured as the duration from when the dolphin was released from the '*send location*' to when the trainer bridged the dolphin at the '*choice location*.'

As with the previous analysis, we included both single burst pulses and bouts of burst pulses, at the '*choice location*,' and excluded bouts that spanned the bridge. A GLMM was conducted to assess whether swim time correlated with the likelihood of the production of single burst pulses versus bouts while accounting for individual differences among dolphins. The results showed no significant differences in swim time when a bouts versus single burst pulses were produced, $\chi^2(1) = 0.52$, $p = .47$. The mean swim time for when bouts were present was 10.04 s (SD = 5.89), and for when single burst pulses were present was 11.59 s (SD = 6.70). Despite the lack of correlation with swim time in this study, the timing of the majority of these burst pulses occurring before the trainer's bridge remains a promising avenue for further understanding additional positive affective states, like excitement/interest.

Do the burst pulses at the 'choice' location vary in duration from those produced at the 'send' location?

Since burst pulse calls occurred at both the send and the choice locations, we wondered if the calls themselves might be longer at the 'choice location', as an indicator of higher excitement, due to either committing to a choice or anticipating a reward. We utilized a GLMM to investigate the relationship between location (send vs. choice) and the length of burst pulse, as a possible indicator of the animal's level of excitement or arousal between these contexts. Remember that the '*send location'* indicates where the dolphin echolocates the sample object before swimming to the '*choice location*' where it will make its selection. For this, we combined data from both 2022 and 2023. The duration of burst pulses at the '*choice location*' (M = 0.43, 95% CI [0.26 - 0.61]) did not significantly differ from their duration at the '*send location'* (M = 0.44, 95% CI [0.24 - 0.63], p = .98). While this does not support that the animals' excitement might be particularly high at the choice location, it does offer some further support for the notion that burst pulses may signal excitement even when they do not occur in conjunction with reinforcement.

Discussion

Burst pulses were present in 74% of the trials, aligning closely with the findings of Ridgway et al. (2015), who reported victory squeals approximately 89% of the time. However, in contrast to Ridgway et al.'s (2014, 2015) observations that victory squeals occur after reinforcement, in our study, 75.8% of burst pulses at the 'choice' location occurred immediately *before* the trainer's bridge. This pattern suggests that these pulses may be related to the dolphins' interest and excitement rather than a direct response to reinforcement. Although we are uncertain about classifying the burst pulses from our study as 'victory squeals,' they likely indicate a positive emotional response, perhaps reflecting the dolphins' confidence in responding correctly and anticipation of upcoming reinforcement or excitement over simply committing to a choice.

Ridgway et al. (2015) briefly suggest that, even in their study, burst pulses might occasionally occur just before the trainer's bridge, indicating potential anticipatory behavior. This observation, in conjunction with our data, raises the intriguing possibility that these vocalizations may convey multiple positive affective states. Affective neuroscience research, for example, shows that dopaminergic responses modulate the incentive salience of a cue –the association between a stimulus and an imminent reward (Berridge, 2007). In our study, the target touched by the animals may have become an incentive-salient cue, triggering a dopaminergic response. This dopaminergic response has been proposed as a potential driver of burst pulse production occurring around reinforcement (Ridgway et al., 2014), but this relationship has yet to be empirically tested.

Burst Pulses: Excitement and Interest

Our results indicate that burst pulses occurred at higher rates when the subject's response was correct, which could be seen as support for a victory squeal or associated incentives, rather than a general excitement over performing the task. It is worth noting, however, that, at the time these data were collected, overall success in the Match-to-Sample task with these dolphins had not yet been achieved, and they showed high variability in performance. Though they produce more burst pulses when correct, the fact that these calls happen more often right before the bridge than after suggests that they may be less about getting a trial right or wrong and more about a measure of commitment, interest or excitement.

This observation aligns with the broader notion that dolphins use vocalizations to convey emotional states, but the specific patterns differ depending on the type of vocalization. For example, our findings on burst pulses contrast with results from a dolphin whistle study (Janik et al., 1994), which employed methods very similar to ours. Janik et al. (1994) investigated variations in the vocal behavior of a bottlenosed dolphin by analyzing whistles produced in three contexts: isolation, correct choices, and incorrect choices during a discrimination task. During trials, the dolphin selected one of two objects, and vocalizations were recorded and analyzed. Unlike our findings, whistles were produced more frequently after incorrect responses and showed specific acoustic variations. These included an increase in the duration of certain portions of the whistle during incorrect trials and a reduced frequency range, meaning the pitch varied less, resulting in a narrower span between the highest and lowest frequencies. These findings suggest that the dolphin's vocalizations convey context-specific information related to task outcomes. The differences in correct/incorrect trials between burst pulses and whistles underscore the complexity of vocalizations in dolphins, where different types of sounds may serve distinct purposes.

We present data indicating that, alongside victory squeals, dolphins likely convey other emotional states, such as excitement and interest, through their vocalizations. While there is limited knowledge about animal vocalizations related to interest, insights can be drawn from studies involving humans. Interest is recognized as a positive emotion (Silvia, 2008; Smith & Ellsworth, 1985) that typically accompanies a strong desire to engage and pay attention, aligning with positive emotions like happiness, pride, surprise, hope, and challenge (Smith & Ellsworth, 1985). The distinction between these emotions often hinges on the anticipated effort required for engagement (Smith & Ellsworth, 1985). From this list, it appears that our dolphins may be experiencing hope and challenge alongside interest, which seems to align well with the behavior and context we observed in them. On the other hand, boredom is a negative emotion defined by disinterest in interacting with the surrounding world, indicating both low mental energy and minimal attention to the environment (Eastwood et al., 2012; Lilley et al., 2017).

We examined the potential role of motivation by analyzing swim times. Although this analysis did not yield significant results, we plan to investigate such motivational indicators more thoroughly in the future. By understanding how interest and boredom influence dolphin behavior, we can enhance our insight into their motivations. Moreover, recognizing the importance of positive affect, such as interest, is vital for effectively managing dolphin welfare, as their well-being encompasses not only the absence of negative emotions but also the presence of positive ones (Boissy et al., 2007; Breifer et al., 2012; DeVere & Kuczaj, 2016).

Further supporting the possibility of their linking to other affective states, we observed that burst pulses often occur in clusters or "bouts" of multiple bursts. Our data show that bouts were more likely to occur on correct trials than single bursts were, although they do not show a greater tendency to co-occur with faster swim times. Future research should explore other ways in which bouts may reflect variations in affect and engagement. In Hector's dolphins (*Cephalorhynchus hectori*), the increase in number of pulses, called 'cries,' were observed during aerial behaviors, like leaping out of the water, as well as during aggressive actions (Dawson, 1991). The authors suggest that such aerial behaviors likely signify excitement. If this is the case, our dolphins may indicate excitement when vocalizing in bouts of bursts, especially during the decision-making process. A similar effect has been seen in whistles—an increased rate of whistle repetition in dolphins has been documented during heightened activity (see Norris et al., 1994; Probert et al., 2023).

Throughout most of our analysis, we considered bouts as a single vocal unit or expression. It is possible that several affective states, like interest followed by victory, are communicated within a bout, particularly in the cases where the bout spans the trainer's bridge. Although this study does not address it, our future work plans on examining whether the bursts occurring before the trainer's bridge differ from those that happen after the bridge during these bouts. We intend to examine the sound characteristics of burst pulses. while taking directionality into account, to further explore if multiple states are being conveyed.

Burst pulse duration and individual variability

In addition to our previous analyses, we explored the duration of burst pulses. Au & Hastings (2008) suggest that one possible function of burst pulses following an echolocation click train is to signal a shift in affective states, such as satisfaction upon task completion. In contrast, burst pulses produced outside click trains may serve different purposes, such as indicating interest, excitement, aggression, or other social functions. Contrary to our expectations of observing significant differences in duration between burst pulses at the '*send location*' and those at the 'c*hoice location*,' our analysis revealed no overall duration difference. This lack of differentiation may be attributed to both contexts' warranting an excited state from which burst pulses are produced.

Notably, several dolphins (PEL, SNA, and BAI) displayed clear differences in burst pulse production between the '*send*' and '*choice*' locations, producing bursts at significantly higher rates at the '*send location*' than the other dolphins (Figure 4). These individual differences underscore the importance of considering the unique behavioral and vocal characteristics of dolphins, as highlighted by previous research (e.g., Clegg et al., 2018; Herman, 2002; Highfill & Kuczaj, 2010; Ridgway et al., 2015). Variations in personality may also influence dolphins' responses to external stimuli (Lilley et al., 2017; Probert et al., 2023). Dolphins have been documented to exhibit distinct and stable personalities (Highfill & Kuczaj, 2007), suggesting that future analyses could benefit from integrating personality data to investigate whether specific dolphins display predispositions toward particular affective states and associated vocalizations (Miller et al., 2022, unpublished data).

Limitations

Research Setting

Especially in forced-choice tasks like the ones used in this study, it is common for dolphins to show bias (such as to a particular location or object) when choosing, such that the biased alternative is selected over the correct answer. As part of our training policy, the trainers aim to ensure that the animals have a high success rate and limited opportunities to fail. When multiple incorrect trials occur, trainers tended to intervene to provide positive reinforcement, including offering "errorless" trials so the session ended positively. Perhaps, if the dolphins had been permitted to fail more often, we would have seen a difference in their affective use of sound more closely associated with success and reward, or conversely, with frustration or even aggression.

Another factor influencing our study is that, during sessions, many other dolphins occupy enclosures near our working animals. As a result, it can be hard to confirm that the recorded vocalizations came from the animals actually participating in the match-to-sample trial. However, our methodology does allow us to combine observational data about the dolphin's location in the enclosure with acoustic data to align the occurrence of calls with the specific behaviors. Nonetheless, in addition to nearby dolphins producing sound, the environment is generally loud, with boats and ships frequently passing by. Due to this excessive background noise, sounds can be masked. Thus, we must note that the absence of a burst pulse does not definitively indicate that the dolphin did not emit one; the recording equipment may not have been able to detect it.

Directionality

To accurately characterize sound characteristics and decode specific information, especially in a burst pulse, it is essential to consider the position of the dolphin's head in relation to the hydrophone and observe how the sound pattern changes with different movements (Branstetter et al., 2012). Proper alignment of a hydrophone along the central axis of a dolphin's beam is crucial due to the directionality of burst pulses. While we were, as mentioned above, able to make observations of the animals' position during trials, the subtle differences in recorded sounds that depend on their precise angle of incidence led us, to date, to analyze only the presence/ absence of the burst pulses, rather than specific qualities of those sounds.

Terminology

It is important to note that there is considerable ambiguity in the terminology used to describe internal states, particularly when discussing concepts such as cognition, arousal, and emotion (see Abramson,2013; Kremer et al., 2020). These terms are often defined inconsistently, leading to confusion when interpreting animal behavior. Clarifying these terms is essential for understanding dolphin vocalizations, as these internal states may not only reflect an affective state but also serve as a means of communication, potentially influencing the listener's own affective state (Bachorowski & Owren, 2003; Kuczaj et al., 2013; Paul et al., 2005).

Future Directions

In future studies, we hope to explore the changes in frequency, amplitude, and directionality of burst pulse calls to develop a model that addresses the dynamic aspect of these signals. By combining video and audio data, we can examine how robust these signals are at different angles and whether we can extract information from them that is potentially meaningful to the animals. Once we have accounted for their directionality, we can investigate what information may be encoded in these pulses in different contexts. One way to do this would be to incorporate the cepstral coefficient in the sound analysis. The cepstral coefficient is a powerful tool in sound analysis due to its ability to succinctly capture and represent the spectral features of complex signals such as burst pulses with sweeping frequencies (Halkias & Ellis, 2008; Noda et al., 2019). This tactic may help us extract meaningful information to understand these signals better.

To contextualize these findings, studies of human vocalizations offer a useful comparison. Limited studies involving human vocalizations suggest that voice onset and offset can vary depending on the expressed emotion (Juslin & Laukka, 2003). For example, abrupt onsets are typically associated with emotions like happiness and anger, while slower onsets convey sadness and tenderness. Such observations of humans can inform our investigations of whether similar patterns exist in dolphin vocalizations and warrant further investigation. Additionally, there is an intriguing question regarding whether the functional role of burst pulses at the end of a click train differ from those produced independently, and warrants further investigation in the future.

Finally, future analysis can explore the cumulative effects of an emotional episode over time and how these may change with the expectation of reward/ no reward. For instance, we hope to examine how a sequence of outcomes (success or failure) may play a role in the dolphin's continued interest in engaging in the task. For example, if dolphins choose incorrectly multiple times in a row, would this change their burst pulse production?

Conclusion

In conclusion, our study sheds light on the complex nature of burst pulses in dolphins and their potential link to positive affective states. The observed patterns in burst pulse production suggest that these vocalizations may be more closely related to the dolphins' interest and engagement rather than a simple indicator of correct performance on a task. The individual variations in burst pulse production also highlight the importance of considering the unique personalities of dolphins in understanding their vocalizations and behavior. While our study has provided valuable insights, further research is needed to fully comprehend the role of burst pulses in dolphin communication and behavior. Understanding these vocalizations is crucial for gaining a deeper understanding of their emotional experiences and social interactions.

Acknowledgments

We extend our heartfelt gratitude to Dr. Mark Xitco, Director of the U.S. Navy Marine Mammal Program in San Diego, as well as the Navy's marine mammal training team, for their crucial support during this study. We would also like to extend our gratitude to audio interns Beau Wade, Anh Tran, and Maya Philips, as well as the dolphin trainers Hailey Crow, Kayla Haas, Michael Storm, June Stancil, Rylie Pereira, Dana Dalrymple, Angela Christian, and Shelby Cossey, all students from the University of California, San Diego, for their crucial roles in data collection. Lastly, we are profoundly grateful to the dolphins involved in this research, whose extraordinary presence continues to inspire and amaze us.

References

Abramson, C.I. (2013). Problems of teaching the behavorist perspective in the cognitive revolution. *Behavioral Sciences*, *3*, 55–71. https://www.mdpi.com/2076-328X/3/1/55.

Ashby, F.G., Isen, A.M., & Turken, U. (1999). A neuropsycholigcal theory of positive affect and its influence on cognition. *Psychological Review*, *106*(3), 529–550. https://doi.org/10.1037/0033-295X.106.3.529.

Au, W. W. L. (1993). *The Sonar of Dolphins*. Springer. https://doi.org/10.1007/978-1-4612-4356-4.

Au, W.W.L. & Hastings, M.C. (2008). *Principles of Marine Bioacoustics.* Springer. https://doi.org/10.1007/978-0-387-78365-9.

Au, W.W.L., Popper, A.N., & Fay, R.R. (2000). *Hearing by Whales and Dolphin.* Springer. https://doi.org/10.1007/978-1-4612-1150-1.

Bachorowski, J.A., & Owren, M.J. (2003). The sounds of emotion: The production and perception of affect-related vocal acoustics. In P. Ekman, J.J. Campos, R.J. Davidson, & F.B.M. de Waal (Eds.), *Emotions inside out: 130 years after Darwin's the expression of the emotions in man and animals* (pp 244–265). New York Academy of Sciences. https:// doi.org/10.1196/annals.1280.012.

Banse, R., & Scherer, K.R. (1996). Acoustic profiles in vocal emotion expressions. *Journal of Personality and Social Psychology*, *70(3)*, 614–636. https://doi.org/10.1037/0022-3514.70.3.614

Berridge, K. C. (2007). The debate over dopamine's role in reward: The case for incentive salience. *Psychopharmacology*, *191(3)*, 391–431. https://doi.org/10.1007/s00213-006-0578-x

Blomqvist, C., & Amundin, M. (2004). High-frequency burst-pulse sounds in agonistic/aggressive interactions in bottlenose dolphins, *Tursiops truncatus*. In J.A. Thomas, C.F. Moss, & M. Vater, (Eds.), *Echolocation in Bats and Dolphins* (pp 425–431). The University of Chicago Press.

Boissy, A., Manteuffel, G., Jensen, M.B., Moe, R.O., Spruijt, B., Keeling, L.J., Winckler, C., Forkman, B., Dimitrov, I., Langbein, J., Bakken, M., Veissier, I., & Aubert, A. (2007). Assessment of positive emotions in animals to improve their welfare. *Physiology & Behavior*, *92*(3), 375–97. https://doi.org/10.1016/j.physbeh.2007.02.003.

Branstetter, B.K., Moore, P.W., Finneran, J.J., Tormey, M.N., & Aihara, H. (2012). Directional properties of bottlenose dolphin (*Tursiops truncatus*) clicks, burst-pulse, and whistle sounds. *The Journal of the Acoustical Society of America*, *131*(2), 1613–1621. https://doi.org/10.1121/1.3676694.

Briefer, E.F. (2012). Vocal expression of emotions in mammals: Mechanisms of production and evidence. *Journal of Zoology*, *288(1)*, 1-20. https://doi.org/10.1111/j.1469-7998.2012.00920.x

Caldwell, M.C., Caldwell, D.K., & Tyack, P. (1990). Review the signature whistle hypothesis for the Atlantic Bottlenose Dolphin, *Tursiops truncatus*. In S. Leatherwood, & Reeves, R. (Eds), *The Bottlenose Dolphin: Recent Progress in Research*. Academic.

Clegg, I.L.K., Elk, C.E.V., & Delfour, F. (2017). Applying welfare science to bottlenose dolphins (*Tursiops truncatus*). *Animal Welfare*, *26(2)*, 165–176. https://doi.org/10.7120/09627286.26.2.165.

Clegg, I.L.K., Rodel, H.G., Boivin, X., & Delfour, F. (2018). Looking forward to interacting with their caretakers: Dolphins' anticipatory behavior indicates motivation to participate in specific events. *Applied Animal Behavior Science*, *202*, 85–93. https://doi.org/10.1016/j.applanim.2018.01.015

Cook, M.L.H., Sayigh, L.S., Blum, J.E., & Wells, R.S. (2004). Signature whistle production in undisturbed free-ranging bottlenose dolphins (*Tursiops truncatus*). *Proceedings of the Royal Society of London B, 271*(1543), 1043–1049. https://doi.org//10.1098/rspb.2003.2610

Dawson, S.M. (1991). Clicks and communication: The behavioral and social contexts of Hector's dolphin vocalizations. *Ethology, 88*(4), 265-276. https://doi.org/10.1111/j.1439-0310.1991.tb00281.x

Diener, D., Nickerson, C., Lucas, R.E., & Sandvik, E. (2002). Dispositional affect and job outcome. *Social Indicators Research*, *59*(3), 229–259. https://doi.org/10.1023/A:1019672513984.

de Waal, F.B.M. (2011). What is animal emotion? *Annals of the NY Academy of Sciences*, *1224 (1)*, 191–206. https://doi.org/10.1111/j.1749-6632.2010.05912.x

DeVere, A.J., & Kuczaj II, S.T. (2016). Where are we in the study of animal emotions? *WIREs Cognitive Science*, *7*(5), 354–362. https://doi.org/10.1002/wcs.1399

Delfour, F., & Charles, A. (2021). Understanding and assessing emotions in marine mammals under professional care. *International Journal of Comparative Psychology, 34,* 1–17. https://doi.org/10.46867/ijcp.2021.34.00.01

Dibble, D.S., Van Alstyne, K.R., & Ridgway, S. (2016). Dolphins signal success by producing a victory squeal. *International Journal of Comparative Psychology*, *29*, 1–10. https://doi.org/10.46867/ijcp.2016.29.00.14

Dudzinski, K.M. (1996). *Communication and behavior in the Atlantic spotted dolphin (Stenella frontalis): Relationships between vocal and behavioral activities*. [Unpublished doctoral *dissertation*]. Texas A & M University.

Dupjan, S., Schon, P.C., Puppe, B., Tuchscherer, A., & Manteuffel, G. (2008). Differential vocal responses to physical and mental stressors in domestic pigs (*Sus scrofa*). *Applied Animal Behavior Science, 114* (1-2), 105–115. https://doi.org/10.1016/j.applanim.2007.12.005

Ellsworth, P. C., & Scherer, K. R. (2003). Appraisal processes in emotion. In R. J. Davidson, H. H. Goldsmith, & K. R. Scherer (Eds.), *Handbook of Affective Sciences* (pp. 572–595). Oxford University Press. https://doi.org/10.1093/oso/9780195130072.001.0001.

Esch, H.C., Sayigh, L.S., Blum, J.E., & Wells, R.S. (2009). Whistles as potential indicators of stress in bottlenose dolphins (*Tursiops truncatus*). *Journal of Mammalogy*, *90*(3), 638–650. https://doi.org/10.1644/08-MAMM-A-069R.1

Eskelinen, H. C., Winship, K. A., Jones, B. L., Ames, A. E., & Kuczaj, S. A. (2016). Acoustic behavior associated with cooperative task success in bottlenose dolphins (*Tursiops truncatus*). *Animal Cognition, 19*(4), 789–797. https://doi.org/10.1007/s10071-016-0978-1

Fredrickson, B. L. (2001). The role of positive emotions in positive psychology: The broaden-and-build theory of positive emotions. American Psychologist, 56(3), 218–226. https://doi.org/10.1037/0003-066X.56.3.218

Gotz, T., Verfub, U.K., & Schnitzler, H.U. (2006). 'Eavesdropping' in wild rough-toughed dolphins (*Steno bredanensis*)?, *Biology Letters*, *2(1)*, 5–7. https://doi.org/10.1098/rsbl.2005.0407

Halkias, X.C., & Ellis, D.P.W. (2008). A comparison of pitch extraction methodologies for dolphin vocalization. *Canadian Acoustics*, *36*(1), 74-80. https://api.semanticsscholar.org/CorpusID:109176555.

Herman, L.M. (2002). Vocal, social, and self-imitation by bottlenose dolphin. In C. Nehaniv & K. Dautenhahn (Eds.), *Imitation in animals and artifacts* (pp. 63-108). MIT Press.

Herman, L.M. (2010). What laboratory research has told us about dolphin cognition. *International Journal of Comparative Psychology, 23*(3), 310–330. https://doi.org/10.46867/ijcp.2010.23.03.07.

Herman, D.L. & Tavolga, W.N. (1980). Communication systems of cetaceans. In L.M. Herman, (Eds), *Cetacean behavior: Mechanisms and function* (pp. 149–197), Wiley.

Herzing, D.L. (1996). Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins, *Stenella frontalis* and bottlenose dolphins, *Tursiops truncatus*. *Aquatic Mammals, 22.2*, 61-79. https://doi.org/10.12966/abc.02.02.2015.

Herzing, D.L. (2000). Acoustics and Social Behavior of Wild Dolphins: Implications for a Sound Society. In W.W.L. Au, R.R. Fay, & N. Popper (Eds.), *Hearing by Whales and Dolphins Springer Handbook of Auditory Research* (pp. 225–272). Volume 12, Springer. https://doi.org/10.1007/978-1-4612-1150-1_5.

Herzing, D.L. (2015). Synchronous and rhythmic vocalizations and correlated underwater behavior of free-ranging Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*) in the Bahamas. *Animal behavior and cognition*, *2*(1), 14–29. https://doi.org/10.12966/abc.02.02.2015

Highfill, L.E., & Kuczaj II, S.A. (2007). Do bottlenose dolphins (*Tursiops truncatus*) have distinct and stable personalities? *Aquatic Mamm*als, *33 (3)*, 380-389. https://doi.org/10.1578/AM.33.3.2007.380.

Highfill, L.E., & Kuczaj II, S.A.(2010). How studies of wild and captive dolphins contribute to our understanding of individual differences and personality. International Journal of Comparative Psychology, *23(3),* 269-277. https://doi.org/10.46867/ijcp.2010.23.03.09.

Isen, A. M., Nygren, T. E., & Ashby, F. G. (1988). Influence of positive affect on the subjective utility of gains and losses: It is just not worth the risk. Journal of Personality and Social Psychology, 55(5), 710–717. https://doi.org/10.1037/0022-3514.55.5.710

Janik, V.M. (2000). Food-related bray calls in wild bottlenose dolphins (*Tursiops truncatus*). *Proceedings of the Royal Society B, 267* (1446), 923–927. https://doi.org/10.1098/RSPB.2000.1091

Janik, V.M., Todt, D., & Dehnhardt, G. (1994). Signature whistle variations in bottlenose dolphins, *Tursiops truncatus*. *Behavioral Ecology and Sociobiology*, *35*(4), 243–248. https://doi.org/10.1007/BF00170704.

Janik, V.M., Sayigh, L.S., & Wells, R.S. (2006). Signature whistle shape conveys identity information to bottlenose dolphins. *PNAS,* 103(21), 8293-8297. https://doi.org/10.1073/pnas.0509918103.

Janik, V. M., & Sayigh, L. S. (2013). Communication in bottlenose dolphins: 50 years of signature whistle research. *Journal of Comparative Physiology A*, *199*(6), 479–489. https://doi.org/10.1007/s00359-013-0817-7

JASP Team. (2024). JASP (Version 0.16.3) [Computer software]. Retrieved from https://jasp-stats.org/.

Jones, B., Zapetis, M., Samuelson, M.M., & Ridgway, S. (2020). Sounds produced by bottlenose dolphins (*Tursiops*): a review of the defining characteristics and acoustic criteria of the dolphin vocal repertoire. *Bioacoustics*, *29*(4), 300–440. https://doi.org/10.1080/09524622.2019.1613265.

Johnson, C.M., & Herzing, D.L. (1991, December 5). Social use of the tactile effects of dolphin vocalizations. *9th Biennial Conference of Biology of Marine Mammals,* Chicago, IL.

Juslin, P.N., & Laukka, P. (2003). Communication of emotions in vocal expression and music performance: different channels, same code? *Psychological Bulletin*, *129*(5), 770–814. https://doi.org/10.1037/0033-2909.129.5.770.

Killebrew, D.A., Mercado, E., Herman, L.M., & Pack, A.A. (2001). Sound production of a neonate bottlenose dolphin. *Aquatic Mammals*, *27*(1), 34–44.

Kremer, L., Holkenborg, S.E.J.K., Reimert, I., Bolhuis, J.E., & Webb, L.E. (2020). The nuts and bolts of animal emotion. *Neuroscience and Biobehavioral Reviews*, *113*, 273–286. https://doi.org/10.1016/j.neubiorev.2020.01.028

Kuczaj II, S.A., Highfill, L.E., Makecha, R.N., & Byerly, H.C. (2013). Why do dolphins smile? A comparative perspective on dolphin emotions and emotional expressions. In S. Watanabe & S. Kuczaj (Eds.), *Emotions of Animals and Humans: Comparative Perspectives* (pp. 63-85). Springer. https://doi.org/10.1007/978--431-54123-3_4.

Lammers, M.O., Au, W.W.L., & Herzing, D.L. (2003). The broadband social acoustic signaling behavior of spinner and spotted dolphins. *The Journal of the Acoustical Society of America*, *114*(3), 1629–1639. https://doi.org/10.1121/1.1596173.

Lammers, M.O., & Oswald, J.N. (2015). Analyzing the acoustic communication of dolphins. In D.L. Herzing & C.M. Johnson (Eds.), *Dolphin communication and cognition: Past, present, and future* (pp. 107–137*).* MIT Press. https://doi.org/10.7551/mitpress/9939.003.0008.

Lazarus, R. S. (1991). *Emotion and Adaptation*. Oxford University Press. https://doi.org/10.1093/oso/9780195069945.001.0001.

Lilley, M.K., Kuczaj, S.T., & Yeater, D.B. (2017). Individual differences in nonhuman animals: examining boredom, curiosity, and creativity. In J. Vonk, A. Weiss, & S.A. Kuczaj (Eds.), *Personality in nonhuman animals* (pp. 257-275*)*, Springer International Publishing. https://doi.org/10.1007/978-3-319-59300-5_13.

Luis, A.R., Couchinho, M.N., & dos Santos, M.E. (2016). A quantitative analysis of pulsed signals emitted by wild bottlenose dolphins. *PLoS ONE*, *11*(7), e0157781. https://doi.org/10.1371/journal.pone.0157781

Lyubomirsky, S., King, L., & Diener, E. (2005). The benefits of frequent positive affect: Does happiness lead to success? *Psychological Bulletin*, *131*(6), 803–855. https://doi.org/10.1037/0033-2909.131.6.803

Macfarlane, N., Janik, V., Jensen, F.H., McHugh, K., Sayigh, L., Wells, R., & Tyack, P.L. (2017). Signature whistles facilitate reunions and advertise identity in bottlenose dolphins. *The Journal of the Acoustical Society of America*, *141 (5)*, 3543. https://doi.org/10/1121/1.4987492

Mellor, D.J. (2015). Positive animal welfare states and encouraging environment-focused and animal-to-animal interactive behaviours. *New Zealand Veterinary Journal*, *63*(1), 9–16. https://:doi.org/10.1080/00480169.2014.926800

Mendl, M., Burman, O.H., & Paul, E.S. (2010). An integrative and functional framework for the study of animal emotion and mood. *Proceedings of the Royal Society of London B*, *277*(1696), 2895–2904. https://doi.org/10.1098/rspb.2010.0303.

Miller, E.C., Johnson, C.M., & Harris, C.R. (2022). *Bottlenose dolphin personality and affective states*.[Unpublished manuscript]. Department of Psychology, University of California.

Noda, J.J., Travieso-Gonzalez, C.M., Sanchez-Rodriguez, D., & Alonso-Hernandez, J.B. (2019). Acoustic classification of singing insects based on MFCC/LFCC fusion. *Applied Science*, *9*(19), 4097. https://doi.org/10.3390/app9194097

Norris, K.S., Wursig, B., Wells, R.S., & Wursig, M. (1994). *The Hawaiian Spinner Dolphin,* University of California Press. https://doi.org/10.1525/9780520913547.

Overstrom, N.A. (1983). Association between burst-pulse sounds and aggressive behavior in captive Atlantic bottlenosed dolphins (Tursiops truncatus). *Zoo Biology, 2* (2), 93–103.https://doi.org/10.1002/zoo.1430020203.

Paul, E.S., Harding, E.J., & Mendl, M. (2005). Measuring emotional processes in animals: the utility of a cognitive approace. *Neuroscience & Biobehavioral Reviews*, *29*(3), 469–491. https://doi.org/10.1016/j.neubiorev.2005.01.002.

Probert, R., James, B.S., Elwen, S.H., & Gridley, T. (2023). Vocal cues to assess arousal state of bottlenose dolphins (*Tursiops* spp.) involved in public presentations. *Journal of Zoological and Botanical Gardens*, *4*(4), 711–727. https://doi.org/10.3390/jzbg4040050.

Quintana-Rizzo, E., Mann, D.A., & Wells, R.S. (2006). Estimated communication range of social sounds used by bottlenose dolphins (*Tursiops truncatus*). The *Journal of the Acoustical Society of America*, *120* (3), 1671–1683. https://doi.org/10.1121/1.2226559.

Ridgway, S.H., Carder, D.A., & Romano, T.A. (1991). The victory squeal of dolphins and white whales on the surface and at 100 m or more in depth. *The Journal of the Acoustical Society of America*, *90(4)*, 2335. https://doi.org/10.1121/1.402199.

Ridgway, S.H., Moore, P.W., Carder, D.A., & Romano, T.A. (2014). Forward shift of feeding buzz components of dolphins and belugas during associative learning reveals a likely connection to reward expectation, pleasure, and brain dopamine activation. *The Journal of Experimental Biology*, *217 (16)*, 2910–2919. https://doi.org/10.1242/jeb.100511.

Ridgway, S. H., Samuelson, D., Van Alstyne, K., & Price, D. (2015). On doing two things at once: dolphin brain and nose coordinate sonar clicks, buzzes, and emotional squeals with social sounds during fish capture. *Journal of Experimental Biology*, *218 (24)*, 3987–3995. https://doi.org/10.1242/jeb.130559.

Ridgway, S.H., Dibble, D.S., & Kennemer, J.A. (2018). Timing and context of dolphin clicks during and after mine simulator detection and marking in the open ocean. *Biology Open*, *7*(2), bio031625. https://doi.org/10.1242/bio.031625.

Roseman, I. J., & Smith, C. A. (2001). Appraisal theory: Overview, assumptions, varieties, controversies. In K. R. Scherer, A. Schorr, & T. Johnstone (Eds.), *Appraisal processes in emotion: Theory, methods, research* (pp. 3–19). Oxford University Press. https://doi.org/10.1093/oso/9780195130072.003.0001.

RStudio Team. (2024). RStudio: Integrated Development for R (Version 1.4.1717) [Computer software]. RStudio, PBC. Retrieved from http://www.rstudio.com/.

Silvia, P.J. (2008). Interest- the curious emotion. *Current Directions in Psychological Science*, *17* (1), 57 – 60. https://doi.org/10.1111/j.1467-8721.2008.00548.x.

Seyfarth, R.M., & Cheney, D. (2003). Meaning and emotion in animal vocalizations. *Annals of the NY Academy of Sciences*, *1000*, 32-55. https://doi.org/10.1196/annals.1280.004.

Shiota, M.N., Campos, B., Oveis, C., Hertenstein, M.J., Simon-Thomas, E., & Keltner, D. (2017). Beyond happiness: building a science of discrete positive emotions. *American Psychologist*, *72*(7), 617–643. https://doi.org/10.1037/a0040456.

Shiota, M.N., Sauter, D.A., & Desmet, P.M.A. (2021). What are 'positive' affect and emotion? *Current Opinion in Behavioral Sciences*, *39*, 142–146. https://doi.org/10.1016/j.cobeha.2021.03.007.

Smith, C.A., & Ellsworth, P.C. (1985). Patterns of cognitive appraisal in emotion. *Journal of Personality and Social Psychology*, *48*(4), 813–838. https://doi.org/10.1037/0022-3514.48.4.813

Smith, C. A., & Kirby, L. D. (2009). Putting appraisal in context: Toward a relational model of appraisal and emotion. *Cognition & Emotion*, *23*(7), 1352–1372. https://doi.org/10.1080/02699930902860386.

Smolker, R., Mann, J., & Smuts, B. (1993). Use of signature whistles during separations and reunions by wild bottlenose dolphin mothers and infants. *Behavavioral Ecology and Sociobiology, 33*, 393–402. https://doi.org/10.1007/BF00170254.

Snowden, C.T. (2003). Expression of emotion in nonhuman animals. In R.J. Davidson, K.R. Scherer, & H.H Goldsmith (Eds.), *Handbook of affective sciences* (pp. 457-480). Oxford University Press. https://doi.org/10.1093/oso/9780195126013.003.0024.

Soltis, J., Leong, K., & Savage, A. (2005). African elephant vocal communication II: Rumble variation reflects the individual identity and emotional state of callers. *Animal Behavior, 70*(3), 589–599. https://doi.org/10.1016/j.anbehav.2004.11.016.

Tyack, P. (1986). Whistle repertoires of two bottlenose dolphins, *Tursiops truncatus*: mimicry of signature whistles?, *Behavioral Ecology and Sociobiology, 18*, 251–257. https://doi.org/10.1007/BF00300001.

Tyack, P.L. (2000). Dolphin social behavior and communication. In J. Mann, R.C. Connor, P.L. Tyack, & H. Whitehead (Eds.), *Cetacean Societies: Field Studies of Dolphins and Whales* (pp. 270-307). University of Chicago Press.

Wang, Z. T., Whitlow, W. L. Au., Rendell, L., Wang, K. X., Wu, H. P., Wu, Y. P., Liu, J. C., Duan, G. Q., Cao, H. J., & Wang, D. (2016). Apparent source levels and active communication space of whistles of free-ranging Indo-Pacific humpback dolphins (*Sousa chinensis*) in the Pearl River Estuary and Beibu Gulf, China. *PeerJ*, *15*(4), e1695. https://doi.org/10.7717/peerj.1695.

Watson, D., Clark, L.A., & Tellegen, A. (1988). Development and validation of brief measures of positive and negative affect: the PANAS scales. *Journal of Personality and Social Psychology*, *54*(6), 1063–1070. https://doi.org/10.1037//0022-3514.54.6.1063.

Whitham, J.C., & Miller, L.J. (2024). Utilizing vocalizations to gain insight into the affective states of non-human mammals. *Frontiers in Veterinary Science*, *11*, 1366933. https://doi.org/10.3389/fvets.2024.1366933.

Xitco, M.J. & Roitblat, H.L. (1996). Object recognition through eavesdropping: passive echolocation in bottlenose dolphins. *Animal learning & behavior,* 24(4), 355–365. https://doi.org/10.3758/BF03199007.

Financial conflict of interest: No stated conflicts.
Conflict of interest: No stated conflicts.

Submitted: *February 5th, 2025*
Resubmitted: *April 3rd, 2025*
Accepted: *April 22nd, 2025*