



Dolphins Signal Success by Producing a Victory Squeal

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As a result of their experiences, animals come to expect certain things to happen in certain contexts. The importance of expectation in learning has been demonstrated in a number of studies. (Kuczaj & Xitco, 2002, p. 194)

. . .lower animals... manifestly feel pleasure and pain, happiness, and misery
– Darwin, *The Descent of Man*

We have long observed dolphins producing recognizable sounds—bursts of pulses with sweeping peak frequencies—at prey capture. We call this the victory squeal. When dolphins forage, there are three sequential sounds: sonar clicks, terminal buzz, and the victory squeal. When dolphins find a fish with sonar clicks, but reject the fish during the terminal buzz phase, they omit or truncate the victory squeal. We also observe dolphins producing the victory squeal after a trainer's bridge, which serves as secondary reinforcement, bridging the time gap between the dolphin's performance and delivery of food reinforcement. It signals to the dolphins that they performed correctly and that reward is forthcoming. Before training, the victory squeal was largely occurred with fish capture, but after successive trials and learning, the dolphins shifted this response to follow the bridge. The victory squeal immediately following the bridge suggests the dolphin expects reward. Although there are no direct studies of dopamine release in cetaceans, early brain stimulation studies demonstrated consistent timing that may link the victory squeal with brain dopamine release. In the current study, we asked if dolphins might produce the victory squeal after task completion, but without the trainer's bridge. Dolphins carried cameras, recording video and sound, while performing tasks in the open ocean, away from trainers and other animals, during swimmer/mine marking and disk retrieval. In each task, we observed the victory squeal immediately upon completion of task components. We suggest that the victory squeal signals that these experienced dolphins recognized their success.

Dolphins are capable of learning novel tasks based on a number of psychological principles concerning expectancy. Animals learn to expect specific outcomes based on retaining and recalling information from prior experiences in similar contexts (Kuczaj & Xitco, 2002). Based on an animal's response to a given stimulus, reinforcement is either given or withheld. Thus the animal learns from past performances. Dolphins learn to expect rewards based on past experiences. Animals may plan their behavior in a meaningful way (Kuczaj, Gory, & Xitco, 2009) and can recognize order by having an appreciation for the relationship between actions and outcomes (Kuczaj, Gory, & Xitco, 1998).

When one investigator (SR) observed sounds produced by bottlenose dolphins (*Tursiops truncatus*) brought in from the wild, a peculiar sound initially referred to as a feeding buzz was heard as the animals seized fish thrown into their enclosure. This occurred at Point Mugu, California in 1963. The pool was fitted with hydrophones and speakers broadcasting sounds that all nearby could hear. The striking pulse bursts were heard each time a dolphin seized a fish. Others have also observed *T. truncatus* buzzing as they took fish. In a group of bottlenose dolphins at Marineland of Florida, Wood described these feeding sounds as mewling and rasping (Wood, 1953). Kellogg mentioned that echolocation became almost continuous as a dolphin approached and took a preferred fish (Kellogg, 1959). Norris noted that a dolphin emitted a brush of pulses as

it took a fish (Norris, Prescott, Asa-Dorian, & Perkins, 1961). In later years, we found that these same sounds were transposed from the instant of fish capture to the instant of a secondary reinforcer, a bridge, indicating that a dolphin had completed the task successfully. This secondary reinforcer could be a tone or other sound or even the cessation of a sound used in training (Ridgway, Carder, & Romano, 1991; Ridgway, Moore, Carder, & Romano, 2014). These sounds produced by dolphins associated with eating fish and responding to reinforcers have come to be called victory squeals (Branstetter, Moore, Finneran, Tormey, & Aihara, 2012; Finneran, 2013; Ridgway, Dibble, Van Alstyne, & Price, 2015; Ridgway et al., 1991, 2014).

We have studied the victory squeal (VS) as part of the sequence of sounds dolphins make as they find and take fish. For that study, the dolphins were habituated to carrying cameras placed on their foreheads with soft rubber suction cups (Ridgway et al., 2015). This study was the first to match sound and video from free-swimming dolphins during location, pursuit and capture of fish. A hydrophone in the far field near the fish also recorded sound. From these two perspectives, we studied the time course of dolphin sound production while video recording fish capture. Our observations identified the instant of fish capture. We found three consistent acoustic phases: (1) sonar clicks locate the fish; (2) about 0.4 s before capture, the dolphin clicks become more rapid to form a second phase, the terminal buzz (TB); (3) at or just before capture, the buzz turns to the VS, which may last 0.2 to 20 s after capture. The squeals are pulse bursts that vary in duration, peak frequency, and amplitude.

The VS may affect prey to ease capture, may be a way to communicate the presence of food to other dolphins, or it may be a reflection of emotional pleasure triggered by brain dopamine release. Here we investigated the VS in tasks that were not directly related to fish capture, but that occurred before a bridge was given by the trainer. Through simultaneous video and audio recordings, we could begin to study what elicited over 200 VSs while the dolphins were performing the various tasks during the investigation.

Method

Subjects

Three dolphins, aged 33, 34 and 51 years (Table 1), with long histories of participation in trained tasks, swam alongside boats in the open ocean wearing cameras (GoPro Hero4 silver and black [San Mateo, CA]; Garmin VIRB [Canton of Schaffhausen, Switzerland]) temporarily attached to their forehead or harness. These cameras recorded video and also sound at bandwidths of 0-16 kHz (GoPro) and 0-13 kHz (VIRB).

Procedure

The three dolphins swam alongside their trainer's boat within and outside of San Diego Bay. They participated individually in different tasks on multiple days, far away from trainers, at least 750 m away from other dolphins. One dolphin (TEN), who participated in marking practice buried mines, wore a camera attached dorsally on her harness, providing a limited view of the rostrum. Two dolphins (SPL, BLU), participating in swimmer marking and disc retrieval studies, wore forehead cameras that provided a clear view of the dolphin's rostrums. These two dolphins had previous experience wearing forehead cameras attached to soft suction cups during fish capture studies (Ridgway et al., 2015). The dolphins voluntarily accepted the suction cup cameras. Cameras remained adhered to the dolphin's forehead during swimmer marking and disc retrieval sessions, while the animals swam rapidly, causing no apparent discomfort. Suction cups have long been used to attach sensors and tracking devices to dolphins (Ridgway, 1965; Tyack, 1985). To corroborate the GoPro acoustic recordings, a broadband hydrophone with a bandwidth from 0-125 kHz (B&K 8101, Brüel & Kjær, Denmark with Dodotronic HydroMic 250 amplifier/digitizer, CIBRA, Italy) was placed in the water at a depth of 1-2 m behind the targets, within the approaching dolphin's narrow sonar beam (Au, 1993; Finneran et al., 2014). An additional GoPro camera was inserted near this hydrophone, together capturing sound and video near the disc or swimmer, providing an additional vantage point during the investigation. Upon task completion, dolphins did not always receive a reward because they were reinforced on a variable schedule.

Table 1
Characteristics and Task Designation of the Three Bottlenose Dolphins (Tursiops truncatus) Used in the Experiments

ID	Species	Sex	Length (cm)	Weight (kg)	Age (yrs)	DOB	MMP (yrs of participation)	Origin
TEN	<i>T. truncatus</i>	F	249	175	33	06/15/83	28	MS, MMA
SPL	<i>T. truncatus</i>	F	251	188	34	06/15/82	29	MS, MMA
BLU	<i>T. truncatus</i>	F	251	201	51	06/15/65	45	MS, MMA

Note. The three dolphins were collected from the wild in the Mississippi Management Area (MS, MMA) in the Gulf of Mexico. These dolphins have been with the Marine Mammal Program (MMP) for 28-45 years. ID, dolphin individual identification; F, female.

Task 1. Disc retrieval studies involved the dolphin BLU and a disc that floated near the surface (Figure 1). BLU’s task included two recognizable opportunities per trial to produce a VS for predetermined stimuli: (1) contacting the disc and (2) surfacing at the boat. Once arriving at a remote location in the bay, the trainer stationed BLU at the boat to place the camera. Each trial began once the trainer turned on the camera and the disc was placed in the water. BLU was then signaled to search for and retrieve the disk. Upon returning to the boat with the disc, she was given reinforcement and the camera was turned off, terminating the trial.

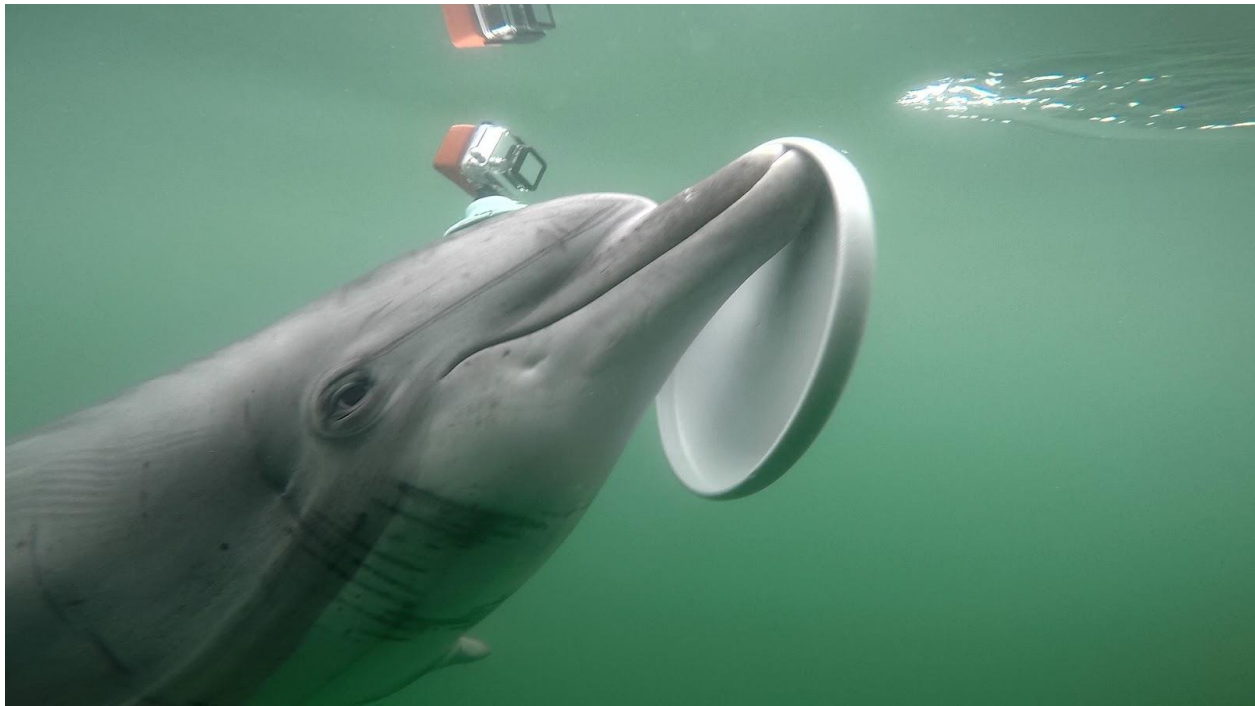


Figure 1. View from the camera near the far-field hydrophone as the dolphin contacts a disc. The camera attached temporarily to the dolphin’s forehead by a rubber suction cup is positioned forward to record the instant of contact with the disc during retrieval trials.

Task 2. Swimmer marking sessions included the dolphin SPL. SPL’s task included five components per trial, providing five opportunities to produce a VS for predetermined stimuli: (1) locate swimmer, (2) return to boat, (3) indicate detection/get marker, (4) mark swimmer, and (5) return to boat. When the boat and dolphin arrived at a remote location to begin trials, SPL stationed in front of her trainer to receive the forehead camera. After SPL received the camera and the swimmer was in the water, the camera was powered on. Once the boat engines were started, SPL was signaled to begin searching for swimmers as she swam alongside the trainer’s boat. If the dolphin identified a swimmer, she returned back to the boat, signifying detection results by pressing the corresponding paddle. SPL

was then presented with a swimmer marking device comprised of two parts that disassembled when SPL made contact with the swimmer. The first part was a cone that the dolphin was trained to insert its rostrum into. The second part was attached to the cone and upon contact with the swimmer separated from the cone and floated to the surface, allowing the location of the swimmer to be identified (Figure 2). Once SPL was given the marker, she relocated the swimmer and began her approach. Upon marker deployment, SPL returned to the boat, completing the chain of behaviors and received reinforcement.



Figure 2. View from a camera near the far-field hydrophone during swimmer marking trials. A dolphin temporarily places its rostrum inside a swimmer marking device, a cone (nose cup) attached to a buoyant marker, used to identify the location of a swimmer.

Occasionally, when the dolphin made contact with the swimmer, the marker did not deploy. SPL still produced a VS, although would abruptly truncate the vocalization if the marker failed to deploy and would reposition herself to mark the target again. The camera was powered off and after repeated trials, the session concluded.

Task 3. Buried practice mine marking investigations involved the dolphin TEN. TEN voluntarily accepted the harness camera (GoPro Hero4 black, silver; Garmin VIRB), allowing it to remain on the dolphin during all components of the task even while swimming rapidly. TEN's task also included five components per trial providing five opportunities to produce a VS for predetermined stimuli: (1) locate the mine, (2) return to boat, (3) indicate detection/get marker, (4) mark the mine, and (5) return to boat, completing the behavior. When the boat arrived at a practice mine field, TEN stationed at the boat in front of her trainer while the camera was secured to her harness and powered on. Upon receiving the search signal, TEN began using sonar to locate the hidden mine on or under the sea floor. If the dolphin identified a mine, she returned back to the boat, signifying detection results by pressing the corresponding paddle. If TEN indicated to the trainer a mine had been detected, she was given a marker. Once the marker had been placed on her

rostrum she was signaled to set the marker near the location of the mine. After marking the mine, TEN returned to the boat to receive reinforcement while divers on the second boat identified the outcome of TEN’s placement of the marker. If the divers established the mark had been successful, TEN was given additional reinforcement and the camera was turned off, ending the trial.

Victory squeals associated with surfacing at the boat were categorized separately from task associated VSs because they could be produced for a variety of reasons. For example, VS responses surfacing at the boat could be produced for task completion, anticipation of receiving a fish reward, receiving the marker or for interacting with the trainer.

All acoustic data was imported into Audacity and displayed with Adobe Audition for VS identification during each task. VS presence was visually and audibly confirmed by investigators when apparent burst pulses of frequencies that varied and swept over time were present on the spectrogram. Underwater photographs taken by the GoPro near the target were formatted with Adobe Photoshop and enhanced in Adobe Lightroom.

Results

During five sessions, BLU participated in 62 disc retrieval trials during which a total of 66 VSs were recorded (Table 3). Of the total number of VSs recorded from these sessions, 35 (53%) were associated with contacting the disc. Twenty-eight VSs (42%) that were associated with surfacing at the boat and three other VSs (5%) were not task-associated. The fraction of retrievals and boat surfacing that resulted in VSs are slightly different, 56% and 45%, respectively. Simultaneous audio and video recordings showed that of the 35 VSs associated with disc contact, 34 of them started just before contact. In only one trial, VS production began just after contact had been established. The reasons for the three *other* VS recordings are unknown, but did not appear to be associated with any part of the task. Because BLU participated in about 15 trials per session, we investigated whether more VSs were present at the beginning of the session versus the latter part. In 3 of the 5 sessions almost all VSs occurred in the first half of the session. In the remaining two sessions, VSs occurred nearly equally throughout the beginning and end of the session.

Table 2
Dolphins and Tasks Eliciting a VS Response

Categories	Animal ID		
	TEN*	SPL*	BLU
Search and locate target	✓	✓	✓
Return to boat	✓	✓	✓
Indicate detection and get marker	✓	✓	NA
Mark target	✓	✓	NA
Return to boat	✓	✓	NA

Note. The asterisk (*) denotes animals whose task was a chain of behaviors.

SPL participated in 19 swimmer marking trials producing a total of 60 VS responses (Table 3). As previously mentioned each trial was separated into five identifiable components: (1) locate swimmer, (2) return to boat, (3) indicate detection/get marker, (4) mark swimmer, and (5) return to boat, completing the chain of behaviors (Table 2). SPL contacted the diver 19 times, resulting in 19 VSs. Contact in 7 of the 19 trials did not result with the marker deploying and identifying the location of the swimmer. Nevertheless, a VS was recorded every time contact was made with the swimmer regardless of whether the marker successfully deployed. There were 25 (42%) additional VS responses associated with swimmer sessions ([1], [2]), nine (15%) with surfacing at the boat, and seven (12%) were not task associated and grouped into the other category. Two of the VSs in this other category were associated with SPL finding and returning a lost camera, the reason for the remaining five VSs could not be determined from the field of view the GoPro provided.

Table 3
Participants and Results with Associated Tasks

Animal ID	TEN	SPL	BLU
Camera location	Harness	Forehead	Forehead
Sessions (<i>N</i>)	5	3	5
Trials (<i>N</i>)	23	19	62
Task	(1) Mine detection and (2) Marking	(1) Swimmer detection and (2) Marking	(1) Disc retrieval
VS associated with final task (<i>N</i>)	13 (14%)	19 (32%)	35 (53%)
VS associated with intermediate tasks (<i>N</i>)	10 (11%)	25 (42%)	NA
VS associated with surfacing at boat (<i>N</i>)	58 (62%)	9 (15%)	28 (42%)
VS other (<i>N</i>)	13 (14%)	7 (12%)	3 (5%)
Total VSs recorded (<i>N</i>)	94	60	66

Note. TEN and SPL participated in different chained behaviors comprised of a (1) detection and (2) marking a target. BLU participated in a behavior that had only one task, disc retrieval. Victory Squeals (VSs) associated with tasks and surfacing at the trainer’s boat were calculated for each trial. *N* denotes number of sessions, trials, total VSs produced and VSs associated with: final task, intermediate tasks, surfacing at boat, and other. NA = not applicable. VSs associated with final task includes: marking mine, marking swimmer, contacting disc for retrieval. VSs associated with intermediate tasks (mine and swimmer marking) include: before touching paddle (swimmer marking), receiving marker and returning empty marker (swimmer marking). VSs in the other category include: passing divers, hand-stationing at boat, swimming alongside boat, finding camera, returning camera, during camera placement and for reasons resulting from an unknown stimulus. Total VSs recorded comprises VS associated with final task, intermediate task, surfacing at the boat and for other reasons.

TEN also participated in 23 trials, searching for buried practice mines, during which a total of 94 VSs were recorded. Because the most mines were buried, it was not possible from the video recordings to know with certainty, whether the dolphin successfully marked the mine. Furthermore, because the camera was on the dolphin’s harness, it was not always possible to correlate the acoustic recordings with a rostral perspective to aid in determining what particular activity was associated with the onset of VS production. Nevertheless, we can draw inferences from the dolphin’s behavior. As with the SPL trials, each trial was separated into five similar components: (1) search and locate mine, (2) return to boat, (3) indicate detection/get marker, (4) mark mine, and (5) return to boat, completing the chain of behaviors (Table 2). Of the 94 VSs recorded, we believe 13 (14%) were associated with successfully marking the mine and 10 (11%) with intermediate tasks associated with the marker. Fifty-eight (62%) of the VSs occurred upon surfacing at the boat, and 13 (14%) were categorized as “other”. The other category was comprised of encountering a diver, boat following, hand stationing and five for unknown reasons.

A total of 104 trials among the three different tasks were performed producing 220 VS responses (Table 3). Of all 220 audio recordings of VS responses, only five were longer than 2 s in duration. Unfortunately, this VS occurred in the other category and its source of stimulus is unknown due to the limited view the harness camera provided. The VSs produced for fish captures were not included in the task related results. In addition to VSs, a cacophony of dolphin sounds were recorded including sonar clicks, terminal buzzes and whistles. TEN produced repetitive whistles of similar form throughout the trials after marking a mine or immediately before surfacing in front of trainer. SPL also produced repetitive whistles, but of a different frequency-amplitude structure while swimming alongside the boat during swimmer detection.

Discussion

Similar to previous delphinid sonar studies, the inter-click interval between projected sonar clicks decreased as the dolphins closed in on the targets (Jensen, Bejder, Wahlberg, & Madsen, 2009; Morozov, Akopian, Burdin, Zaitseva, & Sokovykh, 1971; Ridgway et al., 2015; Wisniewska, Johnson, Nachtigall, & Madsen, 2014). Here we identify the onset of VS production on completion of trained tasks, without immediate reward and away from the trainer. We matched sound and video from the perspective of the dolphin with sound and video near the target. In our current study, dolphins usually terminated VS production within 2 s of contacting the target. In the previous study (Ridgway et al., 2015) some of the VS lasted much longer when dolphins contacted and ate a larger fish and the VS lasted throughout consumption. Although the duration of VSs are shorter for task completions that are not directly associated with primary reinforcers (food), these task completions still elicit a response that appears to be pleasurable.

For years, dolphin vocalizations (i.e., VSs) associated with reward expectation have been heard. When new behaviors are initially trained, if dolphins recognize familiarity, they may generalize previously learned behaviors to try and succeed at the novel task. For instance, dolphins learn to place their rostrum on a target pole when it is first presented. During preliminary training to acclimate the dolphins to research equipment, the animals often generalized the hydrophone with a target pole by stationing their rostrum on the hydrophone when they were instructed to complete an unfamiliar task. Often the dolphin produced a VS upon contact with the hydrophone. After successive trials, the dolphin typically learned to ignore the hydrophone and complete the new task. The dolphin then produced a VS upon completion of the task or for completing a portion of the task involved in a chain of behaviors. Thus it appears the dolphin generalized prior experience and equipment to try and learn the new behavior.

Martin, Phillips, Bauer, Moore, and Houser (2003) found that when dolphins search for practice mines, a VS is often produced at different steps within the chain of behaviors. During current practice mine marking and swimmer marking trials, multiple VSs were also observed at various steps within the task. When VSs were present in our current study, regardless of the task or participant, the high pulse rate emissions resembled previously described VS structure, varying in peak frequency and amplitude throughout production of the sound (Ridgway et al., 2014, 2015).

The victory squeal occurs after a trainer's bridge or secondary reinforcer (Ridgway et al., 2014). The VS also occurs during prey capture (Ridgway et al., 2015). It appears that dolphins produce a VS with expectation of receiving a food reward with delight on fish capture. Our novel findings demonstrate that over time, dolphins learn to expect a reward for tasks (e.g., marking, disk retrieval) that do not directly involve fish capture or a bridge. Thus, the animals produce a VS response when they perceive that they have succeeded at a task. The delay between task component completion and reward reception in this study is significantly longer compared to the nearly instantaneous timing between expectation and reward during fish capture trials. The dramatically delayed timing in reinforcement associated with non fish capture tasks may suggest that, for such tasks, a component of the victory squeal response may be an automatic expression of the animal's triumph over their performance when they experience success or anticipate a reward.

Additional odontocete species have been found to produce unique sounds associated with contacting prey during foraging. For instance, the sperm whale, beluga, narwhal, porpoise, beaked whale and Irrawaddy dolphins produce conspicuous sounds during prey capture (Aguilar de Soto et al., 2012; DeRuiter et al., 2009; Gordon, 1987; Johnson, Madsen, Zimmer, De Soto, & Tyack, 2004; Kastelein, Nieuwstraten, & Verboom, 1995; Miller, Pristed, Møshl, & Surlykke, 1995; Ridgway et al., 1991; Van Parijs, Parra, & Corkeron, 2000).

These vocalizations may be analogous to the bottlenose dolphin VS in appearance, but require further investigations before a conclusion can be drawn as to their function or evolutionary purpose.

A variety of other nonhuman animals display victory responses, but primarily in the context of competition with another animal; In other words, these actions mainly serve as a method of communication (Grafe & Bitz, 2004; Mesterton-Gibbons & Sherratt, 2006). The dolphins in our study produced the sound alone, far away from other dolphins and trainers, suggesting that the vocalization individual expression of emotion. The observation that the dolphins seem to “know” when they have done a good job without receiving immediate primary reinforcement (food) or communication (bridge) from the trainer supports the proposition that the VS may have elements of joy engendered by brain dopamine release. Therefore, we again suggest that the dolphin VS is an emotional outburst caused by an innate response when the animal experiences success.

Although it is difficult to directly study animal emotions, data suggests that dolphins have the capacity to experience complex emotions (Bekoff, 2000; Kuczaj, Highfill, Makecha, & Byerly, 2013; Kuczaj & Horback, 2013; Ridgway et al., 2014). The frequency with which dolphins produce a VS suggests that it may be an uninhibited emotional outburst. The structure of the dolphin brain suggests that emotional sounds may be less inhibited than in some other species. The dolphin’s frontal lobe is relatively small, as is the cingulate, or limbic, cortex (Manger, 2006; Morgane, Jacobs, & McFarland, 1980), both of which are involved in the modulation of the expression of emotional behaviors in other mammals (e.g., Knight, Staines, Swick, & Chao, 1999). Reduced action of these cortical regions has not been explicitly demonstrated experimentally in dolphins due to the technical and ethical difficulties of undertaking such a study, however, the mesolimbic dopaminergic reward pathway appears to be expanded in dolphins compared to other mammals (Manger, Fuxe, Ridgway, & Siegel, 2004), which together with the small prefrontal and cingulate cortex indicates that suppression or modulation of emotional, or reward-based, behaviors may not be particularly strongly developed in dolphins, which in turn may lead to the regular production of the VS by dolphins observed in this study. This potentially limited cortical inhibition and expanded mesolimbic system might explain why dolphins appear to start producing a VS and then abruptly stop upon deciding to reject and not eat a fish (Ridgway et al., 2015).

The VS follows the trainer’s bridge by about 200 ms suggesting an emotional response to dopamine release driven by expectation of reward (Ridgway et al., 2014). Following this work, we studied the time course of the different sounds that dolphins use to forage for food. The VS was produced at the instant of fish capture and continued as the dolphin ate the fish (Ridgway et al., 2015). Now, we show that the VS is often produced during non fish capture tasks at the instant a task is completed. Like the VS produced when a fish is captured and like the VS produced after the trainer’s bridge, the VS produced at the instant of intermediate and final task completion suggests an emotional expression, possibly induced by dopamine release, signaling that dolphins recognize task completion. Our current evidence does not support the VS being used as a food call, but rather our observations support the idea that the VS may be a reflection of emotion and not necessarily for communicating the presence of food to surrounding animals (Ridgway et al., 2014; Wisniewska et al., 2014). The VS may be important in understanding the emotional complexity of the dolphin brain. The context of the emotional VS sounds produced in these studies, suggests that dolphins “know” when they have successfully completed a trained behavior.

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