Linköping University | Department of Physics, Chemistry and Biology
Master's thesis, 60 hp | Educational Program: Physics, Chemistry and Biology
Spring term 2021 | LITH-IFM-A-EX—21/3969--SE

The Whistle caller concept - Signature whistles as call-over signals for Bottlenose dolphins (*Tursiops truncatus*) under human care

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1 Abstract

Dolphins use stereotyped, individually distinctive, frequency modulated whistles, referred to as signature whistles, in order to broadcast their identity. In this study, we trained six dolphins at Kolmården Zoo, Sweden, to be called over, either upon hearing their own signature whistle (SW) or upon hearing a biologically irrelevant ”trivial” sound (TS), with the aim to prove the Whistle caller concept. The Whistle Caller concept is based on the fact that dolphins occasionally use other dolphins' signature whistles in order to address specific group members and convene.

Our hypotheses were that (1) dolphins call-over trained using their SW would learn the behaviour faster than dolphins trained using TSs, and (2) dolphins trained with their SW would be able to discriminate between different SWs better than dolphins trained with a TS would be at discriminating between different TSs.

Three out of three dolphins were successfully call-over trained using their SW, and two out of three dolphins using their assigned TS. When discriminating between different sounds, two of the dolphins trained using their SW performed significantly better than one of the dolphins trained using a TS. However, there were large intra-group differences in the results, indicating that we cannot eliminate the possibility that these results stem from individual differences in these dolphins' ability to learn new behaviours overall, rather than an understanding of the sounds they heard.

We suggest that future studies focus on (1) male-female differences in discrimination success when applying the Whistle caller concept, (2) how the characteristics of the trivial sounds affect discrimination success, and (3) the option of calling more than one animal at a time by sending out several SWs in succession.

Keywords:

Signature whistle, Bottlenose dolphin, *Tursiops truncatus*, zoo animals, animal training, animal welfare, dolphin communication, bioacoustics, the Whistle caller concept.

2 Introduction

2.1 Dolphin vocalisations

The Bottlenose dolphin (*Tursiops truncates*) is a social species whose primary form of communication is through sounds (Herzing, 2000; Janik, 2009). Their ability to communicate through visual or tactile signals demands close enough proximity to see or touch each other, and their communication through taste and smell is debated, as it is yet unclear which and how well dolphins perceive chemical cues through these senses (Kishida *et al*., 2007; Kremers *et al*., 2016; Kremers *et al*., 2016). Sound, however, can convey information over larger distances and several dolphin species therefore generate a broad range of different vocalisations – often divided into whistles, burst pulse sounds and clicks. Whistles and burst pulse sounds are mostly used for communication and the latter category include pops, barks and squawks, whereas clicks are primarily used for navigation and orientation purposes through echolocation (Au, 1993; Herzing, 1996; Herzing, 2000). Whistles have been observed to be used in several different contexts such as during foraging, for group cohesion purposes and as excitement vocalizations to name a few (Herzing, 1996). In this study, however, we focus on one particular type of whistle – the signature whistle.

Signature whistles are stereotyped, individually distinctive frequency modulated whistles that were first described by Caldwell and Caldwell in 1965. Each signature whistle has its own frequency modulation pattern that can range from 1 kHz to 41.8 kHz (Sayigh & Janik, 2010; Hiley *et al*., 2017) but usually stays within 8-18 kHz (Herzing, 1996). They are often made up of several repeated loops that last for about 0.3-0.5 s each (Caldwell *et al.*, 1990). These whistles develop through vocal learning during a calf's first year of life and are thought to be influenced by the calf's acoustic environment (Mello *et al.*, 2005; Fripp *et al*., 2005). The different frequency modulation patterns in these whistles carry information that broadcasts the identity of the whistle owner (Caldwell *et al*., 1990; Janik *et al*., 2006), and are thus thought to be cohesion calls, used when groups of dolphins meet at sea (Herzing, 1996; Janik & Slater, 1998; Esch *et al*., 2009; Quick & Janik, 2012). They also facilitate mother-offspring cohesion, as mothers can use their own signature whistle in order to retrieve their calf if they are apart, and vice versa (Bebus & Herzing, 2015; King *et al.*, 2016). In dolphins that have been separated from their group, signature whistles account for almost all (80-100%) of their emitted whistles (Caldwell & Caldwell, 1965; Janik &

Sayigh, 2013). Because of this, signature whistle rates may be used as an indicator of acute stress (Esch *et al*., 2009). However, an increased whistle rate does not have to imply that stress has increased, but rather be a result of an increased need for communication (Esch *et al*., 2009). Results presented in Caldwell *et al*. (1990) also suggest that stress can cause some dolphins to produce signature whistles with a larger number of loops than what they commonly would, while other dolphins may do the opposite.

2.2 Copying of signature whistles

Although rare, dolphins sometimes copy each other's signature whistles, possibly in order to address, or answer a specific individual (Janik & Slater, 1998; King *et al*., 2013; King *et al*., 2014). This has for example been seen during forced separations of mother-calf pairs, and between close associates that match each other's whistles as an affiliative signal (King *et al*., 2013; King *et al*., 2014). Matching of both signature and non-signature whistles, as well as other vocalizations, have been observed during for example cooperative feeding events and in male alliances during cooperative mate guarding (King & Janik, 2015; King *et al*., 2019). However, when signature whistle copying occurs, the dolphin adds extra features to the copied whistle (changing frequencies or using different numbers of loops) supposedly in order for the copy to be recognized as such (King *et al*., 2013). If these extra features were not added to a signature whistle copy, it is hypothesized that signature whistles as a method for identification would not be sustainable, as it would cause confusion among group members (King *et al*., 2013). Between close associates, this confusion would likely not be as pronounced, and instead hypothetically be an effective way of addressing a specific whistle owner.

2.3 Dolphin training

For dolphins under human care, signature whistles have been seen to increase after training sessions (Lopez Marulanda *et al*., 2016). Lopez Marulanda *et al*. (2016) argue that this might be a result of how the dolphins are grouped during training sessions – when the session is over, the dolphins use their signature whistles in order to regroup and reconvene with individuals that they prefer.

Incorporating signature whistles as a part of dolphin training has, to our knowledge, not been done before. However, Lima *et al*. (2018) showed in their study that dolphins could indeed discriminate between human-made sounds both in water and in air. In their study, Lima *et al*. (2018) trained dolphins to respond to an individually specific instrument when played under water. When a signal was played, the individual to whom it belonged approached the sound source, thereby working as a call-over signal. They then proceeded by playing the instruments above water and could see that the dolphins were able to recognise discriminate between these sounds when played in air as well. Lima *et al*. (2018) suggest that future studies should investigate whether dolphins could associate these acoustic cues with individual identities. In the current study, we take this into consideration, using both signature whistles and human-made, non-biologically relevant, sounds in the training of six bottlenose dolphins at Kolmården Zoo, Sweden.

2.4 Current call-over training and the Whistle caller concept

During the routine dolphin training at Kolmården Zoo, Sweden, all animals are called over by the trainers using a hand-slap on the water surface, which generate an approximately 100 ms long underwater pulse sound that can be heard by the dolphins. When all dolphins are gathered at the poolside, the trainer uses visual cues, such as pointing and making eye contact, to select one or more dolphins for individual training, or “sending” them to another station where another trainer takes over. This is a rather complicated and time-consuming procedure, which sometimes leads to the dolphins misunderstanding the trainers’ signals, creating frustration for both the animals and the trainers. The hand-slap can also be hard for the animals to hear if they are distracted or if the sound is masked by noise, for example during play.

Although dolphins can discriminate between different acoustic cues in air, the dolphin ear is not adapted to receive airborne sounds (Hemilä *et al*., 2010), suggesting that an underwater call-over signal would be more effective than one in air (for example a trainer’s voice). Also, using individual call-over signals during feeding has been observed to decrease dominance and aggressive behaviour in pregnant sows, indicating that individual calls anticipating feeding, can increase animal welfare (Manteuffel *et al*., 2010).

The Whistle caller concept is based on the fact that dolphins imitate another individual's signature whistle to make contact with it and convene (King *et al.*, 2013). Thus, by playing a recorded signature whistle of a dolphin in the water, it should be possible to call that dolphin, while all the other individuals understand that they are not addressed. Using other, non-biologically relevant sounds as call-over signals have been tried successfully before (Lima *et al*., 2018). We hypothesise that by using signature whistles, it will be easier for the dolphins to grasp the concept, and thus make the training of an individual call-over faster, compared to when non-biologically relevant sounds are used. This was tested by training six adult dolphins' at Kolmården Zoo, Sweden, to be called over by either an artificially produced "trivial" sound (TS) or by the dolphin's own signature whistle (SW).

The aim of this study was thus to prove the Whistle caller concept of using signature whistles as individual call-over signals for dolphins in human care. The hypotheses were (1) that the dolphins trained with their own SW would learn their new call-over signal faster than dolphins trained with a biologically irrelevant TS, and (2) that upon hearing other sounds, dolphins trained with their own SW would be able to discriminate between their own SW and other SWs better than dolphins trained with a TS would learn to discriminate between their own TS and other TSs.

3 Materials and methods

3.1 Study subjects

This study was conducted at Kolmården Zoo, Sweden, where eleven dolphins were housed during the beginning of this study. Six of the adult dolphins (Tab. 1) were chosen to participate in the study and randomly assigned to be trained either with their SW or with a TS, using a random team generator. The 2-year old calves (Finn, Alana and Neptun) and two of the adult dolphins (Luna and Nephele) were excluded from the study due to time limitations (Tab. 1).

Table 1. Age, sex, parental and offspring information about the dolphins at Kolmården Zoo, Sweden.

Individual	Year of birth	Sex	Mother	Father	Offspring
Nephele	1983	F	Wild	Wild	Pärla Neptun
Ariel	1996	F	Vicky	Flip	Peach Alana
Lyra	1999	F	Lotty	Flip	Fenah
Luna	2001	F	Vicky	Flip	-
David	2004	M	Doris	Eduardo	Finn Alana Neptun
Fenah	2008	F	Lyra	Pichi	Finn
Pärla	2012	F	Nephele	Pichi	-
Peach	2015	F	Ariel	Pichi	-
Finn *	2018	M	Fenah	David	-
Alana *	2018	F	Ariel	David	-
Neptun *	2018	M	Nephele	David	-

* Calves

Abbreviations: F = Female, M = Male.

3.2 Housing

The dolphin facility at Kolmården Zoo consists of three pools (Fig. 1), but during this study, one of them (the 900 sqm Laguna) was under renovation and thus not accessible to the dolphins until January 2021. Therefore, the dolphins only had access to the 800 sqm show pool and the smaller, 170 sqm holding pool, in the backstage area. The Whistle caller training took place in the show pool.

The Laguna was re-opened in January 2021, shortly prior to the arrival of two new male dolphins (Cecil and Guama from Parc Asterix, France), and the transfer of the previous breeding male David to Selwo Marina in Spain.

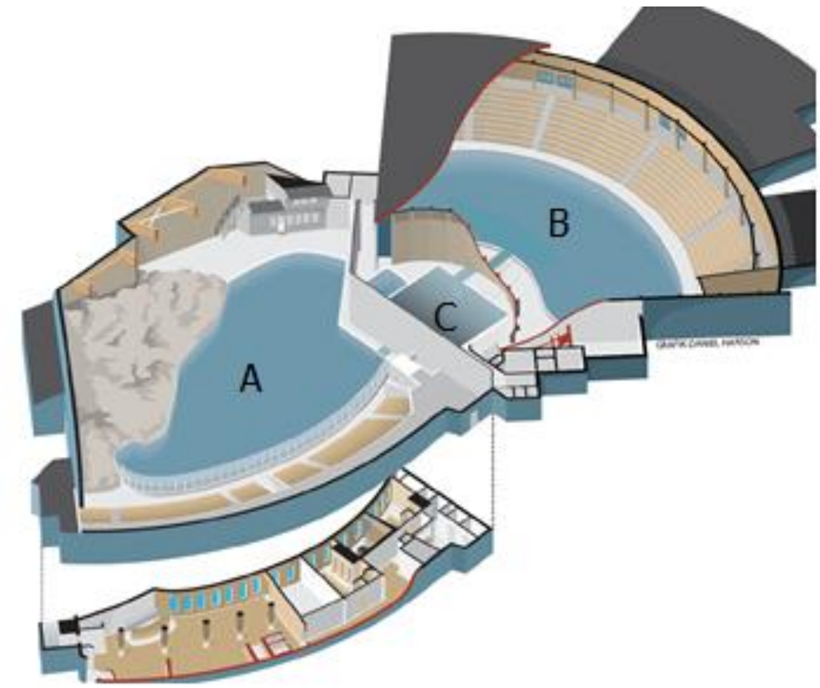


Figure 1. Schematic drawing of the 900 sqm Laguna (A), the 800 sqm show pool (B) and the 170 sqm holding pool (C) at the dolphinarium at Kolmården Zoo, Sweden.

3.3 Recording and identifying signature whistles

During sixteen days between June and September 2020, vocalisations of all eleven dolphins (Tab. 1) at Kolmården Zoo were recorded. The recordings were made using an HS/70 hydrophone (Sonar Research and Development, Ltd, Beverley, East Yorkshire,U.K.), an Etec A1001 preamplifier (Etec aps, Frederiksvaerk, DK), and an Edirol R-09HR digital recorder (Roland Systems Group, Copenhagen, DK) connected to a Dell laptop running the software SeaWave 2.0 (CIBRA - University of Pavia, Italy), which provided a running spectrogram allowing us to see the frequency contours of the whistles in real time.

The hydrophone was lowered into the center and mid-water of the 800 sqm, 4 m deep show pool (Fig. 1) from a footbridge in the ceiling, in order to minimize the acoustic reflections from the pool walls. Whenever a whistle, that was not masked by other sounds such as echolocation clicks, was heard or seen in the spectrogram, the time on the recorder was noted, as well as which dolphin was closest to the hydrophone at that particular time. Using the software Audacity 2.4.1 (http://www.audacityteam.org/), the noted times from all recordings were visually examined. If a whistle was present in bouts of several with an inter-whistle interval of 1-10 s, it was marked as a potential SW. These whistles were then paired with their possible source using both under and above water observations and compared with data from previous studies of the dolphin group, in which four of the dolphins' (Ariel, Lyra, Luna and Nephele) signature whistles had already been identified (Mello, 2005). For one of the remaining dolphins (Fenah), an old video recording from one of the trainers assisted in identifying her signature whistle.

Using the times noted during the process of recording the whistles, the clearest SW for each of the dolphins were cut out and "cleaned" from noise using Adobe Audition 1.0, (Adobe Systems Inc., San Francisco, CA 94103, USA), in order to make the whistles as clear and free from background noise as possible. All individual SWs were successfully identified (Fig 2-3), however, the quality of the recordings varied.

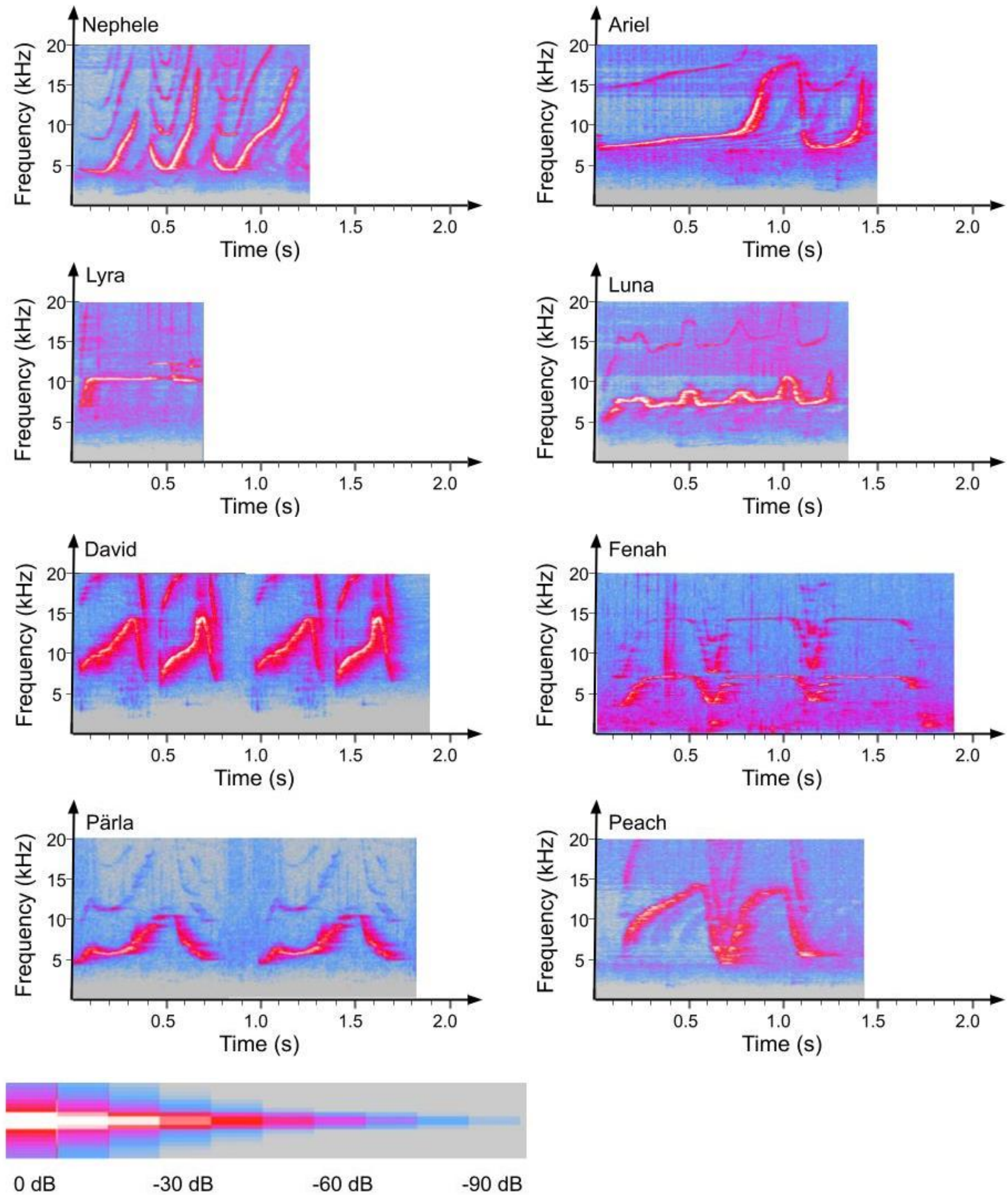


Figure 2. The signature whistles of the 8 adult bottlenose dolphins at Kolmården Zoo, Sweden. Y-axis shows the sound frequency in kHz, and X-axis shows the duration of the sound in seconds. Colours represent the sound pressure level in dB. The signature whistles of David and Pärla are played twice in order to increase the length of their signature whistle playback for the sake of the call-over training taking part in this study.

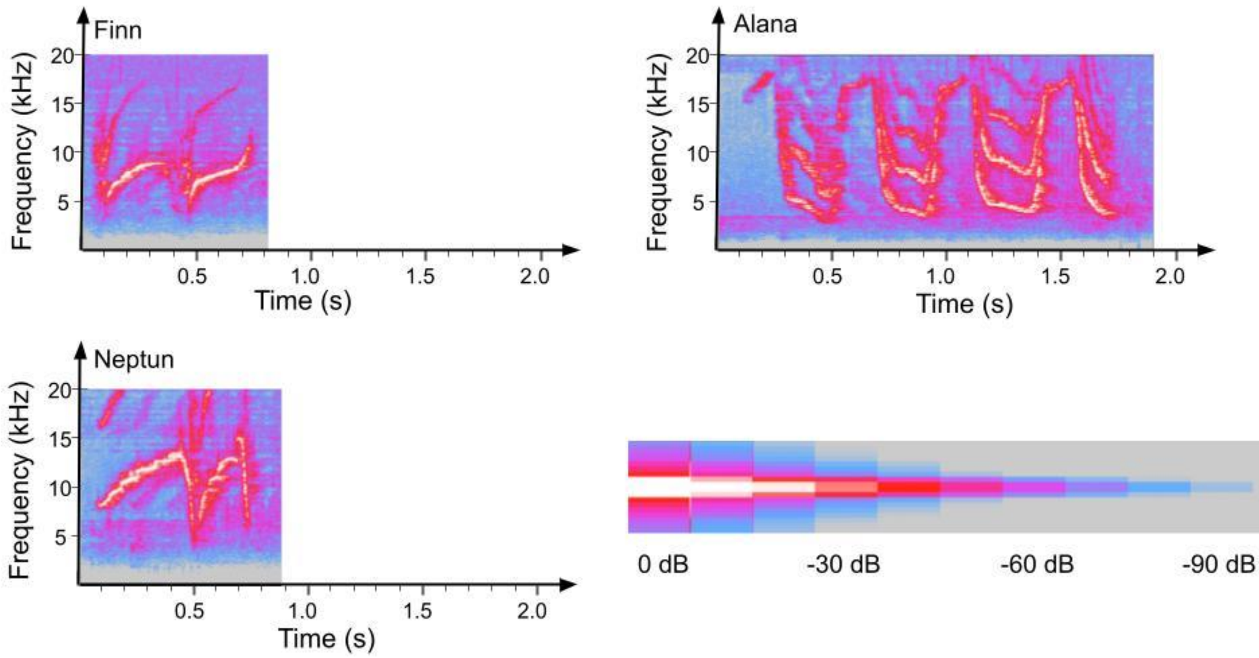


Figure 3. The signature whistles of the 3 bottlenose dolphin calves at Kolmården Zoo, Sweden. Y-axis shows the sound frequency in kHz, and X-axis shows the duration of the sound in seconds. Colours represent the sound pressure level in dB.

3.4 Creating the "trivial" sounds

The "trivial" sounds (TS) used in this study were created using Adobe Audition 1.0. They consisted of several short tones (0.2 s) arranged in different patterns, within the range of 5-18 kHz. The sounds were made to last for approximately 2 s in total. Ten different TSs were produced – two of these were used during desensitization training of the dolphins (Fig. 3), four as individual call-over signals (Fig. 4), and four were used as discrimination sounds (DTS) (Fig. 5).

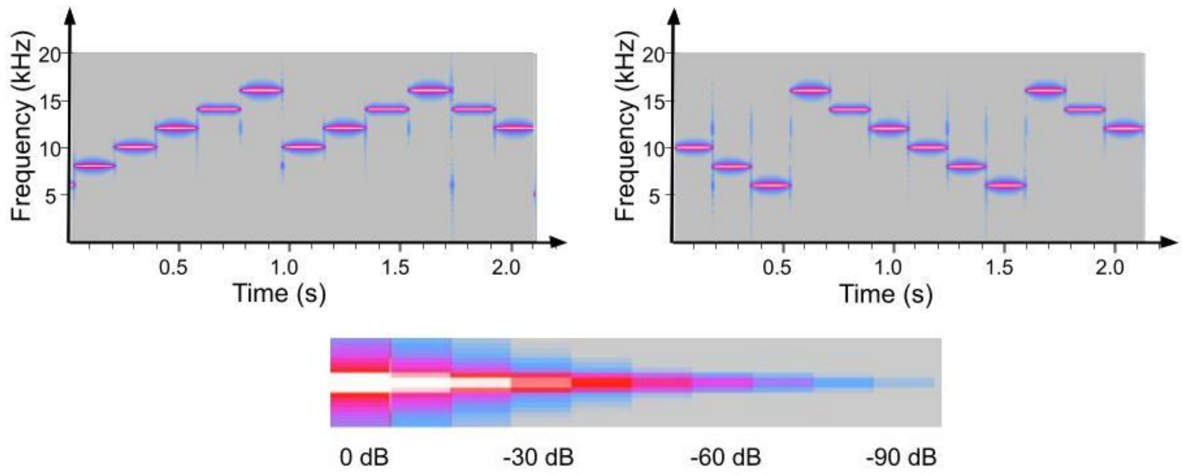


Figure 3. Two computer generated “trivial” sounds used during the desensitisation of the bottlenose dolphins at Kolmården Zoo, Sweden. Y-axis shows the sound frequency in kHz, and X-axis shows the duration of the sound in seconds. Colours represent the sound pressure level in dB.

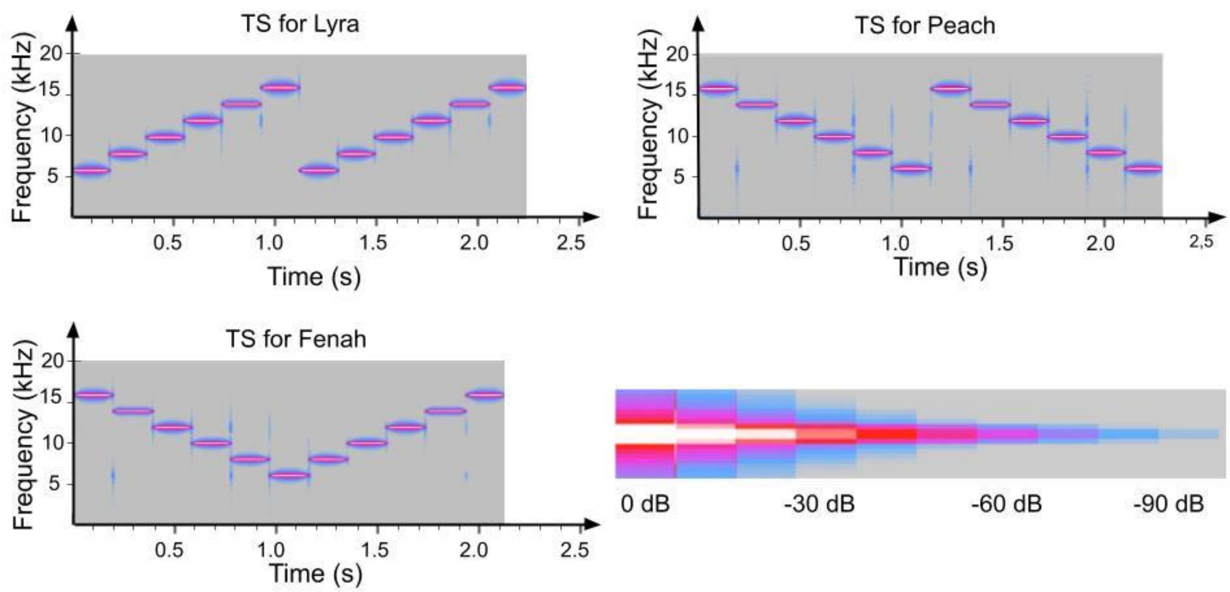


Figure 4. Computer generated “trivial” sounds (TS) used as individual call-over signals for three bottlenose dolphins (Lyra, Peach and Fenah) at Kolmården Zoo, Sweden. Y-axis shows the sound frequency in kHz, and X-axis shows the duration of the sound in seconds. Colours represent the sound pressure level in dB.

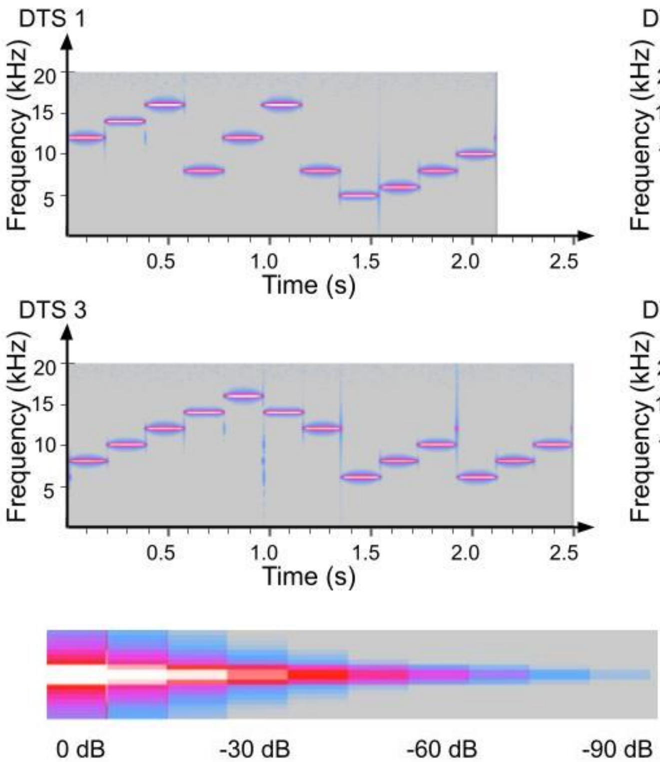


Figure 5. Computer generated "trivial" sounds used as discrimination sounds (DTS). The sounds were used as comparisons to other trivial sounds, already established as call-over signals for three bottlenose dolphins at Kolmården Zoo, Sweden. Y-axis shows the sound frequency in kHz, and X-axis shows the duration of the sound in seconds. Colours represent the sound pressure level in dB.

3.5 The Whistle caller and target setup

A prototype of the Whistle caller (Fig. 6) was built by ÅF Consult, Stockholm, consisting of the following components:

- A CAT S30 mobile phone
- A master unit with a Raspberry Pi card, memory card, 30W output gain.
- Underwater speaker DNH Aqua-30

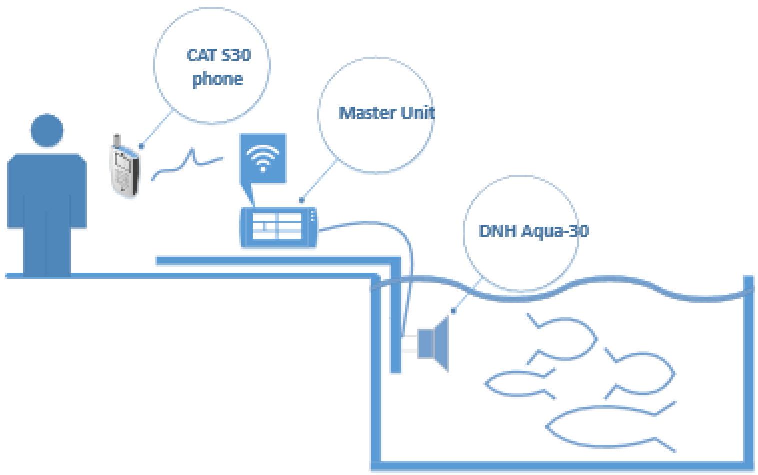
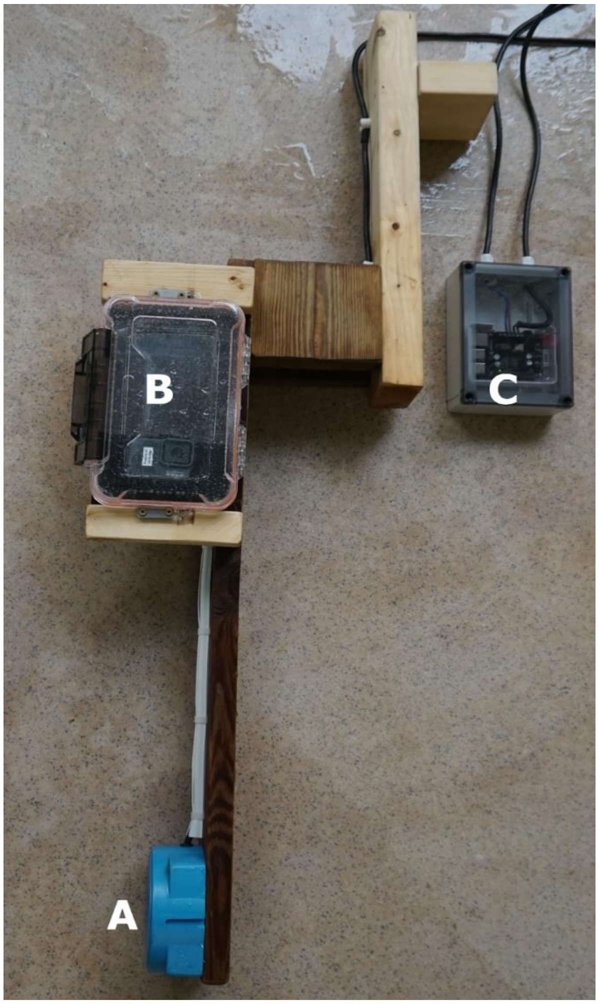


Figure 6. The Whistle Caller. A CAT S30 phone, connected via Wi-Fi to a master unit, was used to choose sounds to play through the DNH Aqua-30 underwater speaker.

The CAT mobile phone connects with the Raspberry Pi via Wi-Fi. Using a custom-made app in the phone, the sounds stored on the memory card in the master unit can be selected and played through the speaker. Several sounds can be selected, and then played in the selected succession.

The Whistle caller underwater speaker was mounted on a wood structure that could be fixed anywhere along the poolside (Fig. 7). On this structure, a waterproof plastic box was also mounted, in which a GoPro Hero 4 camera was placed during the training sessions in order to video record the dolphins' underwater behaviours (Fig. 7). The box was partially above the water surface, allowing the camera to connect to a mobile phone via Bluetooth. In addition to this, another GoPro Hero 4 camera was mounted on a similar wooden structure (Fig. 8) that was deployed 2 m to the right of the Whistle caller, from the dolphin's point of view (Fig. 9). This setup could hold up to three targets, i.e., vertical wooden poles with plastic floats at the end (Fig. 8). The dolphins were already trained to station by such targets, touching it with its beak. By fixing the targets on this structure instead of letting a person hold them, the training was more standardised, removing the possibility of giving unintentional cues to the dolphins by the person holding the targets.



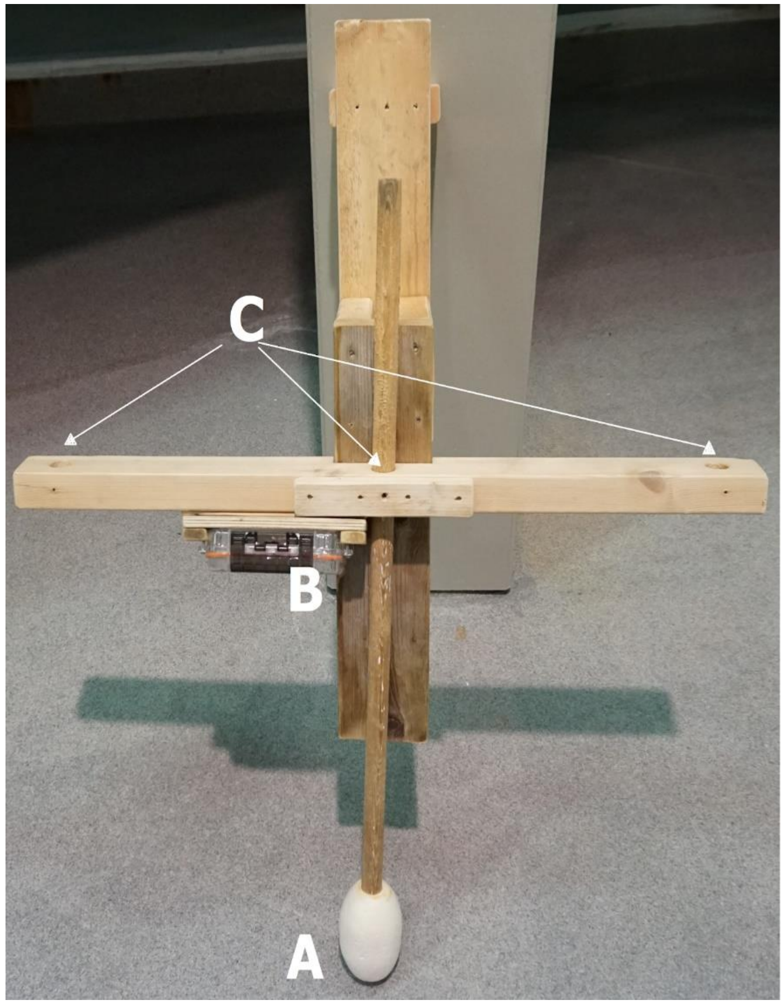


Figure 7. The Whistle caller and wooden structure used in the current study. The Whistle caller includes an underwater speaker (A), a waterproof plastic box for a GoPro Hero 4 camera (B) and the master unit (C) that was connected to a CAT S3 phone via Wi-Fi through a custom-made app from which sounds played through the speaker could be chosen.

Figure 8. The target structure used in the current study, includes a target (A) and a waterproof plastic box for a GoPro Hero 4 Camera (B). The holes on the horizontal board (C) gives the structure capacity to hold up to three targets at a time.

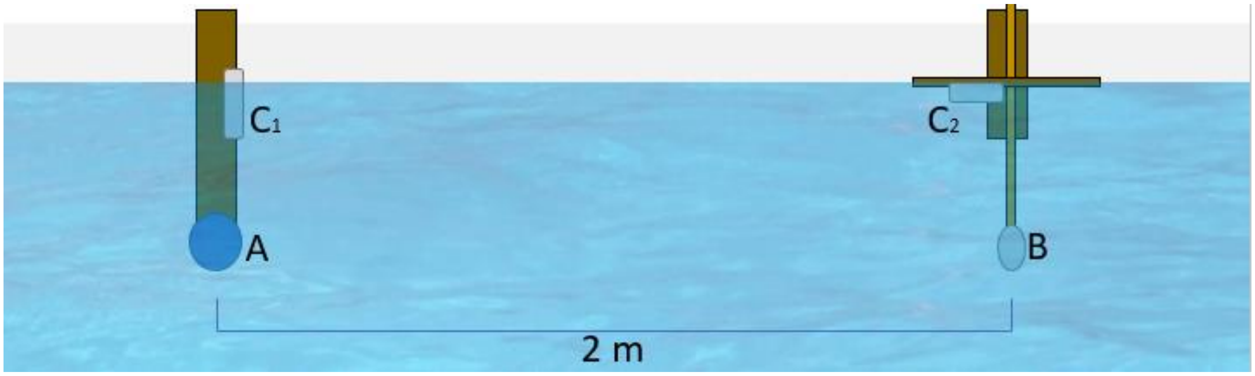


Figure 9. Schematic drawing of the training setup with A) the Whistle caller speaker, B) the target, and C_1) and C_2) the waterproof boxes for the GoPro Hero 4 cameras.

3.6 Preparation and desensitisation training

Previous to the study, all eight adult dolphins had been trained to stay stationed on a target as part of their routine handling procedures. They were also trained to leave their target upon hearing the current general call-over signal, a hand-slap on the water surface.

These dolphins had, prior to this experiment, not been exposed to neither the Whistle caller structure nor sounds being emitted through an underwater speaker. Therefore, they were gradually habituated to both the Whistle caller, and sound emissions from the speaker in 18 short desensitisation sessions. During these sessions, two of the trivial sounds that were not to be used as individual call-over signals later on in the study, were played (Fig. 3).

Upon playing the first sound in the first desensitisation session, all dolphins swam freely in the show pool (Fig. 1). The speaker was mounted on the pool wall in the middle of the visitor side of the pool. After observing the dolphins' behaviour for a few minutes after a sound had been played, the trainers called over all animals to the opposite side of the pool, relative to the speaker position, using the hand slap and rewarded the ones that approached. This procedure was repeated one to three times per session, in five consecutive sessions, depending on the dolphins' responses, and there was one such session a day between 24th-29th of September 2020. Two of the animals (Lyra and Neptun) were visibly distressed after the first desensitization session, but after the fifth session, all individuals approached the trainers upon hearing the signal, thus associating it with a potential reward, suggesting that the sounds were no longer associated with negative, stressful emotions, but rather with positive ones. Between the 30th of September and the 5th of October, the dolphins were exposed to the desensitisation sounds while staying on a hand target with their lower jaw below the water surface, thus ensuring that they would be able to hear the sounds from the speaker on the opposite side of the pool. This was done in six additional desensitisation sessions. Once all dolphins managed to stay calm and stationed at their hand target while the sounds were played, two more sessions were carried out where the sounds were played while the dolphins performed other routine trained behaviours such as standing up-side down with their tails above the water surface, jumping, and swimming from A to B.

Desensitisation was also needed after the arrival of the two new male dolphins, Cecil and Guama in January 2021. Thus, the same two desensitisation sounds were used again in three more sessions mid-February 2021.

3.7 Proof of concept

The adult dolphins were, as mentioned above, randomly divided into two groups, one of which would be exposed to a SW and the other to a TS (Tab. 1). In addition to this, they were also paired with an individual from the other group, so that one SW and one TS individual were trained in parallel (Tab. 2). The individual with whom each dolphin was paired, as well as the order in which the pairs were trained, was decided after consulting the trainers. This to make sure that the paired individuals were as equal as possible, regarding their usual success rate when learning new behaviours. Which TS that was assigned to each dolphin in the TS group was randomly determined.

Table 2. Semi-randomized pairs, the order in which they participated in the training and how they were divided into groups depending on which call-over signal they were assigned.

Training order	SW	TS
1	Ariel	Lyra
2	David	Peach
3	Pärla	Fenah

Abbreviations: SW = Signature whistle, TS = Trivial sound

Two of the dolphins in the SW group, David and Pärla, had SWs with durations of less than 1 s (Fig. 2). This short duration was considered to increase the risk of the call-over sound being masked by disturbances from the surroundings. Thus, sound files with their SWs played twice in a row were created for these two individuals.

3.7.1 Call-over training

In order to teach the dolphins their new call-over signal, they were first trained to just move towards the Whistle caller speaker when their SW or assigned TS was played. During the first few sessions, the call-over signals were played at source levels about 20 dB lower than that of the final call-over signals and was gradually increased until it reached its intended level. This was done to desensitize the dolphins to sounds transmitted by the Whistle caller speaker while they were in close proximity to it, minimizing the risk of frightening them. The trainers used other, already established cues such as a hand slap on the water surface next to the loudspeaker, making hand gestures and pointing, or looking towards the Whistle caller speaker to help the dolphin to understand what was expected from it. These cues were gradually phased out until the trainers deemed that the dolphins could perform the behaviour without any other cues than the SW/TS itself. They were then introduced to a target, approximately 2 m to the right of the Whistle caller (Fig. 9), from the dolphin's perspective, on which they were trained to stay stationed until their SW/TS was played, using a Go/No go paradigm. If the dolphins left the target station before their SW/TS was played or stayed longer than 2 s after their sound had ended (i.e., an incorrect No go-response), they were not rewarded. If they left the target, moving towards the Whistle caller speaker at any time between the start of their SW/TS and 2 s after it had ended (i.e., a correct Go-response), they were rewarded. They were also rewarded for staying on the target when no sound was played (i.e., a correct No go-response) - this to make sure that neither the Whistle caller, nor the target station, was more attractive than the other, thus influencing the dolphins' tendencies to either swim towards the Whistle caller speaker or stay by the target station when their SW/TS was played.

The number of SWs/TSs played, cues used, correct as well as incorrect Go- and No go-responses were noted during each session of call-over training.

One dolphin in pair 3 (Fenah) was trained in the Laguna during her 22nd-38th sessions of the call-over training and 1st-3rd sessions of the discrimination sessions as a consequence of another dolphin being ill and in need of separation in the medical pool (Fig. 1). Distances between the Whistle caller speaker and the target were the same, however, there were no opportunities to fasten the target setup, and she was therefore trained to stay stationed on a regular target held by a trainer during the remaining sessions (including her last two discrimination sessions in the show pool). To minimise possible bias in the form of unintentional cues from the trainer holding the target, the trainer was not informed about what kind of sound (SW/TS or DSW/DTS) was played.

The new call-over signal was considered established once an individual performed the correct response during all trials in at least three separate training sessions following each other. This included both correct Go-responses (leaving the target station upon hearing the SW/TS) and correct No go-responses (staying on the target station when no SW/TS was played). These last three training sessions contained a minimum of six trials, three with correct Go-responses, and three with correct No go-responses. The order and duration of these last three trials were randomised before each session, and the trainers were not allowed to change this predetermined schedule. An exception to the rule of these three last sessions following each other, was only given once, to Fenah, as she was severely distracted by other dolphins during her second to last session of call-over training. However, she still had to complete three sessions with all trials correctly performed before considered to have learnt the behaviour.

The call-over training of the first dolphin pair (Ariel and Lyra) included several different methods before the one described above was adopted. A predetermined training protocol designed before beginning their training, with the aim to make the training as standardised as possible, turned out not suitable for this task. This was mainly because the target station was too far away, on the opposite side of the pool, from the Whistle caller, but also because the only cue used was the hand slap, which was not enough to guide the dolphins towards the desired response. Therefore, this training protocol was progressively changed until it became the less standardised method described above, with the target close to the speaker and including more non-acoustic cues.

3.7.2 Alternative training procedure

An alternative training procedure was considered, but finally not chosen. It was based on adding a hand slap sound immediately preceding (approximately 20 ms) the onset of the SW/TS, and then gradually fading out the hand slap. It was, however, deemed impossible to time a manual hand slap to the broadcasted SW/TS with enough precision and consistency and also to gradually fading it out. Also, since the target station was so close to the speaker, the dolphin would have been able to see the trainer doing the hand slap, which would have interfered with the fading out of this cue. Therefore, the hand slap was recorded, and the sound was added to the file with the SW/TS. After consulting the trainers, this method was not chosen for two main reasons; (1) the dolphins were thought to not recognize the hand-slap playback as a hand-slap, but rather as a feature of the SW/TS, and (2) the dolphins were thought to focus too much on the hand-slap and not on the sound immediately following it, thus resulting in them being trained to be called-over by the hand-slap playback rather than the SW/TS itself, prolonging the training procedure rather than making it more effective.

3.7.3 Discrimination sessions

Immediately after an individual was considered to have learned the new call-over signal (indiscriminately a SW or a TS), they were trained to discriminate between different SW/TS. For this part of the training, the same setup was used as for the call-over training. The only difference was that instead of only hearing their own SW/TS, other SWs/TSs were also played. For the SW group, these other SWs were the those from four other adult dolphins in the group (Nephele, Lyra, Peach and Fenah), and for the TS group it was other TSs, here referred to as discrimination trivial sounds (DTS; Fig. 5), constructed in the same way as the TS, but containing different frequency modulation patterns than that of their assigned TS.

If a dolphin made a correct Go-response, i.e., left the target and approached the Whistle caller speaker when their own SW/TS was played, it was rewarded as usual, but if it left the target upon hearing one of the other sounds i.e., an incorrect Go-response, it was not rewarded. If the dolphin stayed at the target station when a discrimination SW or TS (DSW or DTS) was played and did so until 2 s after the beginning of the sound, i.e., a correct No go-response, it was rewarded. It was also rewarded if it turned its head towards the Whistle caller speaker as if it was about to approach it, but then turned back towards the target and stayed there since turning back towards the target was considered a choice to stay, i.e., a correct No go-response. If a dolphin left the setup during the session, or in other ways showed frustration or a lack of motivation, the session was ended on a positive note with an easy trial (for example staying only a few seconds on the target) to not further damage the dolphin's motivation to take part in the training.

The order in which the dolphin was exposed to the different sounds was randomly determined. The first session included three trials where the dolphin was rewarded for just staying at the target when no sound was played, three trials with DSW/DTS and three trials with their own SW/TS. However, as the dolphins advanced in the discrimination, the rewards for correct No go-responses when no sound was played, were gradually phased out - this to avoid making the target station more attractive for the dolphins, as most of the rewards would be given there. If a dolphin continued to approach the Whistle caller speaker when DSW/DTS was played (incorrect Go-response), the rewards by the target station for correct No go-responses were kept on the same level as during the first discrimination session.

Some of the sessions included more No go rewards, and some included extra trials with SW/TS or DSW/DTS, but this was only allowed if the dolphin was considered not to have had a fair chance to respond correctly. For example, if other dolphins interrupted the training session, or if intermittent noise (for example due to the renovation of the Laguna) might have masked or taken the attention away from the played sounds. Except for the first pair of dolphins (Ariel, who's discrimination continued for a total of 21 sessions, and Lyra, who never reached the criteria for beginning the discrimination training), the remaining animals took part in five discrimination sessions each. The order of all the Go/No go trials, and the duration between stationing at the target and the SW/TS or DSW/DTS being played, was randomly determined before each session.

3.8 Data analysis

The collected data was analysed in Google Sheets using the add-on XLMiner Analysis ToolPak. For detection of inter-pair differences during call-over training, ANOVA and t-tests (two tailed assuming unequal variance) were used (alfa=0.05). T-test was also used for comparisons of the results from the discrimination sessions.

4 Results

4.1 Pair overview

4.1.1 Ariel and Lyra

Ariel and Lyra were the first two dolphins to begin the call-over training, and since the training protocol used at the beginning of this project was not effective, they were exposed to several changes in the training protocol throughout their training.

For Ariel, it required 45 sessions (Fig. 10) before she reached the criteria allowing her to begin with the discrimination training. The gradual transition of the training procedure for Ariel and Lyra – from the standardised method tried at first, to the more liberal method used for the 2nd and 3rd pairs, started by training session 9. However, it was not until session 34 that the final setup (used from the start for the remaining two dolphin pairs) was introduced.

Lyra followed the same training protocol, and changes in it, as Ariel. However, Lyra never reached the criteria allowing her to begin with the discrimination training. In total, she took part in 67 training sessions (including the first 8 sessions where the standardised but not successful method was used), with mixed results (Fig. 11). The trendline for correct responses indicate that she might have reached the criteria had her training continued (Fig. 11), however, her motivation during the training sessions was low, complicating the entire training procedure, resulting in a decision to discontinue her training with the Whistle caller. This will be discussed further in section 5.2.1.

There were no significant intra-pair differences with regards to the number of trials with sounds ($P=0.660$, two tailed t-test) or cues used ($P=0.064$, two tailed t-test) during the call-over training sessions. However, Lyra had significantly more trials with no sounds being played ($P<0.001$, two tailed t-test). This was done to increase the number of correct No go-responses in order to counteract her tendency to leave the target in advance of her assigned TS being played (incorrect Go-response).

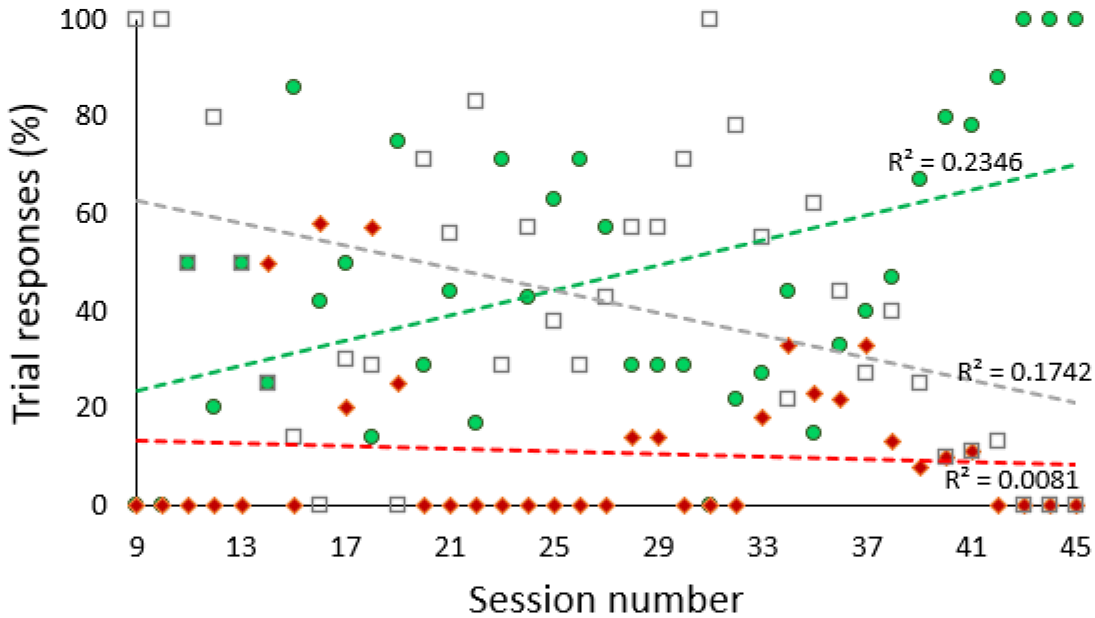


Figure 10. Results from the call-over training with the bottlenose dolphin Ariel who was trained to be called over by a playback of her own signature whistle. The percentage of trials (Y-axis) in each session (X-axis) resulting in a correct response (●), an incorrect response (◆) or including help in the form of a cue (□) (hand or head gesture made by the trainer) and corresponding trendlines and R^2-values. The X-axis starts at the 9th training session as this was when the transition from a standardised training procedure to a more liberal one, allowing more cues, started (used for the remaining dolphins in this study). This transition was gradual and continued until the 34th training session.

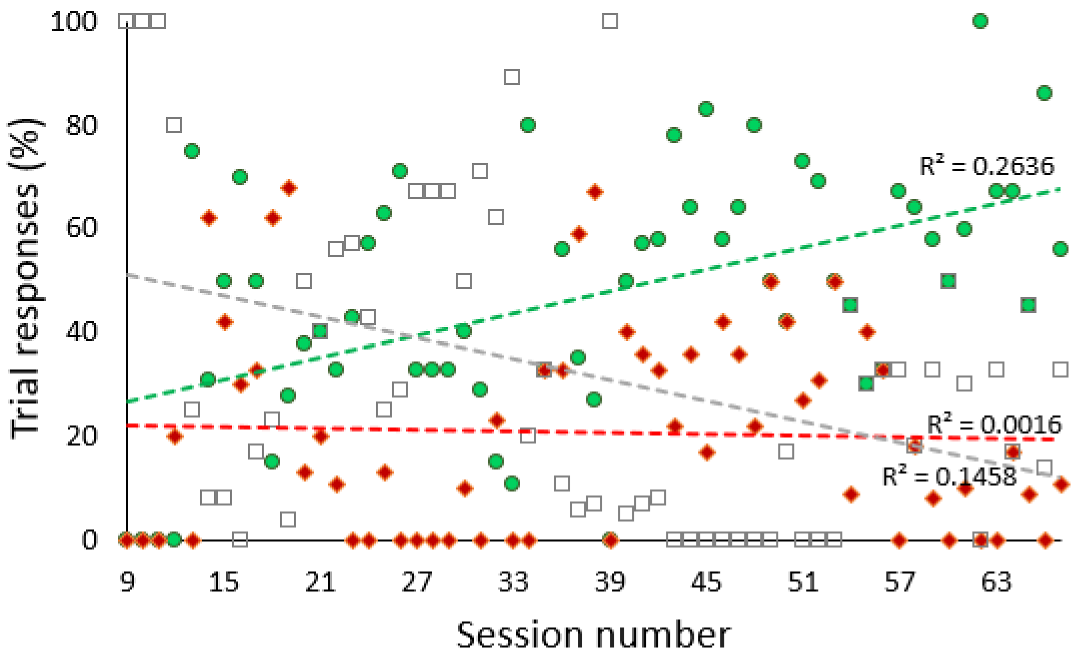


Figure 11. Results from the call-over training with the bottlenose dolphin Lyra who was trained to be called over by a playback of a biologically irrelevant, computer-generated "trivial" sound. The percentage of trials (Y-axis) in each session (X-axis) resulting in a correct response (●), an incorrect response (◆) or including help in the form of a cue (□) (hand or head gesture made by the trainer) and corresponding trendlines and R^2-values. The X-axis starts at the 9th training session as this was when the transition from a standardised training procedure to a more liberal one, allowing more cues, started (used for the remaining dolphins in this study). This transition was gradual and continued until the 34th training session.

During her first five discrimination training sessions, Ariel responded correctly in 83,3 % of the trials when her SW was played (20 out of 24), and in 35 % of the trials when a DSW was played (7 out of 20) (Fig. 12). To the DSWs belonging to Peach and Nephele, Ariel responded correctly (No go) in 50 % of the trials (2 out of 4 for both), of the DSW belonging to Lyra, in 33 % of the trials (2 out of 6), and to the DSW belonging to Fenah, in 16,7 % of the trials (1 out of 6). In total, she responded correctly in 61,4 % (27 out of 44) of the trials with sounds during these first five discrimination sessions. She responded with a correct No go-response during all trials with no sound, in total 15 trials, during these sessions (on average three times per session).

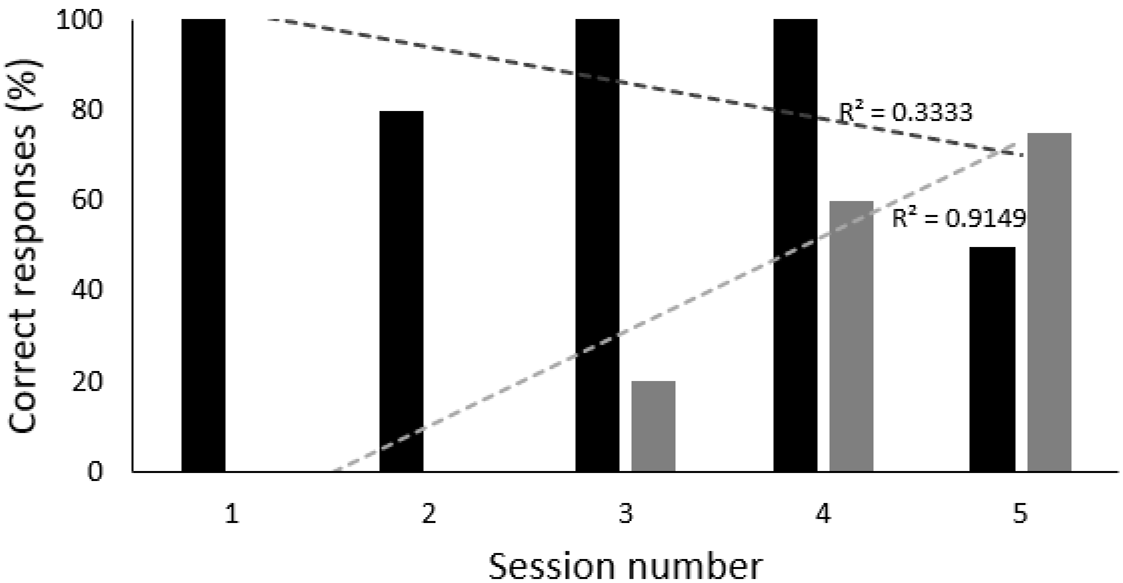


Figure 12. The percentage of correct responses (Y-axis) and corresponding trendlines and R^2-values, during the first five discrimination sessions (X-axis) with the bottlenose dolphin Ariel. Correct responses include a Go-response to her own signature whistle (■) and a No go-response to any of four other dolphins' signature whistles (■).

Looking at all 21 discrimination sessions with Ariel, she responded correctly in 74 % of the trials when her SW was played (74 out of 100), and in 56,5 % of the trials when a DSW was played (48 out of 85) (Fig. 13). She responded correctly in 73 % of the trials (16 out of 22) when the DSW belonging to Nephele was played, in 62 % (13 out of 21) when the DSW belonging to Lyra was played, in 57 % (13 out of 23) when the DSW belonging to Peach was played and finally, in 32 % (6 out of 19) when the DSW belonging to Fenah was played. In total, she responded correctly in 69,5 % (122 out of 185) of the total number of trials during her 21 sessions of discrimination.

She responded correctly in all trials with no sound during all 21 discrimination sessions and was thus rewarded by the target 36 times for correct No go-response (on average 1.64 times per session).

The trendline for correct responses to her own SW, with an R^2-value of 0.33 (Fig. 12), indicates a downward trend for this response during the first five discrimination sessions. However, when looking at all 21 sessions (Fig. 13), an R^2-value of 0.09 indicates that this downward trend is minor.

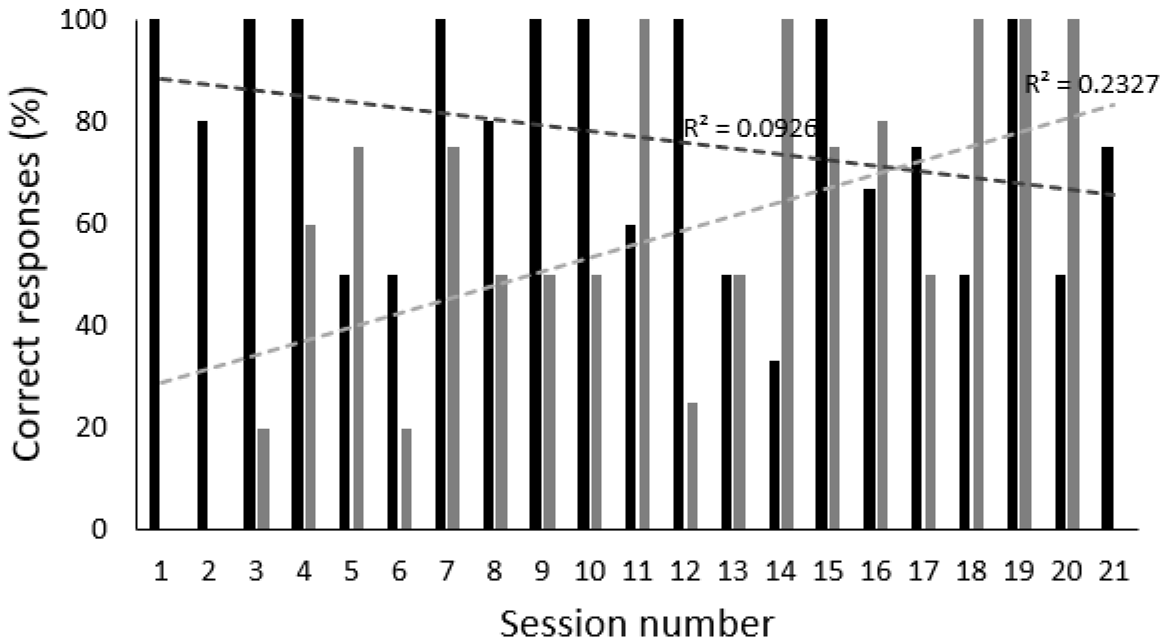


Figure 13. The percentage of correct responses (Y-axis) and corresponding trendlines and R^2-values, during all 21 discrimination sessions (X-axis) with the bottlenose dolphin Ariel. Correct responses include a Go-response to her own signature whistle (■) and a No go-response to any of four other dolphins' signature whistles (■).

4.1.2 David and Peach

For David and Peach it took 24 and 20 training sessions, respectively, to reach the criteria allowing them to begin with the discrimination training (Fig. 14-15). No significant intra-pair difference was found with regards to the number of trials with sounds (P=0.491, two tailed t-test), number of trials without sounds (P=0.371, two tailed t-test) or cues used (P=0.359, two tailed t-test) during the call-over training sessions.

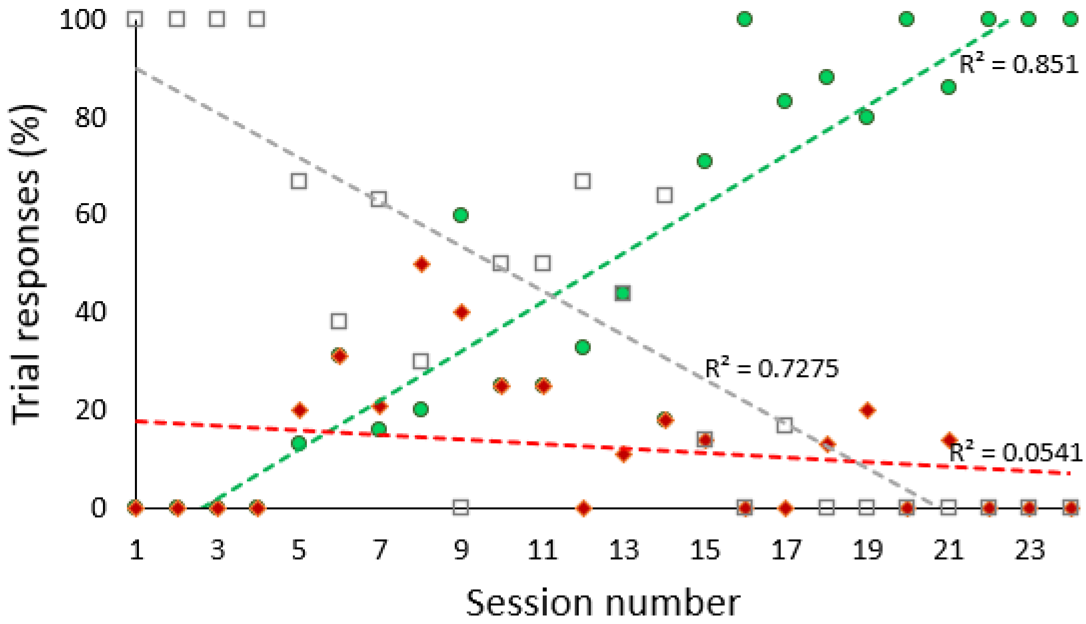


Figure 14. Results from the call-over training with the bottlenose dolphin David who was trained to be called over by a playback of his own signature whistle. The percentage of trials (Y-axis) in each session (X-axis) resulting in a correct response (●), an incorrect response (◆) or including help in the form of a cue (□) (hand or head gesture made by the trainer) and corresponding trendlines and R^2-values.

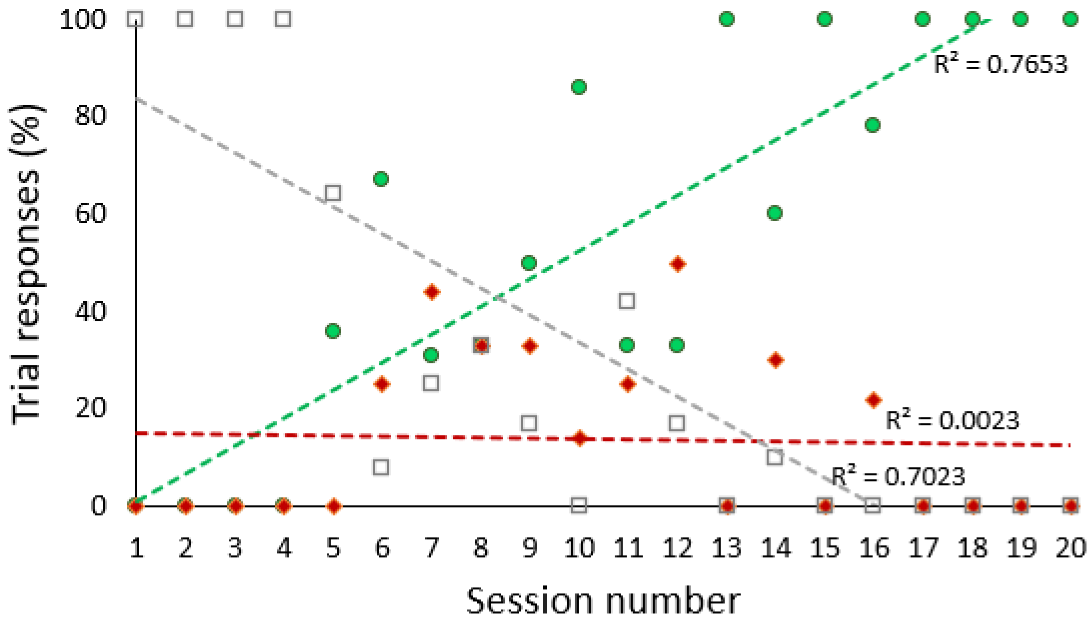


Figure 15. Results from the call-over training with the bottlenose dolphin Peach who was trained to be called over by a playback of a biologically irrelevant, computer-generated "trivial" sound. The percentage of trials (Y-axis) in each session (X-axis) resulting in a correct response (●), an incorrect response (◆) or including help in the form of a cue (□) (hand or head gesture made by the trainer) and corresponding trendlines and R^2-values.

To his own SW, David responded correctly in 79 % of the trials (19 out of 24). When a DSW was played, he responded correctly in 70 % of the trials (14 out of 20) (Fig. 16). To the DSWs belonging to Nephele and Lyra, he responded correctly in 100 % of the trials (6 and 4, respectively), but with the DSWs belonging to Peach and Fenah, he responded correctly only in 60 % (3 out of 5) and 20 % (1 out of 5) of the trials, respectively. In total, David responded correctly in 75,5 % (33 out of 44) of all the trials.

Already during the first discrimination session, progress could be seen with regards to him staying by the target when a DSW was played. Thus, the number of trials with no sound was reduced after the first discrimination session. David responded correctly during all trials with no sound and was thus rewarded by the target a total of five times for a correct No go (on average one time per session).

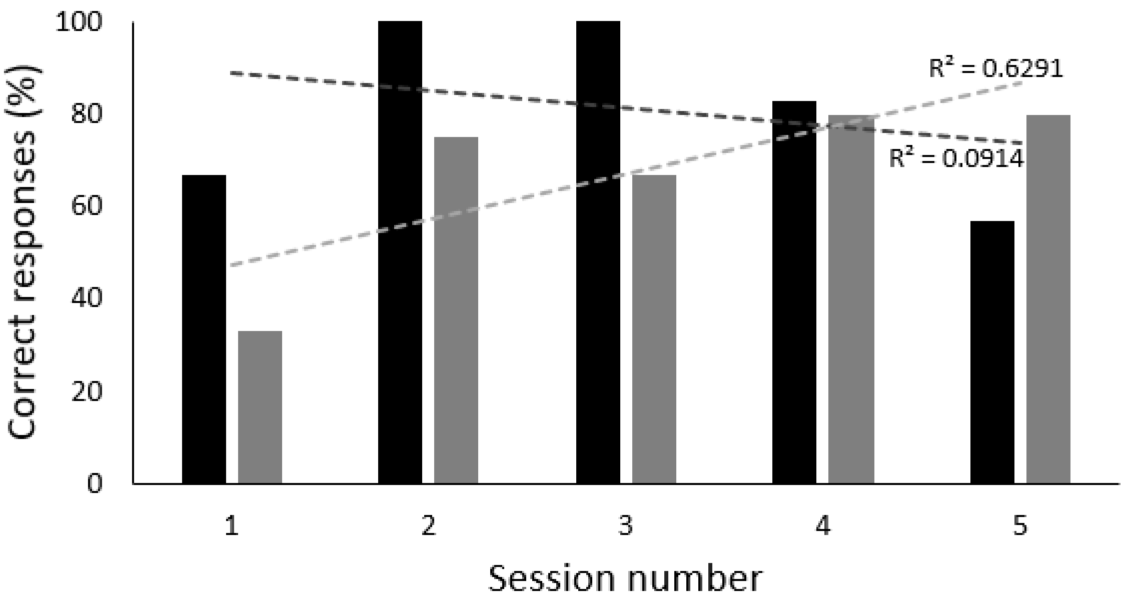


Figure 16. The percentage of correct responses (Y-axis) and corresponding trendlines and R^2-values, during the five discrimination sessions (X-axis) with the bottlenose dolphin David. Correct responses include a Go-response to his own signature whistle (■) and a No go-response to any of four other dolphins' signature whistles (■).

During the discrimination training, Peach responded correctly in 88 % of the trials when her call-over TS was played (14 out of 16) but was incorrect in all of the trials when any of the DTSs were played (15 out of 15) (Fig. 17). Thus, she responded correctly in 45,2 % (14 out of 31) of the total number of trials in her five discrimination sessions. As no progress could be seen, in her No go-response to a DTS, the number of trials with no sound was maintained, and she was continually rewarded for staying by the target when no sound was played. This to make sure that the target station and the Whistle caller speaker were equally attractive throughout all five discrimination sessions. Peach responded correctly during all trials with no sound and was thus rewarded by the target 17 times for correct No go-responses (on average 3,4 times per session).

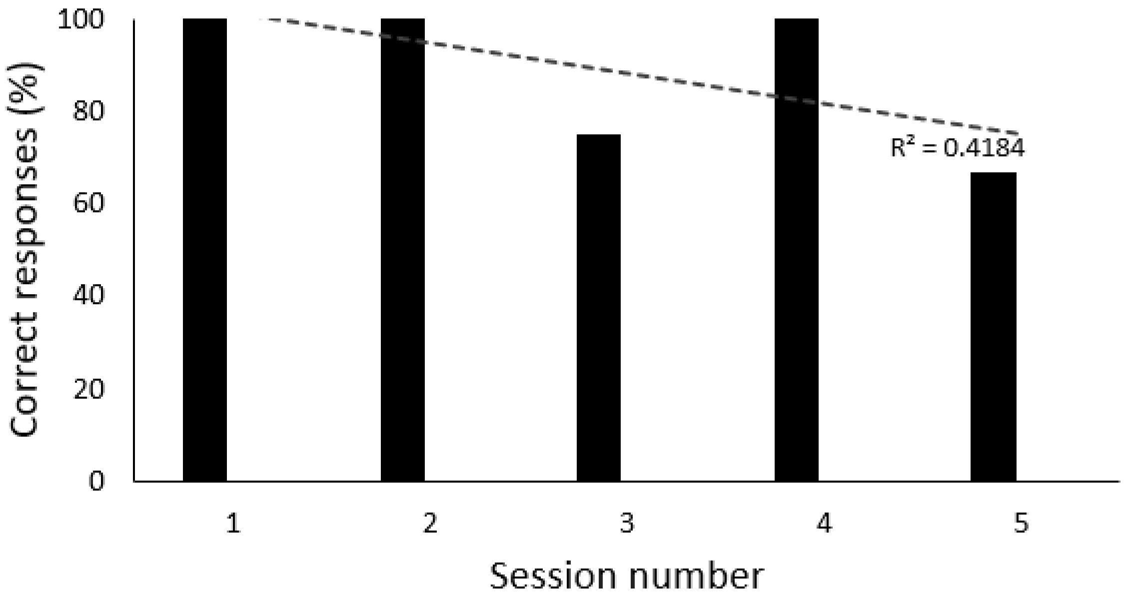


Figure 17. The percentage of correct responses (Y-axis) and corresponding trendlines and R^2-values, during the five discrimination sessions (X-axis) with the bottlenose dolphin Peach. Correct responses include a Go-response to her assigned call-over signal, a “trivial” sound (a biologically irrelevant computer-generated sound consisting of a sequence of tones) (■) and a No go-response to any of four other “trivial” sounds (■).

4.1.3 Pärla and Fenah

Pärla reached the criteria for the discrimination training after 17 sessions, whereas Fenah did so after 38 sessions (Fig 18-19). Both Pärla and Fenah had a break in their call-over training between the 19th of January and the 20th of February (between their 10th and 11th training sessions) due to the arrival of the two new male dolphins, Cecil and Guama. No significant intra-pair difference could be seen with regards to the number of cues used (P=0.639, two tailed t-test) during the call-over sessions. However, Fenah had significantly more trials both with and without sounds (P<0.05 and P<0.01, respectively, two tailed t-test).

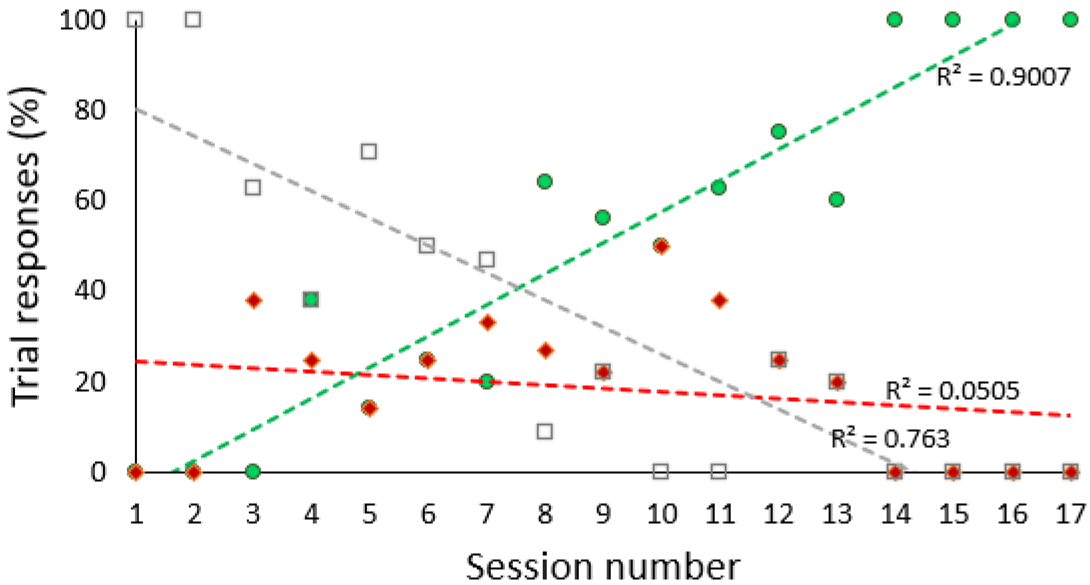


Figure 18. Results from the call-over training with the bottlenose dolphin Pärla that was trained to be called over by a playback of her own signature whistle. The percentage of trials (Y-axis) in each session (X-axis) resulting in a correct response (●), an incorrect response (◆) or including help in the form of a cue (□) (hand or head gesture made by the trainer) and corresponding trendlines and R^2-values.

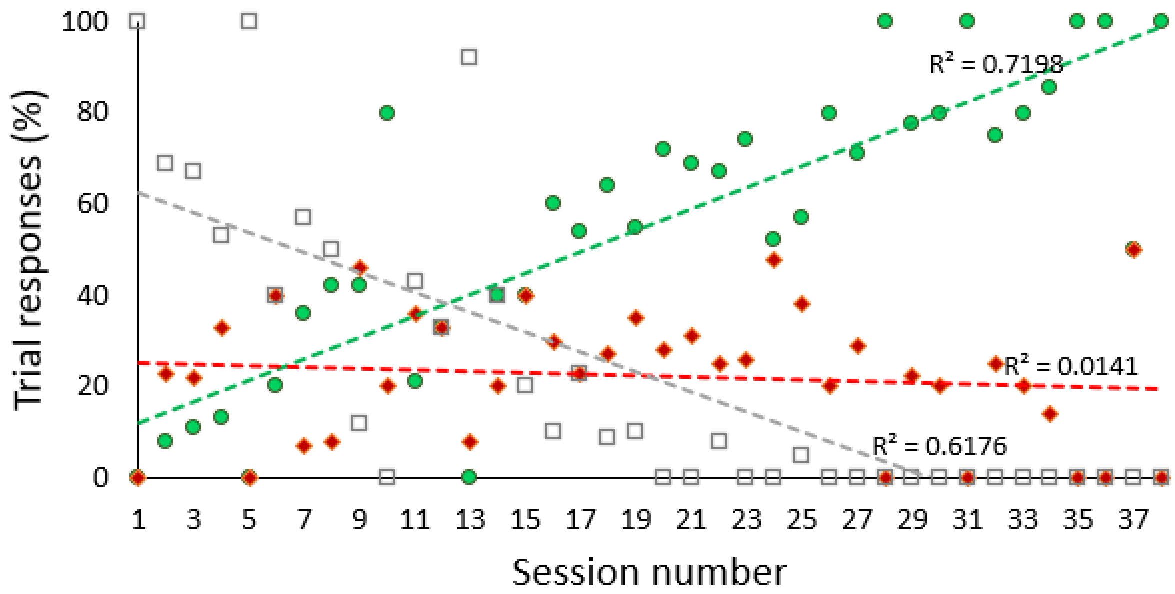


Figure 19. Results from the call-over training with the bottlenose dolphin Fenah that was trained to be called over by a playback of a biologically irrelevant, computer-generated "trivial" sound. The percentage of trials (Y-axis) in each session (X-axis) resulting in a correct response (●), an incorrect response (◆) or including help in the form of a cue (□) (hand or head gesture made by the trainer) and corresponding trendlines and R^2-values.

In her five discrimination sessions, Pärla responded correctly to her own SW in 94% of the trials (17 out of 18) and to a DSW in 11% of the trials (2 out of 18) (Fig. 20). To the DSWs belonging to Lyra, Peach and Fenah, Pärla responded incorrectly in all trials, and to the DSW belonging to Nephele, she responded correctly in 50% of the trials (2 out of 4). She responded correctly in 54% (19 out of 35) of the total number of trials in her five discrimination sessions.

As Pärla responded correctly to the DSW belonging to Nephele in her second discrimination session, the number of trials with no sounds was reduced. Pärla responded correctly during all trials with no sound and was thus rewarded by the target a total of nine times for a correct No go-response (on average 1.8 times per session).

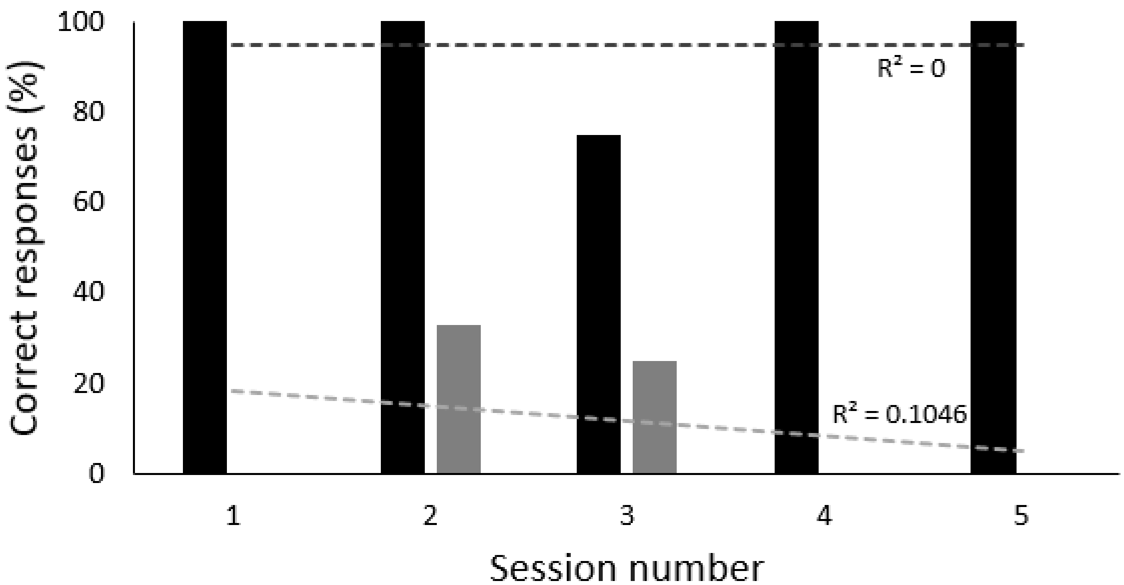


Figure 20. The percentage of correct responses (Y-axis) and corresponding trendlines and R^2-values, during the five discrimination sessions (X-axis) with the bottlenose dolphin Pärla. Correct responses include a Go-response to her own signature whistle (■) and a No go-response to any of four other dolphins' signature whistles (■).

Fenah responded correctly in 31.6 % of the trials when her call-over TS was played (6 out of 19) and 66.7 % of the trials when a DTS was played (12 out of 18) (Fig. 21). To DTS1 and DTS2 she responded correctly in 25 % (1 out of 4) and 83.3 % (5 out of 6) of the trials, respectively. To both DTS3 and DTS4 she responded correctly in 75% of the trials (3 out of 4). Looking at the total number of trials in her five discrimination sessions, Fenah responded correctly in 49 % of the trials (18 out of 37). However, she responded with an incorrect Go-response in 3 out of 6 trials with no sounds during the first session (i.e., she left the target when no sound wads played). Apart from these three incorrect responses, she responded correctly to all trials with no sound and was thus rewarded by the target a total of nine times for a correct No go-response (on average 1.8 times per session).

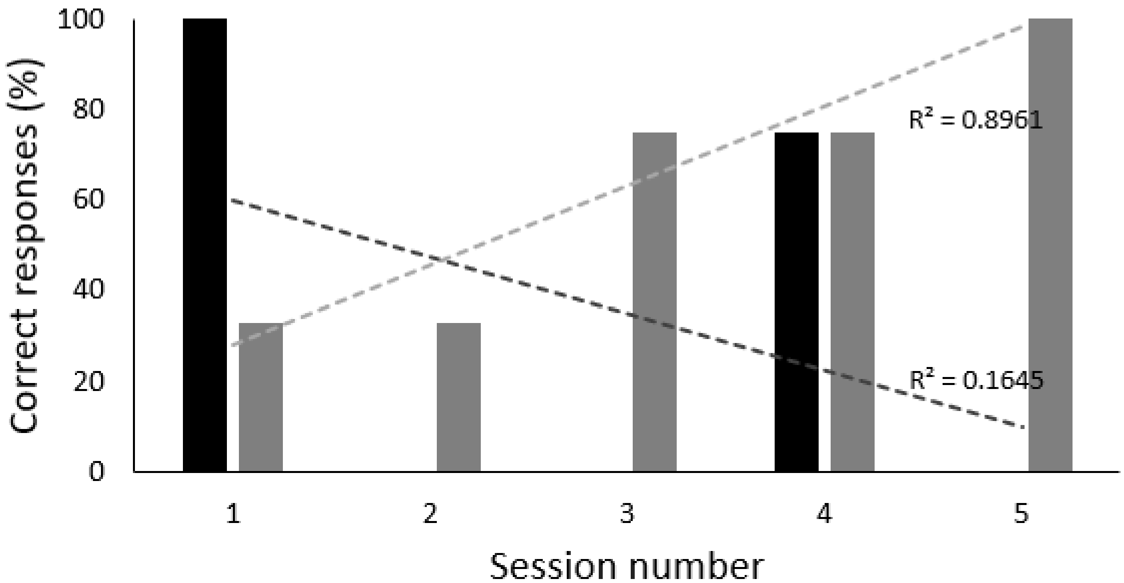


Figure 21. The percentage of correct responses (Y-axis) and corresponding trendlines and R^2-values, during the five discrimination sessions (X-axis) with the bottlenose dolphin Fenah. Correct responses include a Go-response to her assigned call-over signal, a "trivial" sound (a biologically irrelevant computer made sound consisting of a sequence of tones) (■) and a No go-response to any of four other "trivial" sounds (■).

4.2 Statistical analysis

4.2.1 Call-over training

No significant differences were found between any of the dolphins with regards to the number of cues used during the call-over training (P=0.442, ANOVA). However, looking both at the trials with no sounds (No go trials), and at the trials with SW/TSs being played (Go trials), a significant difference was found between several of the dolphins (Tab. 3). The call-over training with Fenah included significantly more trials with no sounds than that of Ariel, Peach, David and Pärla, and significantly more trials with sounds than Lyra, Ariel and Pärla (Tab. 3). Similarly, the call-over training with Lyra included significantly more trials with no sounds than that of Ariel, Peach, David and Pärla (Tab. 3).

Table 3. Average, and t-test p-values from the comparisons of (1) the number of trials with no sounds, (2) the number of trials with sounds, and (3) the number of trials with cues, used during the call-over training of the six bottlenose dolphins taking part in this study.

		Lyra		Ariel		Peach		David		Fenah		Pärla
(1) No sound	*Av.*	***3.84***	*Av.*	***1.89***	*Av.*	***2.20***	*Av.*	***1.71***	*Av.*	***4.13***	*Av.*	***2.06***
	Ar	**P<0.001**	Ly	**P<0.001**	**Ly**	**P=0.016**	**Ly**	**P<0.001**	Ly	P=0.697	**Ly**	**P=0.007**
	Pe	**P=0.016**	Pe	P=0.559	Ar	P=0.559	Ar	P=0.669	**Ar**	**P=0.001**	Ar	P=0.734
	Da	**P<0.001**	Da	P=0.670	Da	P=0.371	Pe	P=0.371	**Pe**	**P=0.011**	Pe	P=0.816
	Fe	P=0.697	**Fe**	**P=0.001**	**Fe**	**P=0.011**	**Fe**	**P<0.001**	**Da**	**P<0.001**	Da	P=0.498
	Pä	**P=0.007**	Pä	P=0.734	Pä	P=0.816	Pä	P=0.498	**Pä**	**P=0.005**	**Fe**	**P=0.005**
(2) Sound	*Av.*	***5.30***	*Av.*	***5.49***	*Av.*	***5.95***	*Av.*	***6.58***	*Av.*	***7.74***	*Av.*	***5.53***
	Ar	P=0.660	Ly	P=0.660	Ly	P=0.359	Ly	P=0.076	**Ly**	**P=0.001**	Ly	P=0.732
	Pe	P=0.359	Pe	P=0.530	Ar	P=0.530	Ar	P=0.141	**Ar**	**P=0.003**	Ar	P=0.954
	Da	P=0.076	Da	P=0.141	Da	P=0.490	Pe	P=0.490	Pe	P=0.057	Pe	P=0.637
	Fe	**P=0.001**	**Fe**	**P=0.003**	Fe	P=0.057	Fe	P=0.214	Da	P=0.214	Da	P=0.247
	Pä	P=0.732	Pä	P=0.954	Pä	P=0.637	Pä	P=0.242	**Pä**	**P=0.017**	**Fe**	**P=0.017**
(3) Cues	*Av.*	***2.57***	*Av.*	***3.29***	*Av.*	***2.45***	*Av.*	***3.38***	*Av.*	***2.55***	*Av.*	***2.18***
	Ar	P=0.064	Ly	P=0.064	Ly	P=0.871	Ly	P=0.307	Ly	P=0.981	Ly	P=0.540
	Pe	P=0.871	Pe	P=0.263	Ar	P=0.263	Ar	P=0.914	Ar	P=0.243	Ar	P=0.099
	Da	P=0.307	Da	P=0.914	Da	P=0.359	Pe	P=0.359	Pe	P=0.906	Pe	P=0.759
	Fe	P=0.981	Fe	P=0.243	Fe	P=0.906	Fe	P=0.376	Da	P=0.376	Da	P=0.208
	Pä	P=0.540	Pä	P=0.099	Pä	P=0.759	Pä	P=0.208	Pä	P=0.639	Fe	P=0.639

Bold text indicates significant p-values.

Gray text has already been presented in previous columns.

Abbreviations: *Av*. = Average values, Ly = Lyra, Ar = Ariel, Pe = Peach, Da = David, Fe = Fenah, Pä = Pärla

To test for differences in either cued response ratio or correct go-response ratio between the SW group and the TS group, a mixed repeated measures ANOVA was used, with time when each pair was trained as the repeated measure (within subject factors) and sound type as between-subject factors. Both cued response and correct go-response ratios varied over time (P<0.01, Tab. 4). No significant differences in responses to TSs and SWs were found (P<0.05, Tab. 4). However, the response to the different sound types, in terms of both cued response and correct go-response ratios were different in the different pairs as indicated by significant Time × Sound type interaction (Tab. 4).

Table 4. Results of the mixed repeated measures analysis of variance for the effect of time (each trained pair of bottlenose dolphins taking part in this study) and sound type (signature whistle or trivial sound) on cued response ratio or correct go-response ratio.

Source	Cued response ratio			Correct go-response ratio		
	Df	F	P	Df	F	P
Within subject						
Time	2	6.4	< 0.01	2	6.5	< 0.01
Time × Sound type	2	4.0	< 0.01	2	5.5	< 0.01
Error	70			70		
Between subject						
Intercept	1	145	< 0.001	1	106	< 0.001
Sound type	1	0.1	0.8	1	0.01	0.9
Error	35			35		

4.2.2 Discrimination sessions

Looking at the percentage of correct responses in the discrimination sessions (for Ariel, the first five), no significant difference with regards to responding correctly to their own SW/TS could be found between any of the dolphins (Fig. 22), although the results were almost significant between Pärla and Fenah ($P=0.055$, two tailed t-test), with Pärla responding correctly more often than Fenah. However, to the discrimination sounds, both David and Fenah responded correctly significantly more often than both Pärla ($P<0.005$ and $P<0.05$, respectively, two tailed t-test) and Peach ($P<0.005$ and $P<0.05$, respectively, two tailed t-test) (Fig. 22). Significant intra-individual differences for Ariel, Peach and Pärla indicate that these individuals gave correct responses significantly more often to the playback of their own SW/TS as compared to the playback of a DSW/DTS (Fig. 22).

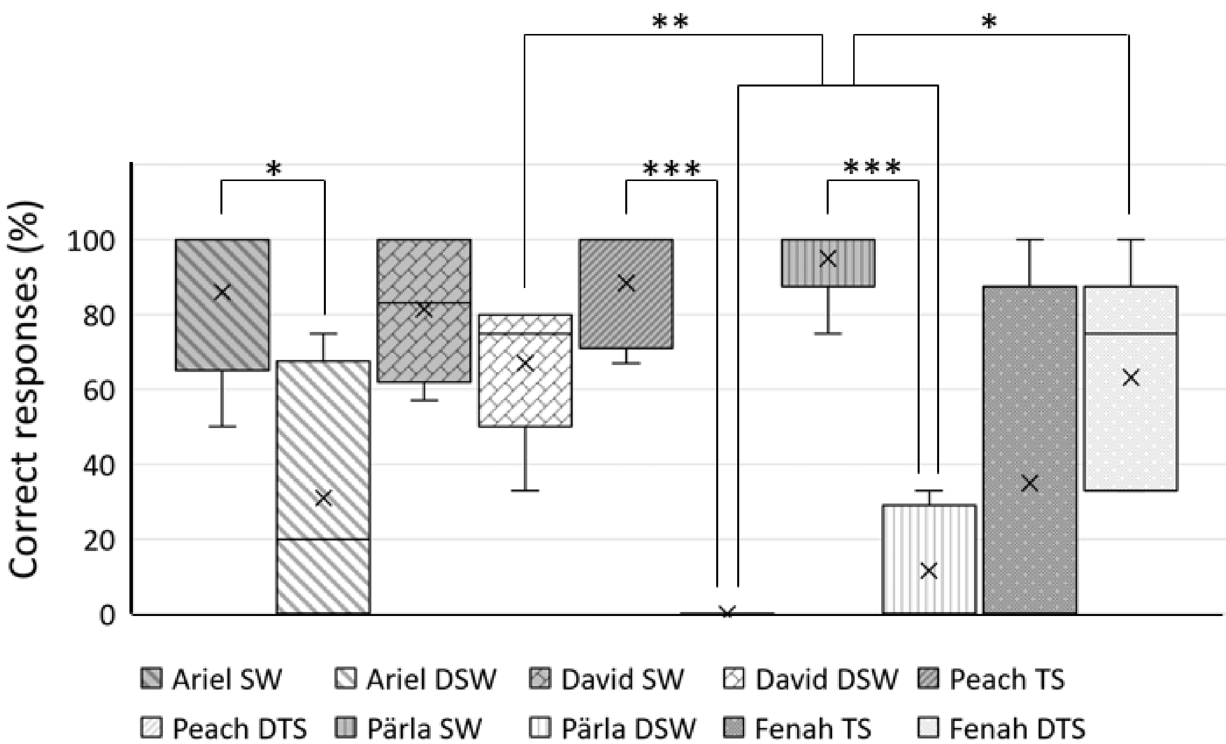


Figure 22. The percentage of correct responses (Y-axis) to either the assigned call-over signal (SW = signature whistle or TS = "trivial" sound), or a discrimination sound (DSW = another dolphin's signature whistle or DTS = another "trivial" sound) for each of the bottlenose dolphins (X-axis) taking part in the five discrimination sessions in this study. The whiskers show the highest and lowest values, "X" shows the mean values and lines show the median values. Brackets indicate where significant differences were found, * = p<0.05, ** = p<0.005, *** = p<0.0005.

When looking at the total percentage of correct responses, including both SW/TS and DSW/DTS trials, Peach and Fenah, both trained with a TS, performed below chance level in two out of five sessions each, whereas none of the dolphins trained with a SW did (Fig. 22).

Again, when looking at the total percentage of correct responses, including both SW/TS and DSW/DTS trials, both Ariel and David responded correctly significantly more often than Peach (P<0.01 and P<0.05, respectively, two tailed t-test) (Fig. 23). Ariel responded correctly significantly more often than Pärla (P<0.05, two tailed t-test) (Fig. 23), however, comparing David's results to Pärla's, these were only almost significant (P=0.054, two tailed t-test).

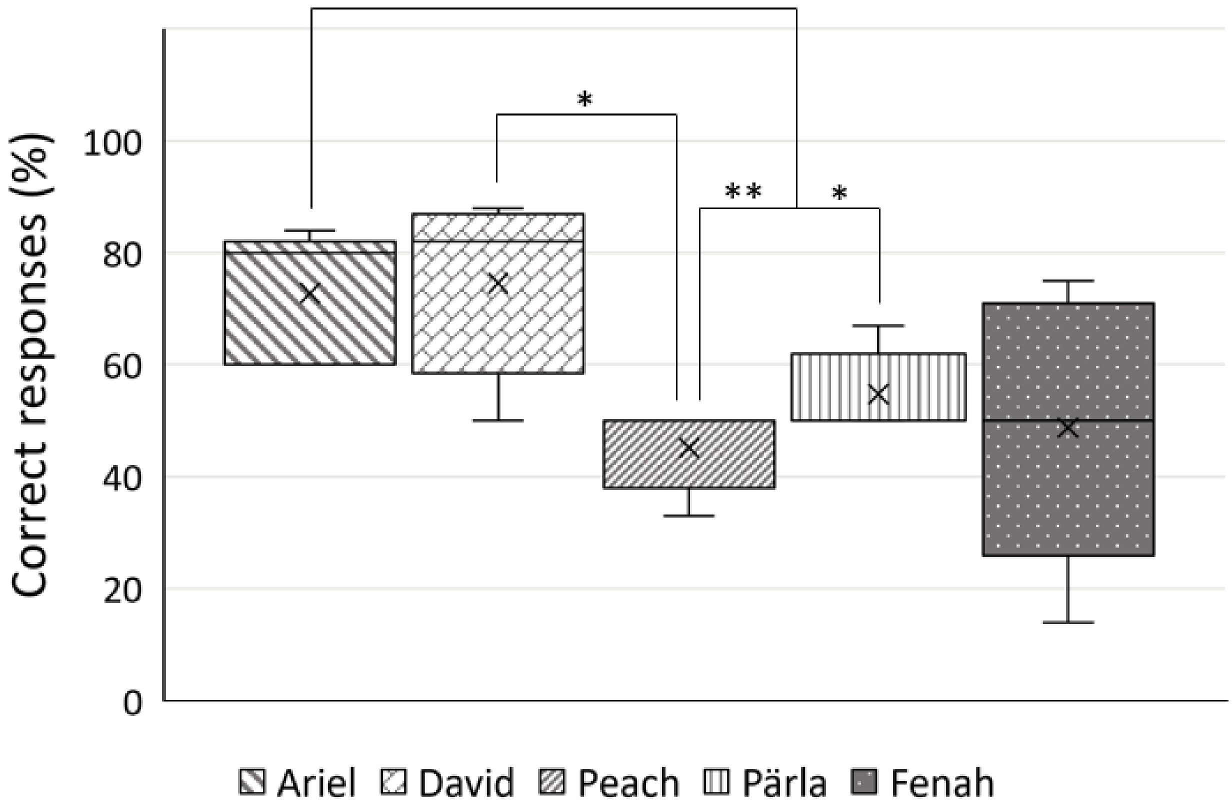


Figure 23. The percentage of the total amount of correct responses (Y-axis), including both trials with assigned call-over signals (signature whistles or "trivial" sounds) and discrimination sounds (other dolphins' signature whistles or other "trivial" sounds) with the bottlenose dolphins (X-axis) taking part in the five discrimination sessions in this study. Ariel, David and Pärla were trained with a playback of their own signature whistle (SW) whereas Peach and Fenah were trained with "trivial" sounds (TS). The whiskers show the highest and lowest values, "X" shows the mean values and lines show the median values. Brackets indicate where significant differences were found, * = $p<0.05$, ** = $p<0.005$.

5 Discussion

In this study, six adult dolphins at Kolmården Zoo, Sweden, were trained to approach an underwater speaker when either their own SW (signature whistle) or a non-biologically relevant

TS ("trivial" sound) was played, and their ability to discriminate between their own and others' SWs and their assigned TS and other TSs, was tested. Two out of three dolphins were successfully trained to be called over, using their assigned TS, but neither of them was able to discriminate between their assigned, and other TSs. All three dolphins trained to be called over, using their own SW, were successful in this task, and two of them were, at least to a degree, able to discriminate between their own SW and the SWs of other dolphins in the group.

5.1 Call-over training

5.1.1 Willingness to participate

Five out of six dolphins were successfully trained to be called over upon hearing their SW or their assigned TS, whereas one (Lyra) did not reach the criteria required to begin the discrimination training. We have identified two main possible causes for this. Firstly, she was put through several different training strategies before the final training setup and procedure was settled. This, according to the trainers, is in general not optimal when shaping a new behaviour, as it may cause confusion for the animal. However, the other dolphin in the first pair, Ariel, did learn how to perform the desired behaviour once trained using the final setup and procedure, indicating that this may not be the only reason why Lyra did not succeed in her task.

Secondly, documentation made for another study, between 2020-11-16 and 2021-01-10, on the "willingness to participate" (WtP) in positive reinforcement training, indicate that Lyra's overall average WtP score was the lowest (3,36) out of all the adult dolphins at Kolmården Zoo (an average of 3,69) during this period (I. Clegg & E. Ström, personal communication, February 9, 2021). The average WtP scores for Lyra and Ariel from their 39th session (November 16, 2020) until the end of their training, show that Ariel (with a WtP score of 3,84) was more willing to participate in the training than Lyra (with a WtP score of 3,35) (I. Clegg & E. Ström, personal communication, February 9, 2021). Furthermore, WtP-scores from the training of David and Peach (starting on November 17, 2020) show that also they had higher average WtP-scores than Lyra (David 3,75 and Peach 3,81) (I. Clegg & E. Ström, personal communication, February 9, 2021).

Clegg *et al*. (2019), showed in their study that a dolphin's willingness to participate in positive reinforcement training can be used as a potential welfare indicator. Thus, Lyra's low WtP-score and following difficulty in learning the desired call-over response, may have been caused by some unidentified welfare factors. It cannot be excluded, though, that Lyra might have been less inclined to respond positively to her TS than Ariel to her SW. Lyra was the only animal with a SW with almost no frequency modulation (Fig. 2), whereas the TS she was assigned included two upsweeps of several tones between 5 and 18 kHz (Fig. 4). Whether this played a role in her call-over training development or not, cannot be answered without further studies, investigating differences in the frequency modulation of SWs and TSs and how these differences correlate to the call-over training results.

As the third pair (Pärla and Fenah) began their call-over training on the 5th of January, WtP-scores were only available from the first five days of their call-over training and were not used in this study.

5.1.2 Learning speed

There were large individual differences in how fast each dolphin learned the complete call-over response during the call-over training, i.e., staying stationed on the target and only leaving it and swimming towards the Whistle caller when their assigned SW/TS was played. As mentioned above, Lyra and Ariel were subjected to several different training procedures, which may explain their seemingly slow learning process. However, when it comes to Fenah, the high number of sessions required for her to learn the correct response was surprising. Fenah went through the same training procedure as, and in parallel with, Pärla. However, Pärla learned the correct response after 17 sessions compared to Fenah's 38 sessions. As no data on Fenah's willingness to participate (WtP) in positive reinforcement training was available, we neither can nor cannot rule out the possibility of motivation being the reason for her slower learning process. Also, as Fenah is the offspring of Lyra (Tab. 1) (who clearly also displayed difficulties in learning the correct response) one may want to investigate further what possible role genes may play in the ability to learn not only this, but also other conditioned behaviours.

5.1.3 David's vocal behaviour

David's results were of particular interest as he was previously described by the trainers as a very quiet individual. This was confirmed while trying to record all the individual SWs in the beginning of the study, where David's SW was one of the whistles seen on the least number of recordings. During the call-over training, as David began to grasp the concept of approaching the Whistle caller speaker when his SW was played, his vocal behaviour increased. He began to couple his approach by producing his SW throughout each training session. Although uncommon, dolphins sometimes mimic each other's SWs, likely in order to address specific individuals (King *et al*., 2013). Often, this copying occurs as a response right after the owner of the SW has whistled (Janik & Slater, 1998; King *et al*., 2013). It is possible that David's increased whistling was in fact him copying the playback of his own SW. This is, however, unlikely as even though the increased use of this SW was limited to the training sessions with the Whistle caller at first, it soon spread to other training sessions as well. Furthermore, as an individual's own SW commonly is the response when answering other animals' SWs (Caldwell & Caldwell, 1965), it is, according to us, also likely the response when addressed with a copy of their own SW. If so, it would explain David's increased use of his SW after hearing the playback from the Whistle caller speaker. However, it is also possible that he was unintentionally reinforced by the trainer when using his SW, and that he began to associate making his SW with the reward he was given during the training sessions with the whistle caller.

Although these observations were not systematically documented, both trainers and the observer were of the opinion that the Whistle caller playback of David's SW worked as somewhat of an on-switch, causing him to use his SW considerably more often after, than before taking part in this project.

5.2 Discrimination sessions

5.2.1 Possible effects from the call-over training

Looking at the total percentage of correct responses during the discrimination, all SW dolphins performed above chance level in all of the five sessions (Fig. 22). Both TS dolphins, however, performed below chance level during two out of five sessions each (Fig. 22). One of these dolphins, Peach, seemed very confident in her approach, continuing with a Go-response regardless of what sound was played (TS or DTS), in almost all trials. The other dolphin trained with a TS, Fenah, seemed less confident as she more randomly chose to stay or go, but tended to stay at the target in response to both her TS and the DTSs. This difference between Peach and Fenah in their tendency to give either an incorrect Go- or an incorrect No go-response may stem from their history during the call-over training. Fenah's call-over training included significantly more trials with no sound ($P<0.05$, two tailed t-test) (i.e., staying by the target) than Peach's training (Tab. 3). Thus, Fenah's history of rewards at the target station may have prompted her, more so than Peach, to give a No go-response rather than a Go-response, when unsure.

5.2.2 Response delay

One thing that is likely to have had an impact on the results in the discrimination training is how fast an individual responded to a sound. For example, Peach was mostly very quick in her response, leaving the target and swimming towards the Whistle caller speaker as soon as a sound had begun, whereas David, although still determined in his approach, was not as quick to leave the target. This somewhat slower response from David may have been mistaken by the trainer as an active choice to stay by the target station when a DSW was played. If he was then rewarded while still at the target, this may have aided him in learning when to stay and when to approach the Whistle caller speaker, whereas Peach never got this chance. However, when looking at the underwater video recordings from the discrimination sessions with these individuals, it is clear that the time between the playback of David's SW and his response was shorter than that between a DSW being played and him being rewarded for staying by the target. Thus, this difference in response time between the two individuals is unlikely to have given David an unfair advantage, but rather that Peach's fast response gave her disadvantage when performing this task.

5.3 Signature whistle use and development

In this study, one male and two females were assigned to the SW-group. The male, David, performed better in the discrimination sessions following the call-over training compared to the females. In the literature on the subject of dolphin signature whistle use, much points to male and female dolphins both using their SW in order to keep in contact with their social group, but that they also benefit from this individual identity broadcasting in different ways - females use their signature whistle in order to keep vocal contact with their calf (Bebus & Herzing, 2015; King *et al.*, 2016), whereas males have been observed to use it to form alliances and affiliative social bonds between themselves and other males (King *et al*., 2018). Males have also been seen to use vocal learning to match other non-signature whistles, to converge on a shared whistle within their alliance (Smolker & Pepper, 2001; Watwood *et al*., 2004; King *et al*., 2019). According to Sayigh *et al*. (1990) and Sayigh *et al*. (1995) male and female dolphins also differ in how similar their SW is to that of their mother's. Sayigh *et al*. (1995) compared the signature whistles of 42 free-ranging dolphin calves with those of their mothers, living in Sarasota Bay, Florida. They found that female dolphin calves produced signature whistles that differed from those of their mothers, while male calves were more likely to produce whistles similar to those of their mothers but also developed whistles different for their mothers. They hypothesised that since female calves often stay in the same matrilineal group as their mother throughout their life, there may be a selective pressure for them to develop a signature whistle distinct from those of their mothers and other members of the matrilineal group (Sayigh *et al*., 1990). Males on the other hand, disperse from their natal group, and are thought to either (1) benefit from a SW similar to those of their mothers as they may be used to recognize kin, avoid inbreeding or influence dominance (Sayigh *et al*., 1990), or (2) not have been exposed to the same selection pressures as females, and thus do not receive either benefits, nor disadvantages from having either similar or different SWs to those of their mothers. However, Fripp *et al.* (2005) further investigated the similarities between the SWs of calves and that of other dolphins in their surroundings, and presented new evidence suggesting that calves may instead model their SWs on the SWs of dolphins in their community with whom they only associate rarely.

5.3.1 Male-female differences

Taking the male-female difference in SW use discussed in section 5.3 into consideration, there might be an innate evolutionary reason for why David performed better during his five discrimination sessions than any of the other dolphins in this study. Perhaps male dolphins have a greater need for recognizing and responding to their own whistle than females do, and perhaps females instead tend to be more responsive to the SWs of others (such as their calves). This theory needs to be tested more in depth in future studies. However, male-female differences have already been observed with regards to both environmental enrichment and during other cognitive tasks (Clark *et al*., 2013; Eskelinen *et al*., 2015). For example, Eskelinen *et al.* (2015) observed that subadult and male dolphins were significantly more likely to participate in enrichment sessions than females were. Similarly, Clark *et al*. (2013) could see that, when presenting dolphins with cognitive enrichment in the form of an underwater maze device, males interacted with the maze regularly whereas females did not. Future studies should focus on male-female differences in dolphin behavior and communication.

5.4 Method

5.4.1 Training procedure

In this study, the dolphins were trained in pairs, including one dolphin from the SW and one from the TS group. This was done in order to minimise biases in intra-pair comparisons (such as trainers refining their training technique with time, seasonal changes, and deviations from the daily routines). For example, on the 23rd of January 2021, the breeding male David (the only adult male dolphin in the group at the time) was returned to Selwo Marina in Spain, where he was originally from. In his place, two new breeding males, Cecil and Guama, from Parc Asterix, France, arrived at Kolmården Zoo. This event caused a break of approximately four weeks in the training of the third pair of dolphins, due to social disturbances in the group and focus on their introduction. This may have affected the learning development for these two dolphins. However, as the two dolphins in each pair were trained in parallel, this was not considered a bias in intra-pair comparisons.

Both the call-over and discrimination training was executed by two different trainers. One trained the first pair (Ariel and Lyra) and another one trained the second (David and Peach) and third (Pärla and Fenah) pair. As the call-over training was not as standardized as the discrimination training, inter-pair comparisons of the results from the call-over training may have been biased by the two trainers' slightly different training techniques.

5.4.2 The whistle caller and target set up

When broadcasting the sounds through the Whistle Caller speaker, there was sometimes a delay of up to 1 s between pushing the "send" button on the mobile phone, and the sound being emitted from the loudspeaker. Although this was rare, it caused the timing of the secondary reinforcement to be slightly off in a few trials in the call-over training. No instances of such a delay were documented from the discrimination trials.

5.4.3 "Trivial" sounds and signature whistle recordings

Janik *et al*. (2006) claimed that it is the frequency modulation pattern, rather than the voice features, that carries the identity information in a SW. This was taken into consideration when creating the TS and DTS variants used in this study. The individual call-over TSs were organized in simple up and down "staircase" sweeps of tones, whereas the DTSs had unique patterns of tones with both organized sweeps and irregular tone sequences. All DTSs began on different frequencies in order to make them different from each other already on the first tone, and none of them began on the same frequency as any of the TSs used as individual call-over signals. As all the TS and DTS variants used in this study had unique frequency modulation patterns, they should, in theory be possible to distinguish from one another. However, the overall duration of the TS and DTS variants did not vary as much as the duration of the SWs and DSWs did.

The quality of the SW recordings greatly varied between individuals. For example, Nephele's SW was captured on the recordings many times, and often when she was in close proximity to the hydrophone, making the recording and hence the playback of her SW of good quality (Fig. 2). Fenah's SW, on the other hand, was severely polluted by background noise that could not be removed using the noise reduction feature in Adobe Audition (Fig. 2). If redone, more time should be devoted to recording the SWs.

As described in King *et al*. (2013), SW copies often include features that make them stand out as a copy. In this project, no extra features were intentionally added to the SW playbacks, although the noise may be regarded as such. It is difficult to say if this had an impact on the results. On the other hand, each dolphin must be aware that when hearing its own SW, it must be generated by someone else. Since the training was designed so the speaker was in direct proximity of the target station the subject would inevitably recognize that the source was the speaker and not one of the other dolphins.

5.4.4 Timing of the secondary reinforcement

As described in section 3.7.3, the dolphins were expected to make a decision on whether to stay by the target or leave it and approach the Whistle caller speaker within 2 s after the beginning of the DSW/DTS. The average duration of the DSWs were 1,4 s while the average duration of the DTSs were 2,3 s. This means that the dolphins in the TS group would be rewarded for staying by the target before the DTS being played had ended. It is difficult to say whether this would make the discrimination easier or harder for the dolphins in the TS group as compared to those in the SW group, and one may argue that, instead of counting seconds from the beginning of the DSW/DTS, one should count the seconds after the end of the sound. However, it was clear, from the videos from the call-over training sessions before the discrimination, that the dolphins' active choice to stay or go, was made almost as soon as the sound had begun. As the timing of the secondary reinforcement after a desired response is important when training animals (Browne *et al.*, 2011; Feng *et al.*, 2016), we considered it to be a greater bias had we waited too long after the dolphins' actual decision to stay or go was made. Thus, after consulting the trainers, reinforcing two seconds after the beginning of the sound, was decided for both the SW and the TS group.

6 Conclusion

In this study, five out of six dolphins were observed to learn a new call-over signal consisting of either their own signature whistle (SW) or a non-biologically relevant "trivial" sound (TS). When exposed to other dolphins' SWs or other TSs, two dolphins, both from the SW group, were observed to successfully discriminate between their own SW and those of other dolphins. The only male in this study was the one most successful in the discrimination task. Although not regularly documented for the sake of the study, he was also observed to increase his use of his signature whistle, both during and in connection to the sessions, as he progressed in his training. This was also expanded to other training sessions.

The results in this study suggest that it is indeed possible to train dolphins to be called over, using both biologically and non-biologically relevant sounds. Furthermore, the results suggest, in accordance with the hypothesis of this study, that discrimination between a dolphin's own SW and the SWs of others, is more likely to be successful than discrimination between an assigned TS and other TSs. However, due to the small sample size in this study, we cannot say for sure that these results do not simply stem from individual differences in learning abilities of the trained dolphins.

We recommend further testing of the Whistle caller concept and its applicability in the husbandry routines of dolphins under human care and suggest that future studies focus on (1) male-female differences in discrimination success when applying the Whistle caller concept, (2) how the characteristics of the trivial sounds affect discrimination success, and (3) the option of calling more than one animal at a time by sending out several SWs in succession.

7 Societal and ethical considerations

All training and tests of the dolphins in this study were in compliance with the current Swedish animal welfare laws (ethical authorisation 5.2.18-5974/15, regarding education, ethological research, training of animals and simple sampling procedures). All training was conducted using positive reinforcement, and the dolphins were allowed to leave the training sessions at any point if they did not want to participate. The learning of novel behaviours, such as those in this study, can work as an important form of cognitive enrichment and has large welfare benefits (Westlund, 2014; Clark, 2017). Additionally, this study provided acoustic enrichment in the form of sounds being played from the Whistle caller speaker, as well as visual and physical enrichment as the entire dolphin group often manipulated and interacted with the Whistle caller equipment that was lowered into the pool. When introducing novel objects to dolphins, these can sometimes have unintended effects on the behaviour of the animals (Lyn *et al.*, 2020). Thus, the dolphins in this study were successively desensitised to the Whistle caller setup and sounds being emitted from the speaker during a total of 16 sessions. Signs of stress (fast swimming around in the pool or avoiding the Whistle caller) were only seen during the first three desensitisation sessions, and to counteract these negative associations to the Whistle caller, the dolphins were rewarded soon after each desensitisation sound had been played. Once desensitised to it, the dolphins did not display any stress related behaviours in relation to the Whistle caller sounds; however, one cannot rule out the possibility of them, although not showing it, still experiencing some degree of discomfort. If so, the Whistle caller project may have had unintended negative impact on the animals, and this should be further investigated in future studies with the Whistle caller.

To our knowledge, this is the first study to test the use of signature whistles as individual call-over signals. If established in dolphins under human care, individual call-over signals have the potential to make training sessions more effective by facilitating separating the dolphins into sub-groups when divided between trainers. Also, it would allow for trainers to request specific dolphins while others would understand that they were not addressed. By testing the hypothesis that signature whistles would be easier for dolphins to discriminate between, compared to other sounds, this study contributes not only to streamlining training sessions, but also to the understanding of the role of signature whistles in dolphin communication.

Using individual call signals to signal individually selective feeding has been seen to lower dominance behaviour in pregnant sows (Manteuffel *et al*., 2010). This gives us reason to believe that individual call-over signals such as the SWs used in this study can improve animal welfare in a range of different species. This study may therefore not only contribute to a welfare improvement in zoo kept animals, but for animals under human care in general.

8 Acknowledgements

First of all, I would like to thank Kolmården Zoo and the staff at the dolphinarium for allowing me to study their dolphins and be a part of their team. A special thank you to Therese Höglin and Josefin Larsson for their contribution during the training process, and to Elin Ström and Isabella Clegg for allowing me to use their collected data (WtP-scores) in my study. I would also like to acknowledge ÅF Consult, Stockholm, making this study possible by creating all of the Whistle caller components, and Rahmat Naddafi for helping out with the statistical analysis.

Lastly, a big thank you to my supervisor Mats Amundin for entrusting me with this project, and for supporting and encouraging me throughout the process.

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