Cover Image: Bottlenose Dolphin Crater Feeding (Photo by Shane Gross)

Experimental evidence for electroreception in the bottlenose dolphin (*Tursiops truncatus*)

Dissertation

to obtain the degree
Doctor Rerum Naturalium (Dr. rer. nat.)
at the Faculty of Mathematics and Natural Sciences
University Rostock

Sensory and Cognitive Ecology

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Rostock, April 11, 2022

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Date of defense: August 19th, 2022

Experimenteller Nachweis der

Elektrorezeption beim Großen Tümmler

(*Tursiops truncatus*)

Dissertation

zur

Erlangung des akademischen Grades

doctor rerum naturalium (Dr. rer. nat.)

der Mathematisch-Naturwissenschaftlichen Fakultät

der Universität Rostock

Sensorische und Kognitive Ökologie

vorgelegt von

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aus Erlangen

Rostock, den 11. April 2022

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Diese Doktorarbeit wurde am 19. August 2022 im Rahmen eines wissenschaftlichen Kolloquiums verteidigt.

Für meinen Papa...

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ABSTRACT

Passive electroreception is a sensory modality of many aquatic animals and is predominantly used for short-range prey detection. Best known in the elasmobranchs, the ability to detect electric fields of biological origin has also been demonstrated in the monotreme platypus and echidna, as well as the delphinid species *Sotalia guianensis*. Mainly foraging on benthic prey, electroreception could complement the dolphin's other sensory modalities to facilitate prey detection. The hairless vibrissal crypts on the upper rostrum serve as the electrosensory units. Similarities in vibrissal crypt anatomy and innervation—as well as the fact that benthic foraging is also common in the bottlenose dolphin (*Tursiops truncatus*)—suggest that passive electroreception might also be found in this species. In this study, the ability of the bottlenose dolphin to detect electric fields in water was first tested by using a complex behavioral experiment. Trained with a go/no-go task using acoustic stimuli, four animals where subsequently tested for stimulus generalization within and across modalities using novel acoustic, optical, tactile, as well as direct current (DC) and alternating current (AC) electric stimuli. Based on the formation of an abstract concept of the go/no-go task, all animals responded spontaneously to the novel electric stimuli on the first trials. Using classical psychophysical techniques, detection thresholds for DC signals were determined for two dolphins at 2.4 and 5.5 μV cm^{-1}, respectively, a sensitivity similar to that of the Guiana dolphin. Thresholds for low-frequency AC signals decreased with increasing frequency. Though less sensitive than sharks or rays, these results show that electroreception in bottlenose dolphins could act supplementarily to other sensory modalities and facilitate short-distance prey-detection during bottom-feeding.

ZUSAMMENFASSUNG

Viele wasserlebende Tiere besitzen passive Elektrorezeption und verwenden diese hauptsächlich für die Beuteerkennung im Nahbereich. Die Fähigkeit zur Wahrnehmung elektrischer Felder biologischen Ursprungs ist vor allem von den Haien und Rochenartigen bekannt, wurde aber auch beim Schnabeltier und dem Schnabeligel (Monotremata), sowie bei der Delphinart *Sotalia guianensis* (Guayana-Delfin) nachgewiesen. Auf der Suche nach benthischer Nahrung könnte die Elektrorezeption die anderen Sinnesmodalitäten des Delfins ergänzen und das Auffinden der Beute erleichtern. Die haarlosen sog. Vibrissenkrypten auf dem Oberschnabel dienen als Elektrorezeptoren. Ähnlichkeiten in der Anatomie und Innervierung der Vibrissenkrypten, sowie die Tatsache, dass auch beim Großen Tümmler (*Tursiops truncatus*) benthische Nahrungssuche typisch ist, lassen vermuten, dass passive Elektrorezeption auch bei dieser Art vorkommt. In dieser Studie wurde die Fähigkeit des Großen Tümmlers, elektrische Felder im Wasser wahrzunehmen, mit einem komplexen Verhaltensexperiment untersucht. Vier Tiere wurden mit einer Go/No-Go-Aufgabe mit akustischen Reizen trainiert und später auf Reizgeneralisierung innerhalb und zwischen den Sinnesmodalitäten mit neuen akustischen, visuellen, taktilen sowie elektrischen Gleichstrom- und Wechselstromreizen getestet. Mittels der Bildung eines abstrakten Konzepts der Go/No-Go-Aufgabe reagierten alle Tiere sofort beim ersten Versuch auf die neuen elektrischen Reize. Für zwei Delfine wurde mittels klassischer psychophysikalischer Methoden die Wahrnehmungsschwelle für Gleichstromfelder bei 2,4 bzw. 5,5 µV cm^{-1} ermittelt. Die Sensitivität entspricht damit der des Guyana-Delfins. Die Schwellenwerte für niederfrequente Wechselstromfelder nahmen mit zunehmender Frequenz ab. Obwohl die Empfindlichkeit geringer ist als die von Haien oder Rochen, zeigen die Ergebnisse, dass die Elektrorezeption auch beim Großen Tümmlern als Ergänzung zu anderen sensorischen Modalitäten wirken und die Beuteerkennung auf kurze Distanz während der Nahrungssuche am Boden erleichtern kann.

1. INTRODUCTION

Marine mammals possess a number of sensory systems specially adapted to their aquatic lifestyle. This is not only reflected in their species-specific adaptations of already established sensory systems such as hearing and vision, but above all it is the development of new specialized sensory systems during the transition from land to water beyond the classical terrestrial sensory modalities. These modified and specialized sensory systems enable cetaceans, pinnipeds, and sirenians to assess and integrate all available sensory information on a multimodal level, which is not only essential for prey detection and capture, but also to navigate in the oceans, find mates, or avoid predators (Nachtigall, 1986; Torres, 2017).

The vibrissal system of seals and manatees, for example, is not only used for active touch (Bauer et al., 2012; Dehnhardt & Dücker, 1996; Dehnhardt & Kaminski, 1995; Grant et al., 2013), but also represents a highly developed system for the reception of hydrodynamic stimuli—for example, associated with fish movements and other object-caused distortions to the hydrodynamic flow (Dehnhardt et al., 2001; Gaspard et al., 2013, 2017; Hanke et al., 2010; Krüger et al., 2018; Wieskotten et al., 2010). This effective hydrodynamic receptor system enables seals and sea lions to pursue trails of fish without any visual cues and hunt even in dark or turbid waters (Dehnhardt et al., 1998, 2001).

Audition is widely considered the most important sensory system in cetaceans. Whales and dolphins use sound to navigate, find prey, avoid predators, and for communication (Au, 1993; Thewissen & Nummela, 2008; Tyack, 2000)—bottlenose dolphins (*Tursiops truncatus*) can hear frequencies from 150 Hz up to 150 kHz (Au et al., 2000). Especially when hunting fish species that produce loud sounds, some toothed whale species (Odontoceti), including bottlenose dolphins, also rely on passive listening for initial prey detection (Barros & Wells, 1998; Gannon et al., 2005; Milmann et al.,

2016). Nevertheless, toothed whales primarily rely on echolocation to navigate, explore, and assess their environment, and especially during foraging when vision is limited (Harley et al., 2003; Tyack & Clark, 2000). Odontocetes produce ultra-sonic click sounds with their phonic lips at frequencies between 10 and 300 kHz (for a review, see Kuroda et al., 2020). These clicks are projected into the water through the melon, a fatty structure in a dolphin's forehead that acts as an acoustic lens (Au, 1980). The returning echoes from their surroundings are received with the lower jaw and used to determine the distance, size, and location of objects (Au, 1993). Using this highly effective biosonar, dolphins can discriminate objects differing in form and size (Nachtigall & Patterson, 1980; Pack & Herman, 1995) and locate even small objects at distances up to more than 100 m (Au, 1990, 1993; Au et al., 1980; Au & Snyder, 1980; Harley et al., 2003; Murchison, 1980). While most dolphins possess good visual abilities in air and under water (Herman et al., 1975; Madsen & Herman, 1980; Mobley & Helweg, 1990) or use tactile perception, especially during socialization (Dudzinski, 1998), the evolution of echolocation nevertheless constitutes the prime example of a highly specialized sensory adaptation to the aquatic environment in marine mammals.

However, some foraging strategies require additional sensory adaptations. Behavioral and anatomical evidence suggest that the Guiana dolphin (*Sotalia guianensis*), a small dolphin species inhabiting the coastal waters from Honduras to Brazil, possesses passive electroreception, the ability to detect bioelectric fields in water (Czech-Damal et al., 2012). Such bioelectric fields provide a valuable source of sensory information as constant direct current (DC) fields are generated by ion flow on mucous membranes such as at the gills or the mouth of fish (Bedore & Kajiura, 2013; Kalmijn, 1972). Gill movements, respiratory behavior, or muscle contractions modulate this standing DC field with low-frequency alternating current (AC, ≤ 20 Hz) potentials (Kalmijn, 1972; Wilkens & Hofmann, 2005). In the study by Czech-Damal et al. (2012), a

male Guiana dolphin learned to respond reliably to weak DC electric fields as small as 4.6 µV cm^{-1}. The authors identified the hairless vibrissal follicles on the Guiana dolphin's upper rostrum as the electrosensory units (Czech-Damal et al., 2012). All dolphins and whales, like almost all mammals, possess vibrissal hairs during at least one stage of their life (Henneberg, 1915; Japha, 1912; Ling, 1977; Yablokov & Klevezal, 1969). In baleen whales (Mysticeti) and two representatives of the river dolphins (*Inia geoffrensis* and *Platanista* spp.), these hairs are still visible in adult animals, although it remains to be shown for the river dolphins whether they are actually real vibrissae with a sinus system (Ling, 1977; Mercado III, 2014). In all other toothed whales (Odontoceti), the vibrissal hair shafts disappear within the first weeks after birth, and only the hairless follicles remain visible as rows of 2–20 small pores on both sides of the upper rostrum (Cozzi et al., 2017; Drake et al., 2015; Japha, 1912; Ling, 1977; Nakai & Shida, 1948). While the vibrissae may play a role in neonates to locate the maternal nipple (Czech, 2007), the hairless follicles of adult dolphins have long been considered rudimentary. The morphological study of different toothed whale species (the bottlenose dolphin, the Guiana dolphin, the harbor porpoise [*Phocoena phocoena*], and the Franciscana dolphin [*Pontoporia blainvillei*]), however, revealed that the hairless follicle-sinus complexes (F-SCs) are not rudimentary but are structurally modified, highly innervated sensory units, possibly serving electroreception (Czech-Damal et al., 2012). Thus, the hairless F-SCs were renamed "vibrissal crypts" (Czech, 2007) because they lack characteristic structures of a mammalian F-SC as defined by Rice et al. (1986), such as a hair shaft, hair papilla, or a blood sinus. Instead, the ampullary-shaped invagination of the skin together with a rich innervation by the trigeminal nerve of up to 300 axons per crypt are strongly reminiscent of the ampullae of Lorenzini of sharks and or the mucous gland electroreceptors of the platypus (Czech-Damal et al., 2012; Manger et al., 1998; Manger & Pettigrew, 1996; Murray, 1974). Furthermore, the large lumen is filled with a dense

meshwork of corneocytes and keratinous fibers (Czech-Damal et al., 2012). Rich in glycoproteins (Baum et al., 2000, 2001), it is suggested that this gel-like substance is electrically conductive and thus could enhance signal transduction, similarly to the biogel found in the electroreceptors of sharks and or the platypus (Czech-Damal et al., 2012; Josberger et al., 2016; Tricas & Carlson, 2012).

The ecological relevance of passive electroreception is underlined by the fact that it has evolved independently several times across multiple taxa (King et al., 2018). While passive electroreception is best known from sharks and rays, it is found in all non-teleost fish, in all Mormyrids and Gymnotids, as well as in all catfish species. Furthermore, it is also found in the platypus (*Ornithorhynchus anatinus*) and two more monotreme species, the western long-beaked echidna (*Zaglossus bruijnii*) and the short-beaked echidna (*Tachyglossus aculeatus*).

Electroreception specialists like sharks, rays, or the platypus display a preference for benthic feeding using their electroreceptive sense to deliberately forage on prey hidden in the sediment (Dehnhardt et al., 2020; Kalmijn, 1974; Manger & Pettigrew, 1995; Tricas & Sisneros, 2004). Benthic feeding strategies have been observed across many dolphin species, including the Guiana dolphin (Rossi-Santos & Wedekin, 2006), bottlenose dolphins (Kaplan et al., 2019; Mann & Sargeant, 2003; Nowacek, 2002; Quigley et al., 2022; Rossbach & Herzing, 1997), or harbor porpoises (Heithaus & Dill, 2009). Stomach-content analyses confirm the Guiana dolphin's preference for bottom-dwelling fish (Di Beneditto & Siciliano, 2007; Santos et al., 2002). While digging into the sediment, the electrosensory capabilities of the Guiana dolphin could then act as a supplementary short-range sense when vision and/or echolocation become less effective (Czech-Damal et al., 2012; Dehnhardt et al., 2020). "Crater-feeding" or "bottom-grubbing" describes a feeding technique in bottlenose dolphins in which the animals dig vertically into the seafloor to search for hidden fish (Kaplan et al., 2019;

Mann & Sargeant, 2003; Rossbach & Herzing, 1997). In addition to these similarities in foraging behavior, a high morphological resemblance of their vibrissal crypts to those of the Guiana dolphin raises the question as to whether electroreception could also be present in the bottlenose dolphin or other delphinid species (Czech, 2007; Czech-Damal et al., 2012; Hüttner et al., 2022, with histological data from N. Czech). The vibrissal crypts of the bottlenose dolphin display similar morphological modifications to the electroreceptors of the Guiana dolphin: They are comparable in size, ampullary shape, innervation, and blood supply, and a vibrissal shaft is also absent (Czech, 2007; Czech-Damal et al., 2012). However, recent anatomical evidence from a light microscopic study of mostly neonate bottlenose dolphins suggests a mechanoreceptive or proprioceptive function that could enable the dolphin to detect water movements and low-frequency oscillations (Gerussi et al., 2020). Based on their findings, Gerussi et al. (2020) conclude that the vibrissae also remain complete in adult *Tursiops*, including a hair papilla, and an intact vibrissal shaft, rich innervation, and blood supply. However, in adults the vibrissal shaft remains inside the follicle but does not reach the opening of the follicle (Gerussi et al., 2020). In each case, the rich innervation with free endings definitely indicates a sensory function. However, more studies are needed to verify the functional roles of the bottlenose dolphin's vibrissal crypts.

To address whether bottlenose dolphins possess passive electroreception, I designed a behavioral study with four bottlenose dolphins at Nuremberg Zoo, Germany. Using a stimulus generalization test, the dolphins were trained to indicate the presence of an electric field using the go/no-go task. In a normal go/no-go setting, an animal is trained to indicate the presence of a stimulus by leaving a so-called "station." If no stimulus is presented, the animal has to reject a go response and stay in the station (Holt & Schusterman, 2002; Schusterman, 1980). The go/no-go task has been used in different studies investigating the sensory detection and cognitive abilities of dolphins and other

marine mammals. Among others, Nachtigall and Hall (1985) chose the go/no-go task to examine the ability of bottlenose dolphins to detect different flavors. They demonstrated that bottlenose dolphins possess basic taste abilities and can identify the tastes of sour, sweet, salty, and bitter (Nachtigall, 1986; Nachtigall & Hall, 1985). In another experiment, Ralston and Herman (1995) used the go/no-go behavior to train a dolphin to recognize frequency contours of different sounds and tested the dolphin's ability to generalize the trained rule to novel stimuli. A whistle response by the dolphin was defined as the correct go response, while no sound emitted by the dolphin after presentation of the contrasting frequency was considered a correct rejection. For the purpose of the present study, it was important to begin training the dolphins for the go/no-go task with stimuli addressing one of their established sensory modalities. After they learned the task in one sensory modality, new stimuli addressing other sensory modalities were introduced to test whether the animals could generalize the go/no-go task in a modality-independent manner. I used this stimulus generalization test because testing for a novel sensory modality that has never been studied in an animal could cause certain problems and thus may lead to a false-negative result: The dolphins could fail to respond to the electric fields not due to the fact that they did not sense the electric stimulus, but because they had no previous experience with the novel stimulus. Moreover, a lack of experience with the go/no-go task itself or focusing on other sensory input instead could have prevented the dolphins from responding correctly (Hanke & Dehnhardt, 2013; Scholtyssek et al., 2015). Thus, in the first part of this study, the go/no-go task was first established using only acoustic stimuli. Then, and prior to testing for electroreception in the bottlenose dolphin and based on the ability of bottlenose dolphins to generalize rules and form concepts (for further review, see Herman et al., 1989, 1994), the ability of the four dolphins to generalize the go/no-go behavior to novel stimuli within and across other modalities like vision and touch was tested. If the

dolphins are able to generalize the response behavior whenever they perceive sensory input to one of their renowned sensory modalities, this would represent an ideal starting point to test for passive electroreception in the bottlenose dolphin. Besides determining whether dolphins are in principle able to detect electric fields in water, the main objective of this study was to examine the sensitivity of the system and to determine the detection thresholds for weak electric fields. Thus, the detection threshold of bottlenose dolphins for DC electric fields was determined by using classical psychophysical techniques. Because naturally occurring bioelectric fields typically consist of DC as well as AC components, additional tests were performed in a final experiment to determine whether the dolphins are also able to detect low-frequency AC electric fields.

2. METHODS

2.1 PART I: ESTABLISHMENT AND GENERALIZATION OF THE GO/NO-GO BEHAVIOR

The first part of my thesis consisted of three stages. Stage 1 included the establishment and training of the go/no-go behavior with acoustic stimuli. Stage 2 involved testing whether the dolphins could generalize the go/no-go behavior to novel stimuli within the acoustic modality. Finally, stage 3 comprised testing whether the dolphins could transfer the go/no-go behavior to novel stimuli across other modalities.

2.1.1 Subjects

Subjects were four bottlenose dolphins (*T. truncatus*). Anke, a 33-year-old female (wild-born, approximately 1983), had previous experience participating in cognitive tasks. She had previously performed in experiments on lateralization (Kilian et al., 2000) and the ability to form equivalence classes (von Fersen & Delius, 2000). The other three animals—Dolly and Donna, two 10-year-old females (born at Zoo Duisburg, Germany, 2007), and Kai, a sub-adult 5-year-old male (born at Dolfinarium Harderwijk, the Netherlands, 2010)—had all been well trained but were experimentally naïve. All animals lived together in a group of 7–10 bottlenose dolphins and 6–10 California sea lions (*Zalophus californianus*) at Nuremberg Zoo, Germany. The enclosure consisted of an indoor area (dolphinarium) connected to six outdoor pools (dolphin lagoon, see Figure 1) of various sizes and depth. The total water volume of the enclosure was approximately 7 million liters of saltwater. The total water area was approximately 1,900 m² with a maximum depth of 7 m. Usually, one experimental session was conducted per day with one dolphin at a time, on five days per week. Kai performed all experimental sessions in outdoor pool no. 1 (see Figure 1) and on some days in the main indoor pool. Experimental sessions with the three females were first carried out outdoor (see Figure 1) but later only in a round indoor pool (see Figure 1).

On some occasions, a second animal was present in the same pool. In this case the second dolphin was handled by a separate trainer in order to not disturb the session.
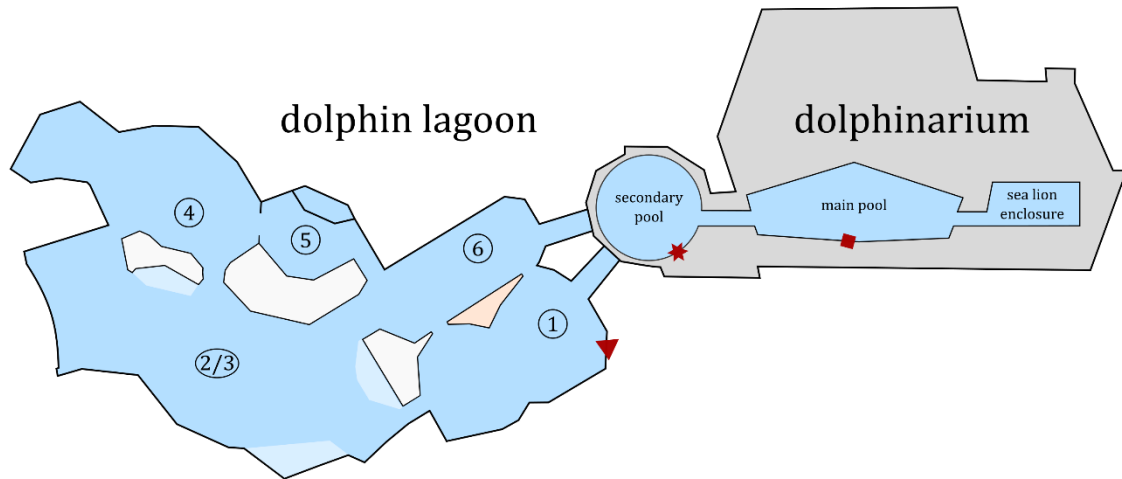
Figure 1: Pool plan of the dolphin enclosure. Experimental sessions were performed in outdoor pool no. 1 (red triangle), the secondary pool of the indoor dolphinarium (red star). Due to husbandry requirements, Kai also performed some sessions in the show pool of the dolphinarium (red square).

2.1.2 Experimental setup

The experimental apparatus for multimodal stimulus presentation was built from polyvinyl chloride (PVC) tubes. It was lowered into the pool before the beginning of each experimental session. The main experimental compartment consisted of a cube-formed tube structure of approximately 1.0 m long × 1.0 m wide × 1.0 m high (see Figure 2). For a trial, after a hand signal given by the trainer, the tested dolphin swam headfirst into the apparatus through a square opening at the front side of the apparatus. With its head inside the apparatus, the dolphin then stationed itself on a target (red ball) and placed its lower jaw on a U-shaped resting platform that had been installed in front of the target (see Figure 2). Both the target and the resting platform ensured a consistent position of the dolphin's head during each trial. All sessions were conducted by the experimenter and a trainer who was handling the dolphin. The trainer sat on the opposite side of the pool while the experimenter sat on land, behind the submerged

apparatus. Both the trainer and the experimenter were positioned out of the dolphin's sight as soon as he or she stationed correctly inside the apparatus. Additionally, a visual cover (white tarp, 110 cm × 80 cm) was fixed to the apparatus above the animal's station (target and resting platform) to prevent any unintentional visual cueing by the experimenter (see Figure 2). The experimenter observed the dolphin's behavior on a small LCD monitor connected to an underwater camera attached to the apparatus and directed toward the animal's station (WoSports® Fish Finder, see Figure 2). For documentation purposes, experimental sessions could be recorded by a second camera (GoPro Hero 4 Black, GoPro, USA) that was also attached to the apparatus.
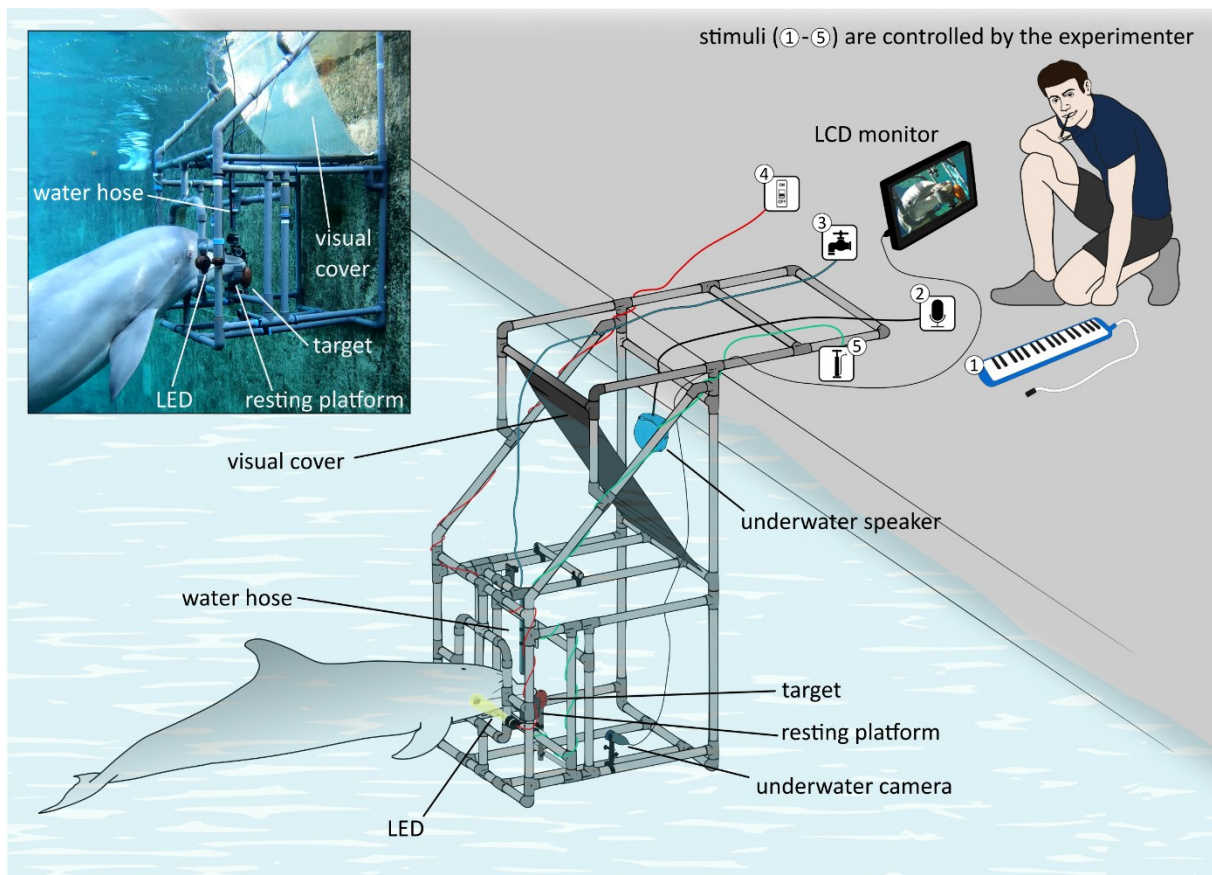
Figure 2: View of the experimental setup during generalization tests. The dolphin swims into the apparatus through the square opening and touches the target while placing its lower jaw on the resting platform. The experimenter sat behind the submerged apparatus, and thus was not visible to the stationing dolphin. The visual cover excluded any unintentional cueing by the experimenter. Using an underwater camera connected to a small LCD monitor screen, the experimenter observed the dolphin's behavior during the experiment. The experimenter controlled the presentation of the different stimulus types used during this part of the study: (1) melodica sounds manually produced by the experimenter on land, (2) pure tones, (3) water jet, (4) lights on/off, and (5) air bubbles.

2.1.3 Experimental phases and stimuli

In total, 54 different stimuli were presented to the dolphins during the first part of this study, addressing their auditory, visual, and tactile modalities (see Table 1).

2.1.3.1 Stage 1: Establishment of the go/no-go behavior

To train the dolphins with the go/no-go behavior, I used three different acoustic stimuli: a police whistle, a metal rattle—both presented above the water—and a dog clicker presented under water (see Table 1). During each training session, go and no-go trials were presented counterbalanced in a randomized order. The number of trials per session was increased until the dolphins performed well for 20 trials per session. The learning criterion for successful acquisition of the go/no-go task was defined as $\geq 80\%$ correct choices (hits and correct rejections combined, binomial test, $P < 0.0001$) accompanied by a false alarm rate $\leq 20\%$ (binomial test, $P < 0.0001$) over three consecutive sessions of 20 trials.

2.1.3.2 Stage 2: Generalization of the go/no-go behavior within the acoustic modality

In the second stage, new acoustic stimuli were introduced to test each dolphin's ability to generalize the go/no-go behavior within the auditory modality. The new stimuli included 25 melodica key sounds (Thomann Melodica, 37 keys, range: f to f''') that were played manually by the experimenter for 3 s. The 25 stimuli included 15 single tones between 0.3 and 1.4 kHz with a frequency difference ≥ 0.04 kHz and 10 double tones with two keys played simultaneously (0.3–1.2 kHz). The frequency differences between the two pressed keys of each double tone ranged from 0.05 to 0.18 kHz.

Likewise, 21 digitally generated pure tones were presented via an underwater speaker (DNA Aqua 30, see Figure 2). The pure tones were produced by running *Audacity® Recording and Editing Software* (version 22.1, Audacity Team, 2017), between 8 and 15 kHz at intervals of 0.5 kHz. The underwater speaker was placed in the

center of the apparatus above the visual cover and connected to a second speaker in air (Bose Roommate II Powered Speaker, Bose Corporation, USA) that was powered by a 12 V battery pack (GP Recyko 210AAHCB 2050 mAh). The experimenter played the sounds simultaneously on both speakers to control stimulus presentation, using a small audio player (iPod Nano, 3rd generation, 2007, Apple Inc., USA) that was connected to the second speaker in air.

An ordinary bike bell ring served as a third acoustic stimulus class (see Table 1). The bike bell was fixed to one of the tubes of the apparatus underwater and was rung manually by the experimenter by pulling a string tied to the bell.

Generalization performance was measured by each dolphin's performance on the first trial of each novel sound. The dolphins also needed to maintain an overall performance of $\geq 80\%$ correct responses and a false alarm rate of $\leq 20\%$ (chi-square test, $P < 0.001$) over all sessions, during which the novel stimuli were introduced to reach the criterion. The novel sounds were presented 2–4 times per session in a randomized order. Melodica sounds were tested first, and as long as the dolphins reached the learning criteria, the pure tones were introduced next. The bike bell was introduced last. Over the course of stage 2, the training sounds were replaced successively with the novel stimulus types.

2.1.3.3 Stage 3: Transfer of the go/no-go behavior across modalities to optical and mechanical stimuli

In stage 3, each dolphin's ability to transfer the go/no-go behavior across modalities to optical and mechanical stimuli was tested. Again, the novel stimuli were randomly interspersed 2–4 times per session. Thus, step by step, the dolphins were confronted with an increasing number of different stimuli addressing different sensory modalities. The transfer criterion was defined as a correct first trial response and an averaged hit rate of $\geq 80\%$ over the first 15 trials presented over 5–8 sessions of each

novel stimulus. As in stage 2, the dolphins also needed to demonstrate an overall performance of ≥ 80% correct choices (hits and correct rejections combined) while showing a false alarm rate ≤ 20% during these sessions. To address the visual modality, three serially connected underwater LED lights were used to present optical stimuli. One LED was installed on each side of the dolphin's head and directed toward his or her eyes. The distance between the respective LED and the dolphin's eye was approximately 25 cm (see Figure 3). The third LED light was installed above the animal's station on the upper side of the apparatus and was directed upward. It was only visible to the experimenter and served as a control light to monitor stimulus presentation. A dimmer switch was interposed to control brightness. For the "light on" stimulus, the lights were switched on manually by the experimenter for 3 s (Table 1). Second, a reversed optical stimulus was created by switching the lights on before the trial started, and the dolphin was sent to swim into the apparatus by its trainer. Now, switching off the lights served as the go stimulus (see "light off," Table 1).

Table 1: Stimulus categories presented within different modalities that were used during Part I of this study.

STIMULUS CATEGORY	STIMULUS NAME	STIMULUS DESCRIPTION
Establishment of the go/no-go behavior		
Acoustic stimuli	Training sounds	Dog clicker, police whistle, metal rattle manually presented by the experimenter
Generalization of the go/no-go behavior within the acoustic modality		
Acoustic stimuli	Melodica sounds	25 different melodica sounds played by the experimenter on land
	Pure tones	21 digitally produced sine wave pure tones presented via underwater speaker
	Bike bell	Bike bell rung underwater
Transfer of the go/no-go behavior across different modalities		
Optical stimuli	Lights on	LED lights switched on
	Lights off	LED lights switched off (LED lights were switched on before the dolphin entered the apparatus)
Mechanical stimuli	Water jet	Water jet directed at the upper rostrum
	Air bubbles	Air bubble flow directed at the lower rostrum

Two types of mechanical stimuli were used: a weak jet of water directed at the upper jaw of the dolphins and a flow of air bubbles toward the lower jaw of the dolphins (see Table 1). For the water jet, a thin tube was fixed to the PVC structure and was connected to the facility's water supply. The tube opening was installed approximately 10.0 cm above the position of the dolphin's rostrum (Figure 3). The water jet was generated by opening the valve. The stimulus duration was again defined as 3 s, and together with the strength of the water jet it was controlled manually by the experimenter.

To generate the flow of air bubbles, a thin flexible tube connected to a common aquarium air pump was fixed to the apparatus below the dolphin's resting platform (Figure 3). As soon as the pump was switched on by the experimenter, a weak flow of air bubbles exited the tube opening, rose upward, and touched the lower jaw of the dolphin (see Table 1). The stimulus duration (3 s) was again controlled manually by the experimenter.

To mask any secondary acoustic cues associated with the onset of the non-acoustic stimuli and that the dolphins could have used to respond to the novel stimuli, a significant white noise–like background sound was generated underwater. Therefore, using a water hose connected to the general water supply, a strong jet of water was directed onto the water surface next to the apparatus (G. Dehnhardt, personal communication.
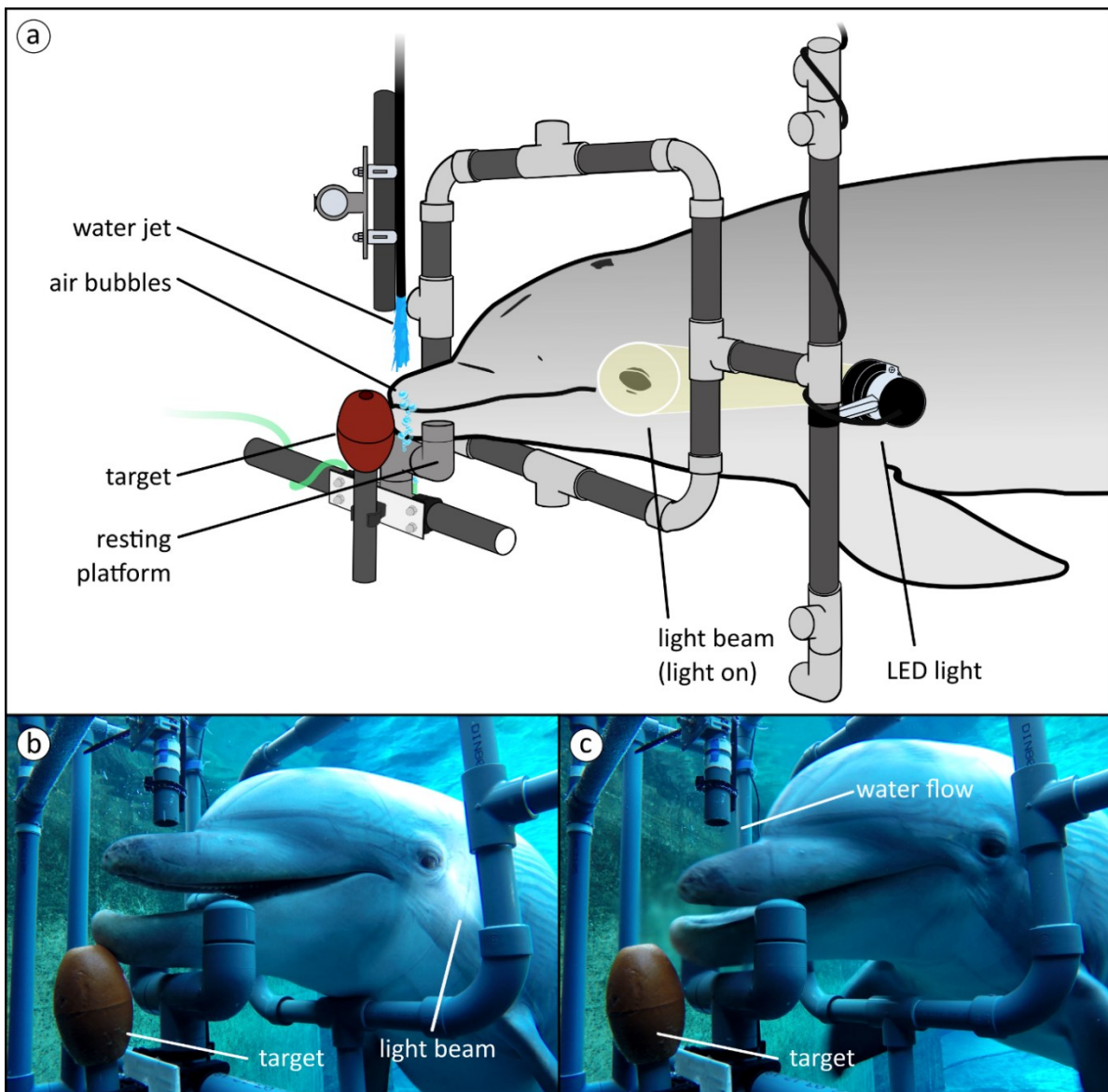
Figure 3: Stimulus presentation setup. Overview of the experimental setup. The dolphin (Anke) enters the experimental apparatus and touches the target with her rostrum. A total of 53 different stimuli were presented to the dolphins over the course of this part of the study. Training sounds (dog clicker, police whistle, metal rattle, not shown), and melodica sounds (not shown) were presented manually by the experimenter above the water. Sine wave pure tones were presented via an underwater speaker, hidden by the visual cover, above the dolphin's station (not shown). A bike bell, fixed to the apparatus underwater, was rung manually by the experimenter using a string tied to the bell handle (not shown). Two LED lights were attached to both sides of the stationing dolphin's head. They were switched on (lights on) or off (lights off) by the experimenter to generate two different optic stimuli. A water tube (black tube) connected to the facility's water supply created a water jet that was directed at the dolphin's upper jaw after the experimenter opened the valve. A second thin flexible tube (green tube) was attached to the apparatus below the resting platform and was connected to a small air pump above the water. As soon as the experimenter switched on the pump, a small stream of air bubbles directed at the dolphin's lower jaw was created. **(b)** The light beam of the LEDs is visible around the eye of the dolphin. One LED light was installed on each side of the head of the stationing dolphin. **(c)** The water jet is visible around the upper rostrum emerging from the opening of the thin water tube (black).

2.1.4 Experimental procedure

All sessions were carried out by the experimenter and a trainer. Unless otherwise stated, I was always the experimenter. Usually, one session was run per day with each dolphin on five days a week. During one session, the dolphins received approximately 20% of their daily diets (1–1.5 kg of herring, sprat, capelin, squid, and mackerel).

Each session typically consisted of 20 go and no-go trials, presented in a pseudo-randomized sequence (Gellermann, 1933; Holt & Schusterman, 2002). A trial started once a dolphin was sent to swim into the apparatus. Then, following the classical go/no-go paradigm, either a go trial (stimulus present) or a no-go trial (stimulus absent) was carried out. During a go trial, stimulus presentation started approximately 3 s after the dolphin reached the station and touched the target. The dolphins then had to respond within 5 s after the stimulus onset by leaving the apparatus (*hit*). During no-go trials, the dolphins were required to remain stationed for at least 12 s (*correct rejection*). Correct responses were secondarily reinforced by the experimenter with a short whistle sound followed by a food reward from the trainer. The trainer had no information about the type of trial, in order to eliminate any unintentional cues by the trainer. False responses—no responses during go trials (*misses*) or responses during no-go trials (*false alarms*)—were signaled to the dolphin with three short consecutive whistles and were not reinforced.

2.2 PART II: PASSIVE ELECTRORECEPTION IN THE BOTTLENOSE DOLPHIN

In Part II of my thesis, I tested the four bottlenose dolphins for their ability to detect weak electric fields in water. Based on my assumption that bottlenose dolphins have passive electroception, I first tested whether the dolphins were able to also transfer the go/no-go behavior to this modality. To do so, DC electric field stimuli were

randomly interspersed, just like the mechanical and optical stimuli had been in Part I. Subsequently, detection thresholds for DC as well AC electric fields were determined.

2.2.1 Subjects and general experimental procedure

Experiments were conducted with the same four animals and followed the same experimental procedure and setup that was established in Part I: Sessions were conducted by the experimenter (myself) and a trainer with one dolphin at a time. The trainer handled the dolphin and sent the animal into the apparatus to start a trial. He rewarded the dolphin with fish if its decision to leave the apparatus or to stay was correct. The experimenter controlled electric stimulus presentation according to a pseudo-randomized sequence of 20 counterbalanced go/no-go trials (Gellermann, 1933). As before, he observed the dolphin's behavior during each trial on the small video monitor. Correct responses were defined as the dolphins leaving the apparatus after they detected an electric stimulus or staying inside the apparatus if no stimulus was presented. Correct choices were secondarily reinforced with a short continuous whistle blow from the experimenter. The dolphins were then rewarded with fish by the trainer and sent back to the apparatus for the next trial. Incorrect responses were signaled to the dolphin with three short consecutive whistles, followed by no reward.

2.2.2 Electric stimulus generation

Electric fields were generated by a battery-powered, custom-made electric field generator (EFG, version 2.0, 2014, University of Rostock, Germany) that served as a constant current source. The electric field generator was connected to two copper wire electrodes to form an electric circuit. The electrodes (1 cm long, 2 mm in diameter, and 1 cm apart from each other) were encapsulated in epoxy and cast into a PVC tube 26 mm in diameter. The electrodes were attached to the tube structure of the apparatus and positioned 5–10 cm from the dolphins' vibrissal crypts on their upper rostrums (see

Figure 4). The distance between the upper rostrum and the tip of the stimulus electrodes was consistent for each animal throughout the experimental period, as stationing both on the target and on the resting platform ensured a consisted rostrum position during every trial.
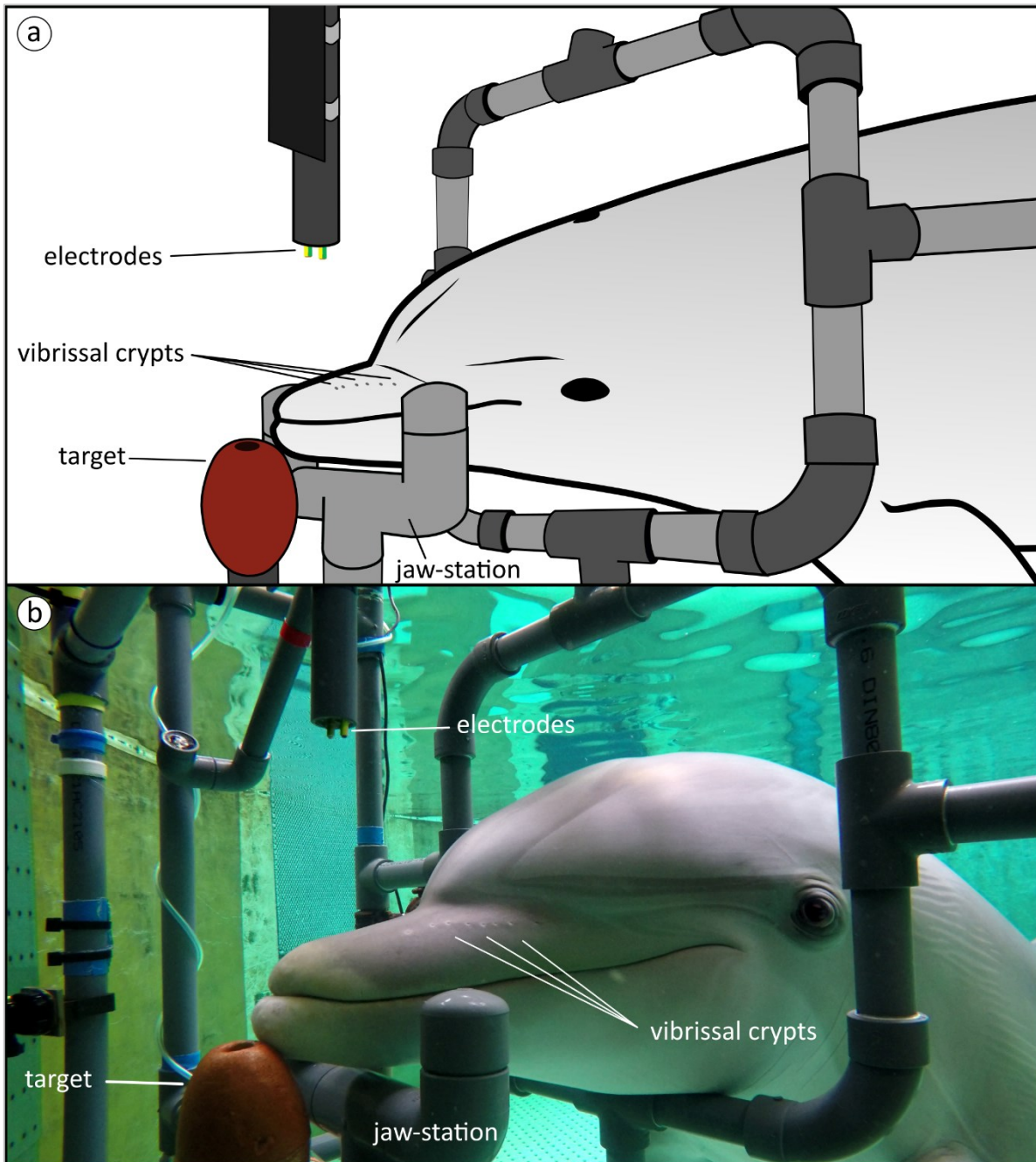
Figure 4: Schematic (a) and live view (b) of the experimental setup during a trial. The dolphin touches the target and stays in a constant position. The electrodes are located approximately 10 cm directly above the dolphin's vibrissal crypts on the upper rostrum. If an electric stimulus was presented, the dolphin was trained to leave the apparatus ("hit") and return to its trainer. A correct response was reinforced by the experimenter with a short continuous whistle sound, followed by a food reward from the trainer. During stimulus-absent trials, the dolphin was required to stay in station for at least 12 s. This "correct rejection" was also secondarily reinforced by the experimenter and followed by a fish reward from the trainer.

As long as comparatively strong electric fields were generated over the course of the study, tiny air bubbles emerged from one of the two copper wires due to electrochemical processes. With the electrodes positioned directly above the rostrum, these air bubbles could have provided secondary visual and/or acoustic cues for the dolphins. While bottlenose dolphins possess good visual abilities in air and underwater, their visual capabilities directly in front of them are limited. Even though the visual field of dolphins overlaps up to $20-30°$ (Mass & Supin, 2018) in front of them, their distinctive head anatomy causes a small blind area directly in front of the melon (Cozzi et al., 2017; Dral, 1975; Xitco et al., 2004). As the electrodes were positioned within this blind area, visual secondary cues associated with electrolytic processes were considered unlikely. The use of acoustic cues was prevented by generating a white noise background sound by a jet of water directed at the water surface.

The stimulus generator was powered by three 12 V batteries. Two of the 12 V batteries were connected in series and served as the power source for electric field stimulus presentation. The stimulus strength was adjusted by switching between 12 and 24 V. Additionally, the electric field strength was adjusted by using a multi-turn wirewound potentiometer (VISHAY SPECTROL, Model 534, 10 turns, 10 kΩ, VISHAY Intertechnology, Malvern, PA, USA). The electric field generator was connected to a digital TrueRMS multimeter (Voltcraft VC870, Conrad Electronics SE, Germany) to monitor the applied current. AC and DC electric fields were used during the course of this study. DC electric fields were generated by presenting a square-wave pulse. AC electric fields were generated by presenting a periodic square wave signal. Electrolytic processes at the stimulus electrodes altered the square wave signal, generating a sinusoidal-similar AC electric signal. Three different frequencies were tested: 1, 5, and 25 Hz. For DC and AC signals, the stimulus duration was defined as 3 s and was controlled by a timer chip (NE555).

Electric field stimulus strength was measured before and after each session with two non-polarizable Ag/AgCl electrodes (1 cm long, 0.1 mm thick, 1 cm apart). The Ag/AgCl electrodes (1 cm long, 0.1 mm thick, 1 cm apart) were connected to the electric field detector (EFD, version 2.0, 2014, University of Rostock, Germany), a custom-made amplifier based on an instrumental amplifier (AD620, Analogue Devices, Norwood, MA, USA). The measure electrodes were placed below the stimulus electrodes at the location of the vibrissal crypts of the dolphins. To ensure precise measurements of the electric field strength, the position of the vibrissal crypts of each animal was determined by measuring the rostrum of each dolphin to the nearest millimeter. Because the dolphins touched both the target and the resting platform, the position of their rostrums remained consistent throughout the entire study. For each dolphin, the measure electrodes were positioned exactly at the position of the nearest vibrissal crypt.

The EFD was connected to a TrueRMS multimeter (Voltcraft VC870, Conrad Electronics SE, Germany) to monitor and record the electric field strength. The recording frequency was approximately 2 Hz. DC electric fields were monitored by using a battery powered laptop running a measuring and recording software (VC 870 Interface Program, Version 4.2.6, Voltcraft, Conrad Electronics SE, Germany) that was connected to the multimeter via USB. AC electric field strength and frequency were monitored with a digital oscilloscope (RIGOL DS1052E, Dual Channel, 50 MHz, RIGOL Technologies, Beijing, China) that was connected to the EFD. AC and DC electric field strengths were calculated and recorded by the experimenter using Microsoft Excel (2016).

2.2.3 Transfer of the go/no-go behavior to electric stimuli

To test whether bottlenose dolphins possess electroreception, I first tested whether the four animals could transfer the go/no-go behavior to electric stimuli. Weak DC electric fields in water were introduced first. Considering the detection threshold of

approximately 4.6 µV cm^{-1} for weak DC electric fields in the Guiana dolphin (Czech-Damal et al., 2012), initial tests were performed with a stimulus intensity well above the threshold of the Guiana dolphin of approximately 1.5 mV cm^{-1}. At the beginning, 3–5 electric stimuli were interspersed randomly during one session among the familiar acoustic, optical, or mechanical stimuli. The overall hit rate on DC electric stimulus trials was calculated. The criteria for a successful transfer of the go/no-go behavior to electric stimuli were ≥ 80% hits over at least 30 consecutive electric stimulus trials and at least 80% correct choices and a maximum false alarm rate of 20%. Next, the electric field strength was reduced to 1.0 and 0.5 mV cm^{-1}, respectively, with 32–34 trials each.

2.2.4 Determining the sensory detection threshold of the bottlenose dolphin for DC electric fields

Each bottlenose dolphin's detection threshold for DC electric fields was determined by using classical psychophysical methods. First, the number of electric stimuli presented per session was increased and the other stimulus types from Part I were faded out session-by-session until only electric stimuli were used during sessions. Then, similarly to Czech-Damal et al. (2012), the threshold was determined by using a combination of the staircase method and the method of constant stimuli, and the theoretical detection threshold was defined as the electric field strength that would be detected 50% of the time (Gescheider, 1976, 1997). Starting from 1.0 mV cm^{-1}, a stimulus intensity to which they had already responded highly significantly in the mixed sessions, the stimulus intensity was reduced gradually by using a set of predetermined stimuli between 1,000 and 2 µV cm^{-1}. For each stimulus strength, a minimum of 30 trials were presented over at least three consecutive sessions. The next weaker electric field strength was introduced if the dolphin's response rate to one stimulus strength remained ≥ 80%.

2.2.5 Determining the sensory detection threshold of the bottlenose dolphin for AC electric fields

After determining the thresholds for DC electric fields, the dolphins were tested to determine whether they could also detect AC electric fields. Test sessions with AC electric fields were performed only with Donna and Dolly. The three different frequencies (1, 5, and 25 Hz) were tested separately. For each stimulus frequency, a stimulus strength clearly above the previously determined DC electric field threshold was tested first. Again, for each stimulus intensity a minimum of 30 trials were performed over at least three consecutive sessions. The detection threshold was defined as the electric field strength that would be detected 50% of the time (Gescheider, 1976, 1997).

2.2.6 Control experiment for the exclusion of secondary acoustic cues

A control measurement was carried out to rule out potential secondary acoustic cues associated with the electric field presentation. Therefore, a hydrophone (Model D/140, Neptune Sonar Ltd, United Kingdom) was placed in the center of the experimental apparatus, in the same position as the center of a dolphin's head during a trial. The hydrophone was connected via two Etec 100-A preamplifiers to a National Instruments USB 6251 A/D converter, which was connected to a battery-powered laptop with a custom-made LabVIEW sound recording software ("Biologger using NI USB-63x6," programmed by Alain Moriat, National Instruments, USA; courtesy of Magnus Wahlberg, University of Southern Denmark). DC and AC stimuli were presented in the exact same manner as during an experimental session. The full technical details of the recording setup are specified in the appendix (see section 7.1). The recordings were carried out in cooperation with Kolmården Wildlife Park, Sweden, and were conducted by Mats Amundin, PhD, at Nuremberg Zoo. No audible artifacts could be measured, ruling out any secondary acoustic cues that could have indicated the presence of an electric stimulus to the dolphins.

3. RESULTS

3.1 PART I: ESTABLISHMENT AND GENERALIZATION OF THE GO/NO-GO BEHAVIOR

3.1.1 Stage 1: Establishment of the go/no-go behavior

The performance of each of the dolphins in the last three sessions to reach the learning criteria was highly significant (see Table 2). Anke habituated quickly to the general experimental procedure and reached the learning criteria after 109 trials. Dolly needed 820 trials to complete 20 trials per session. Donna was highly neophobic toward the experimental apparatus; thus, the number of trials per session had to be increased and decreased frequently at the beginning of training to maintain high motivation. In total, it took Donna 1,058 trials over 81 sessions to meet the criteria. Due to continuing poor motivation as soon as the number of trials was increased, Kai never performed more than 10 trials per session. He met the criteria of ≥ 80% correct choices over three consecutive sessions after 210 trials.

Table 2: The performance of the four dolphins during the go/no-go behavior training until they completed three consecutive sessions with 20 trials. The number of sessions and trials varied among the four dolphins. The overall performance (hits and correct rejections combined), the hit rate, and the false alarm rate of the four dolphins were all significantly different from chance level.

		ESTABLISHMENT OF THE GO/NO-GO BEHAVIOR		
Dolphin	Number of trials	Overall performance (%)	Hit rate (%)	False alarm rate (%)
Anke	109	85.0**	86.7**	16.7**
Dolly	820	95.0***	91.7***	0.0***
Donna	1,058	91.7***	96.7***	13.3***
Kai	210	96.7***	100.0***	6.7**

Level of significance (binomial test): * $P < 0.01$, ** $P < 0.001$, *** $P < 0.0001$

3.1.2 Stage 2: Generalization of the go/no-go behavior within the acoustic modality

First, I analyzed each dolphin's first trial performances for each individual novel sound, as well as their averaged overall performance (hits and correct rejections combined) and false alarm rate over all sessions during which the novel stimuli were

introduced. Second, for each new stimulus type, I calculated the all-time hit rate on all trials of the different novel stimulus types presented until the end of the study. Kai and Donna did not participate in all generalization tests due to scheduling conflicts with the daily training routine (e.g., animal presentations, medical training, or visitor programs) of the zoo. Kai was only tested with the melodica sounds, and Donna did not participate in tests using the bike bell stimulus.

The dolphins showed a highly significant averaged first trial performance over the 25 melodica sounds with at least 23 correct responses (see Table 3). Anke was the only animal to fail to respond correctly on the very first melodica sound trial. Over all sessions during which the novel stimuli were introduced (7–22 sessions, see Table 3), Anke, Dolly, and Donna's overall performances and false alarm rates were also significant. Kai did not reach the predefined learning criterion of ≤ 20% false alarms. However, with 21.6% false alarms over 22 sessions (111 no-go trials), his false alarm rate was still significantly different from the level of chance (binomial test, $P < 0.0001$; see Table 3) and the experiment was continued as planned. As shown in Figure 5, each dolphin responded well to all tested melodica sounds until the end of the study, with at least 87.5% hits.

Anke, Dolly, and Donna responded correctly to all 21 pure tones on their first trials (see Table 3). With at least 95.8% correct choices and ≤ 8.9% false alarms, their performances over all sessions during which the pure tones were introduced (Anke: 11 sessions, Dolly: 14 sessions; Donna: 6 sessions; Table 3) were also highly significant. Their all-time hit rates (see Figure 5) also remained at a high level.

Additional generalization tests using the bike bell were only conducted with two animals (Anke and Dolly, see Table 3). Both animals immediately responded without error to the novel stimulus on their first trials and over their first 15 trials. The overall session performance and false alarm rate of both dolphins during these sessions was also

highly significant (see Table 3). Their all-time hit rates (see Figure 5) over all bike bell trials were also highly significant at 100.0% (Dolly, 101 trials, binomial test, $P < 0.0001$) and 99.0% (Anke, 101 trials, 100 hits, binomial test, $P < 0.0001$).
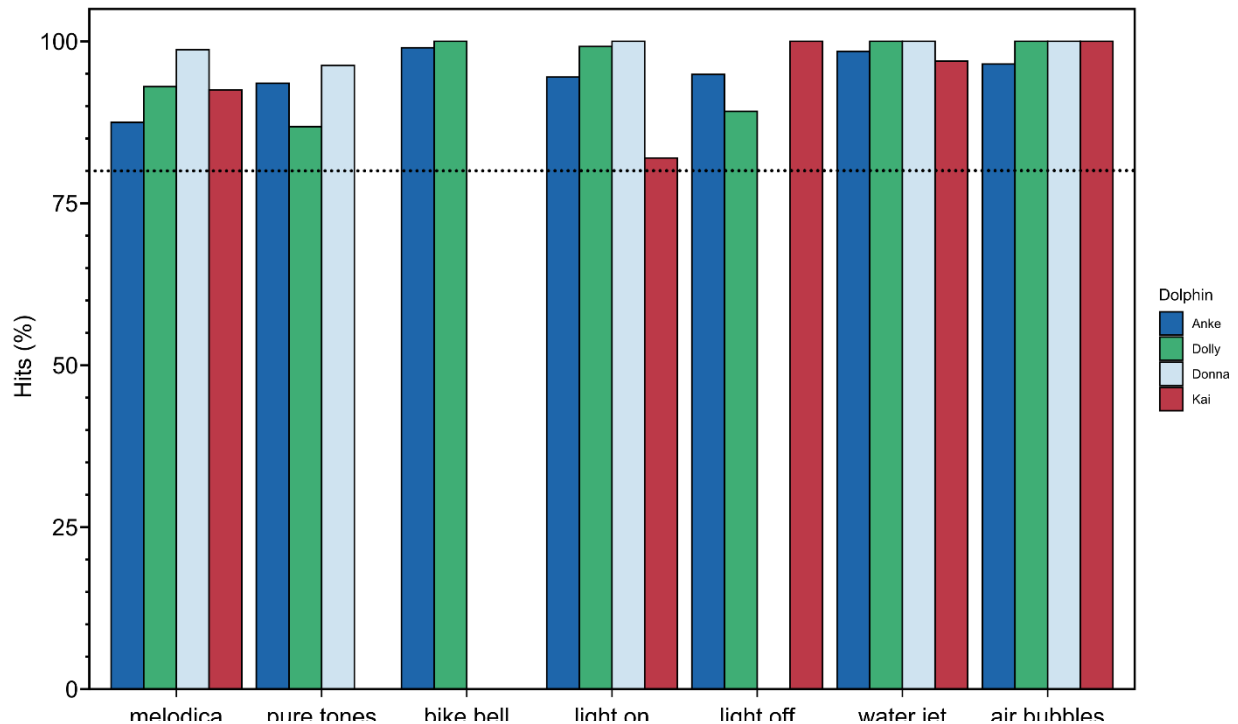
Figure 5: All-time performance over all trials for each dolphin and each novel stimulus type used during generalization and transfer tests. Each dolphin demonstrated significant performances of ≥ 80% hits (dashed line) for all stimulus types.

Table 3: The performance of the dolphins during acoustic go/no-go generalization and across modality transfer tests. For melodica sounds and the pure tones, a pooled first trial performance of ≥ 80% correct go responses (hits) was defined as a successful generalization. For the bike bell as well as the two optical and mechanical stimuli, a hit rate of ≥ 80% over the first 15 trials was defined as a successful generalization/transfer. Moreover, the dolphins had to maintain an overall performance of ≥ 80% correct choices and ≤ 20% false alarms over all sessions during which the novel stimulus types were introduced (first 15 trials per stimulus type).

ACOUSTIC GO/NO-GO BEHAVIOR GENERALIZATION						
Dolphin	Stimulus type	Number of sessions	Number of first trials	First trial performance (%)	Overall session performance (%)	Overall false alarm rate (%)
Anke	Melodica sounds	7	25	92.0***	87.9***	18.6***
	Pure tones	11	21	100.0***	96.8***	8.9***
	Bike bell	5	15	100.0***	89.0***	16.0***
Dolly	Melodica sounds	16	25	100.00***	94.5***	9.3***
	Pure tones	14	21	100.0***	97.9***	4.5***
	Bike bell	8	15	100.0***	95.5***	8.1***
Donna	Melodica sounds	13	25	92.0***	96.2***	3.7***
	Pure tones	6	21	100.0***	95.8***	6.7***
Kai	Melodica sounds	22	25	96.0***	83.3***	21.6***

Level of significance (binomial test): * $P < 0.01$, ** $P < 0.001$, *** $P < 0.0001$

3.1.3   Stage 3: Transfer of the go/no-go behavior across modalities to optical and mechanical stimuli

3.1.3.1   Visual modality

Dolly, Donna, and Kai responded spontaneously to switching on the lights on their first trials and continued to perform significantly throughout the first 15 trials and over all trials until the end of the study (see Table 4). Donna and Dolly responded correctly on each of the first 15 trials (100.0% hit rate, binomial test, $P < 0.0001$, see Table 5). Kai's performance, with a hit rate of 93.3% over the first 15 trials (binomial test, $P = 0.0005$, see Table 4), as well as the overall performance and the false alarm of all three dolphins during these sessions (5–8 sessions, see Table 4), were also significant. Anke failed to immediately transfer the go/no-go behavior to the visual modality. She did not respond correctly on the first trial and her pooled hit rate over the first 15 trials dropped below the level of chance to only 21.4 % (see Table 5). Over time, Anke's performance increased to 94.5% hits over all light-on trials presented until the end of the study (490 trials, see Figure 5).

Anke and Kai also immediately responded to the light-off stimulus on their respective first trials and showed no errors during the first 15 trials (see Table 4). Anke continued to respond reliably to the lights being switched off and showed a highly significant all-time hit rate of 94.9% across 185 total trials (see Figure 5). Due to social management measures, Kai only performed 15 trials with this stimulus. Although Dolly responded correctly on the first trial, she did not reach the learning criterion after the first 15 trials with only 40.0% hits (binomial test, $P = 0.8491$, see Table 4). However, her performance increased to 85.0% hits over 185 trials until the end of the study (see Figure 5).

3.1.3.2 Tactile modality

The four dolphins showed highly significant transfer performances to the two mechanical stimuli. For both stimuli addressing the tactile modality, they responded correctly on their first trials and maintained a highly significant hit rate after the first 15 trials and over all trials (see Table 4). Dolly and Donna even showed 100.0% hits for both stimulus types (Dolly: 248 water jet trials and 231 air bubble trials; Donna: 47 water jet trials and 54 air bubble trials)

Table 4: Performance over the first 15 trials for each novel stimulus type during go/no-go transfer across modality tests for each dolphin. A successful generalization was defined as ≥ 80% hits over the first 15 trials accompanied by an overall performance of ≥ 80% correct choices as well as ≤ 20% false alarms.

GO/NO-GO TRANSFER ACROSS SENSORY MODALITIES					
Dolphin	**Stimulus type**	**Number of sessions**	**Hit rate first 15 presentations (%)**	**Overall session performance (%)**	**Overall false alarm rate (%)**
Anke	Light on	5	26.7	86.0***	4.0***
	Light off	8	100.0***	95.0***	9.4***
	Water jet	5	100.0***	97.0***	0.0***
	Air bubbles	6	86.7*	92.2***	8.5***
Dolly	Light on	5	100.0***	98.1***	4.3***
	Light off	5	40.0	84.0***	12.5***
	Water jet	4	100.0***	96.3***	0.0***
	Air bubbles	5	100.0***	94.0***	15.0***
Donna	Light on	6	100.0***	95.0***	10.0***
	Water jet	5	100.0***	93.3***	13.3***
	Air bubbles	7	100.0***	95.7***	7.1***
Kai	Light on	8	93.3**	91.3***	15.0***
	Light off	7	100.0***	78.8***	27.3*
	Water jet	8	100.0***	86.3***	15.0***
	Air bubbles	6	100.0***	80.3***	27.7*

Level of significance (binomial test): * $P < 0.01$, ** $P < 0.001$, *** $P < 0.0001$

3.2 PART II: PASSIVE ELECTRORECEPTION IN THE BOTTLENOSE DOLPHIN

3.2.1 Transfer of the go/no-go behavior to electric stimuli

The first presentation of electric stimuli resulted in highly significant performances by all animals. All four dolphins responded correctly to the interspersed electric fields of 1.5 mV cm^{-1} on their first trials and on all trials during the first session of each dolphin (see Table 9). Anke, Dolly, and Donna continued to show a highly significant hit rate of at least 93.3% over the first 15 trials (see Table 5) and maintained this performance after 32–34 trials, with a hit rate of at least 84.4% (see Figure 6). Although Kai responded correctly on all four trials in the first session, his average hit rate dropped to 60% after the first 15 trials (equal to chance level, binomial test, P = 0.6072). Kai was trained for 48 more trials over 15 sessions, but his performance decreased further to 14.6% over these trials, leading to an overall hit rate (60 trials) of only 25.0%. After responding spontaneously to the first electric field stimuli at the beginning, this heavy drop in his performance can be explained by the fact that he was generally poorly motivated to participate in the experiment, even before the tests for electroreception began. Therefore, I discontinued experimental sessions with Kai.

Table 5: Individual transfer performances on the first trial, during the first sessions with DC electric stimuli presented and over the first 30 trials. Only 12 trials were carried out with Kai until training had to be interrupted repeatedly due to animal management issues.

Dolphin	Electric field strength	Correct first trial response	First session performance (hits/trials)	Hit rate (%) over first 15 trials
		GO/NO-GO TRANSFER TO ELECTRIC FIELD STIMULI		
Anke	1.5 mV cm^{-1}	*Yes*	4/4	93.3**
Dolly	1.5 mV cm^{-1}	*Yes*	4/4	100.0***
Donna	1.5 mV cm^{-1}	*Yes*	4/4	100.0***
Kai	1.5 mV cm^{-1}	*Yes*	3/3	60.0

Level of significance (binomial test): * P < 0.01, ** P < 0.001, *** P < 0.0001

Anke, Dolly, and Donna continued to show a significant performance of at least 83.3% hits when the electric field strength was reduced to 1.0 and 0.5 mV cm^{-1},

respectively, with 32–34 trials each. Dolly even responded correctly on all trials with electric fields of 1.5, 1.0, and 0.5 mV cm^{-1} (see Figure 6).
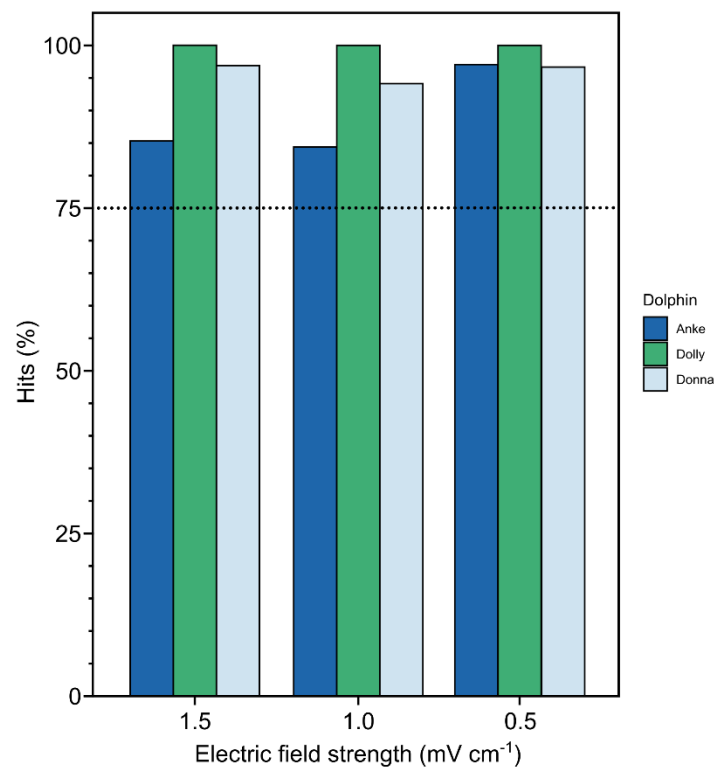
Figure 6: Hit rates of the dolphins "Anke," "Dolly," and "Donna" to electric fields of 1.5, 1.0, and 0.5 mV cm^{-1}. All dolphins maintained a highly significant performance after 32–34 trials with an electric field strength of 1.5, 1.0, and 0.5 mV cm^{-1}.

One dolphin (Anke) showed an interesting behavior once the electric stimuli were introduced. She deliberately started to move her rostrum toward the stimulus electrode before leaving the apparatus, bringing her vibrissal crypts closer the source of the stimulus (Figure 7). Occasionally, she also touched the two copper wire electrodes with her upper rostrum after the offset of the electric field. During later test sessions, Dolly showed similar behavior after she had entered the experimental apparatus, moving her rostrum horizontally from one side to the other directly below the stimulus electrodes. Usually, she then proceeded to touch the target and stationed correctly.
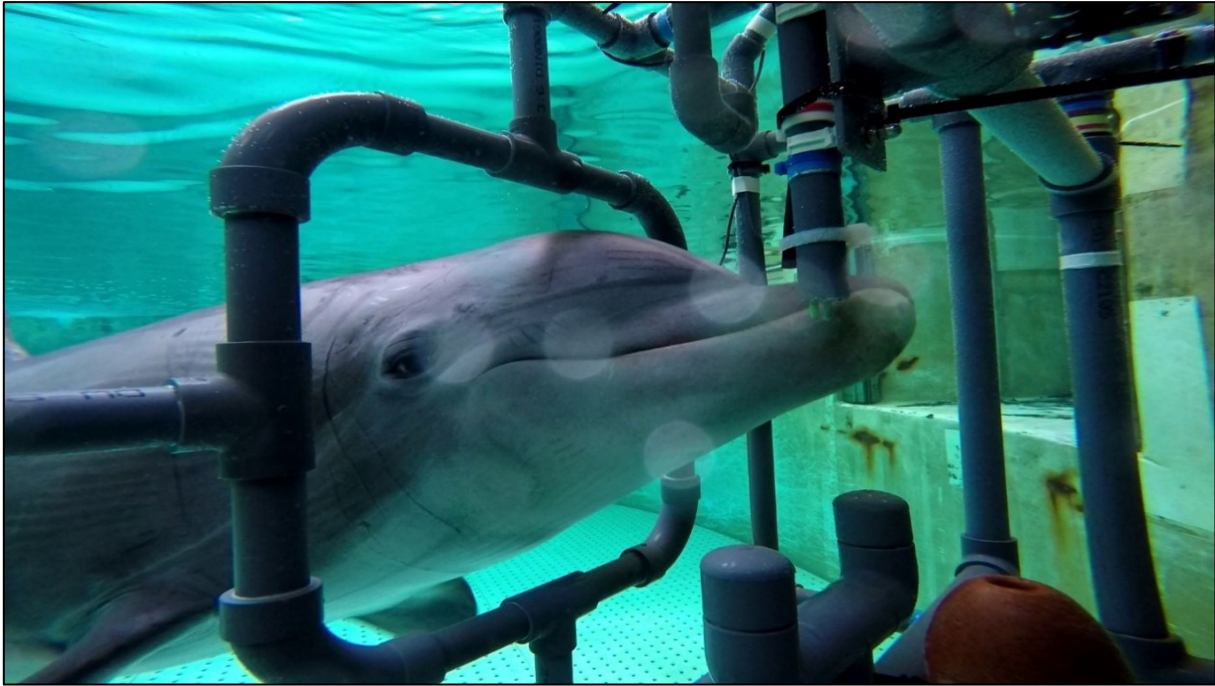
Figure 7: Anke's response to electric field stimuli. After the onset of the electric field, Anke leaves the target and moves her upper rostrum and the vibrissal crypts toward the stimulus electrodes.

3.2.2 DC electric field detection threshold

Threshold determination was carried out only with Anke, Dolly, and Donna. The performances of the three dolphins remained unchanged after presenting only the electric stimuli (i.e., after they were no longer mixed with the acoustic, optical, and mechanical stimuli).

When the stimulus intensity was reduced, up to an electric field strength of 125 µV cm^{-1}, Anke's performance remained at a highly significant level (see Figure 8). After the first 30 trials, Anke failed to reach the predefined learning criterion of $\geq$ 80% hits. Moreover, her false alarm rate was high at 23.3%. Thus, additional training sessions were carried out. While her performance on no-go trials improved significantly to < 10.0% false alarms (chi-square test, P < 0.05), her hit rate decreased from a significant level of 76.7% throughout the first 30 trials to only 51.4% over the next 35 trials, which led to an overall hit rate of 63.1%. After Anke started to show poor motivation during this stage of the study, I decided to terminate experimental sessions without determining

a precise threshold. Considering only her performance during the last 35 trials, which was equivalent to chance level, Anke's threshold may be in this range. Nevertheless, combined data show that Anke successfully learned to respond to DC electric stimuli. In total, 397 electric stimuli of different electric field strengths were presented during 80 sessions over the course of 11 months. Her average overall performance on all electric stimulus trials was significant at 80.1% hits (binomial test, $P < 0.0001$).
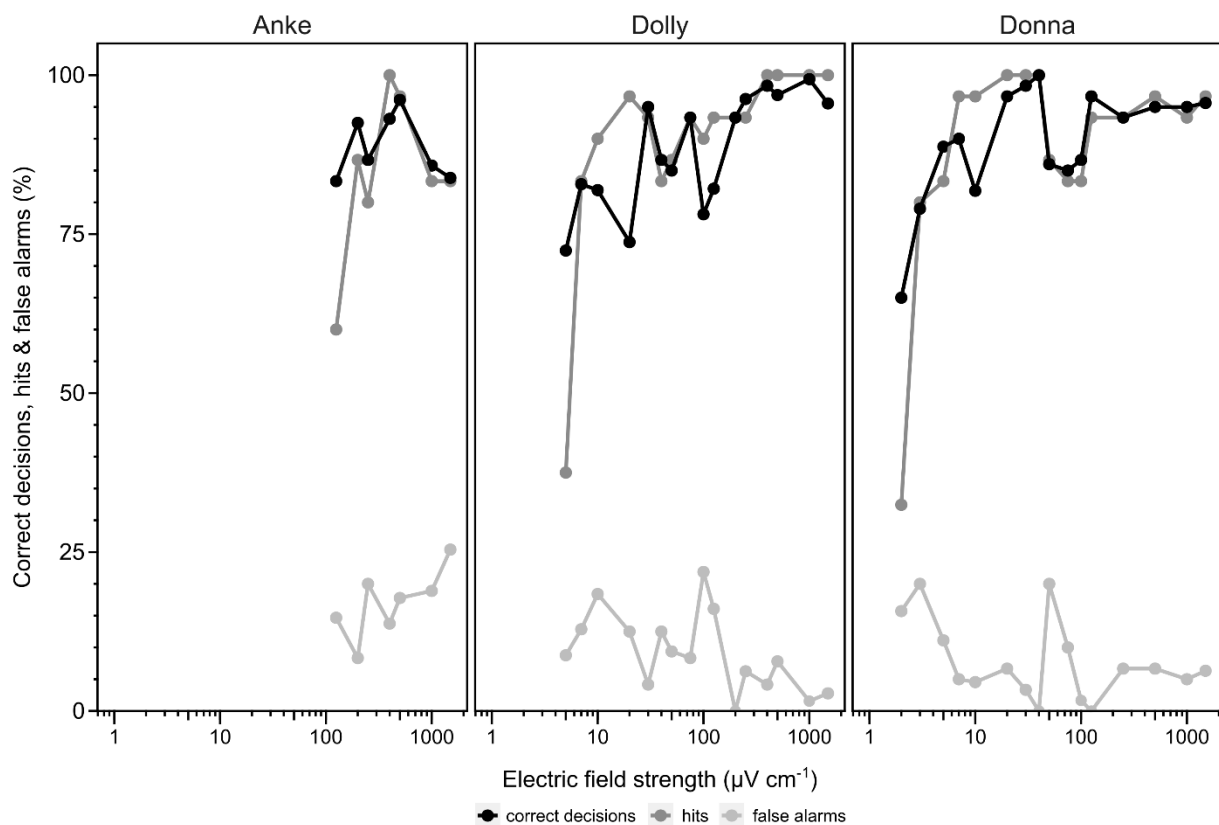
Figure 8: Performance in relation to electric field strength by the dolphins "Anke," "Dolly," and "Donna." Dolly and Donna performed significantly until the electric field strength was reduced below 10.0 μV cm^{-1}. Anke's performance dropped to chance level after the electric field strength was reduced to 125.0 μV cm^{-1}.

Dolly performed well at all stimulus strengths between 1.0 mV cm^{-1} and 125 μV cm^{-1}, with a hit rate of at least 93% hits over the first 30 trials of each stimulus strength (see Figure 8). At 1.0, 0.5, and 0.4 mV cm^{-1}, she even achieved 100% correct responses over the first 30 trials. At 125 μV cm^{-1}, her performance dropped temporarily to 77.7% after the first three sessions. She needed a total of 7 training sessions until her performance improved and reached 93.3% hits over the last 30 trials. There was an

almost identical improvement in performance through additional training sessions at a field strength of 100 µV cm⁻¹ (69.4% hits on the first 36 trials vs. 90.0% on the last 30 trials). Subsequently, Dolly reached at least 80% hits immediately over the first 30 trials with electric field strengths between 75 and 30 µV cm⁻¹ (75 µV cm⁻¹: 93.3%; 50 µV cm⁻¹: 86.6%; 40 µV cm⁻¹: 83.3%; and 30 µV cm⁻¹: 93.3%). With electric fields strength of 20, 10, and 7 µV cm⁻¹, Dolly again needed significantly more training sessions (16, 20, and 13, respectively), but then ultimately demonstrated high hit rates of 96.6%, 90.0%, and 83.3% (see Figure 9). Her performance at 5.0 µV cm⁻¹ never exceeded the level of chance. By interpolating Dolly's performance at the last electric field strength above threshold (7 µV cm⁻¹) and the first one below threshold (5 µV cm⁻¹), Dolly's detection threshold at a theoretical hit rate of 50 % was determined at 5.5 µV cm⁻¹ (see Figure 9).

Up to an electric field strength of 20 µV cm⁻¹, Donna showed a very consistent and significant performance, achieving at least 83% hits (see Figure 8). At 40, 30, and 20 µV cm⁻¹, she even achieved 100% correct responses on stimulus-present trials. After the stimulus strength was reduced to 10 µV cm⁻¹, her performance dropped significantly to only 40.0% hits after 30 trials, and she needed a total of 15 training sessions until the hit rate increased (96.7% on the last 30 trials). With a field strength of 7 µV cm⁻¹, Donna's hit rate also initially dropped but quickly improved again to 96.7% hits over the last 30 trials after a total of 7 sessions. Donna then showed a hit rate of at least 80% with electric field strengths of 5 µV cm⁻¹ (83.3%) and 3 µV cm⁻¹ (80%). Her performance fell to only 33.3% hits over 30 trials at 2 µV cm⁻¹. Based on data interpolation, Donna's detection threshold was determined at 2.4 µV cm⁻¹ (see Figure 9).
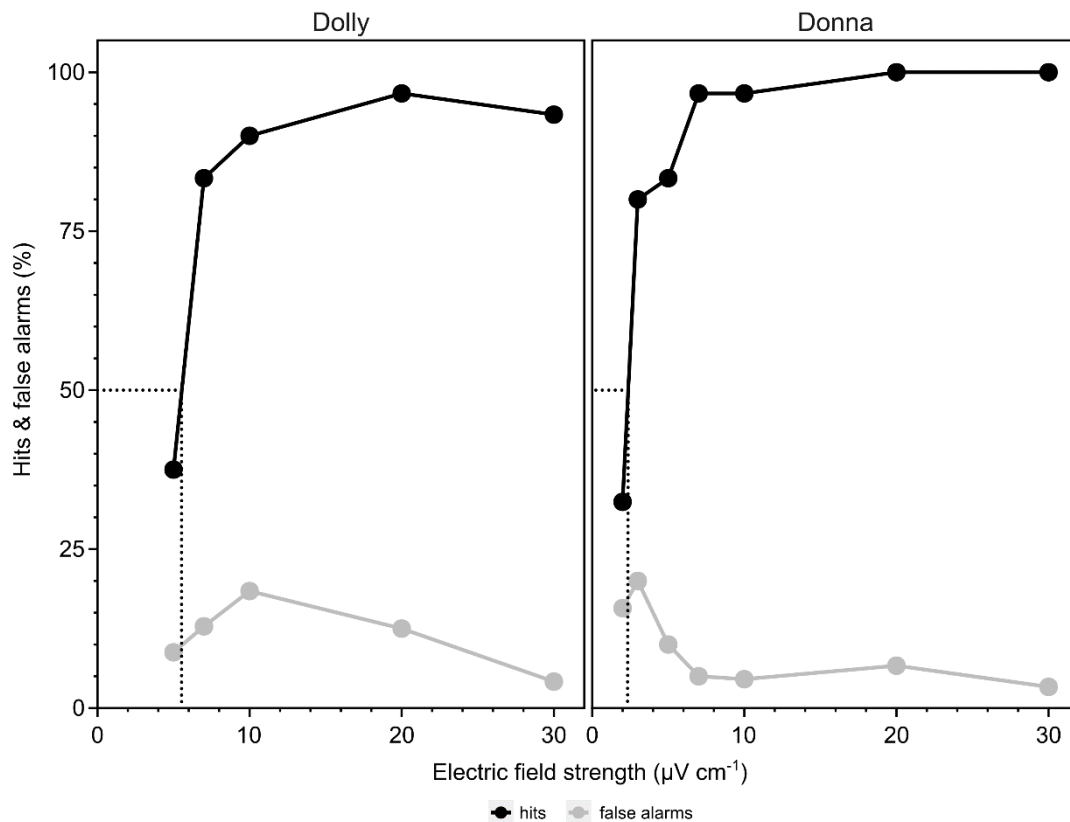
Figure 9: Psychometric functions for the dolphins "Dolly" and "Donna." Hit rate in relation to electric field strength (black circles) and the average false alarm for each stimulus intensity (gray circles) are shown. Absolute detection thresholds were determined as the stimulus intensity with a theoretical hit rate of exactly 50.0%: 5.5 µV cm^{-1} for Dolly and 2.4 µV cm-^{1} for Donna.

3.2.3 AC electric field detection threshold

Threshold determination for 1 Hz AC electric fields started with a stimulus strength clearly above the previously determined detection thresholds for DC fields (see Figure 10). Up to a field strength of 35 µV cm^{-1}, Dolly reliably detected all tested stimulus strengths with at least 80% hits (see Figure 10). At 30 µV cm^{-1}, her hit rate dropped to 60%, and stimuli of 20 µV cm^{-1} she no longer detected. The resulting sensory threshold for 1 Hz AC electric fields was subsequently identified at 28.9 µV cm^{-1} (see Figure 10). Donna responded reliably to AC electric field intensities ≥ 15 µV cm^{-1} (see Figure 11). However, she was not able to detect the stimuli when the electric field strength was attenuated to 10 µV cm^{-1}, and her performance dropped significantly below the level of chance (30.0% hits, chi-square test, $P < 0.05$). Based on data interpolation, Donna's

theoretical detection threshold for 1 Hz AC signals was determined at 11.7 µV cm⁻¹ (see

Figure 11).

When 5 Hz AC electric stimuli were introduced, Dolly's performance never

exceeded the level of chance (binomial test, $P > 0.05$). At 50.0 µV cm⁻¹, Dolly correctly

left the apparatus only three times on 14 trials (hit rate: 21.4%, see Figure 10). Even after

the electric field intensity was increased to 75.0 and 100.0 µV cm⁻¹, her performance only

increased slightly to 40.0% hits for both stimulus strengths.

Figure 10: Psychometric functions for 1 and 5 Hz AC stimuli for the dolphin "Dolly." The hit rate in relation to electric field strength (black icons) and the average false alarm rate for each stimulus intensity (gray icons) are shown. Absolute detection thresholds for 1 and 5 Hz AC stimuli were determined as the stimulus intensity with a theoretical hit rate of exactly 50.0% at 28.9 µV cm⁻¹ for AC stimuli with a frequency of 1 Hz. For electric fields with an AC frequency of 5 Hz, the stimulus-specific hit rate did not exceed the level of chance at 50.0%.

On the contrary, Donna still was able to reliably detect 5 Hz AC electric fields.

However, after this new stimulus quality was first introduced with a stimulus strength of

25.0 µV cm⁻¹, Donna failed to reach the learning criteria with only 76.7% hits over the

first 30 trials (4 sessions) and a false alarm rate of 25.0% during these sessions. She

required 9 additional training sessions until her hit rate increased to ≥ 80% and her false alarm rate improved to below 20% again (see Figure 11). After the stimulus strength was reduced to 20 µV cm^{-1}, Donna failed to detect the 5 Hz AC fields. Over 32 trials (7 sessions), she responded correctly only 8 times (hit rate: 25.0%), corresponding to a theoretical absolute detection threshold of 22.3 µV cm^{-1}. Donna also was able to detect to 25 Hz AC stimuli with electric fields of at least 40 µV cm^{-1}. Reducing the electric field strength to 30 µV cm^{-1} resulted in a significant drop in her performance, with a hit rate of only 16.7% (chi-square test, $P < 0.05$). Accordingly, Donna's detection threshold for 25 Hz AC fields was determined at 35.3 µV cm^{-1} by interpolating the percentage of correct responses (hits) at the last stimulus strength above threshold and the hit rate at the first stimulus strength below threshold (see Figure 11).
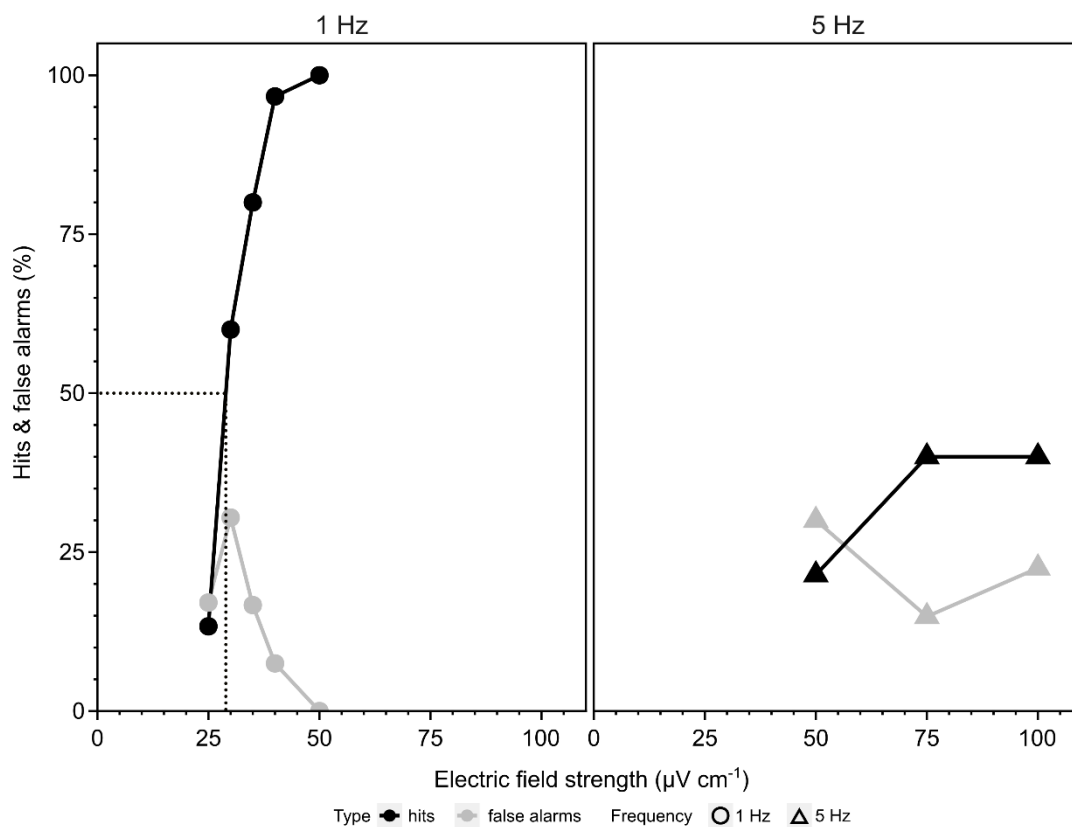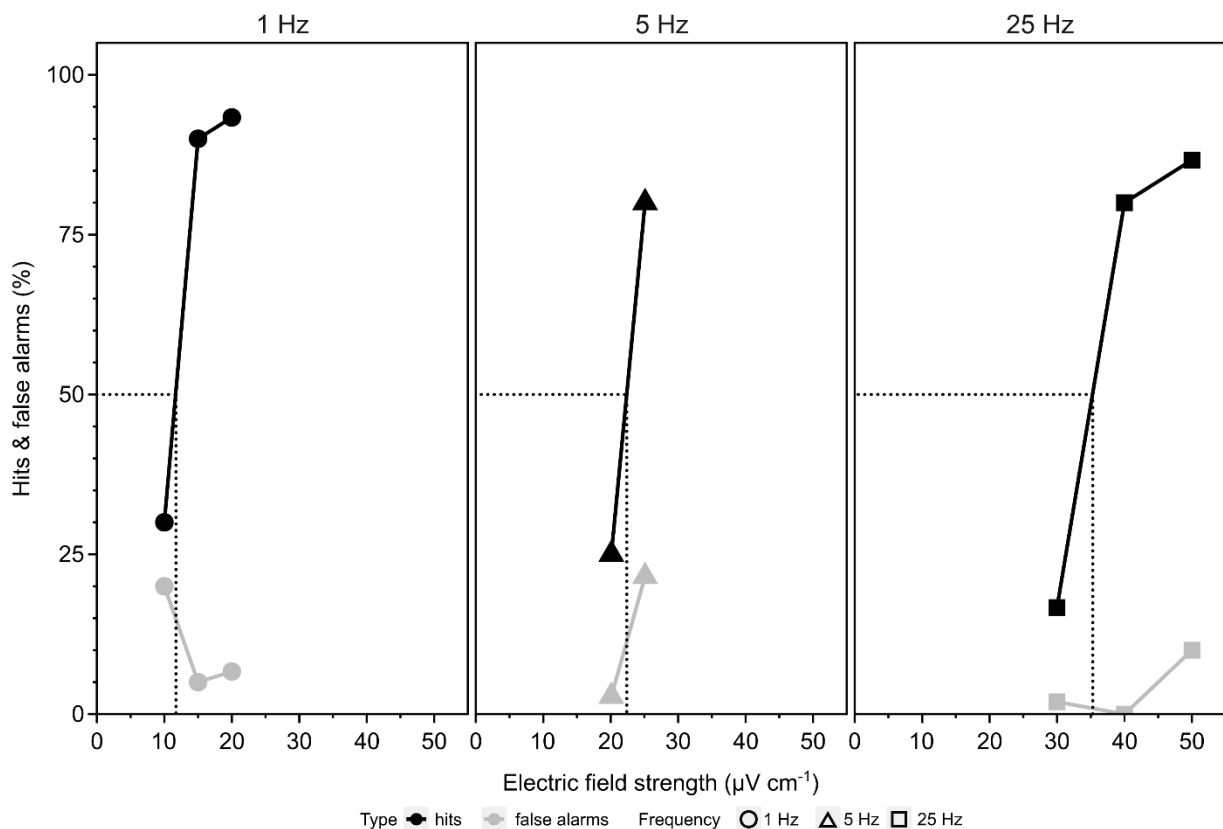

Figure 11: Psychometric functions for 1, 5, and 25 Hz AC stimuli for the dolphin "Donna." The hit rate in relation to the electric field strength (black icons) and the average false alarm rate for each electric field strength (gray icons) are shown. Absolute detection thresholds for all three AC frequencies were determined as the stimulus intensity with a theoretical hit rate of exactly 50.0%: 11.7 µV cm^{-1} for 1 Hz, 22.3 µV cm^{-1} for 5 Hz, and 35.3 µV cm^{-1} for 25 Hz.

4. DISCUSSION

4.1 GO/NO-GO GENERALIZATION AND CONCEPT FORMATION

The results show that bottlenose dolphins are able to generalize a response paradigm learned on the basis of only one sensory modality to the extent that they form an abstract concept of the detection task. After the dolphins were trained with the go/no-go behavior using only a few acoustic stimuli, they transferred it to novel acoustic stimuli as well as across modalities to new optical and mechanical stimuli. All dolphins also spontaneously transferred the go/no-go behavior to the novel electric field stimuli on the first trials and throughout the subsequent trials. These findings provide more evidence that the animals had developed an abstract concept of the go/no-go behavior and that any form of sensory input across their different sensory modalities would trigger a correct go response.

4.1.1 Stage 1: Establishment and learning of the go/no-go behavior

All four dolphins successfully learned to apply the go/no-go behavior to the acoustic training stimuli. However, as a relatively long training period was necessary, different factors may have affected the dolphins' learning success. First, neophobia toward the experimental apparatus itself hindered at least one dolphin (Donna) from learning the task more quickly. Second, the slow learning progress might be explained by the lack of experience with behavioral experiments.

4.1.2 Stage 2: Generalization

After being trained with three different training sounds, in the second stage, the dolphins were presented with novel sounds to achieve generalization of the go/no-go behavior within the acoustic modality. Generalization is indicated by a successful transfer of a previously learned relation to new stimuli on the first trial and maintaining a transfer performance equal to training performance (Daniel et al., 2016; Herman et al.,

1989; Herrnstein, 1979; Katz et al., 2007; Roitblat & von Fersen, 1992; Wright & Katz, 2007). The fact that almost all dolphins immediately transferred the go/no-go behavior to the novel acoustic stimuli (melodica sounds, pure tones, bike bell) on their first trials and maintained a high performance over the first 15 trials of each novel acoustic stimulus type provides strong evidence that the dolphins learned to generalize the previously established go/no-go task within the auditory modality.

4.1.3 Stage 3: Concept formation

The results show that bottlenose dolphins can apply a specific response behavior to novel stimuli within and across modalities. A number of studies have already highlighted the bottlenose dolphin's ability to transfer abstract relationships between objects to different sensory modalities. In several matching tasks, Pack, Herman, and colleagues have shown that dolphins could integrate sensory information across their modalities "echolocation" and "vision" and could successfully identify objects that they perceived only visually with the identical object perceived only through echolocation, and vice versa (Herman et al., 1998; Pack & Herman, 1995; Pack et al., 2002, 2004). Rather than testing for the cross-modal transfer of the perception of a stimulus across modalities, in this study I tested whether the dolphins had learned the go/no-go rule on a conceptual level.

In general, concept learning allows animals to quickly sort novel objects, events, or behaviors into different categories or classes without the necessity of learning by trial and error (Murphy, 2010; Thompson, 1995; Zentall et al., 2002, 2008). Categorization thus promotes cognitive economy and is based on generalization across all members of a category and discrimination between different categories (F. S. Keller & Schoenfeld, 1950; Rosch, 1978). Through concepts, all members within each category or class are considered to be equivalent and become interchangeable and elicit the same behavioral response (Lazareva & Wasserman, 2018; Rosch, 1978; Schusterman et al., 2000).

Equivalence within one class is achieved through common features in physical appearance (perceptual concepts) shared by all members, a common functional purpose (associative concepts), or an abstract relation between stimuli (abstract concepts) (Castro & Wasserman, 2017; Herrnstein et al., 1976; Katz et al., 2007; Zentall et al., 2002).

Until stage 2 of this study, only acoustic stimuli were used, and the generalization performance of the dolphins might have been facilitated by physical similarities because they were all presented within the auditory modality (Katz et al., 2007; Wright & Katz, 2006). In the last stage, however, common features between the novel stimuli were absent, and the dolphins were required to abstract the relation between the detection of a stimulus and the corresponding go response to be able to respond to the novel stimuli presented across different modalities. Similarly to generalization, concept formation is measured by an animal's ability to transfer the learned relation to novel stimuli on the first trial (Castro & Wasserman, 2017; Lazareva & Wasserman, 2018; Roitblat & von Fersen, 1992; Thompson, 1995; Wright & Katz, 2006; Zentall et al., 2002; Zentall & Hogan, 1975). Learning cannot facilitate an animal's performance only during the first trial; thus, a correct first trial response can only be accomplished through the formation of a concept (Pack et al., 1991; Roitblat & von Fersen, 1992; Wright & Katz, 2006). Although only a relatively small number of different stimuli were used for each sensory modality, the high first-trial performances of the dolphins with the novel stimuli convincingly indicate that they conceptualized the initially trained rule of "sound means go, no sound means stay" to an abstract go/no-go concept of "sensory input means go, no sensory input means stay."

Another hallmark for the formation of an abstract concept is maintaining a transfer performance with novel stimuli that is equivalent to training performance (Herman et al., 1994; Roitblat & von Fersen, 1992; R. K. Thomas & Boyd, 1973; R. K. Thomas & Noble, 1988; Thompson, 1995; Zentall & Hogan, 1975). The dolphins in this

study not only immediately responded to the novel optical, mechanical, and electric stimuli on the first trial, but they also sustained a significant performance over all subsequent trials. This robust transfer performance provides more evidence that the animals not only were able to generalize the go/no-go task within the auditory modality, but indeed learned to respond to the novel stimuli based on the formation of an abstract concept of go/no-go.

Anke failed the first transfer test to another modality using the light-on stimulus, suggesting an initial limitation of her concept of go/no-go (i.e., it was confined to stimuli within the acoustic modality). However, her performance in subsequent tests during which more novel stimuli were introduced indicates that she also learned the go/no-go concept, supporting the principle that when trying to facilitate concept formation in animals, training set size and training stimulus variety can sometimes be critical (Daniel et al., 2016; Galizio et al., 2018; Herman et al., 1993). This was shown in a comparative study by Wright and Katz (2006), who analyzed the extent to which learning of the same/different (S/D) concept in pigeons and primates depends on the size of the training set. The authors concluded that a small training set leads only to item-specific learning, while large training sets facilitate concept formation, as indicated by an increase in transfer performance from chance level to > 80%. Other studies with pigeons and primates have also demonstrated S/D concept learning only after training with a large number of different training stimuli (Bodily et al., 2008; Daniel et al., 2015; Katz & Wright, 2006; Katz et al., 2002; Wright & Katz, 2007). Anke's initial failure to transfer the go/no-go behavior to the visual modality suggests a similar relation between stimulus variety during training and her transfer performance. Until stage 3, stimuli were only composed of different sounds. Although Anke demonstrated generalization of the go/no-go behavior within the acoustic modality, training with acoustic stimuli only might have limited her success of learning a modality-independent go/no-go concept.

The introduction of this novel stimulus dimension may have also initially confused Anke and thus prevented a successful transfer (Scholtyssek et al., 2013). On the contrary, Herman et al. (1993) trained a dolphin with a visual matching task using six different objects. After reaching the learning criterion, the dolphin immediately matched six new objects and was correct on all first trials, indicating rapid concept formation after training with only a few exemplars. In this study, after the stimulus set was increased by introducing the second optical stimulus and the mechanical stimuli during the later transfer tests, Anke seemed to have expanded her attention beyond the acoustic modality and had no problems transferring the go/no-go behavior to these new stimulus dimensions, and thus eventually learned the go/no-go task at a conceptual level.

Putting these results into a wider context, the presented data expand our understanding of the cognitive ability of bottlenose dolphins to generalize rules and to form concepts. Most studies on conceptual behavior in dolphins and other non-human animals have concentrated on the direct relation between two or more stimuli. However, in my study, the dolphins were not required to learn and conceptualize a specific relation between two stimuli (e.g., same/different). Instead, they accomplished to abstract the relation between the detection of an arbitrary stimulus and a specific behavior and to transfer this relation to novel stimuli across different modalities. Similar findings are rare and only a few species have demonstrated the ability to transfer a concept across modalities after learning it within only one modality. One example is a study by Meck and Church (1982a, 1982b), who demonstrated that rats successfully transferred the abstract concept of "duration" learned within the auditory modality to the visual modality. Dolphins have been shown to match complex shapes using the modalities of vision and echolocation in either direction and can transfer this concept to novel object pairs (Herman et al., 1998; Pack & Herman, 1995; Pack et al., 2002, 2004). Harley et al. (1996) have provided additional evidence for echoic-visual cross-modal

concept formation. In my study however, rather than integrating acoustic, echoic, visual, or tactile information, stimuli addressing any modality, to the extent tested, became equivalent and therefore interchangeable.

4.2 ELECTRORECEPTION IN THE BOTTLENOSE DOLPHIN

The immediate and reliable transfer of the go/no-go task to new acoustic, optical, and mechanical stimuli by the four animals represented an ideal starting point to test for electroreception in bottlenose dolphins. Consistently, all dolphins responded correctly when they were presented with weak electric fields on their first trials. Above all, their spontaneous and robust transfer as well as their performance on subsequent trials—with decreasing electric field strength—have undoubtedly established passive electroreception as a sensory modality in the bottlenose dolphin. The dolphins were able to detect weak DC electric fields as low as 2.4 µV cm^{-1} and low-frequency ($\leq$ 25 Hz) AC electric fields in water. Next to the platypus (Scheich et al., 1986), the long-billed and short-billed echidna (Pettigrew, 1999), and the Guiana dolphin (Czech-Damal et al., 2012), the bottlenose dolphin is only the fifth mammalian species that has been shown to possess passive electroreception.

The control experiment by Czech-Damal et al. (2012) already showed that the vibrissal crypts on the upper rostrum serve as the electroreceptors in odontocetes. With its vibrissal crypts covered by an insulating rubber shell, their subject no longer responded to the electric stimuli. While Gerussi et al. (2020) proposed a proprioceptive instead of an electrosensory function for the vibrissal crypts in the bottlenose dolphin, the results of my study clearly verify that bottlenose dolphins are electrosensitive to weak electric fields in water. Although no exclusion tests were carried out here, the fact that the vibrissal crypts are the responsible functional units is underlined by observations of Anke during this experiment. After presented with an electric stimulus, Anke frequently moved her head upward with the vibrissal crypts toward the electrodes,

and it seemed that she almost touched the copper wires with her upper jaw (see Figure 7). She presented this behavior consistently, from the first electric stimulus trial and throughout the experiment. Anke presumably tried to enhance the perception of the electric stimulus input by moving her electroreceptors closer to the stimulus source, illustrating that the dolphin's vibrissal crypts serve as the electrosensory units.

Different controls and considerations were taken to exclude that the dolphins could use any secondary cues perceived via any of their other modalities to solve the task successfully. First, the trainer never knew the type of an upcoming trial. As the experimenter, my actions were also not visible to the dolphins because I hid behind the visual cover. Furthermore, the control measurement that was carried out confirmed that no acoustic cues correlated with electric stimulus presentation. For the full acoustic analysis carried out by Mats Amundin, PhD., senior advisor, Kolmården Wildlife Park, Sweden, see the appendix (section 7.1). Visual detection of small air bubbles associated with electrochemical processes was excluded because the electrode was placed out of the visual field (Cozzi et al., 2017; Dral, 1975; Xitco et al., 2004). Additionally, these air bubbles only occurred with the stronger electric stimuli and not when the stimulus strength was attenuated to $\leq$ 200.0 μV cm^{-1} during threshold determination. Consequently, when looking at the dolphins' response performances hereafter, the dolphins could have only relied on detecting the electric stimulus to respond correctly. The perception of the bubbles via echolocation can also be virtually excluded. Sonar resolving performance is limited by the shortest wavelength. With peak frequencies of up to 130 kHz (Kuroda et al., 2020; Poché et al., 1982), the shortest wavelength of a bottlenose dolphin click is approximately 1.1 cm. As the air bubbles had diameters < 1 mm, it is highly unlikely that the dolphins could perceive the bubbles by using echolocation.

4.2.1 Detection threshold for DC and AC electric stimuli

Anke, Dolly, and Donna responded best to a standing DC electric field, though reliable thresholds could only be determined for the two younger dolphins (Dolly and Donna). Both of them also demonstrated good detection abilities for low-frequency AC potentials. Sensory thresholds for DC electric fields were in the same order of magnitude as the threshold determined for the Guiana dolphin (4.6 µV cm⁻¹; Czech-Damal et al., 2012). With a threshold of 2.4 µV cm⁻¹, Donna was slightly more sensitive than Dolly at 5.5 µV cm⁻¹. Similarly to the Guiana dolphin, the sensitivity of the two bottlenose dolphins is approximately one order of magnitude higher than that of the platypus, with an average lowest threshold of approximately 50−60 µV cm⁻¹ (Proske et al., 1998; Scheich et al., 1986).

The fact that Anke did not reach the learning criterion at 125 µV cm⁻¹ suggests that she is significantly less sensitive than Dolly and Donna. However, considering the thresholds of Dolly and Donna, Anke's performance is likely a lower estimate of her actual ability to detect electric fields and rather due to other constraints. Instead, Anke's failure to meet the learning criterion could have been due to the fact that at this point during the experiment, she was having a hard time with the repetitive and identical nature of the experimental sessions. If so, these difficulties may have affected her motivation to participate in the experiment in general, which was then reflected in her poor performance in the detection task.

Unlike the other subjects, Kai was not able to maintain a significant performance after the first session with electric stimuli. Even when the electric field strength was increased, he did not reach the criterion and only responded at chance level. However, his poor performance during tests was likely affected by social problems between him and the other male dolphins of the group rather than him being unable to detect the electric signals. Aggression represents a social stressor that can negatively impact the

welfare of dolphins (Waples & Gales, 2002), which in turn affects a dolphin's willingness to participate in training sessions (Clegg et al., 2019). Thus, the observed social problems between Kai and the other animals could have very likely also affected his performance during the electroreception tests. After group management measures ultimately led to the decision to relocate Kai to another facility, no further sessions could be conducted to investigate his ability to detect DC electric fields.

Dolly and Donna also responded well to low-frequency AC electric fields. Dolly was less sensitive than Donna and for both dolphins, the thresholds for AC stimuli were higher than the previously observed thresholds for DC potentials. Dolly's perception threshold for 1 Hz AC signals (28.9 μV cm^{-1}) was almost three times higher than for Donna (11.7 μV cm^{-1}). Moreover, the capability of the two dolphins to detect AC electric fields decreased with increasing stimulus frequency. While Donna was able to detect 5 and 25 Hz signals, she could only do so after the electric field strength had been increased by at least a factor of 2 (see Figure 11). Dolly, on the other hand, never managed to reliably detect alternating electric fields with a frequency of 5 Hz, even after the stimulus intensity was increased to 100 μV cm^{-1}. Similarly, two shark species (*Scyliorhinus canicula* and *Triakis semifasciata*) who have also been tested for their ability to perceive AC electric fields also responded to signals with frequencies > 5 Hz only after the electric field strength was increased by a factor of 2 (Kalmijn, 1974).

4.2.2 Bioelectric fields and theoretical detection range

Naturally occurring electric fields in water are complex and not yet fully understood, but they are best described as a standing DC-dipole field with a superimposed AC component (Bedore & Kajiura, 2013; Kalmijn, 1974). DC potentials are generated by ion leakage at the gills, mouth, cloaca, and siphons (Wilkens & Hofmann, 2005). Respiratory movements of the gills, the head, or the pharynx create low-frequency (< 5 Hz) AC potentials that modulate the standing DC field (Bedore & Kajiura,

2013; Bodznick et al., 1992; Haine et al., 2001; Kalmijn, 1974; Wilkens & Hofmann, 2005). AC potentials of higher frequencies (> 20 Hz) are produced by muscle action potentials associated with muscle movements and nerve impulses (Eeuwes et al., 2008; Kalmijn, 1972, 1974), but they are considered out of the detection range of most electroreceptive species (Bedore & Kajiura, 2013).

Different behavioral experiments demonstrated that elasmobranchs most readily respond to DC stimuli as well as very low-frequency AC electric fields (Eeuwes et al., 2008; Kalmijn, 1971, 1974; Kimber et al., 2011). Electrophysiologically however, the ampullary electroreceptors of elasmobranchs and other electrosensitive fishes are not true DC receptors. But due to their own movement relative to the source, the standing DC electric fields are turned into low-frequency AC stimuli and can thus be detected (Bodznick & Montgomery, 2005; Kalmijn, 1974).

With peak sensitivities from DC up to 10 Hz for most species the electric sense of sharks and rays is well suited to detect the standing and modulated electric fields of their typical prey (Bodznick & Montgomery, 2005; Kalmijn, 1974).

Although it is not yet clear if the electroreceptors of dolphins can detect DC signals directly, the behavioral thresholds determined here show a similar frequency preference for DC up to low-frequency AC signals to the behavioral threshold of sharks and rays. Thus, to the extent tested, it can be seen that the frequency range of the electroreceptive system of bottlenose dolphins also corresponds well with the most prominent electric fields emitted by fish and other potential prey species that are generated by basic functions, rather than the high-frequency electric fields that are generated by muscle activity. While Donna was able to detect electric fields at a frequency of approximately 25 Hz, sharks no longer responded to electric stimuli at frequencies > 16 Hz, even after the stimulus intensity was increased (Kalmijn, 1973, 1974). In addition to the aforementioned morphological parallels in receptor anatomy, this

homology in frequency sensitivity also highlights the convergent adaptation of electroreception across different aquatic taxa (King et al., 2018).

Sharks and rays are by far the most sensitive of the electroreceptive species: Some elasmobranchs still respond to electric fields as low as 5 nV cm^{-1} (Haine et al., 2001; Kajiura & Holland, 2002; Kalmijn, 1982). Estimating a maximum detection range requires information about the magnitude of bioelectric fields generated by typical prey species. Electric potentials generated by marine animals range from 10 to 500 µV cm^{-1} (Kalmijn, 1974). While mollusks produce weaker electric potentials of up to only 10 µV cm^{-1}, teleost fish produce stronger fields between 50 and 500 µV cm^{-1} (Bedore & Kajiura, 2013; Kalmijn, 1974). DC fields of wounded crustaceans even reach values as high as 1.0 mV cm^{-1} (Kalmijn, 1974). Using literature data, Bedore and Kajiura (2013) calculated a mean sensitivity for DC electric fields across different elasmobranch species of approximately 35 nV cm^{-1}. Hence, sharks should be able to detect prey at a maximum distance between 0.3 and 0.7 m (Bedore & Kajiura, 2013). On the basis of behavioral data, Haine et al. (2001) also concluded that elasmobranchs should be able to detect prey from distances of approximately 0.5 m. As electric potentials significantly decay with increasing distance from the source, even the most sensitive elasmobranchs use passive electroreception only for short-range prey detection (Haine et al., 2001). Bedore and Kajiura (2013) calculated the decay of the electric field strength over distance for different DC field-generating species, including common prey species of dolphins (Barros & Wells, 1998; Barros et al., 2000; Pansard et al., 2011; Pate & McFee, 2012). Regarding the thresholds for DC electric fields and on the basis of the calculations by Bedore and Kajiura (2013), bottlenose dolphins should be able to detect typical prey-generated electric fields at distances between 3.0 and 7.0 cm (see Figure 12). Moreover, the sensitivity range for AC electric fields seems to be well suited to perceive the typical AC modulations generated by respiratory movements and could provide additional

information about the location of a fish. Due to the absence of data on the electric field characteristics generated by fish captured during "crater-feeding" (Kaplan et al., 2019), this can only be an estimate, and further research is needed to investigate what role electroreception plays as soon as the dolphins start digging into the sediment. It also remains to be investigated how the electric fields of fish are altered when a fish is wounded or whenever they are distressed. Nonetheless, while the sensitivity measured in dolphins is significantly lower than in elasmobranchs, the perception of prey-generated electric fields could still facilitate the localization of prey at close range.
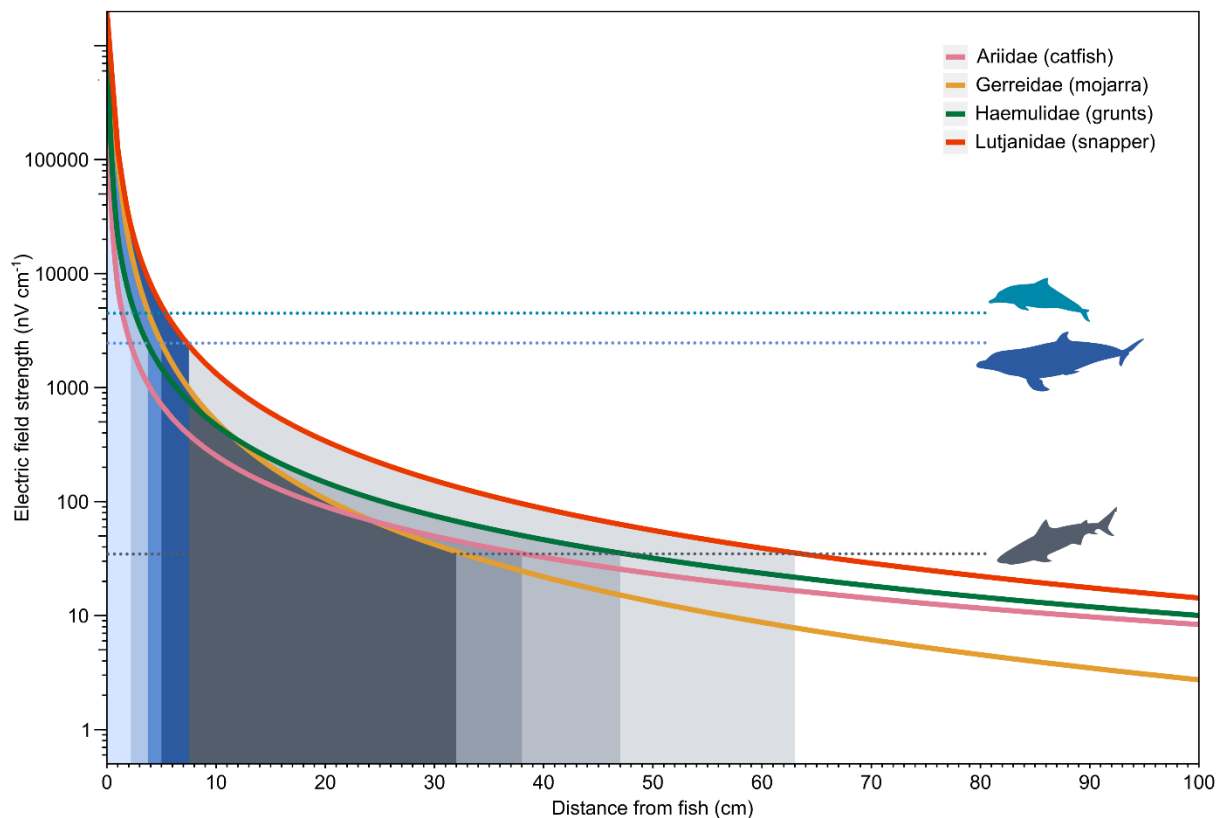
Figure 12: Calculated theoretical detection distances of prey species for the bottlenose dolphin (blue), the Guiana dolphin (cyan), and sharks (gray). Colored lines represent the decay of the electric field over the distance away from the fish (calculations based on Bedore & Kajiura, 2013). Colored spaces below the electric field lines represent the detection range in which the four families of fish (Ariidae, Gerreidae, Haemulidae, and Lutjanidae) are detectable for the sharks (gray areas) and bottlenose dolphins (blue areas). For bottlenose dolphins, a maximum sensitivity of 2.4 µV cm^{-1} (blue dashed line) was used. For sharks, an average sensitivity of 35 nV cm^{-1} (gray dashed line) obtained from the literature information was used (Bedore & Kajiura, 2013). Additionally, the detection threshold of the Guiana dolphin at 4.6 µV cm^{-1} is shown (cyan dashed line). *Adapted from Bedore, C. N., & Kajiura, S. M. (2013). Bioelectric Fields of Marine Organisms: Voltage and Frequency Contributions to Detectability by Electroreceptive Predators. Physiological and Biochemical Zoology, 86(3), 298–311.* https://doi:10.1086/669973.

4.2.3 Ecological implications and sensory integration

It is well known that the primary sensory systems dolphins use during navigation and foraging are audition—passive listening as well as active echolocation—and vision (Au, 1993; Busnel & Fish, 1980; Herman, 1980; Mann et al., 2000; Torres, 2017). Using their acoustic senses and good visual capabilities in air and underwater (Herman et al., 1975) enables dolphins to locate potential prey at short ranges as well as over longer distances. A variety of studies have shown the accuracy and success dolphins achieve in locating objects via echolocation. Objects as small as 8 cm are still easily detected over a distance of > 110 m using echolocation (Au & Snyder, 1980). Experiments with live fish have shown that in their natural environment, a bottlenose dolphin can locate prey up to 93 m away (Au et al., 2007). So, while echolocation, passive listening, and visual recognition drive initial prey localization, little is known about what other sensory modalities besides vision or echolocation, such as electroreception or chemoreception, as well as tactile information or hydrodynamic perception are used by dolphins during the different phases of foraging: detecting, tracking, and ultimately capturing prey (Curio, 1976). Especially as the dolphin approaches its prey, new sensory cues become available and, instead of relying only on their main modalities, the integration of all available sensory cues is essential for successful prey capture (Gardiner et al., 2014). Moreover, if one of the main modalities is limited or not sufficient enough—for example, during "crater-feeding" or "bottom-grubbing," when the dolphins bury themselves into the sand (Mann & Sargeant, 2003; Rossbach & Herzing, 1997; Quigley et al., 2022; Sargeant & Mann, 2009)—combining all of their senses is important to guarantee foraging success (Gardiner et al., 2014; Kelkar et al., 2018; Torres, 2017). Establishing passive electroreception as a supplementary sensory modality in the bottlenose dolphin sheds new light on the complexity of the interplay between the dolphin's different sensory systems during foraging. While bottlenose dolphins may initially locate bottom-

dwelling prey through echolocation or vision while circling the ocean floor (Kaplan et al., 2019; Rossbach & Herzing, 1997), their electric sense could become important as soon as they get very close to their prey. Sharks even rely primarily on electroreception when striking at their prey. Rather than vision or audition, sharks use their olfactory sense to initially detect and track prey (Hobson, 1963; Hodgson & Mathewson, 1971; Hueter et al., 2004). However, Gardiner et al. (2014) have shown the importance of electroreception for successful prey capture. In the absence of electric cues, the three tested shark species frequently failed to capture their prey. Thus, as already proposed by Czech-Damal et al. (2012) for the Guiana dolphin, by providing complimentary information about the precise location of a hiding fish, passive electroreception could increase the bottlenose dolphin's chance to locate prey at short distances, prompting them to strike at and successfully snap it when digging in the sediment.

Dolly's behavior during several trials, especially after the stimulus intensity was reduced, underlines the argument that passive electroreception is a short-range sense. Dolly repeatedly started each trial by moving her rostrum from side to side below the stimulus electrodes after she entered the apparatus and before she touched the target. Similar lateral head sweeps of the electrosensory organ have been reported for the platypus and the paddlefish (*Polyodon spathula*). While the platypus sweeps its bill across the riverbed to search for prey buried in the sediment during foraging (Gregory et al., 1989; Manger & Pettigrew, 1995), the paddlefish also moves its elongated rostrum laterally from side to side during swimming to increase its prey detection (Pettigrew & Wilkens, 2003). In addition, during "crater-feeding," bottlenose dolphins move their head and rostrum through the agitated sediment. Although not intentional, this could presumably also increase the chance of detecting an electric field of a hidden fish similarly to the lateral sweeps of the platypus or the paddlefish.

Altogether, the results undoubtedly establish passive electroreception as a sensory modality in the bottlenose dolphin. Thus, the question arises whether and which other dolphin or whale species could benefit from the ability to perceive electric fields at short distances. Observations of pygmy sperm whales (*Kogia breviceps*) have shown that the vibrissal crypts open widely as soon as the head submerges underwater (Dehnhardt et al., 2020; Dehnhardt & Mauck, 2008). Compared with *Sotalia* and *Tursiops*, the follicle—that is, the electroreceptor—is connected directly to the water body, which may allow for better detection of electric fields. A first indication that sperm whales also perceive electric fields came from the fact that until 1955, there were repeated incidents of sperm whales becoming entangled in underwater telecommunication cables (Heezen, 1957; Wood & Carter, 2008). Only a change in technology from metal core cables, which emitted strong electromagnetic fields, to coaxial cables and finally fiber optical cables, which emit virtually no electric fields into the environment, led to a decrease in such accidents (Wood & Carter, 2008). However, information on the vibrissal crypt anatomy of the pygmy sperm whale is missing, and additional studies are needed to investigate the possibility of an electrosensory system in this species.

Other more promising candidates that might possess passive electroreception are the South Asian river dolphins of the genus *Platanista*. It includes two species, the Ganges River dolphin *Platanista gangetica gangetica*, inhabiting the Ganges, Brahmaputra, and Karnaphuli River systems, and the Indus River dolphin (*Platanista minor*) distributed across the Indus River in India and Pakistan (Braulik et al., 2015; Smith & Braulik, 2018). A thorough investigation of the feeding and sensory ecology of this genus indicates that electroreception could play a role during foraging (Kelkar et al., 2018). Almost entirely blind, *Platanista* can only rely on echolocation and passive listening to locate its prey. However, as these small dolphins mainly inhabit shallow

areas, echolocation is limited at the riverbed due to acoustic interferences. Thus, a supplementary electroreceptive sensory system could very likely increase feeding efficiency and capture success (Kelkar et al., 2018). Similarly to the Guiana dolphin and the bottlenose dolphin, *Platanista* also display a preference for bottom-dwelling fish. Moreover, the so-called "mud-probing" foraging behavior that has been recorded during multiple sightings supports the hypothesis for electroreception in the South Asian river dolphins (Czech, 2007; Kelkar et al., 2018; Reeves & Brownell, 1989). *Platanista* is recognized as one of the most primitively evolved dolphin species (Braulik et al., 2015; Smith & Braulik, 2018), and together with the Amazonian river dolphin *Inia geoffrensis* it is the only extant dolphin species with a visible hair shaft on the upper rostrum maintained through adult life (Ling, 1977). Considering the importance of vibrissae in pinnipeds and sirenians (Dehnhardt et al., 1998, 2001; Gaspard et al., 2013; Reep et al., 2002, 2011), this suggests that the hairs are most likely mechanoreceptors (Bauer et al., 2018; Berta et al., 2015). However, to determine whether these structures have an electroreceptive or mechanoreceptive role, it is first necessary to investigate whether the hairs of *Platanista* or *Inia* are true vibrissae (including a complete blood sinus system) or simply normal but innervated hairs. Hence, additional anatomical and behavioral studies are needed to explore the form and sensory functions of dolphin vibrissae.

4.2.4 Detection of Earth's magnetic field

There are questions that remain to be answered to fully understand how the bottlenose dolphin's ability to detect weak fields in water functions within an ecological context. Beyond foraging, one can also think about an expanded relevance of this sensory system, such as the usability of spatial charge distributions caused by ocean currents and their interaction with Earth's magnetic field, which offers space for new theoretical and empirical approaches in marine mammal research. It has long been

claimed that cetaceans possess magnetoreception, the ability to sense Earth's magnetic field. The evidence comes primarily from observations showing that location and timing of whale strandings often correlate with geomagnetic anomalies (Kirschvink et al., 1986; Klinowska, 1985, 1986a, 1986b, 1988, 1990) or disturbances to the geomagnetic field (GMF) caused by solar storms (Vanselow et al., 2018). Migration routes of fin whales could also be explained by a map-like use of Earth's magnetic field (Walker et al., 1992). In addition to these observational data, Kremers et al. (2014) have provided behavioral evidence that bottlenose dolphins are able to perceive magnetic fields. In an exposure test, the dolphins approached magnetized objects faster than the visually and echo-acoustically identical demagnetized control objects. While this suggests that bottlenose dolphins perceive the magnetic properties of an object, it remains uncertain which sensory structures are involved in the detection of the magnetic field. One possible mechanism could be the presence of magnetite in the dura mater (Bauer et al., 1985), although even with a series of experimental modifications, the authors could not show a spontaneous response to magnetic stimuli based on magnetite. The mechanism sharks use to gather magnetic field information was first proposed by Kalmijn (1974, 1977, 1978, 1981, 1982) and describes the ability of elasmobranchs to perceive self-induced electric fields through electromagnetic induction when moving through Earth's magnetic field, either by their own swimming motion or by the physical movement of the seawater itself. Depending on the swimming direction and the speed, the estimated voltage gradients induced by movement across the horizontal component of the GMF are well within the average detection range of sharks and rays (Formicki et al., 2019; Kalmijn, 1978, 1982; Newton et al., 2019; Paulin, 1995), and thus could be used for orientation during long-range migrations. In a recent magnetic displacement study, B. A. Keller et al. (2021) demonstrated that bonnethead sharks (*Sphyrna tiburo*) can differentiate and use geographic information from Earth's magnetic field during long-distance migrations.

My findings and the existing evidence for electroreception in *Sotalia* strengthen the case for magnetoreception in dolphins, and it remains to be determined whether dolphins can also perceive magnetic fields through electromagnetic induction. The mechanism for magnetoreception in sharks as proposed by Kalmijn (1971, 1973, 1974) is based on the fact that an animal swimming across the horizonal component of the GMF induces a potential difference between the dorsal and ventral side of the body. These potential differences vanish if the fish moves to the north or south—that is, when it swims parallel to the magnetic field lines. Thus, sensing these potential differences that vary according to the swimming direction and speed and could thus be used for orientation (Kalmijn, 1974).

Water flow within the GMF, caused by tidal activity, among other factors, also induces electromagnetic currents, on local and regional scales (von Arx, 1962; Pals, 1982). These electric fields overlap well with the perceptual range of sharks and other passively electroreceptive fish (Pals, 1982). Given the correlation between whale strandings and geomagnetic anomalies, the discovery of electroreception implies in principle the possible mechanism for magnetoreception in dolphins. However, it remains to be tested whether electromagnetically induced electric fields, either caused by swimming through the GMF or by ocean currents, can be detected by dolphins.

5. CONCLUSION

Czech-Damal et al. (2012) provided the first evidence for electroreception in a toothed whale species. Until this study, the Guiana dolphin (*S. guianensis*) was the only dolphin species known to possess this sense. Here, I have demonstrated passive electroreception in a second dolphin species, the Atlantic bottlenose dolphin (*T. truncatus*). First, this finding expands our understanding of cetacean sensory biology. It remains to be seen which other odontocete species also possess an electrosensory system and which other senses have evolved in marine mammals that have not yet been examined. New strategies are needed to investigate these questions. The cognitive approach of this study has proved to be an innovative but straightforward strategy to discover and investigate the electroreceptive system of the bottlenose dolphin. By establishing a generalized concept of the go/no-go task, the dolphins were able to immediately identify a novel electric stimulus as a relevant sensory input and indicated its presence as they had previously learned with other stimulus types. Thus, relying on the cognitive ability of dolphins to form concepts and transfer them across different modalities demonstrates a new and non-invasive approach to further investigate their sensory world.

Taken together, the results of this study provide further insight into the sensory world of cetaceans and how their sensory systems have been adapted to aquatic life. Nevertheless, additional studies are needed to fully understand the importance and distribution of electroreception within the order of cetaceans.

Finally, considering the increasing number of small cetaceans that have become endangered because of human activities, a better understanding of not only a species behavioral and ecological needs like habitat use or population dynamics, but also its sensory demands could help to increase conservation efficiency (Dominoni et al., 2020).

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7. APPENDIX

7.1   CONTROL EXPERIMENT: "TESTING FOR ACOUSTICAL CUES IN TIM HÜTTNER'S ELECTRO-MAGNETIC TEST RIG"

The measurements were carried out in cooperation with Mats Amundin, PhD., senior advisor, Kolmården Wildlife Park, Sweden.

Testing for acoustical cues in Time Hüttner's Electro-magnetic test rig

Carried out by Mats Amundin, Ph.D., senior advisor, Kolmarden Wildlife Park, Sweden

Recording setup

The hydrophone, a Neptune D140, was placed in the center of the dolphin's head position, approximately 30cm from the electrodes and in the same vertical plane. The hydrophone was connected via two Etec 100-A preamplifiers to a National Instruments USB 6251 A/D converter, which was connected to a laptop running a custom-made Labview sound recording program "Bio-logger using NI USB-63x6" (courtesy Magnus Wahlberg, University of Southern Denmark).

Bio-logger settings:

Hydrophone sensitivity -210dB re 1V/uPa

Preamplifier gain: as in notes

Sampling freq. 333 kS/s, 16 bit

USB input device range +/-1V

Results

Recs 1-3 (file name 10-05-39.wav, 10-08-37.wav, 10-09-01.wav): Preamp 50dB

DC pulse 3 s long, starts ca. 5s after rec start. Electrode signal strength 1.0mV/cm. No visible spikes.

Rec 4 (10:09-23.wav): Preamp 60dB

DC pulse 3 s long, starts ca. 5s after rec start. Electrode signal strength 1.6mV/cm. No visible spikes.

Rec 4 (10:09-23.wav): Preamp 60dB

DC pulse 3 s long, starts ca. 5s after rec start. Electrode signal strength 1.6mV/cm. No visible spikes.
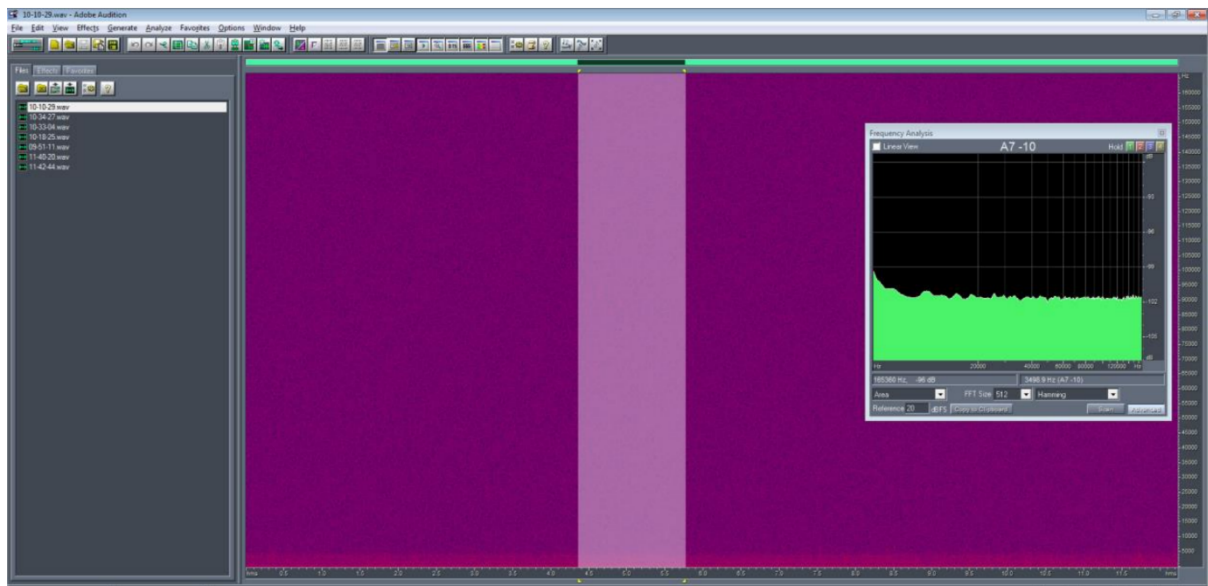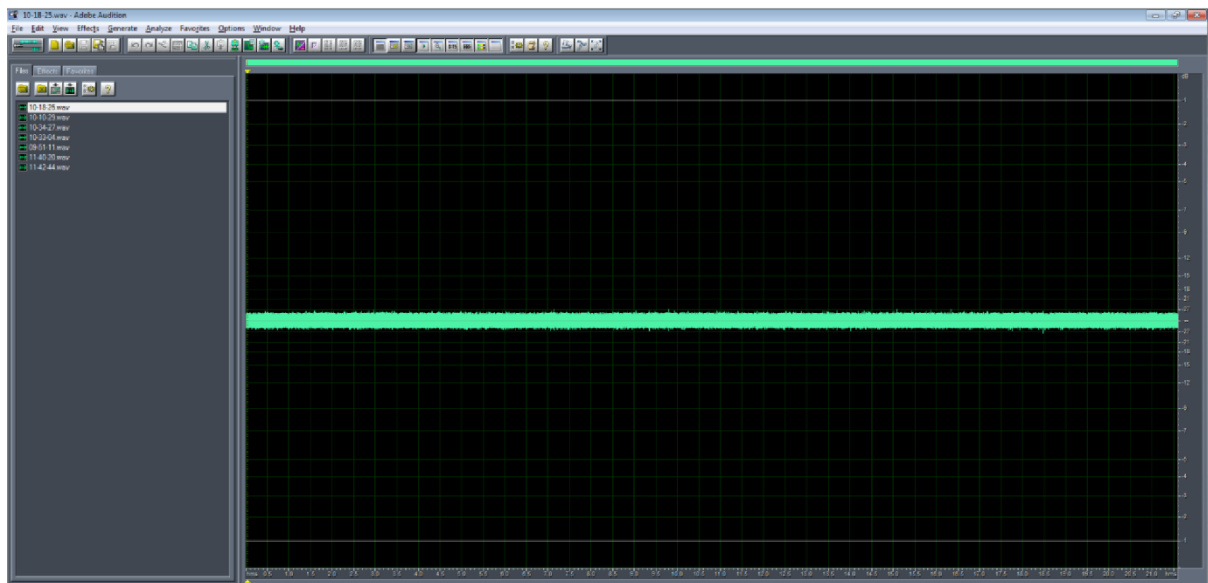

Rec 5 (10:10:29.wav): Preamp 60dB

Switching polarity each 0.5s for 10s. Electrode signal strength +/-1.2-1.8mV/cm. No visible spikes.

Rec 6 (10-18-25.wav): Preamp 60dB.

Switching polarity each 0.5s for 10s. Electrode signal strength +/-1.2-1.8mV/cm. No visible spikes.

Rec 7 (10-33-04.wav): Preamp 60dB.

Switching light on and off twice. Weak peak coincides with switching on first time, stronger at switching off. Only positive pulses. Switching on/off second time generated no peaks.

Rec 8 (10-34-27.wav): Preamp 60dB.

Switching light on and off twice. Both switching on and off first time created spikes. Not so the second time. Both were positive pulses, broadband, with emphasis on frequencies <60kHz (see screen dumps below: switching on pulse above, switching off pulse below).
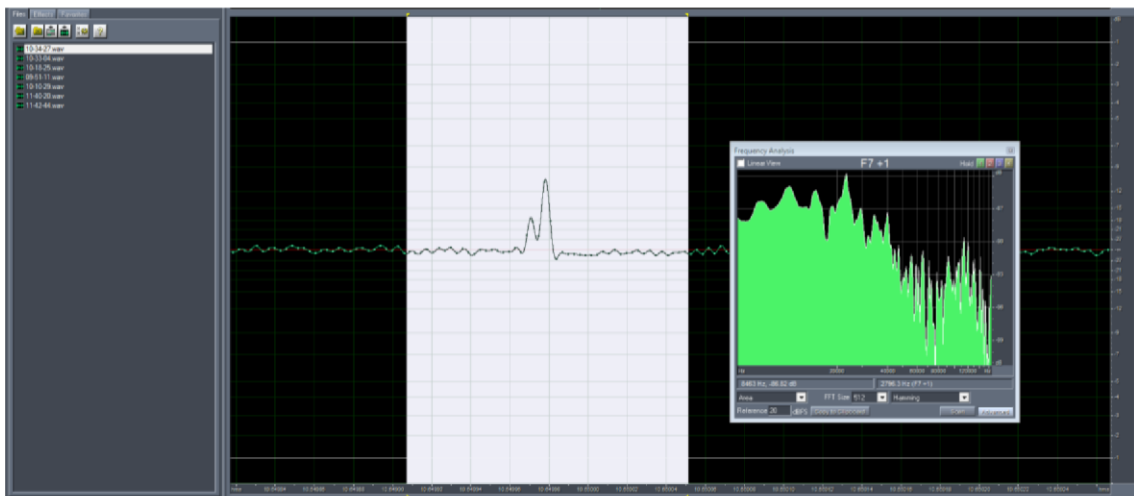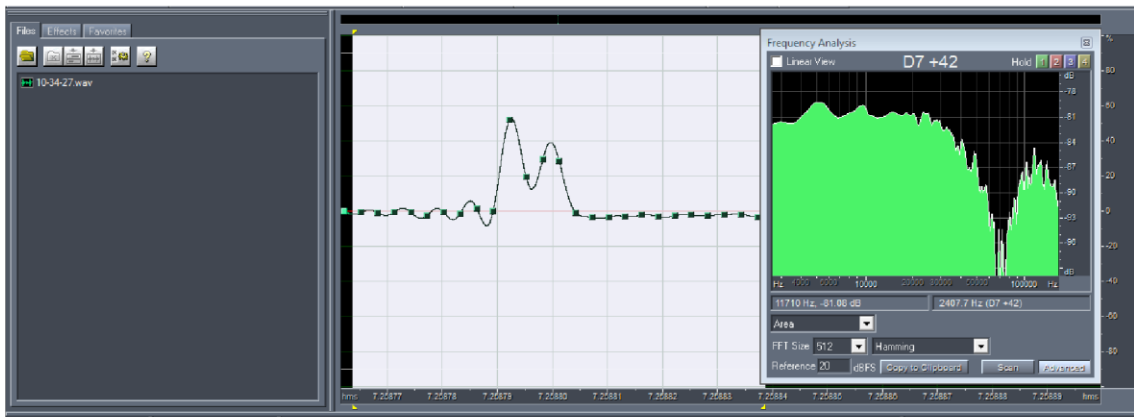
Noise floor

The average RMS power was ca. 39dB re. 1V. With a hydrophone sensitivity of -210dB re 1V per µPa, and a preamp gain of 60dB, this corresponds to a received level of 111 dB peak re 1µPa. This is 60-70dB above the best hearing sensitivity between 10 and 80kHz, meaning that possible lower amplitude spikes from the electrodes would be masked.
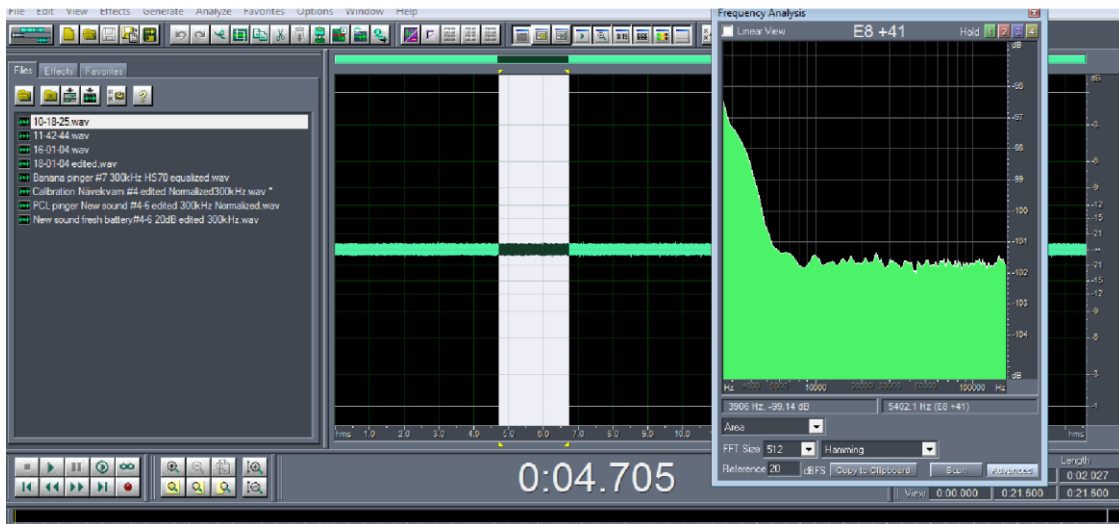
ACKNOWLEDGEMENTS

Without the support of numerous people, this doctoral thesis would not have been imaginable. I would like to take this opportunity to express my sincere gratitude for all the help I received over the past few years.

First and foremost, I want to thank my supervisor, Prof. Dr. Guido Dehnhardt. Dear Guido, thank you very much for believing in me, for your support, and especially for giving me the opportunity to study dolphins. It was a dream come true. Without our valuable and inspiring conversations, both at a professional and personal level, this thesis would not have been possible.

Special thanks are also due to Dr. Lorenzo von Fersen. Dear Lorenzo, thank you for your tremendous support throughout the last few years, for making every day at the zoo exciting and fun, for always having an open ear for my questions, and for always believing in me and in my work. I have never taken that for granted. Thank you for everything!

I would also like to thank Armin and his entire team (Ulla, Karsten, Andreas, Sophie, Basti, Daniel, Anne, Ruta, Guido, Tom, Florian, and Christiane) at the dolphin lagoon for welcoming me into your team, for teaching me the secrets of animal training, and for always finding the time to carry out my numerous experimental sessions. Thank you for the opportunity to work every day with such amazing animals.

A big thank you to the Nuremberg Zoo, its director Dr. Dag Encke and vice-director Jörg Beckmann, who not only provided the financial resources and made the dolphins available for research, but also followed my research at the zoo with great interest. Furthermore, many thanks to the entire technical department of the zoo (Thomas Schiller, Peter Haack, Markus Otzmann, Richard Meixner, Matthias Helgert, and Markus Fiegl) for always finding a solution to any problem I had with my underwater

apparatus. Thank you to Dieter Kühnlein for his help in all administrative questions, Dr. Katrin Baumgartner and Dr. Herman Will for all your support and advice over the years.

To my colleagues at the Marine Science Center, thank you for your help and support from afar, especially Lars for the technical support.

Thanks to Matthias Zürl for his physics lessons.

Many, many thanks to Johannes, Ralph, and Hartmut for their diligent proofreading and valuable comments.

Last but not least, I would like to thank my family, especially my wife Rebecca. You have always believed in me, encouraged me not to lose sight of my goal and let me live my dream. Without you and the joy, strength, and motivation you have given me over the past years, I would never have achieved my goal of proving electroreception in bottlenose dolphins. Thank you!

DECLARATION OF INDEPENDENCY
SELBSTSTÄNDIGKEITSERKLÄRUNG

I hereby solemnly declare that I produced the present Doctoral Thesis independently without external assistance, and that no other than the listed sources of information and references were used, and that the passages taken literally and with regard to the contents from these sources are clearly indicated as such.

Ich versichere hiermit an Eides statt, dass ich die vorliegende Arbeit selbstständig angefertigt und ohne fremde Hilfe verfasst habe, keine außer den von mir angegebenen Hilfsmitteln und Quellen dazu verwendet habe und die den benutzten Werken inhaltlich und wörtlich entnommenen Stellen als solche kenntlich gemacht habe.

Rostock, 11.04.2022   Tim Hüttner