Diving deeper into the dolphin's Umwelt : acoustic, gustatory, olfactory and magnetic perception

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Diving deeper into the dolphin's *Umwelt* :

Acoustic, gustatory, olfactory and magnetic perception

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CHAPTER 1
INTRODUCTION

1. **THE *UMWELT* CONCEPT OF JAKOB VON UEXKÜLL**

In 1909, Jakob von Uexküll established a new concept and with it a new perspective on living creatures' perception of their environment: *Umwelt* (translation from German to English: environment; von Uexküll 1909), meaning subjective universe (Chien 2006). Von Uexküll (1934) conceded animals as subjects and rejected considering them as machines driven solely by reflexes. This opinion was common in the early 20th century, as for example outlined in James (1962). In contrast to the contemporary common opinion (e.g. in the theory of behaviourism), von Uexküll (1934) assumed internal, cognitive processes as equally important as the observable behaviour of an animal and admitted its internal states and motivation.

The subject's *Umwelt* is divided into two parts, the *Merkwelt* and the *Wirkwelt*, both forming a coherent entity (von Uexküll 1909). *Merkwelt* (engl. perceptual world) refers to everything a subject perceives. *Wirkwelt* (engl. active world) refers to everything a subject does. To be perceived by a subject, objects have to possess a feature (*Merkmal*) that matches a subject's receptor (von Uexküll 1909). The perceived stimulus is then processed in the *Merkorgan* (engl. sense organ), for example the brain, where a meaning is attributed to each stimulus. This meaning can change depending on the context or the subject's internal state. Thus, a stimulus can have different meanings to the subject. According to the meaning, the subject's *Wirkorgan* (engl. act organ) will take an action (*Wirkmal*) on or with the object. This closed loop between subject and object is called *Funktionskreis* (engl. functional circle; von Uexküll 1934).

Because of the crucial role of receptors that enable the perception of *Merkmale* and the sensory processing structures (*Merkorgan*), the *Umwelt* is determined by the species' bauplan. Thus, although several species can share the same environment, each has its own *Umwelt* as it differs from another species regarding its sensory abilities. Furthermore, even within the same species individuals do not necessarily share the same *Umwelt* because of morphoanatomical differences, caused for example by genetic defects or events during ontogeny (e.g. a blind and a seeing person may share the same environment but not the same *Umwelt*). Therefore, each individual has its own, self-centred *Umwelt* that is determined by the individual's bauplan (von Uexküll 1934).

Although von Uexküll (1909) admits that species differ in their perception-based experience, he insists on their equality regarding their adaption. According to him "each animal subject, the simple and the complex, are equally adapted to their environment; a simple animal has a simple *Umwelt*, a complex animal a complex one", thus no species can be considered superior to another (von Uexküll 1934).

2.   COMPARISON OF DIFFERENT *UMWELTEN*

It is difficult to determine a species' *Umwelt* from an external point of view because we, as humans, also possess our own *Umwelt*. By simply transferring our perception of reality to another species, we do not respect its specific subjectivity. An object that might be meaningful from the human point of view can be meaningless to another species (Delfour 2010) either because it does not possess the according receptors to perceive the object's feature or because the object, although it can be perceived, does not have a meaning for this species. Therefore, an unbiased study of a species' sensory perception and behaviour is necessary.

Because the perceptual mechanisms tend to be conservative in evolution, information from related species can be valuable (Saslow 2002). Phylogeny (i.e. genetic relatedness) as well as ecological constraints are involved in the evolution of a species' *Umwelt*. It is unclear whether one has more weight than the other.

This dilemma is particularly true for species such as cetaceans that performed a drastic change in lifestyle in the course of evolution. This mammalian order returned from a terrestrial life back into the water, which caused extensive changes in anatomy, physiology, and behaviour (Gatesy et al. 2013). The results of this remarkable transformation are extant cetaceans that include baleen whales (Mysticeti) and toothed whales (Odontoceti). Their closest relatives on land are artiodactyls (even-toed ungulates) including deer, antelopes, gazelles, cattle, sheep, goats, giraffes, pigs, camels, and hippopotami (Thewissen et al. 2009). From all extant artiodactyls, hippopotami are the closest relatives of whales (Gatesy et al. 2013). However, cetaceans evolved about 47 million years ago from a small deer-like ancestor (Thewissen et al. 2009).

The phenotypic differences between cetaceans and artiodactyls are striking. Indeed, whales show many analogous characteristics with other marine species given that their "new" aquatic environment required many profound adaptions, while artiodactyls remained in the terrestrial environment that is characterized by different, partly opposite constraints (e.g. gravity, body dehydration). In the following section we give a summary of what is known about the *Umwelt* of deer, a family that is phylogenetically close to cetaceans, and about the *Umwelt* of cuttlefish, an order that shares the same environment as cetaceans.

2.1. The *Umwelt* of deer

Deer (Cervidae) are prey species that live primarily in forests but inhabit also tundra, grassy landscape or mountainous areas (Geist 2009). All these habitats exhibit high luminosity contrasts and colours, as well as a large range of potential predators. Hence, deer's visual system is adapted to visually contrasted habitats like forests, thus possessing a high visual sensitivity in low-light conditions (e.g. due to a tapetum lucidum). The highly developed vision is also advantageous for a crepuscular prey species as it facilitates the detection of predators (D'Angelo et al. 2008; VerCauteren & Pipas 2003). Behavioural tests proved the assumption that deer can perceive colours (Birgersson et al. 2001) which is suggested to further enhance their predator-detection capabilities (VerCauteren & Pipas 2003). Colour vision is thought to be used also in the context of food selection: deer are herbivorous, selecting suitable diet (plant species or different parts of plants) probably using vision (VerCauteren & Pipas 2003) and odour (Tixier et al. 1998). Chemoreception is further used in intra-specific communication: male deer use excretions, for example from the preorbital gland, for scent marks that are sniffed by both males and females (Mary & Balakrishnan 1984). Chemical analyses revealed that several deer species possess excretions that differ significantly in composition depending on population, sex, and age (Lawson et al. 2001), but also between hierarchical status (Miller et al. 1998). In visually restricted habitats such as forests, acoustic signals are advantageous because they propagate omnidirectionally and are less affected by dense vegetation than visual signals (Catchpole & Slater 1995; Marler 1965). Deer are highly vocal during the reproductive season, where males roar

intensively. Roaring rate is assumed to be an honest indicator of a male's fighting ability (Clutton-Brock & Albon 1979). While males use this signal to evaluate the roaring competitor, females are attracted to males with higher roaring rates (McComb 1987). Some frequency parameters of the roars provide honest (because anatomically limited) information about the caller's age, body weight, and reproductive success, that might be used by other males for rival assessment and by females for mate choice (Charlton et al. 2007; Reby & McComb 2003). Indeed, female deer show a preference for high-pitched roars that are indicative of reproductive success in males, thus using the acoustic information about the caller provided by frequency parameters (Reby & McComb 2003; Reby et al. 2010). While vocalizations are very important during the breeding season, deer are much less vocal at other periods of the year and rely strongly on vision.

2.2. The *Umwelt* of cuttlefish

Cuttlefish (Sepiida) are predatory cephalopods primarily inhabiting shallow-water areas of temperate oceans. Their habitat is characterized by polarized light, numerous possible predator and prey species, as well as a three-dimensional space. Consequently, cuttlefish's highly developed visual system is used for navigation (Alves et al. 2009), camouflage adaption (Kelman et al. 2008), and prey detection (Messenger 1989; Shashar et al. 2000). The cuttlefish's pupil changes its form depending on the light condition: it is O-shaped in darkness and W-shaped in bright light to improve the image contrast (Mäthger et al. 2013). Although colour blind (Mäthger et al. 2006), they have an overall good vision (Marshall & Messenger 1996). Furthermore, cuttlefish are sensitive to polarization characteristics of the light (Shashar et al. 1996). This sensitivity improves their object recognition (Cartron et al. 2013) and their prey detection abilities (Shashar et al. 2000). In general, cuttlefish are visual predators, able for example to estimate the distance of their prey (Messenger 1968). Although they can detect chemical cues of prey (Boal & Golden 1999), they do not approach the odour in the absence of a visual cue (Guibé et al. 2010). However, odour and taste play an important role: prey preferences seem to be odour-driven and taste seems to guide food evaluation (Darmaillacq et al. 2004; Guibé et al. 2010). Other salient environmental

features such as predators, conspecifics, or water composition can also be detected by odours (Boal & Golden 1999). For example, female cuttlefish can detect if a male has recently mated on the basis of chemical cues alone and they show preference for such males (Boal 1997). The sensory systems are already functional in 25 days old cuttlefish embryos, which respond to light stimuli, the odour of predators, and touch (Romagny et al. 2012). Adult cuttlefish also respond to mechanical stimuli: epidermal receptors comparable to the lateral line organ in fish (Budelmann & Bleckmann 1988) allow the perception of local water movements (Komak et al. 2005).

To summarize, both deer and cuttlefish, which are respectively close relatives and habitat neighbours of cetaceans, are highly visual species. Although deer and cuttlefish are phylogenetically not very close, similar environmental constraints, particularly a visually restricted habitat, seem to have favoured similar sensory adaption. However, with regard to the other sensory modalities, both species have different well-developed senses. While deer rely strongly on acoustic signals at certain times of the year (Clutton-Brock & Albon 1979), cuttlefish have no underwater audition (Budelmann & Bleckmann 1988). These common features and differences in the *Umwelt* of deer and cuttlefish raise the question about characteristics of the *Umwelt* of a cetacean species.

3. WHAT IS KNOWN ABOUT THE *UMWELT* OF DOLPHINS?

The order Cetacea comprises two suborders, Mysticeti and Odontoceti. Both suborders are different in terms of morphology, feeding ecology, habitat and behaviour, wherefore knowledge gained about mysticete species can be generalized to odontocete species (and vice versa) only with caution if at all. Mysticeti differ from Odontoceti in their lack of teeth; instead they possess a filter-feeding apparatus made up of baleen plates to feed on zooplankton and small fish (Bannister 2009). They are generally larger than odontocete cetaceans (e.g. blue whale, *Balaenoptera musculus*, with >30 m and >170 tons the largest known animal), mostly living in the open ocean and undertaking long migrations. Therefore, a general "cetacean *Umwelt*" does not exist. A more species-specific perspective is required to approach the *Umwelt*. The odontocete family Delphinidae includes the best studied cetacean species, wherefore they present a

suitable model to outline their *Umwelt*. The analysis of the dolphin's world must begin with a review of the sensory information available to dolphins, which is given in the following paragraphs.

3.1. Audition

Most research effort has been made in the study of dolphins' audition. Audition is the ability to hear, meaning the detection of sound. Sound is an oscillation of pressure (wave) transmitted through air, water, or another medium, that travels five times faster in water than in air. The frequency of the wave determines the pitch of a sound, (i.e. low vs. high). For a given sound frequency, the wavelength is nearly five times longer in water than in air. Generally, high frequencies attenuate rapidly and do not carry very far compared to low frequencies (Nummela 2009). Hearing is evaluated by electrophysiological (auditory evoked potential) or behavioural audiograms. Odontocetes tend to have a 10-octave functional hearing range with peak sensitivity between 40 and 80 kHz (Warzok & Ketten 1999). In bottlenose dolphins (*Tursiops truncatus*), hearing ranges up to 150 kHz, with best sensitivity at 10-80 kHz (Houser & Finneran 2006). The morphology of the odontocete ear, that is exclusively adapted for underwater hearing, differs from that of other mammals already by the lack of outer ear pinnae. Middle and inner ear are located together in the tympano-periotic complex that is surrounded by air cushions in order to acoustically isolate the ear from the skull (Nummela 2009). The primary sound perception path is considered to be the lower jaw that receives the sound energy and transmits it through a fatty tissue in the mandibular canal (mandibular fat pad) up to the tympanic plate (Nummela 2009). This fat pad is composed of triacylglycerol, being similar in density and thus acoustic impedance to water (Varanasi & Malins 1971).

Delphinids produce three different categories of vocalizations: clicks, burst-pulsed sounds and whistles (Janik 2009). Clicks are short broadband signals that can exceed 100 kHz (Richardson et al. 1995) and are mostly used for echolocation. Burst-pulsed sounds consist of rapid click trains (Janik 2009) that are highly directional (Au & Hastings 2008). Into this category fall bottlenose dolphins' bray calls (Janik 2000a), the so called "squawks", "yelps" and "barks" (Schultz et al. 1995) as well as "moans"

or "rasps" (Caldwell & Caldwell 1967). The distinction between echolocation clicks and burst-pulsed sounds is not always easy. Some authors describe a fluent passage between these two categories of vocalizations and that they may merge into the other during sound emission (Au & Hastings 2008). Whistles are tonal, frequency modulated signals with fundamental frequencies lying between 800 Hz (Schultz & Corkeron 1994) and 28.5 kHz (May-Collado & Wartzok 2008) and often several harmonics. Whistles and burst-pulsed sounds can be produced simultaneously (Janik 2009). This corresponds with the generally accepted concept that there are two sites of sound production that can be controlled independently (Dormer 1979), that are composed of two identical sound producing structures consisting of fatty dorsal bursae within a pair of phonic lips, one in the left and one in the right nasal passage (Cranford 2000).

There are two main functions of hearing in dolphins: communication and echolocation (see below). In a habitat where visual contact is not always given, acoustic signals provide a good communication channel even for long-range communication. Most delphinids use whistles for communication, but also pulse sound-based communication exists (e.g. Commerson's dolphins, *Cephalorhynchus commersonii*; Yoshida et al. 2010). Why some delphinid and other odontocete species (e.g. the family of Phocoenidae (porpoises), the pygmy sperm whale, *Kogia breviceps*, and the genus of *Pontoporia*) not produce whistles but only pulse sounds was connected to the orca (*Orcinus orca*) predation risk, that lead to a selective pressure favouring vocalizations restricted to sounds that orcas hear poorly or not at all (i.e. below 2 and above 100 kHz; Morisaka & Connor 2007). Most studies on delphinid communication are concerned with whistles because they are thought to play an important role in social interactions for most delphinid species (Díaz López 2010). Whistles have varying numbers of harmonics and delphinids can distinguish between whistles with and without harmonics (Yuen et al. 2007) but it is unclear which information might be encoded in the harmonics. Whereas the fundamental frequency is relatively omnidirectional, higher order harmonics are more directional (Lammers & Au 2003). Bottlenose dolphins can discriminate tonal sounds that differ in frequency by only 0.2 to 0.8 % (Thompson & Herman 1975) but they seem to pay attention rather to the frequency modulation than to the absolute frequency (Ralston & Herman 1995).

The active space (i.e. the transmission range over which a signal can be detected by conspecifics) for bottlenose dolphins' whistles is determined as 10 to 20 km for frequencies below 12 kHz (Janik 2000b). However, the active space of a sound depends (among other factors such as its frequency) on bottom substrate and water depth. Thus, the same call can be perceptible less than 200 m in a shallow sea grass area of 1.6 m depth or more than 6 km in a sandy bottom area of 3.5 m depth (Quintana-Rizzo et al. 2006).

The ontogeny of whistle repertoire is mainly driven by vocal learning. Neonatal bottlenose dolphins produce whistles as well as burst-pulsed sounds just after birth (Morisaka et al. 2005). With the ability of vocal learning, delphinids are able to acquire and modify new signals in their vocal repertoire through the use of auditory information and feedback, thus infants' and adults' vocal repertoires are different (McCowan & Reiss 1997). Janik (2009) described two different way of learning that can influence the vocal development: contextual learning and production learning. He outlined that in contextual leaning animals learn an association between an existing signal and its context. This context can be a specific behavioural context or a temporal position in a sequence of signals (Janik & Slater 2000). If applied to sound production, this requires control over the delivery of signals that are already in the repertoire, so that they can be produced in novel contexts (Janik 2009). Production learning is defined as instances when the vocalizations themselves are modified in form as a result of experience with those of other individuals; vocal production learning is relatively rare and has only been identified in some bird and mammal species (Janik 2009). The dolphins' ability of vocal leaning is not restricted to a critical or sensitive period as in birds but they retain this ability through their whole life lime (McCowan & Reiss 1997). The use of copying is evident in vocal matching interactions, in which animals respond to a conspecific's whistle with the same whistle type within a short time (Janik 2000c). The occurrence of the same whistle type in the repertoires of two individuals is called vocal sharing, what seems to be frequent in delphinids (e.g. bottlenose dolphins: Azevedoa et al. 2007; McCowan & Reiss 1997; orcas: Ford 1989; Ford 1991; Yurk et al. 2002; see Annex for vocal sharing at the group level in captive orcas). Delphinids are also able to copy non-conspecific sounds from their environment (Foote et al. 2006;

Reiss & McCowan 1993; Richards et al. 1984) and to associate a given sound with an object or context (Reiss & McCowan 1993; Richards et al. 1984). However, why dolphins copy a certain sound of their environment but not another, is still unclear. Perhaps the meaning of the object or context to the dolphin plays a crucial role. Although there is a huge amount of studies concerning the vocal communication of delphinids, many questions are still open due to technical and methodological constraints, such as individually assigned recordings (that are not impossible but often expensive) and unlimited access to the animals. The latter concerns especially studies with direct observation of free-ranging cetaceans, which are not always easy to find and to follow wherefore most studies are restricted to convenient weather conditions and particularly daytime permitting boat trips, leaving the activity at other time periods nearly unknown.

Another important function of sound for odontocetes is echolocation, where they emit sound pulses and listen for returning echoes to generate an auditory scene of their surrounding for navigation and foraging (Madsen & Surlykke 2013; Thomas et al. 2004). Shorter wavelengths have a better spatial resolution, thus high frequencies are better suitable for detecting small objects than are low frequencies (Nummela 2009). In line with this, species inhabiting acoustically complex inshore and river waters use higher frequencies for echolocation (>100 kHz) than near- and offshore species (<100 kHz) that inhabit low object density environments (Warzok & Ketten 1999). Echolocation and sound location are facilitated by rapid auditory temporal processing (Nummela 2009). Beside echolocation, some delphinids are known to detect their prey by passive listening, meaning that they use the sounds produced by their prey to locate it. Noise-producing fish make up indeed a large part of the bottlenose dolphin's diet (Gannon et al. 2005).

In odontocetes, hearing is considered to be the most important sensory modality (e.g. Thewissen 2009) as it is involved in navigation, prey location, and communication (e.g. Mooney et al. 2012). Consequently, the majority of studies address questions related to hearing, sound production, echolocation and communication. At the same time, other sensory modalities are considered to be less important (e.g. Marriott et al. 2013) and therefore reduced or even absent because of trade-offs among the modalities

(Nummela et al. 2013). The following paragraphs will outline what is known about the other modalities.

3.2. Vision

Another important sense to perceive the environment is vision. Vision is the ability to see, meaning the detection of light. When light passes through the water it is differently absorbed, refracted and scattered, depending on the wavelength of the light and the concentration and type of dissolved material in the water. In coastal waters, light of longer wavelength is transmitted better, whereas in the open ocean this is true for light of shorter wavelength (Warzok & Ketten 1999). In general, light decreases with depth. In marine mammals (cetaceans and pinnipeds), visual sensitivity is maximized by a high density of photoreceptors (400 000 per mm² in bottlenose dolphins; Dral 1977) and a tapetum lucidum, i.e. a reflective layer behind the retina, that is reported to be the most developed of any mammal (Dawson 1980). Dolphins have a very good underwater and in-air vision (Herman et al. 1975) and excellent distance estimation (Mobley & Helweg 1990). Both rod and cone receptors have been described in their retina (Perez et al. 1972). Nevertheless, they lack the common dichromatic vision typical for many terrestrial mammals and are probably colourblind (Mass & Supin 2009). The lens of the cetacean eye is very strong and more similar to those in fish compared to the lens of terrestrial mammals (Warzok & Ketten 1999). The delphinid pupil is round under low-light conditions and roughly U-shaped in bright light conditions (Mass & Supin 2009). The cetacean eyes are located laterally (directed ventronasally), allowing a panoramic vision with a 120-130° visual field, and are protected by several anatomical structures inside the eyes from mechanical damage (e.g. due to water pressure) or cooling (Mass & Supin 2009). Both eyes are mobile and are moved independently from each other (Mass & Supin 2009).

Delphinids use their sense of sight in a variety of contexts, from social interactions to prey capture. In short-range communication, visual displays are known to play an important role for delphinids. Postures are thought to signal intent and demeanour of the signal emitter (Dudzinski 1996). The 'S'-posture, in which the dolphin's body is bend into an S-shape (head pointing down, pectoral fins stretched

out), is often described in association with aggressive behaviour including sexual interactions as well as disciplinary behaviour towards infants (Bojaniwski 2002; Dudzinski 1996). The 'S-posture' is known as aggressive stance from other cetaceans too (e.g. humpback whales, *Megaptera novaeangliae*) and might be comparable with the arched head and arched neck position known in many terrestrial mammals during aggressive displays (Dudzinski 1996). The dolphin's 'head-to-head' posture is often accompanied by 'jaw claps', hits, tail hits and 'squawks' (burst-pulsed sounds) that are thought to express irritation or anger (Au & Hastings 2008; Dudzinski 1996). 'Jaw claps' are 'head jerks' also described by Connor et al. (2000) to be included in aggressive behaviours. Furthermore, they mention a distinct posture, in which the dolphin arches the head and flukes down, which may be used to threaten another dolphin. Affiliation between individuals is, among others, expressed by proximity and synchronous movements (Connor et al. 2000) and both could be enhanced by visual acuity. Further, there is some evidence that dolphins use pointing gestures (Xitco et al. 2001) and that complex behaviours such foraging techniques are taught by action imitation that in turn requires observation (Abramson et al. 2013; Bender et al. 2009). Another visual display occurs in reproductive contexts, when dolphins present their genital region to sexually attract their mating partner (Tyack 2000). In addition, the normally white ventral side of bottlenose dolphins can be remarkable pink in periods of high sexual activity (personal observation) what might serve as a visual signal.

But also the inspection of objects, both in water and in air, suggests that cetaceans use their vision to perceive their surroundings. A common behaviour of several cetacean species is spyhopping, i.e. surfacing vertically and lifting the head out of the water (e.g. Jensen et al. 2013; Ford 1984; Whitehead & Weilgart 1991) that seems to serve the inspection of objects over water (Madsen & Herman 1980). Furthermore, dolphins can visually track fish that is flying through the air (after they had hit them very hard with their fluke) and catch them (Wells et al. 1987).

3.3. Somatosensory perception

Somatosensory perception comprises the perception of touch, pain (nociception), temperature, and body position (proprioception). Several different receptors types are

involved (including mechanoreceptors, nociceptors, and thermoreceptors) that are located in the skin and inside the body. To be able to feel the body position is crucial for an air-breathing animal that lives in a three-dimensional underwater habitat in order to orient towards the surface even when no visual cues are available and to feel if the blowhole is above the water (to ensure respiration). The cetacean skin is well innervated and very sensitive to touch (Tyack 2000). Dolphins are most sensitive on their heads (corners of the mouth, eyes, snout, melon, area around the blowhole), reaching a sensitivity comparable to human fingertips or lips (Ridgway & Carder 1990). In the region of the blowhole, large numbers of mechanoreceptors were found that are thought to serve in the perception of pressure change that occurs when the whale/dolphin breaks through the water surface in order to assure that the blowhole is opened for respiration only after surfacing (Bryden & Molyneux 1986). Dolphins are able to perceive pressures as small as 100 mg/mm² (Kolchin & Bel'kovich).

Beside the surrounding water, somatic stimuli can originate from objects in the environment. Rubbing occurs in both captive and free-ranging cetaceans. Several delphinids rub body parts on the substrate, for example pebbles, sand, or along rocky edges (Ford 2009; Rossi-Santos & Wedekin 2006; Smith et al. 1992; Whitehead et al. 2004), what possibly functions in pleasure or hygiene (Dudzinski et al. 2012) but may also be a result of play behaviour (Kuczaj et al. 2006). However, touch is also an important short range communication signal during play, sexual, maternal, and social contexts using the nose or rostrum, flippers, pectoral fins, dorsal fin, flukes, abdomen, and the entire body (Dudzinski et al. 2009a). Tactile contacts between dolphin conspecifics can be observed during aggressive interactions (including also biting etc.) but are also common in affiliative contexts (Dudzinski et al. 2009b; Dudzinski et al. 2010; Dudzinski et al. 2012; Paulos et al. 2008). Affiliation between individuals is expressed by proximity and physical contact (Connor et al. 2000). Physical contact includes contact swimming, gentle stroking with the pectoral fin or rubbing against another individual. Sakai et al. (2006) reported that flipper rubbing in wild Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) is an affiliative behaviour which could be a quantitative measure of social relationships among individuals. Tamaki et al. (2006) reported that flipper-rubbing may contribute to restore friendly relationships between

former opponents or reduce conflicts. Thus, flipper-rubbing may be the cetacean equivalent of primate grooming (Connor 2007; Norris et al. 1994; Tamaki et al. 2006). People working with delphinids in captivity report that petting is appreciated by the animals and can be therefore used as a reinforcer in training (Dudzinski et al. 2009a; personal observation).

3.4. Chemoreception

Especially in aquatic species it is difficult to differentiate the different modalities of chemoreception, i.e. gustation, olfaction, and the vomeronasal sense (Hemilä & Reuter 2008). Chemoreception is sensitive to all substances spread by water, air, or direct contact that can be perceived by the chemical sense organs (Hemilä & Reuter 2008). As cetaceans lack the vomeronasal organ (Thewissen 2009), the following section will focus on gustation and olfaction.

3.4.1. Gustation

Gustation is the ability to taste. Waterborne tastants (i.e. substances that elicit gustatory excitation) are hydrophilic substances, for example amino acids or nucleotides, that are carried by water currents (Hemilä & Reuter 2008). In water, the diffusion of molecules is slower than in air (10^{-9} m²/s versus 10^{-5} m²/s; Dusenbery 1992). Traditionally, gustation provides information about food material already in the mouth, where the taste is perceived by the receptor cells of the taste buds that are located on the tongue, the roof of the mouth, the epiglottis, and the oesophagus (Purves et al. 2001). Several authors suggested that cetaceans in general and odontocetes in particular should have taste sensation (Pihlström 2008; Pfeiffer et al. 2001; Watkins & Wartzok 1985). However, evidence in the literature is difficult to find and only those in favour of gustation in dolphins will be given hereafter (for a more comprehensive review see Chapter 4). A taste system comparable to that of other mammals might exist in bottlenose dolphins. First, on the dolphin's tongue have been found taste buds (reviewed in Kuznetzov 1990), marginal and vallate papillae (known to be potential locations of taste buds; Kastelein & Dubbeldam 1990; Werth 2007), as well as cells that resemble

Von Ebner's glands (also called gustatory glands; Ferrando et al. 2010) that might be chemosensory or important for the sense of taste. Second, it was proposed that the very well developed cranial nerve V (trigeminal nerve; Oelschläger 2008) might provide a pathway to transmit impulses from the oral cavity to the brain (Oelschläger & Oelschläger 2009), called trigeminal chemoreception (Kuznetzov 1990). Unlike other mammals, where cranial nerve VII innervates the tongue's taste buds (Purves et al. 2001), this nerve does not seem to be involved in dolphins' chemoreception but rather in acoustic signal production (Oelschläger 2008). However, cranial nerve V is, just as cranial nerve VII, able to excite the gustatory neurons in the nucleus of the solitary tract in the medulla (Boucher et al. 2003; Purves et al. 2001).

Furthermore, behavioural studies have shown that bottlenose dolphins can perceive sour and bitter (Friedl et al. 1990; Kuznetzov 1990; Nachtigall & Hall 1984) nearly as well as humans; moreover, they were able to detect salty (Friedl et al. 1990; Kuznetzov 1990). Regarding the perception of sweet, there is evidence for both presence (Friedl et al. 1990) and absence (Kuznetzov 1990). In addition to the basic tastes, dolphins were also able to detect urine and faeces (Kuznetzov 1990). Dolphins' high sensitivity to some carboxylic acids, that are not perceived by taste but primarily by smell in other mammals (odorous substances), led to the hypothesis that dolphins do not possess a sense of taste or smell in its typical form but rather a chemical sense called "quasi-olfaction" (Kuznetzov 1990) as it combines characteristics of both taste and olfaction.

Known tastants such as amino acids or nucleotides can be unintentionally released into the water by other animals, for example prey species (Hemilä & Reuter 2008), and provide therefore a possible cue for finding food (Würsig 1986) or evaluating food quality. However, these questions have not been investigated so far. Given the fact that dolphins seem to be able to detect excrements (Kuznetzov 1990), gustation could also be used intra-specifically, for example individual recognition or mate detection (e.g. females' receptiveness). The idea of pheromone mediated behaviour was already suggested for spinner dolphins (*Stenella longirostris*; Norris 1991).

3.4.2. Olfaction

Olfaction is the ability to smell and is considered to be the most primordial, meaning the "oldest", sense (Purves et al. 2001). Airborne odourants (i.e. substances that elicit olfactory excitation) are volatile molecules, for example alcohol or fatty acids, carried by air (Hemilä & Reuter 2008). In terrestrial mammals, odourants dissolve in the olfactory epithelium inside the nasal cavity, where they bind to olfactory receptor cells that transmit the impulse further via cranial nerve I (olfactory nerve; Thewissen 2009). Even when the detected chemicals are carried in water, when the transmission pathway to the central nervous system is via cranial nerve I it is considered to be olfaction, as it is the case in fish (Hara 1994). Therefore, olfaction is also possible in water and does not necessarily require olfactory receptor cells in the nasal cavity.

In odontocetes, the nasal cavity accommodates parts of the echolocation system (Pihlström 2008) wherefore a traditional involvement in olfaction may seem unlikely. However, chemoreceptor cells were found in the nasal cavity of harbour porpoises (*Phocoena phocoena*; Behrman 1989). Cranial nerve I seems to vanish during early ontogenesis (Oelschläger & Buhl 1985). In baleen whales, the olfactory tract is reported to be either considerably reduced/absent (Oelschläger 2008; Pihlström 2008) or present (Thewissen et al. 2011). In toothed whales, the olfactory tract is considered to be absent (Oelschläger 2008; Pihlström 2008), but the olfactory tubercle was found to be well-developed (Oelschläger & Oelschläger 2009).

As other marine but air-breathing species, including another marine mammal (the harbour seal, *Phoca vitulina vitulina*), use odours to locate prey (Kowalewsky et al. 2006; Nevitt et al. 1995; Wright et al. 2011), it was suggested that bowhead whales (*Balaena mysticetus*) and humpback whales may have a functional sense of smell that is used to detect prey (Hagelin et al. 2012; Thewissen et al. 2011). The same could be true for dolphins, by using either airborne molecules as proposed before or waterborne molecules as fish do (Hara 1994). Beside prey detection, fish are able to perceive olfactory cues of predators and conspecifics (Hirvonen et al. 2000), what could be useful information for

dolphins, too. But again, these ideas have not been investigated yet in dolphins. Furthermore, individual recognition or mate detection could be chemically mediated, and as the chemical sense in dolphins is not clearly described (gustation, olfaction, "quasi-olfaction") involvement of smell cannot be ruled out.

3.5. Electro-/Magnetoreception

3.5.1. Electroreception

Electroreception is the ability to perceive an electric field. Bioelectrical fields are generated by every muscle movement and the water medium provides best conditions for conducting the currents. In active electroreception, the animal generates an electric field and senses distortion of this field from objects of varying conductivity in its habitat; in passive electroreception, the animal perceives electric fields generated by an object in vicinity (Czech-Damal et al. 2012). Active electroreception is known for example in electric eels (*Electrophorus electricus*; Souza et al. 2007). Passive electroreception is used for prey detection for example by elasmobranch fishes (Kalmijn 1971) that possess electroreceptors called ampullae of Lorenzini (Murray 1960).

So far, the Guiana dolphin (*Sotalia guianensis*) has been found to be sensitive to weak electric currents such as those emitted by the muscles of prey fish buried in the sediment (Czech-Damal et al. 2012). The electroreceptors are probably in the hairless vibrissal crypts on the rostrum (Czech-Damal et al. 2013). These structures are also present in bottlenose dolphins. Interestingly, most fish prey species in the bottlenose dolphins' diet are bottom-dwellers (Wells & Scott 2009). Thus, the perception of electric fields would improve prey detection.

3.5.2. Magnetoreception

Magnetoreception is the ability to perceive a magnetic field. The Earth's magnetic field is a dipole field that is generated by the generated by Earth's fluid outer iron core (Wiltschko & Wiltschko 1995). Its intensity ranges from over $60\,000$ nT near the magnetic poles to $30\,000$ nT at the magnetic equator, but

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shows minimum values below 26 000 nT at the east coast of South America. In the ocean, the magnetic topography (i.e. variation in the magnetic field) is regular and long-term stable, with hills (i.e. locally higher total intensities) and valleys (i.e. locally lower intensities) symmetrically arranged on both sides of the mid-oceanic ridge; there are some anomalies that run linear on opposite sides of the ridge and some that run perpendicular to those (reviewed in Walker & Dennis 2005). Local anomalies can be caused by differently magnetized rocks (Wiltschko & Wiltschko 1995). Beside spatial variation the geomagnetic field also shows temporal variation caused by solar electromagnetic radiation (leading to regular daily variations) or sun spot activity (leading to irregular fluctuations called magnetic storms; Wiltschko & Wiltschko 1995).

Two main principles are the perception of a magnetic field based on induction or based on magnetite (reviewed in Wiltschko & Wiltschko 1995). The theory of induction-based perception assumes that the electric field, which is generated by the magnetic field, is perceived by electroreceptors; it is dependent on the conductivity of the surrounding medium, thus salt water provides a very suitable medium. Magnetite-based perception is based on ferromagnetic particles such as magnetite (iron oxide). These miniature magnets align themselves in the magnetic field and are connected to the central nervous system. However, the exact pathways of the signal transmission are still unclear (Lohnmann & Johnsen 2000). Magnetite has been found in the dura mater of bottlenose dolphins (Bauer et al. 1985) and short-beaked common dolphins (*Delphinus delphis*) where nerve fibres have been identified on the particles' surface (Zoeger et al. 1981).

Magnetoreception is commonly used for navigation, i.e. orientation based on the geomagnetic field (reviewed in Wiltschko & Wiltschko 1995). As navigational cues such as land marks are limited in oceans, magnetoreception could serve dolphins for orientation, as it was suggested for fin whales (*Balaenoptera physalus*; Walker et al. 1992), but experimental evidence is lacking.

4.   OPEN QUESTIONS ABOUT THE *UMWELT* OF DOLPHINS

The aim of this thesis is to contribute to a better understanding of the dolphin's *Umwelt* by filling some of the knowledge gaps. Up to now, the dolphin's *Umwelt* has only been outlined in parts. With regard to audition, vision, and somatosensory perception, where main research effort has been made, the dolphin's *Umwelt* is relatively well-understood.

Some of the senses are temporally independent, meaning that they are functional at any time of the day. Contrarily, vision is generally limited to day time. Because visual restriction often enhances the use of acoustic signals, the use of vocalizations might be different at night compared to day time. As outlined above, most studies on dolphin vocal behaviour are conducted at day. In contrast to most other mammals, cetaceans do not have a diurnal activity rhythm (i.e. being awake during the day and sleeping during the night) due to their unihemispheric sleep (Lyamin et al. 2008). Consequently, nighttime cannot automatically be considered as inactivity but has to be seen as an equally important part of the dolphin's *Umwelt*. When not being (entirely) sleeping at night, dolphins can be expected to be engaged in different activities or social behaviours and given the fact that they are highly vocal it seems likely that these activities may be mediated by vocalizations (thus studies concerning the vocal activity describe the dolphins' *Wirkwelt* because they investigate what the dolphins are doing). Furthermore, nighttime is the only time without human interaction for dolphins in captivity, thus presenting a particular time where dolphins might express more behaviours relevant to their internal processes. Therefore, a closer investigation of dolphins' vocal activity at night is necessary to complete our knowledge about the dolphin's *Umwelt*. Here we asked: is there a nocturnal activity, measurable by vocal activity (Chapter 3, Paper 1)?

With respect to the dolphins' well-known capacity to copy sounds from their environment, the questions remains open why they do copy a certain sounds of their environment but not another. It has been shown that dolphins produce vocal copies especially in the presence of a certain object that was associated with the original sound (Hooper et al. 2006). This implies that these objects were meaningful to the dolphins. This led to the question whether the production of vocal copies can serve as an indicator for the meaningfulness of the original sound or the object/context with which this sound was associated (Chapter 3, Paper 2).

The second aspect of the dolphin's *Umwelt* concerns the perceptive abilities of different modalities (describing the dolphins' *Merkwelt*, i.e. what the dolphins are perceiving). As the literature review revealed, gustation, olfaction, and magnetoreception are mentioned only casually although they are potentially functional senses. Therefore, information is lacking about their possible relevance for the dolphin's perception of its *Umwelt*. Dolphins are surrounded by a huge amount of chemical information, which are known to be exploited by other marine species, thus we investigated their chemical senses. Because food preferences have been reported in this species, we were wondering whether those might be guided by taste (Chapter 4, Paper 3). Furthermore, prey location is mediated by olfactory cues in other marine species wherefore this raises the question whether dolphins are also able to perceive food-related odours (Chapter 4, Paper 4).

Beside the five traditional senses (hearing, sight, touch, taste and smell), the perception of other cues can also provide useful information about the environment. One of these less intensively studied senses is magnetoreception. Although some spatial observations and anatomical findings suggest that dolphins (and other cetaceans) may be sensitive to the geomagnetic field (Kirschvink et al. 1986; Klinowska 1985; Walker et al. 1992), experimental evidence is lacking. Therefore we asked whether dolphins possess a magnetic sense (Chapter 5, Paper 5).

CHAPTER 2
METHODOLOGY

1. STUDY SPECIES: SOME ADDITIONAL INFORMATION

Common bottlenose dolphins (*Tursiops truncatus*) belong to the odontocete family Delphinidae that includes 35 species, ranging from the less than 1.5 m long Hector's dolphin (*Cephalorhynchus hectori*) to the 9 m long orca. Delphinids probably evolved 11-12 million years ago in the mid- to late Miocene and many of the early delphinid fossils can be assigned to extant genera, particularly to *Tursiops* (LeDuc 2009). The bottlenose dolphin is one of the best studied cetacean species, probably because of its frequent presence both at the coastline and in dolphinariums. This species is found in most of the world's temperate and tropical seas, in coastal as well as offshore waters (Wells & Scott 2009). Coastal bottlenose dolphins often are long-term resident to a specific home area (e.g. Sarasota, Florida; Morey Firth, Scotland; Shark Bay, Australia), meaning that the dolphins have a relatively permanent home range in a given area.

Bottlenose dolphins live in a fission-fusion society meaning that individuals associate in small groups that frequently change in composition and behaviour (Connor et al. 2000). The social relationships within this society are revealed through behaviours expressed in social interactions, repeated over days, months and years (Mann et al. 2000). Affiliation between individuals is expressed by proximity, synchronous movements and physical contact (Connor et al. 2000). Another behaviour that often associates with affiliation is socio-sexual contact that may involve almost any age-sex class combination of individuals, and does not appear in exclusively affiliative or agonistic contexts (Connor et al. 2000).

The development of social relationships seems to begin with long-term bonds between infants who spend considerable time performing social play, cultivating important social relationships and practicing social skills (Connor et al. 2000). Later in life the association patterns are different between females and males. Females have a large network of associates and within this extensive social web, most females associate most strongly with a subset of other females in so-called 'bands' (Connor et al. 2000). Males form 'first-order alliances' meaning pairs or trios that cooperate to form coercively maintained consortships with individual females (Connor et al. 1992). Each pair or trio maintains associations with one or two other pairs or trios, thus forming so-called 'second-order alliances' that cooperate in attempts to take female consorts from other alliances or to defend against such attacks (Connor et al. 1992).

Associations between males and females are tied strongly to females' reproductive state (Connor et al. 2000). In Shark Bay, Australia, mixed-sex-groups are common and females and males were seen foraging together, engage in occasional affiliative contact and often travel and rest together (Smolker et al. 1992). There might exist a kind of 'friendships' between males and females (Connor et al. 2000). Connor et al. (1996) reported an observation in which one alliance appeared to prevent females from being herded or harassed by other males.

Although births can occur all year round there are peaks in spring and summer months (Urian et al. 1996). Females give birth to usually one calf after a gestation period of about 12 months (Perrin & Reilly 1984). Calves are weaned after a lactation period of 1.5 or 2 years but stay with their mothers for up to six years (Wells & Scott 2009). In general sexual maturity is reached by females at 5-13 years and by males at 9-14 years (Wells & Scott 2009). The life span of females is usually longer than that of males, who can reach an age of up to 48 years whereas females can live to more than 57 years (Wells & Scott 1999).

2. STUDY SUBJECTS

We studied a group of captive-born bottlenose dolphins in the facility of "Planète Sauvage" (Port-Saint-Père, France). The group consisted at any time of unrelated males and females at different ages (Table 1) but changed in composition over the course of the thesis. Two dolphins died (Thea, an adult female, and Mininos, a juvenile male) and three dolphins arrived from other facilities (Parel, a juvenile female, as well as Kite and Spat, two juvenile males). Some individuals were already more or less familiar with each other due to a common housing period prior to their arrival at "Planète Sauvage" (Figure 1).

Individuals could be easily identified on the basis of physical differences. Appropriate for identification were for example the shape of the dorsal fin or fluke, differences in the face, or colour patterns of the skin (Figure 2).

Table 1: Individual bottlenose dolphins that participated at different studies over the course of this thesis.

Individual (mother x father)	Sex	Date of birth/death	Place of birth	Arrival at "Planète Sauvage"	Participation
Amtan (Moly x Moby)	F	* 13.05.2001	Dolfinarium Harderwijk (Netherlands)	21.11.2008	Acoustic recordings; Chemoreception (sense of taste/smell); Magnetoreception
Cecil (Louise x Ralph)	M	* 31.05.1984	SeaWorld Orlando (USA)	24.11.2008	Acoustic recordings; Chemoreception (sense of taste/smell); Magnetoreception
Kite (Lucy x Beachie)	M	* 05.10.2005	Dolfinarium Harderwijk (Netherlands)	27.03.2012	Chemoreception (sense of smell); Magnetoreception
Mininos (Athéna x Guama)	M	* 16.08.2004 † 04.10.2012	Parc Astérix (France)	24.11.2008	Acoustic recordings; Chemoreception (sense of taste)
Parel (Roxy x Prince)	F	* 08.06.2008	Dolfinarium Harderwijk (Netherlands)	29.03.2012	Chemoreception (sense of smell); Magnetoreception
Peos (Amaya x Pichi)	M	* 23.06.1999	Parc Astérix (France)	24.11.2008	Acoustic recordings; Chemoreception (sense of taste/smell); Magnetoreception
Spat (Finagain x Tucker)	M	* 22.05.2008	Dolfinarium Harderwijk (Netherlands)	29.03.2012	Chemoreception (sense of smell); Magnetoreception
Thea (Honey x Smarty)	F	* 02.08.1992 † 26.09.2011	Windsor Safari Park (UK)	21.11.2008	Acoustic recordings
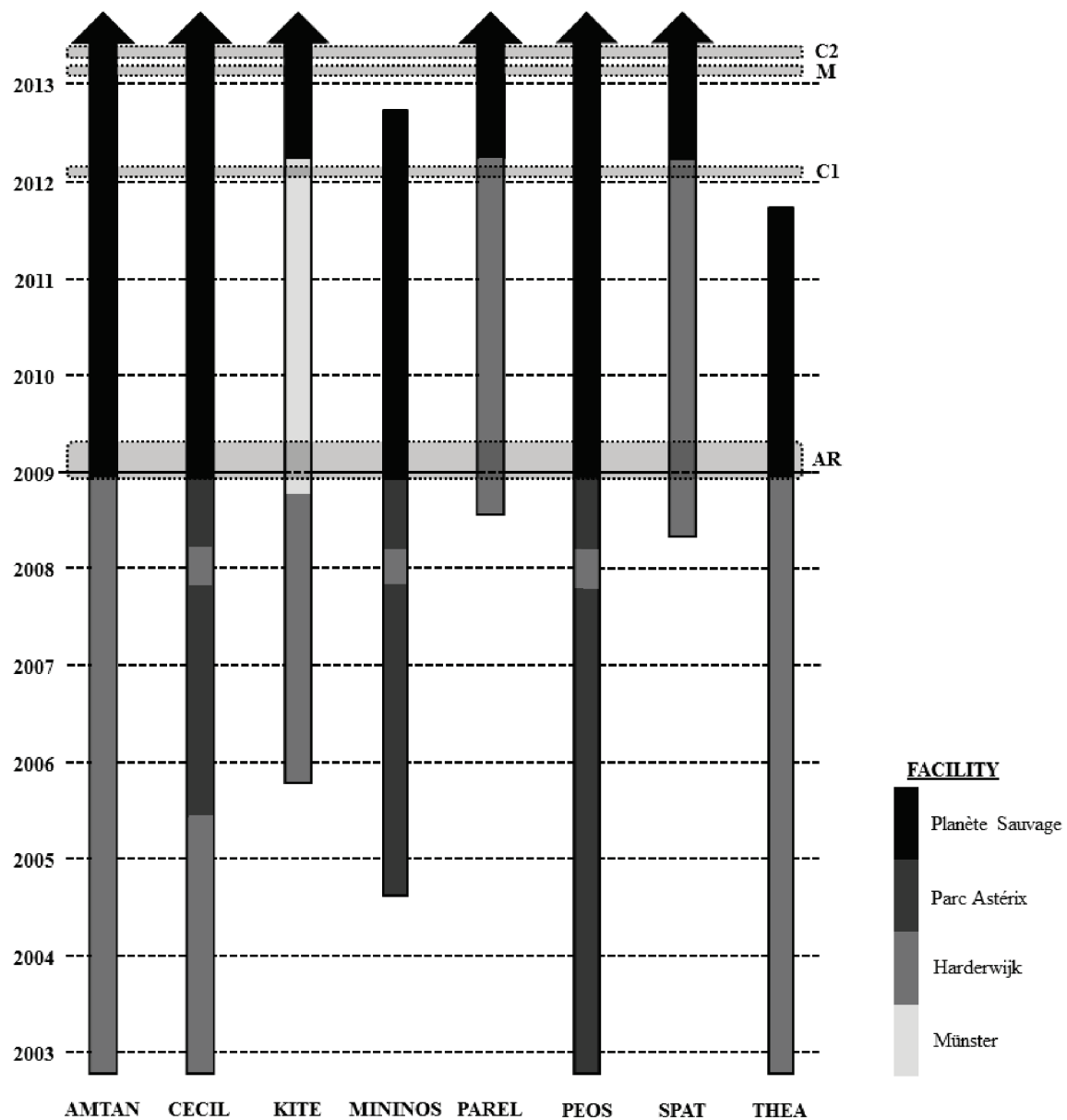
Figure 1: Housing facilities for the last 10 years and taking place of data collections (AR: Acoustic Recordings; C1: Chemoreception – Sense of Taste; C2: Chemoreception – Sense of Smell; M: Magnetoreception) for every individual studied in the course of this thesis.

Figure 2: Physical characteristics of all studied individuals useful for identification (©Planète Sauvage).

3. STUDY SITE

The delphinarium "La Cité Marine" is part of the safari park "Planète Sauvage" situated in Port-Saint-Père, France. Overall, this outdoor facility consists of four pools, covering 2000 m² water surface and containing 7.5 million litres salt water (Figure 3; Table 2). Water temperature can range from 10-28°C, salinity from 25-35%. For cleaning purpose the delphinarium is equipped with mechanical filters as well as an ozone system (in case that ozone does not function properly chlorine is available).
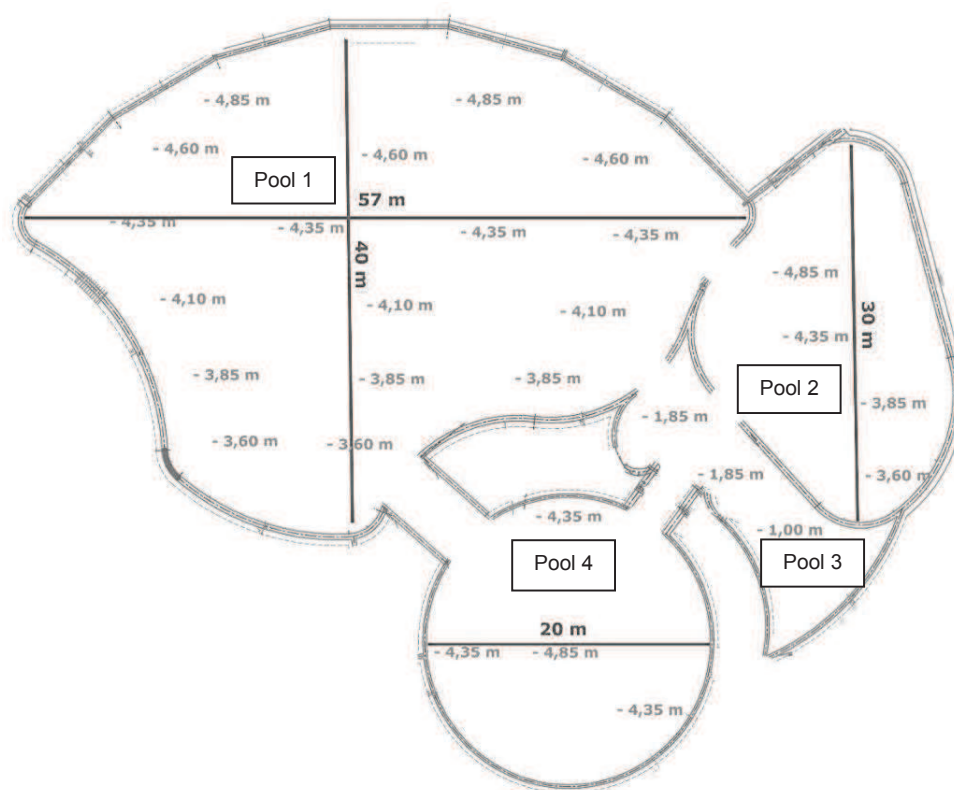
Figure 3: Outline and dimensions of the pools in "Planète Sauvage" (©Planète Sauvage). Values beside lines indicate diameters and negative values indicate the pools' depths at different locations.

Table 2: Dimensions of the pools in "Planète Sauvage".

	POOL 1	POOL 2	POOL 3	POOL 4
Volume (m3)	4950	1280	220	1040
Surface (m²)	1150	330	180	314
Depth (m)	3.60-4.85	4.85	0.00-1.80	4.50
Length (m)	57	30	23	20
Width (m)	40	15	8	20

The four pools are connected by channels that can be closed with gates in case of a necessary separation of a particular individual (e.g. birth or disease). In general, the channels are open during the day, thus the dolphins are free to use all pools. However, every now and then the trainers closed one or several channels for some time in order to habituate the dolphins.

Daily routine lasted from 8 a.m. to 7 p.m. An exemplary day proceeded as follows (in summer, i.e. high season, there were up to four public shows per day whereas in winter the park is closed, thus there were no public shows but training sessions instead):

– 8 a.m.: arrival of the first trainer; inspection of dolphins; preparation of fish
– 9 a.m.: 1st session (feeding without training)
– 10:30 a.m.: 2nd session (training and feeding)
– 11:30 a.m.: 3rd session (training and feeding with public)
– 2 p.m.: 4th session (public show)
– 3:30 p.m.: 5th session (public show)
– 5 p.m.: 6th session (training and feeding with public)
– 6 p.m.: 7th session (feeding without training)
– 7 p.m.: cleaning; inspection of dolphins; departure of last trainer

Training sessions lasted ca. 15 minutes, public shows ca. 30 minutes. Training includes medical training (e.g. acceptance of inspection and palpation of all parts of the body or being touched by medical equipment) as well as training for public shows (e.g., jump on command). Shows started with a prelude: a soundtrack was broadcast from the loudspeakers of the dolphinarium, including music and natural sounds (i.e. sound of waves, sea gull calls, humpback whale calls, and dolphin whistles), and in the meantime the audience would enter the seating rows and take their places. After the prelude, the actual show started during which dolphins' biology and behaviour was explained to the public (e.g. demonstration of body features and physical abilities; explanation of threats such as pollution or overfishing). The shows were accompanied by music and a trainer commented the different activities. To avoid that the dolphins become bored by the shows, the order of the different activities was changed each time. All dolphins were trained from an early age using positive reinforcement (operant conditioning) with fish as primary reinforcer.

The diet of the dolphins was primarily composed of frozen stored fish (herring, capelin, sprat, mackerel, and whiting) and squid, whose quality is controlled regularly through biochemical analyses conducted by an external laboratory. The species composition changed on a daily basis but contained at least three different fish species each day. A daily ration of 5-10 kg per individual (depending on its size) was given throughout the day during the training/feeding sessions.

Free time between the training sessions was enriched from time to time with toys (e.g. foam mat, ball) and water jets, however, dolphins were free to do what they liked.

4. DATA COLLECTION

Four studies have been conducted in order to investigate different sensory modalities and thereby to contribute to fill in the gaps of knowledge about dolphins' perception of their *Umwelt*. With the exception of the acoustic recordings, all data were collected as part of this thesis. The general approach of these studies is based on the spontaneaous responses of the dolphins, meaning that the dolphins were never trained to respond in a certain way to a given stimulus. Contrarily to most other studies no operant conditioning was used (e.g. go/no-go paradigm). With respect to the *Umwelt* concept, this approach offers the advantageous opportunity to study spontaneaous responses based on internal processes that can potentially reflect the significance a given stimulus may have for an individual.

4.1. Acoustic Recordings

The acoustic behaviour of the dolphins in Planète Sauvage has been already investigated in a previous study (Briseño Jaramillo 2009). Over seven month, the dolphins have been recorded in different situations as well as at different times. A part of those recordings, that have been made during eight nights (between 18:00 and 06:00) in April and May 2009 and have not been investigated before, served as data basis for the here presented findings.

To semi-continuously record the dolphins' vocalizations two Nauta SS03-10 hydrophones were placed at opposite sides of pool 1. They were connected to a Marantz PMD 670 recorder (sample rate: 44.1 kHz; resolution: 16 bit; frequency

response: 15-20000 Hz ± 3dB) that in turn was connected to a Dell 390 computer where the sounds were recorded by using ANA software (Richard et al. 1991). Recording sessions lasted between 60 to 80 minutes, after what the batteries needed to be changed, leading to several sessions per night.

At the same time of the acoustic recordings, a human observer was positioned next to pool 1 and counted the number of respirations. Although visual restrictions at night did not allow identification, blows were well audible and therefore easy to count. However, light conditions prevented the collection of other behavioural data.

4.2. Chemoreception

The main challenge of the investigation of chemoreception in dolphins was the lack of previous studies that could have served as a guideline regarding the experimental design or the behaviours to look at. Therefore, we needed to creatively invent new techniques.

4.2.1. Sense of Taste

The study on gustation was conducted in collaboration with Benoist Schaal (Centre des Sciences du Goût, CNRS (UMR 6265), Université de Bourgogne). In January and February 2012, we tested the dolphins' capacity to perceive flavours. Ice cubes present a suitable matrix for presenting flavours because they are easy to produce with different flavours while being visually and tactilely identical. Furthermore, the dolphins expressed a high liking for them. Sometimes trainers gave ice cubes as enrichment to the dolphins after training or feeding where ice cubes are used to meanwhile cool the fish in a metal bowl. The use of ice cubes as enrichment is not uncommon in the husbandry of aquatic species (Warne-Reese 1997). Thus, ice cubes were familiar to all dolphins and no habituation was necessary. Ice cubes were produced with herring, salmon, and shrimp flavours, originally used for human cooking or for baiting fish. Each flavour was diluted in water with which the experimental ice cubes were produced. In order to create ice cubes whose flavour was as close as possible to the original flavour (of herring, salmon, and shrimp), different concentrations were tasted by the experimenter until the best, i.e. neither excessively intense nor lacking flavour, was found.

4.2.2. Sense of Smell

The study on olfaction was conducted in collaboration with Aurélie Célérier and Silvia Campagna (Centre d'écologie fonctionnelle et évolutive, CNRS (UMR 5175), Université de Montpellier). In May and June 2013, we tested the dolphins' capacity to perceive an odour. Therefore, fish was placed in an opaque plastic barrel that was placed next to pool 3 and attached to a pole of a connecting channel (either pool 3/pool 1 or pool 3/pool 2) to prevent it from falling in the pool. Simultaneously, an identical but empty barrel was placed at the other position and served as control (Figure 4). The position for fish/control barrel changed randomly and the dolphins were filmed (Sony Handycam HDR-XR 155 on a tripod) to avoid interaction with and influence of the experimenter.
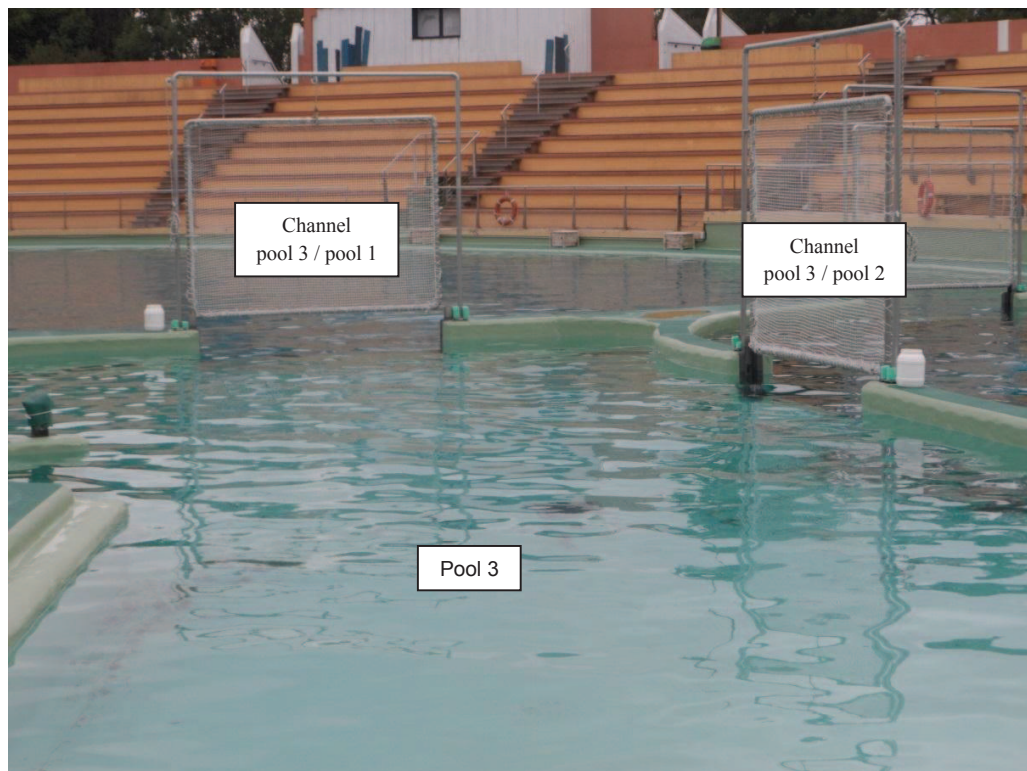
Figure 4: Experimental setup for the experiment "sense of smell" (©Planète Sauvage).

4.3. Magnetoreception

In January and February 2013, we tested the dolphins' capacity to perceive a magnetic field in pool 4. For this experiment we used the same plastic barrels as in the experiment "sense of taste". Inside, a magnetic neodymium block was placed. The barrel was attached to a wooden plank that was placed at the border of the pool in a way that the barrel hung in the water (Figure 5). The same device served as control but with a demagnetized neodymium block inside. This control block had the same dimensions and same density as the magnetized one, therefore the dolphins could probably not discriminate the two stimuli by echolocation (no information were available whether or not a magnetic field influences the properties of the echolocation signal but it seems unlikely). The device was always installed by a person blind to the content of the barrel, i.e. either the magnetic or the demagnetized neodymium block that were presented in a randomized order. The sessions were filmed with a video camera (Sony Handycam HDR-XR 155) on a tripod.
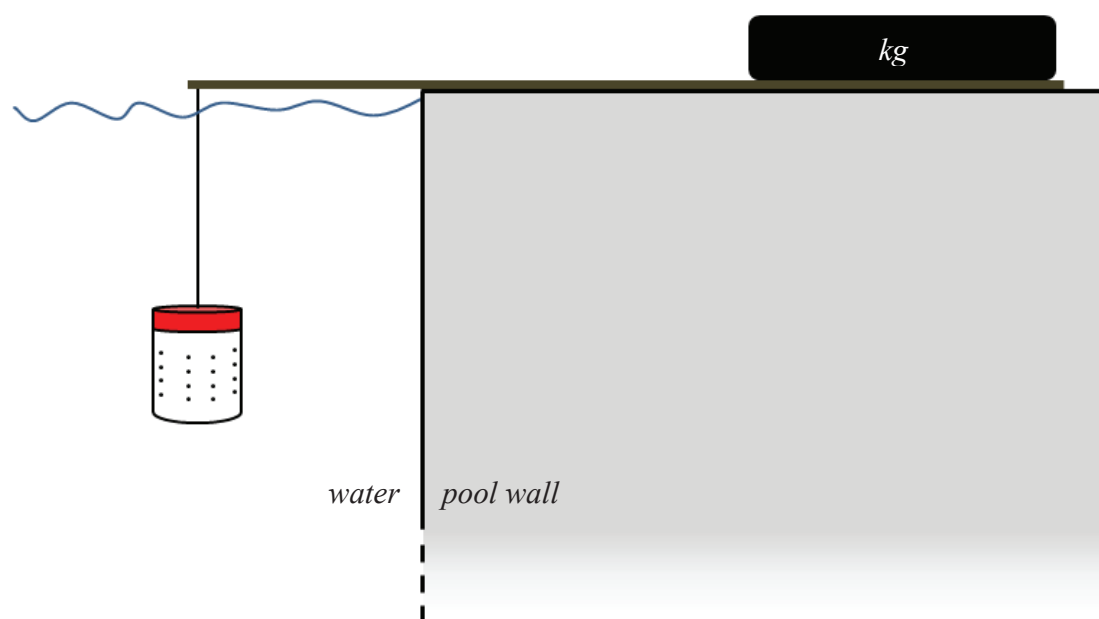
Figure 5: Experimental setup for the experiment "magnetoreception": the perforated plastic barrel hanging 40 cm from the pool wall at a depth of 50 cm, attached to a wooden plank (covered with neoprene to avoid injury and weighted down with a 10 kg block).

5.   DATA ANALYSIS

We used different parametric and non-parametric statistical tests to analyse the data obtained during the experiments. With the exception of the acoustic recordings, all data were available at the individual level. Statistic calculations were done using R software (version 2.15.0, R Development Core Team, www.r-project.org).

5.1.   Acoustic Recordings

Because the identity of the vocalizing dolphin was not available, data were available only at the group level. For temporal analyses, we divided the night by two-hour-intervals, leading to six time periods (i.e., 18:00-20:00, 20:00-22:00, 22:00-00:00, 00:00-02:00, 02:00-04:00, and 04:00-06:00).

First, whistles were visually classified into whistle categories following current bioacoustics methods (Adret-Hausberger 1989; Azevedo et al. 2007; Bazúa-Duran & Au 2002; Díaz López 2011; Lemasson & Hausberger 2011) and the number of whistles per time period was counted to determine the whistle rate of each whistle category. Whistle rates were compared between time periods (Chi²-tests) and between whistle categories (GLM) but also between whistle categories for each time period and vice versa (G-tests). Then, we investigated the temporal organization of vocal sequences, i.e. a series of consecutive whistles of the same whistle type by means of whistle repeatability (indicated by a whistle sequence index, WSI) and the inter-whistle-interval (IWI). WSI and IWI were compared between time periods across whistle categories. For WSI, a non-parametric G-test was used, whereas data on IWI allowed a parametric GLM.

During the analysis of the acoustic recordings, we found not only whistles but also some unusual sounds that have never been recorded previously from these dolphins. To evaluate the first impression that these unusual vocalizations were more similar to the whale calls broadcast during the daily public shows than to the dolphins' own whistles, we used a discriminant function analysis on several measured frequency and time parameters. To go further, a playback experiment with human subjects was conducted and the resulting assignment of sounds (dolphin or whale) was compared by using Wilcoxon tests.

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5.2. Chemoreception

5.2.1. Sense of Taste

Previous studies on dolphins' sense of taste investigated their detection thresholds by using the go/no-go paradigm (Friedl et al. 1990; Kuznetzov, 1990; Nachtigall & Hall 1984) and therefore no information on dolphins' spontaneous responses towards tastes was available. From preliminary observations we knew that dolphins sometimes stayed close to the experimenter but sometimes swam away and were therefore out of sight. That is why the latency to come back and beg for another ice cube was chosen as measure of the dolphin's interest in the previous ice cube flavour. We compared begging latencies between different flavours (LMM) considering the individual's identity as random factor.

5.2.2. Sense of Smell

As no previous studies on dolphins' sense of smell were available, we had no information on how a dolphin's reaction towards an odorous stimulus might look like. In general, however, breathing patterns affect the perception of odourants (Saslow 2002). Therefore we chose to simply take the number of respiration within a range of approximately 2.5 m around the barrels where the smell would be possibly detectable as a measure to investigate whether or not dolphins could perceive the odour. We compared the number of respirations between fish and control by using Wilcoxon tests.

5.3. Magnetoreception

Videos were analysed by an observer who was blind to the content of the barrel visible in the video. Different behaviours of the dolphins that occurred within a range of 1.5 m around the barrel were investigated. Therefore, we overlaid the video image with a border that marked this range. To create this border, we installed the device together with the tripod and the video camera once before the experiment started, and asked a trainer in the water to hold a measuring tape of 1.5 m. Whereas the other end of the measuring tape was at the barrel (hold by another person), the trainer removed herself from the device until the measuring tape was fully stretched out. At this

moment we took a picture with the video camera. This procedure was repeated several times in order to cover all sides of the barrel. Afterwards, the pictures were matched on the computer and the different measurement points were connected to create the border (Figure 6). Using one border for all experimental videos was possible, because the device and the tripod with the video camera were always installed in exactly the same way, therefore ensuring that the pictures filmed with the camera were always the same (i.e. the wooden plank reaching into the picture from the lower right corner with the same distances each time; Figure 6).
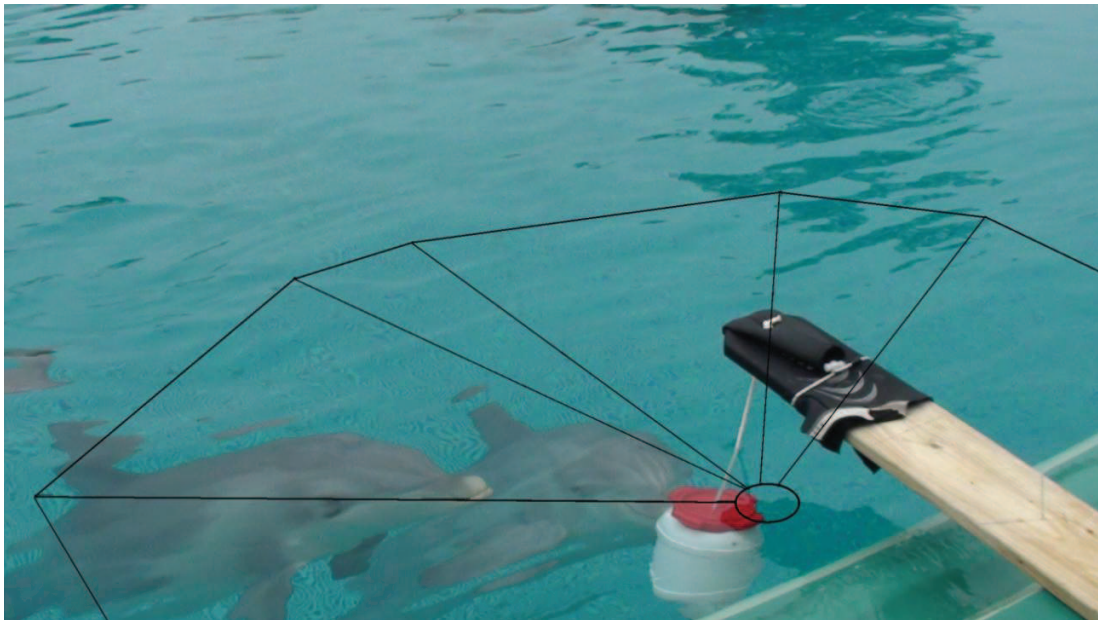
Figure 6: Screen shot from a video recorded during an experimental session of the experiment "magnetorecepotion". The black border was added in the picture to visualize the range of 1.5 m around the barrel within which the behaviours were measured. The circle marks the position of the barrel's lid when it hangs from the wooden plank without being touched (here, the two dolphins have touched the barrel, therefore it moved and the lid is no longer at its original position). The five lines represent the five distance measurements that were performed to create the 1.5 m-area's border.

The behaviours measured were: the latency for the first approach (i.e. entering the 1.5 m range around the device), the time spent within this area, the latencies for the first rostrum contact and the first body contact (i.e. contact with the device by another part of the body than the rostrum), as well as the number and duration of rostrum and body contacts. We compared all variables between magnet and control (Wilcoxon).

6. CONSTRAINTS

In general, working in a zoo offers several advantages such as continuous presence of the animals; however, there are also some constraints. Experiments can only take place between trainings and shows. Especially during the high season in summer, time schedules for experiments were restricted because the number of shows per day increased. On the other hand, winter is often the only time when necessary maintenance work on the facilities can be realised. Therefore, even in months without public shows, the possibility to conduct experiments was sometimes very limited. Highly complex facilities such as dolphinariums can be liable to technical problems, be it the filtration or something else. In the course of this thesis, some unforeseen technical problems occurred, thus obstructed, interrupted or stopped some experiments.

But also the dolphins themselves, as any other study species, can cause some complication. The most extensive impairment was their sexual activity that peaks in spring. In these times, all dolphins were highly engaged in sexual and social behaviours and were absolutely not responsive to anything else than another dolphin. Thus, the dolphins did not participate well (often not at all) neither in trainings or shows nor in experiments, meaning that the dolphins would not react to a trainer's command, a toy, or an experimental device.

In the particular case of this thesis another unexpected incidence occurred: two dolphins died due to illness, leaving the group each time socially unstable for a certain time afterwards.

CHAPTER 3
THE NOCTURNAL *UMWELT* OF DOLPHINS: RICHER THAN EXPECTED

SUMMARY OF PAPER 1

Questions: From the human point of view, the *Umwelt* differs between day and night due to a circadian activity rhythm, i.e. in general being awake during the day and sleeping during the night. Cetaceans are known to have a different type of sleep (unihemispheric in contrast to bihemispheric sleep), wherefore their activity rhythm is not as strictly committed to the same diurnal-nocturnal alternation. Still, nighttime is a particular period (darkness, quiet). However, little is known about the nocturnal *Umwelt* of dolphins. Is there a nocturnal activity, measurable by vocal activity?

Methods: We investigated the nocturnal whistle rate of the Planète Sauvage bottlenose dolphins. In addition, respiration rate served as indicator of physical activity as sleep in dolphins is, among others, characterized by low respiration rates.

Results: We found that the dolphins' vocal production followed a temporal pattern with two peaks of intense whistle activity (8 p.m. and midnight), which were followed by a strong decrease and low respiration rates, resembling the pre-sleep chorusing in other species.

Conclusions: Bottlenose dolphins' nightly activity pattern suggests that active phases alternate with more quiet phases. Although resting/sleeping probably occurs, their vocal activity indicates a more complex activity rhythm compared to simply diurnal/nocturnal rhythm, likely due to the unihemispheric sleep. Thus, the nocturnal *Umwelt* of dolphins can be considered richer than expected.

This paper is under review in ***Animal Behavior and Cognition*** and has been presented in parts at the 2013 International Ethological Conference & the Association for the Study of Animal Behaviour (*IEC 2013*).

PRESLEEP CHORUSING IN CAPTIVE BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*)

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Abstract

Diurnal animals also produce sounds at night. In several roosting species, high vocal activity at the roosting site seems to be a prerequisite to sleep, suggesting a role of vocal chorusing in coordinating resting activities. Dolphins' nocturnal vocal activity has been rarely investigated. However, this animal model is interesting because: dolphin resting behaviour is associated with social synchrony (swimming in tight formations and synchronous breathing) and dolphins' daily social activities are primarily mediated by vocal interactions. Therefore, we recorded the nocturnal vocal and breathing activities of a captive group of five bottlenose dolphins. The temporal pattern revealed two peaks of intense whistle activity (8 p.m. and midnight), which were followed by a strong decrease and low respiration rates, resembling the pre-sleep chorusing in other species. These findings are questioning the significance of nocturnal vocal activity in marine mammals. Contrarily to earlier reports on wild dolphins, these productions are clearly outside a nocturnal feeding context. They shed new light on the potential cognitive and social significance of auditory communication in this poorly known resting context.

Keywords: nocturnal activity; resting; whistle communication; breathing rate; cetaceans

1. INTRODUCTION

Dawn and dusk chorusing have been commonly described in a variety of songbirds (Burt & Vehrencamp 2005) and primates (Schel & Zuberbühler 2012). Different functional hypotheses have been proposed: inter-group spacing (Geissmann & Mutschler 2006), mate assessment or attraction (Galdikas 1983), adaption to sound propagation constraints (Henwood & Fabrick 1979), and intra-group coordination (Boinski & Campbell 1995). The phenomenon is especially striking in roosting species of birds or bats, where vocal activity at roosting sites is very intense and seems to be a prerequisite to sleep (Adret-Hausberger 1982; Kunz 1982). After that, sleeping birds and bats remain silent unless some disturbance occurs when a new (smaller) peak of vocal activity can be observed before resuming resting behaviour and silence (Adret-Hausberger 1982; Kunz 1982). Similar observations have been made in sleeping clusters of Barbary macaques (Ansorge et al. 1992). Vocal activity resumes again before emergence from roosts, e.g. about two hours before, in bats (Kunz 1982). In European starlings, peaks of vocal activity arise before each wave of departure of a bird group, suggesting a role of vocalization in synchronizing and coordinating departures of social groups (Adret-Hausberger 1982; Feare 1984; Hausberger et al. 2008). Vocal signals have also been shown to be involved in synchronizing flight departures in whooper and Bewick's swans (Black 1988) or troop movements in Campbell's monkeys (Ouattara et al. 2009) and howler monkeys (Milton 1980). One possible primary function proposed for nocturnal chorusing has indeed been interactive communication and social coordination (Burt & Vehrencamp 2005; Staicer et al. 1996).

Sleeping clusters in primates as well as nocturnal roosting in birds and bats rely upon social synchrony (Adret-Hausberger 1982; Ansorge et al. 1992; Feare 1984; Hammerschmidt et al. 1994; Hausberger et al. 2008; Kunz 1982). Young Barbary macaques show distress if they are not included in a sleeping cluster (Ansorge et al. 1992; Hammerschmidt et al. 1994). In European starlings, songs seem to help the birds to remain in vicinity of socially related conspecifics (Hausberger et al. 2008). Although little is still known on sleeping behaviour of cetaceans (Lyamin et al. 2008), resting/sleeping behaviour was found to account for 87% of total time at night in captive bottlenose dolphins (Sekiguchi & Kohshima 2003) and is associated with social synchrony during so-called swim-rest, involving two or more individuals (Gnone et al. 2001; Sekiguchi & Kohshima 2003). Wild dolphins also show

resting in tight formations ("carpet formation"; Würsig et al. 1994), and this synchronous swimming is performed with often one eye open on the nearest neighbor's side (Goley 1999). At that stage, dolphins are silent (Gnone et al. 2001; Sekiguchi & Kohshima 2003).

Data on diel patterns of vocalizations in cetaceans are variable. Captive bottlenose dolphins tend to produce more vocalizations at daytime (Moore & Ridgway 1996; Therrien et al. 2012), whereas other cetacean species were found to be vocally more active at nighttime in the wild (Munger et al. 2008; Stafford et al., 2012). Several authors assumed an association between nocturnal foraging and vocal activity in dolphins (Goold 2000; Notarbartolo di Sciara & Gordon 1997). Indeed, bottlenose dolphins increase whistle rate during day feeding events, probably to recruit other individuals (Acevedo-Gutiérrez & Stienessen 2004). However, choruses outside feeding periods have been described at night in humpback whales (Au et al. 2000) as well as at sunrise in bottlenose dolphins (Powell 1966). Overall, increased whistle production has been associated with increased group excitement (Díaz López & Shirai 2009; dos Santos et al. 2005) and socializing (Jones & Sayigh 2002; Quick & Janik 2008). In the wild, solitary animals do not seem to produce whistles (Díaz López & Shirai 2009).

In the present study, we hypothesized that resting behaviour in bottlenose dolphins, as it involves social synchrony (Gnone et al. 2001; Sekiguchi & Kohshima 2003; Würsig et al. 1994), may be preceded by increased vocal activity, possibly reflecting as in roosting birds and bats the excitement preceding resting/sleeping. In order to test this hypothesis, the vocal and respiratory activity of a group of captive bottlenose dolphins was recorded all night long.

2. MATERIAL & METHODS

2.1. Subjects and housing conditions

We studied three male (5, 10, and 25 years old) and two female (8 and 17 years old) captive-born bottlenose dolphins (*Tursiops truncatus*) in the facility of Planète Sauvage (Port-Saint-Père, France). Before they were brought together in Planète Sauvage in December 2008, the males and the females respectively lived together in other delphinariums. Overall, this outdoor facility covers over 2000 m² water surface and contains 7500000 l salt water cleaned with ozone. The diet of the dolphins was primarily composed of fish (herring, capelin, sprat, mackerel, and whiting) and squid.

The daily ration of 5-10 kg per individual (depending on its size) was given throughout the day (between 9 a.m. and 5 p.m.) during nine training and feeding sessions conducted by the dolphin trainers. Sessions includes medical training (e.g., acceptance of inspection and palpation) as well as training for public presentations (e.g., jump on command).

2.2. Data collection

We observed the dolphins at different times, between 6 p.m. and 6 a.m., during eight nights in April and May 2009 (22 hours in total). Observation sessions lasted about one hour each, were repeated 2 to 5 times per night, and were distributed over the different nights in order to cover all night hours. During observations, a Nauta SS03-10 hydrophone was connected to a Marantz PMD 670 recorder (sample rate: 44.1 kHz; resolution: 16 bit; frequency response: 15-20000 Hz ± 3dB) to record the vocalizations. In order to assess in parallel the physical activity of the animals, a human observer (M.B.J.), positioned next to the pool, counted the number of respirations. Although visual restrictions at night did not allow observation or identification, blows were well audible and therefore useful for data collection. For subsequent analyses, data were pooled in six "time periods" lasting two hours (i.e., 6-8, 8-10, and 10-12 p.m., 0-2, 2-4, and 4-6 a.m.), leading to 2 to 6 repetitions (recording at different nights) per time period, with an average recording duration of 221 ± 89 minutes per time period (for details see Table 1).

Table 1: Details about acoustic recordings for each time period, containing the number of recordings that were made at different nights, the total duration of the recordings, and the number of whistles found in these recordings.

Time period	Number of recordings at different nights	Total recording duration [min]	Number of whistles recorded
6-8 p.m.	3	151	35
8-10 p.m.	2	203	135
10-12 p.m.	6	374	83
0-2 a.m.	4	275	164
2-4 a.m.	2	140	17
4-6 a.m.	3	184	44
Sum	19	1327	484
Mean ± SD	3 ± 1.6	221 ± 88.9	81 ± 59.1

2.3. Data analysis

2.3.1. Whistle classification

As we did not have access to callers' identity it was not possible to analyse signature whistles (Caldwell & Caldwell 1965) as it is often done (reviewed by Janik & Sayigh 2013). Moreover, our past investigations at day time confirmed that many whistle types were shared among group members as it is often found in captivity (McCowan & Reiss 1995). Indeed, signature whistles are reported to be often not produced at all in captivity (Janik & Slater 1998). Therefore we used a more global classification method not considering single whistle types but broader whistle categories to address the comprehensive structure of vocal activity.

Whistles were classified into whistle categories according to their number of inflection points and the orientation of their frequency modulation (Azevedo et al. 2007; Bazúa-Duran & Au 2002; Díaz López 2011). The definition for an inflection point was adopted from Pivari and Rosso (2005): a change in the slope of the whistle contour from negative to positive, or vice versa. This classification, also used in classical bioacoustic research (e.g. Adret-Hausberger 1989; Lemasson & Hausberger 2011), led to seven whistle categories (Figure 1).

2.3.2. Whistle and respiration rate

Whistle and respiration rates were counted for each night time period: number of whistles per 120 minutes ("whistle rate") and number of respirations per 120 minutes ("respiration rate"). In a comparative perspective, we also calculated the day whistle rate from recordings made in the same facility with the same group and the same equipment (performed during 4 days in March 2009 between 10 a.m. and 5 p.m.; 16 recording sessions with a total duration of 220 minutes). We considered the obtained day rate (19.64 whistles per 120 minutes) as a baseline rate, since it was comparable with the whistle rate reported in another study in a same-size group of captive bottlenose dolphins (13.62 whistles per 120 minutes; Therrien et al. 2012).

During day and night recordings group condition was calm, i.e., individuals were together as a group and had been in the facility for more than three months. Recordings were never performed during training sessions or public presentation.
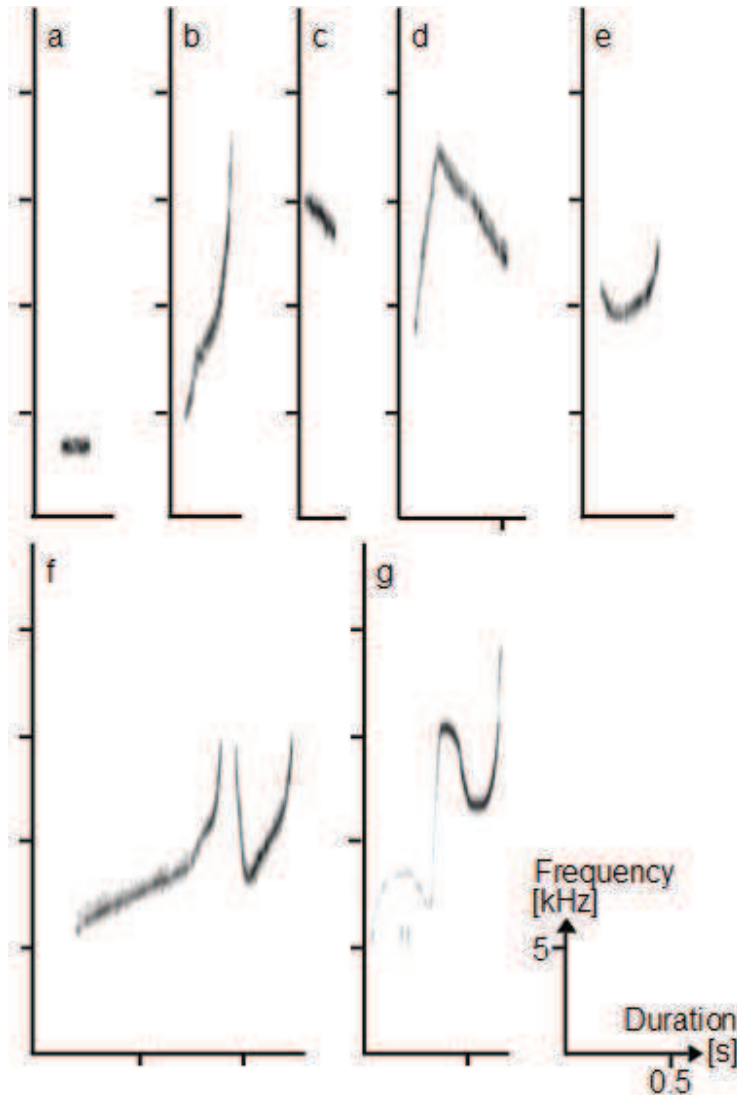
Figure 1: Spectrograms of nocturnal whistle categories emitted by bottlenose dolphins in Planète Sauvage. Whistle categories: (a) "flat": no inflection point, constant frequency contour; (b) "rising": (no inflection point, ascendant frequency contour; (c) "descending": no inflection point, descendant frequency contour; (d) "wave": one inflection point, ascendant-descendant frequency contour; (e) "U-shape": one inflection point, descendant- ascendant frequency contour; (f) "sine": two inflection points; (g) "multilooped": more than two inflection points (Spectrograms drawing: scales standardized; fast Fourier transformation: 1,024 samples; window type: Hann; band filter: 0-2 kHz).

2.3.3. Acoustic and temporal organization of vocal sequences

Whistles were often emitted in sequences, i.e. a series of consecutive whistles of the same whistle type. To describe the proportion of whistle sequences within a given recording, we calculated a whistle sequence index (WSI) as follows:

$$\frac{\text{Number of pairs with two consecutive whistles of the same category}}{\text{Total number of whistle pairs}} * 100$$

WSI ranges from 100, meaning that all whistles are of the same category, to 0, meaning that no whistle is followed by a whistle of the same category. Repetitions can result from a single individual repeating a certain whistle category or from a vocal interaction between individuals. Inter-whistle-interval (IWI) can give some indication of the character of these repetitions: bottlenose dolphins' IWI was reported to be between 1-10 seconds when single individuals repeat a certain whistle category (Janik et al. 2013), but mostly less than 3 second during vocal interactions (Janik 2000). Therefore, IWI, i.e., the time between the end of a whistle and the start of the following whistle, was measured to assess potential vocal interaction activity. We did not determine a maximum IWI above which two whistles were no anymore considered as a pair but included all whistle pairs in this analysis.

2.4. Statistical analysis

All statistic calculations were done using R software (version 2.15.0, R Development Core Team, www.r-project.org).

2.4.1. Whistle and respiration rate

Whistle and respiration rates were compared using Chi²-tests, which were also used for pairwise comparisons (correction: False Discovery Rate (FDR); R package: RVAideMemoire). Whistle rate was compared between whistle categories by using a likelihood ratio test on an additive Generalized Linear Model (GLM), with a Poisson family. Pairwise comparisons were performed

with the contrasts method (correction: False Discovery Rate (FDR); R package: doBy). To go further, whistle rate was compared between whistle categories for each time period by using a G-test. When needed, pairwise comparisons were performed by using multiple G-tests (correction: FDR). The same procedure was used to compare whistle rate depending on time period for each whistle category. Overall whistle rate was compared between night and day using Chi²-test. Spearman's rank correlation evaluated a possible relationship between whistle and respiration rates.

2.4.2. Acoustic and temporal organization of vocal sequences

WSI was compared between time periods by using a G-test, followed by pairwise comparisons (correction: FDR). IWI was compared between time periods by using a GLM with a negative binomial law (R package: MASS), followed by pairwise comparisons with the contrasts method (correction: FDR). Spearman's rank correlation evaluated a possible relationship between WSI and IWI. Overall WSI, average IWI, and average sequence length were compared between night and day using Chi²-tests.

3. RESULTS

3.1. Whistle and respiration rate

During observations, a total of 484 whistles were recorded. Vocal activity varied significantly in the course of the night (Figure 2). Whistles rate was significantly higher than expected at 8-10 p.m. and 0-2 a.m. (N = 6; $34.89 \geq \chi^2 \geq 30.98$, p < 0.001), whereas it was lower than expected at 6-8 and 10-12 p.m. and 2-4 and 4-6 a.m. (N = 6; $5.16 \leq \chi^2 \leq 20.13$, p ≤ 0.023). Highest whistle rate (76 whistles per 120 minutes) was recorded at 8-10 p.m. and was around five times higher than at 2-4 a.m., when we recorded the lowest whistle rate (15 whistles per 120 minutes). Overall, whistle rate was significantly higher at night (43.21 whistles per 120 minutes) compared to day whistle rate (19.64 whistles per 120 minutes; $\chi^2 = 8.83$, p = 0.003). Respiration rate presented a different pattern, globally decreasing from 6-8 p.m. (763 respirations per 120 minutes, i.e. 1.27 respirations/minute/individual) to 4-6 a.m. (574 respirations per

120 minutes, i.e. 0.96 respirations/minute/individual; Figure 2). At 6-8 and 8-10 p.m., respiration rate was significantly higher than expected ($18.30 \geq \chi^2 \geq 7.08$, $p \leq 0.016$), whereas it was lower than expected at 4-6 a.m. ($\chi^2 = 14.19$, $p < 0.001$). Whistle and respiration rates were not correlated (Spearman's rank correlation: $N = 6$; $r_s = 0.696$, $p = 0.125$), however, the lowest respiration rates were observed just after the highest whistles rates.
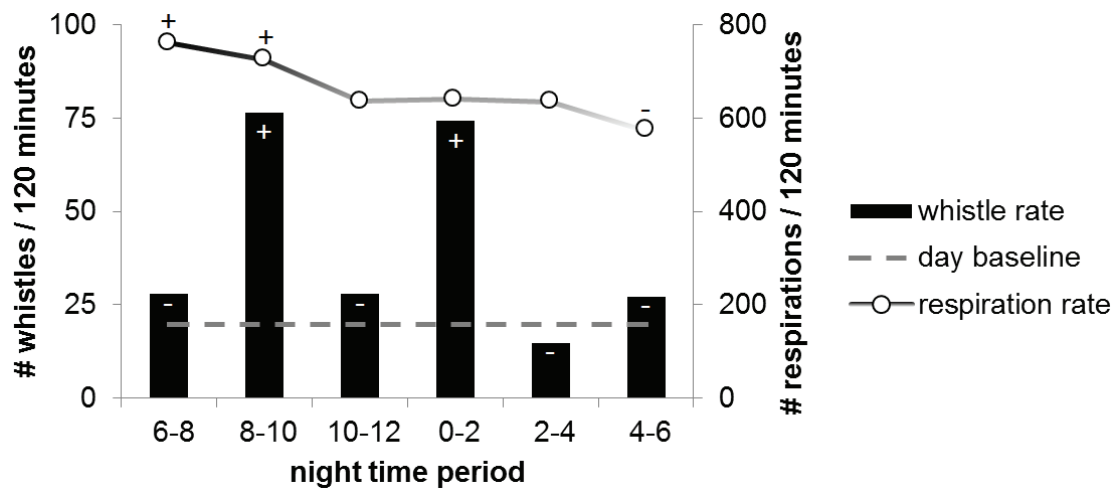
Figure 2: Changes in whistle and respiration rates in the course of the night. Whistle and respiration rates (i.e. number of whistles and respirations, respectively, per 120 minutes) are illustrated with black bars and white circles, respectively. Plus- and minus-signs indicate that the observed rates are significantly higher or lower, respectively, than expected (Chi²-tests; alpha = 0.05). Mean day whistle rate is illustrated as a baseline (grey dashed line).

Whistle rate differed according to whistle category (likelihood ratio test: $N = 42$; $\chi^2 = 131.40$). Overall, regardless of night time period, "multilooped" whistles were preferentially emitted ($p \leq 0.025$), followed by "rising" whistles ($p \leq 0.006$), whereas "wave" whistles had lowest whistle rate ($p \leq 0.005$). Likewise, at day, "multilooped" and "rising" whistles had highest whistles rates and accounted for 80.56% of all whistles recorded during the day reference period. Considering both whistle category and night time period, either were found to affect whistle rate (G-test; whistle category: $N = 7$, $G = 19.40$; time period: $N = 6$, $G = 2.47$; Figure 3). Three whistle categories did not differ statistically in whistle rate between time periods, meaning their whistle rates were consistent in the course of the night ("flat": $G = 2.52$, $p = 0.773$; "wave":

G = 6.74, p = 0.240; "sine": G = 7.69, p = 0.174). Whistle rates of all other whistle categories ("rising", "descending", "U-shape", "multilooped") differed according to time period (40.08 ≥ G ≥ 17.43, 0.004 ≥ p ≥ 0.001). The relative frequency of occurrence of the different whistle categories differed according to time period. Thus, dolphins produced mostly "multilooped" whistles during the first peak at 8-10 p.m. (52.6%; G = 74.09, p < 0.001) and "rising" whistles during the second peak at 0-2 a.m. (32.9%; G = 27.45, p ≤ 0.006).
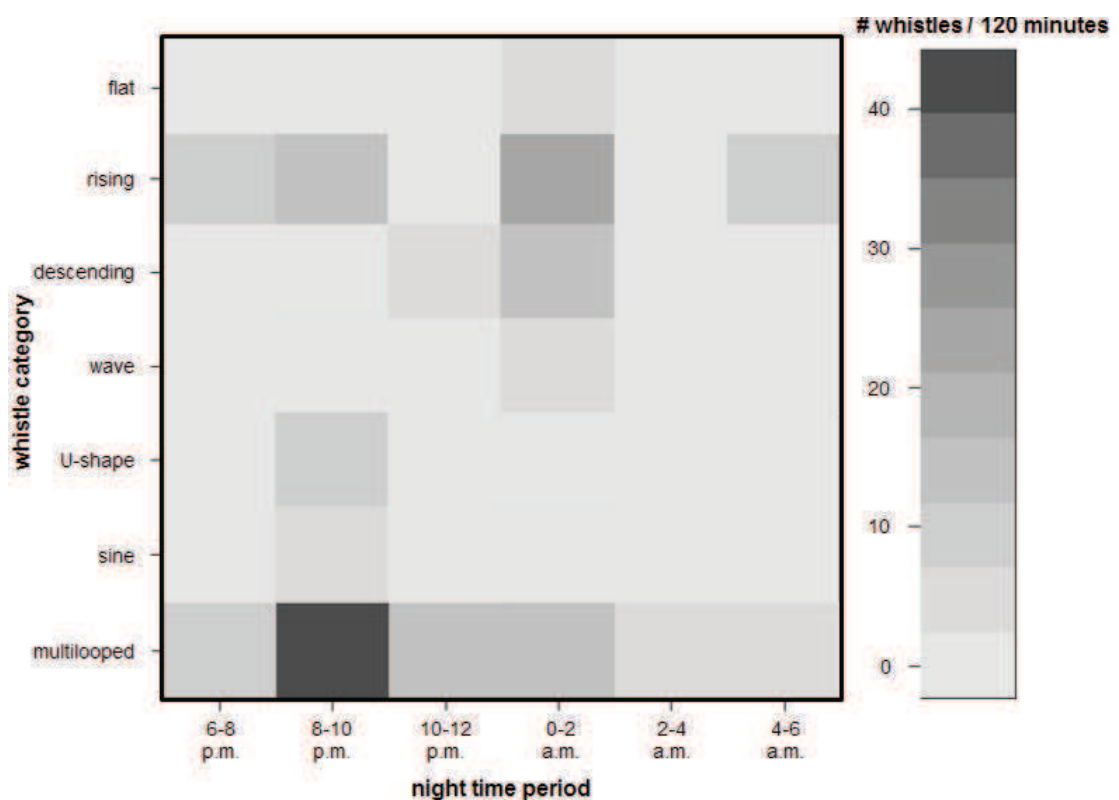
Figure 3: Matrix representing rates of production whistle categories across time periods. The darker the colour, the higher the whistle rate (number of whistles per 120 minutes).

3.2. Acoustic and temporal organization of vocal sequences

At night, almost half (48.5%) of the recorded whistles occurred in sequences, i.e., at least two consecutive whistles of the same category (227 pairs of whistles of the same category out of 468 whistle pairs in total), whereas at day it accounts for more than three quarters (76.47%). In total, we found 79 whistle sequences at night and 5 at

day. The longest sequences were repetitions of "multilooped" whistles (at night: comprising 37 whistles; at day: comprising 15 whistles), the average whistle sequence length was 3.9 whistles at night and 6.2 whistles at day (difference not significant: $\chi^2 = 0.52$, p = 0.469).

Whistle repeatability (indicated by WSI) was below the day baseline of 76.47 ($\chi^2 = 6.26$, p = 0.012). Furthermore, WSI differed significantly between night time periods (G-test: N = 6; G = 21.91, p < 0.001; Figure 4), reaching its maximum at 8-10 p.m. (WSI = 0.64), the time period when whistle rate was highest. Whistles of the same category were repeated more often in early evening (6-8 and 8-10 p.m.) and early morning (4-6 a.m.) compared to the middle of the night (p $\leq$ 0.018).

Nocturnal inter-whistle-interval (IWI) was above the day baseline of 16.12 sec ($\chi^2 = 18.90$, p < 0.001). IWI was around four times higher at 2-4 a.m. compared to all other night time periods (GLM: N = 471; $\chi^2 = 60.41$, p $\leq$ 0.002; Figure 4). This time period is coincident with the time period when whistle rate was lowest. Overall, whistles occurring in sequence (intra-sequence whistles) were separated by shorter IWIs compared to whistles not occurring in sequence (non-sequence whistles), but both followed the same course (i.e., clearly peaking at 0-2 a.m.). WSI and IWI were not correlated (Spearman's rank correlation: N = 6; rS = 0.143, p = 0.803).
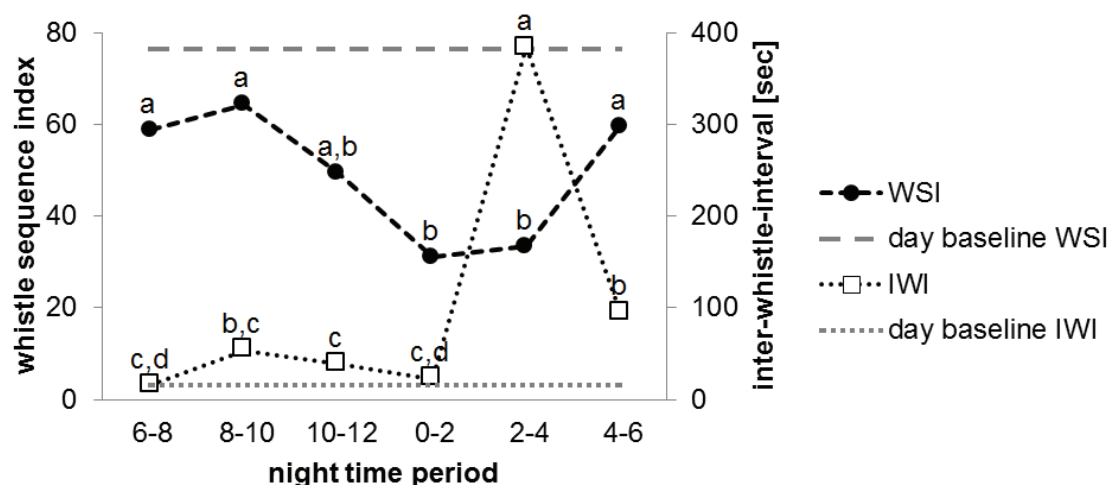
Figure 4: Changes in temporal organization of vocal sequences in the course of the night. Whistle sequence index (WSI) and inter-whistle-interval (IWI) are illustrated with black circles and white squares, respectively. Same letters indicate absence of statistical difference between two given time periods (WSI: G-test; IWI: GLM; alpha = 0.05). Mean day WSI and IWI are illustrated as baselines (grey dashed and dotted line, respectively).

4.   DISCUSSION

Nocturnal underwater acoustic recordings of a group of captive bottlenose dolphins revealed a temporal pattern with two peaks, one early at night (8-10 p.m.) and the other just after midnight. Both were followed by a strong decrease of vocal activity. Although this pattern was not correlated with the breathing pattern, lower breathing rates were observed just after those peaks.

The peaks observed revealed a higher whistle rate than during day recordings which is in accordance both with the finding that some wild dolphins whistle intensively at night (Atem & Monteiro-Filho 2006), and that peaks in vocal activity may occur (Powell 1966). Indeed, at these time periods, increased repeatability of whistle categories and short inter-whistle intervals may suggest that whistle matching interactions between group members did occur (Janik 2000; Janik et al. 2013) and that some degree of excitement could be involved (Díaz López & Shirai 2009; dos Santos et al. 2005). Other cetaceans such as humpback whales also show chorusing at night with peaks before and after midnight (Au et al. 2000).

The very low breathing rates observed after the peaks, especially after 2 a.m., correspond to values associated to bottom or surface resting observed in another study (0.48 and 1.05 respirations/minute/individual, respectively; Sekiguchi & Kohshima 2003). These behaviours were associated with one or two eyes closed, thus potentially to sleep. Sleeping behaviour has been shown to occur mostly at night (0-3 a.m.; Sekiguchi & Kohshima 2003) with low breathing and vocal activity (Gnone et al. 2001; Sekiguchi & Kohshima 2003). However, dolphins are not entirely quiet and sometimes even produce unusual vocalizations that seem to be vocally expressed rehearsals of day events (Kremers et al. 2011 → paper 2).

A previous study on vocal activity of captive bottlenose dolphins using 24h-recordings from 15 days found that both daytime and group composition had influence: whereas vocal activity showed peaks at 9 p.m. and 2 a.m. in a group composed of two adult, two juvenile males, two adult, and two juvenile females; after the two adult males were removed to another facility, only afternoon peaks were observed (Therrien et al. 2012). Maybe males are especially involved in these increased vocal activities, which would explain that these peaks were especially visible in our study, where three males were present.

Finally, the repertoire use was also interesting with more variety and especially "multilooped" whistles at the first peak, while "rising" whistles were predominant at the

second peak. Dolphins tend to use a higher variety of sounds when excited (dos Santos et al. 2005), which suggests that the first peak may indeed recall the roosting choruses observed in a variety of species (Adret-Hausberger 1982; Kunz 1982), which are followed by a quiet phase (here about 0.05 whistles/minute/individual). However, contrarily to bird roosts in undisturbed conditions, a new peak arises later again. This second peak is yet different with a slightly lower whistle rate and the majority of whistles being "rising" that is a whistle category simpler in structure than "multilooped". It may thus correspond to a less "excited" state in the dolphin group, characterized by less complex whistles and less repetitions. Furthermore, other social species are known to use simple call structures in coordination and synchronization contexts (primates: Boinski & Campbell 1995; birds: Black 1988).

Sleep cycle length in dolphins is rarely documented but seems to last 1-2 hours (Ridgway 2002). This may explain the interval between the two vocal peaks observed. Overall, these data suggest that dusk chorusing occurs that precedes a first sleep phase while readjustment after two hours is associated with a renewed, but somewhat quieter vocal activity before a deeper, longer sleep period.

However, alternatively it is possible that the peaks in vocal activity observed in this study result from certain individuals that may be more vocal than others, repeating the same "multilooped" structures. Maybe this increased vocal activity indicates that this individual is more instrumental in coordinating the group's activity.

Chorusing behaviour in cetaceans has begun to be studied only recently and it seems likely that it serves different functions depending on the species. Chorusing in dolphins was mentioned only sporadically, occurring during behaviours that seem to ensure behavioural synchrony and social facilitation, and was assumed to serve in cohesion (Norris et al. 1994).

Our findings contribute to provide further comprehension of vocal nocturnal activity in cetaceans. They suggest that vocal activity may support the social synchrony observed in groups of resting/sleeping dolphins and provide some further explanation for cetacean night choruses. By including a new phylogenetical group, this study contributes to the existing comparative studies on social aspects of chorusing. Finally, this study reveals that integrating more research on dolphins with the literature on birds and other species may lead to new paths in cetacean behavioural research.

Acknowledgements

References

Acevedo-Gutiérrez, A. & Stienessen, S. C. (2004). Bottlenose dolphins (*Tursiops truncatus*) increase number of whistles when feeding. Aquatic Mammals, 30, 357-362.

Adret-Hausberger, M. (1982). Social influences on the whistled songs of starlings. Behavioral Ecology and Sociobiology, 11, 241-246.

Adret-Hausberger, M. (1989). The species-repertoire of whistled songs in the European starling: species-specific characteristics and variability. Bioacoustics, 2, 137-162.

Ansorge, V., Hammerschmidt, K. & Todt, D. (1992). Communal roosting and formation of sleeping clusters in Barbary macaques (*Macaca sylvanus*). American Journal of Primatology, 28, 271-280.

Atem, A. C. G. & Monteiro-Filho, E. L. A. (2006). Nocturnal activity of the estuarian dolphin (*Sotalia guianensis*) in the region of Cananéia, São Paulo State, Brazil. Aquatic Mammals, 32, 236-241.

Au, W. W. L., Mobley, J., Burgess, W.C. & Lammers, M. O. (2000). Seasonal and diurnal trends of chorusing humpback whales wintering in waters off western Maui. Marine Mammal Science, 16, 530-544.

Azevedo, F. A., Oliveira, A. M., Dalla Rosa, L. & Lailson-Brito, J. (2007). Characteristics of whistles from resident bottlenose dolphins (*Tursiops truncatus*) in southern Brazil. Journal of the Acoustical Society of America 121, 2978-2983.

Bazúa-Duran, M. C. & Au, W. W. L. (2002). The whistles of Hawaiian spinner dolphins. Journal of the Acoustical Society of America 112, 3064-3072.

Black, J. M. (1988). Preflight signalling in swans: a mechanism for group cohesion and flock formation. Ethology 79, 143-157.

Boinski, S. & Campbell, A. F. (1995). Use of trill vocalizations to coordinate troop movement among white-faced capuchins: a second field test. Behaviour 132, 875-901.

Burt, J. M. & Vehrencamp, S. L. (2005). Dawn chorus as an interactive communication network. In: Animal communication networks, edited by McGregor, P. K., pp. 320-343. Cambridge University Press, Cambridge.

Caldwell, M. C. & Caldwell, D. K. (1965). Individualized whistle contours in bottlenose dolphins (*Tursiops truncatus*). Nature 207, 434-435.

Díaz López, B. (2011). Whistle characteristics in free-ranging bottlenose dolphins (*Tursiops truncatus*) in the Mediterranean Sea: influence of behaviour. Mammalian Biology 76, 180-189.

Díaz López, B. & Shirai, J. A. B. (2009). Mediterranean common bottlenose dolphin's repertoire and communication use. In: Dolphins: anatomy, behavior, and threats, edited by Pearce, A. G. & Correa, L. M., pp. 129-148. Nova Science Publishers, Inc., New York.

dos Santos, M. E., Louro, S., Couchinho, M. & Brito, C. (2005). Whistles of bottlenose dolphins (*Tursiops truncatus*) in the Sado estuary, Portugal: characteristics, production rates, and long-term contour stability. Aquatic Mammals 31, 453-462.

Feare, C. J. (1984). The starling. Oxford University Press, Oxford.

Galdikas, B. M. F. (1983). The orangutan long call and snag crashing at Tanjung Puting Reserve. Primates 24, 371-384.

Geissmann, T. & Mutschler, T. (2006). Diurnal distribution of loud calls in sympatric wild indris (Indri indri) and ruffed lemurs (*Varecia variegata*): implications for call functions. Primates 47, 393-396.

Gnone, G., Benoldi, C., Bonsignori, B. & Fogani, P. (2001). Observations of rest in captive bottlenose dolphins. Aquatic Mammals 27, 29-33.

Goley, P. D. (1999). Behavioral aspects of sleep in Pacific white-sided dolphins (*Lagenorhynchus obliquidens*, Gill 1865). Marine Mammal Science 15, 1054-1064.

Goold, J. C. (2000). A diel pattern in vocal activity of short-beaked common dolphins, *Delphinus delphis*. Marine Mammal Science 16, 240-244.

Hammerschmidt, K., Ansorge, V., Fischer, J. & Todt, D. (1994). Dusk calling in barbary macaques (*Macaca sylvanus*): demand for social shelter. American Journal of Primatology 32, 277-289.

Hausberger, M., Bigot, E. & Clergeau, P. (2008). Dialect use in large assemblies: a study in European starlings *Sturnus vulgaris* roosts. Journal of Avian Biology 39, 672-682.

Henwood, K. & Fabrick, A. (1979). A quantitative analysis of the dawn chorus: temporal selection for communicatory optimization. American Naturalist 114, 260-274.

Janik, V. M. (2000). Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). Science 289, 1355-1357.

Janik, V. M. & Sayigh, L. S. (2013). Communication in bottlenose dolphins: 50 years of signature whistle research. Journal of Comparative Physiology A 199, 479-489.

Janik, V. M. & Slater, P. J. B. (1998). Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. Animal Behaviour 56, 829-838.

Janik, V. M., King, S. L., Sayigh, L. S. & Wells, R. S. (2013). Identifying signature whistles from recordings of groups of unrestrained bottlenose dolphins (*Tursiops truncatus*). Marine Mammal Science 29, 109-122.

Jones, G. J. & Sayigh, L. S. (2002). Geographic variation in rates of vocal production of free-ranging bottlenose dolphins. Marine Mammal Science 18, 374-393.

Kremers, D., Briseño Jaramillo, M., Böye, M., Lemasson, A. & Hausberger, M. (2011). Do dolphins rehearse show-stimuli when at rest? Delayed matching of auditory memory. Frontiers in Psychology 2, 386.

Kunz, T. H. (1982). Roosting ecology of bats. In: Ecology of bats, edited by Kunz, T. H., pp. 1-55. Plenum Publishing Corporation, New York.

Lemasson, A. & Hausberger, M. (2011). Acoustic variability and social significance of calls in female Campbell's monkeys (*Cercopithecus campbelli campbelli*). Bioacoustics 129, 3341-3352.

Lyamin, O. I., Manger, P. R., Ridgway, S. H., Mukhametov, L. M. & Siegel, J. M. (2008). Cetacean sleep: an unusual form of mammalian sleep. Neuroscience and Biobehavioral Reviews 32, 1451-1484.

McCowan, B. & Reiss, D. (1995). Quantitative comparison of whistle repertoires from captive adult bottlenose dolphins (Delphinidae, *Tursiops truncatus*): A re-evaluation of the signature whistle hypothesis. Ethology 100, 194-209.

Milton, K. (1980). The foraging strategy of howler monkeys. Columbia University Press, New York.

Moore, S. E. & Ridgway, S. H. (1996). Patterns of dolphin sound production and ovulation. Aquatic Mammals 22, 175-184.

Munger, L. M., Wiggins, S. M., Moore, S. E. & Hildebrand, J. A. (2008). North Pacific right whale (*Eubalaena japonica*) seasonal and diel calling patterns from long-term acoustic

recordings in the southeastern Bering Sea, 2000–2006. Marine Mammal Science 24, 795-814.

Norris, K. S., Würsig, B., Wells, R. S. & Würsig, M. (1994). The Hawaiian spinner dolphin. University of California Press, Berkeley and Los Angeles.

Notarbartolo di Sciara, G. & Gordon, J. (1997). Bioacoustics: A tool for the conservation of cetaceans in the Mediterranean Sea. Marine Freshwater Behaviour and Physiology 30, 125-146.

Ouattara, K., Lemasson, A. & Zuberbühler, K. (2009). Campbell's monkeys concatenate vocalizations into context-specific call sequences. Proceedings of the National Academy of Science 106, 22026-22031.

Pivari, D. & Rosso, S. (2005). Whistles of small groups of *Sotalia fluviatilis* during foraging behavior in southeastern Brazil. Journal of the Acoustical Society of America 118, 2725-2731.

Powell, B. A. (1966). Periodicity of vocal activity of captive Atlantic bottlenose dolphin: *Tursiops truncatus*. Bulletin Southern California Academy of Sciences 65, 237-244.

Quick, N. J. & Janik, V. M. (2008). Whistle rates of wild bottlenose dolphins (*Tursiops truncatus*): influences of group size and behavior. Journal of Comparative Psychology 122, 305-311.

Ridgway, S. H. (2002). Asymmetry and symmetry in brain waves from dolphin left and right hemispheres: some observations after anesthesia, during quiescent hanging behaviour, and during visual obstruction. Brain, Behavior and Evolution 60, 265-274.

Schel, A. M. & Zuberbühler, K. (2012). Dawn chorusing in guereza colobus monkeys. Behavioral Ecology and Sociobiology 66, 361-373.

Sekiguchi, Y. & Kohshima, S. (2003). Resting behaviors of captive bottlenose dolphins (*Tursiops truncatus*). Physiology and Behavior 79, 643-653.

Stafford, K. M., Moore, S. E., Berchok, C. L., Wiig, Ø., Lydersen, C., Hansen, E., Kalmbach, D. & Kovacs, K. M. (2012). Spitsbergen's endangered bowhead whales sing through the polar night. Endangered Species Research 18, 95-103.

Staicer, C. A., Spector, D. A. & Horn, A. G. (1996). The dawn chorus and other diel patterns in acoustic signaling. In: Ecology and evolution of acoustic communication in birds, edited by Kroodsma, D. E. & Miller, E. H., pp. 426-453. Cornell University Press, Ithaca.

Therrien, S. C., Thomas, J. A., Therrien, R. E. & Stacey, R. (2012). Time of day and social change affect underwater sound production by bottlenose dolphins (*Tursiops truncatus*) at the Brookfield Zoo. Aquatic Mammals 38, 65-75.

Würsig, B., Wells, R. S., Norris, K. S. & Würsig, M. (1994). A spinner dolphin's day. In: The Hawaiian spinner dolphin, edited by Norris, K. S., Würsig, B., Wells, R. S. & Würsig, M., pp. 65-102. University of California Press, Berkeley and Los Angeles.

SUMMARY OF PAPER 2

Questions: Dolphins are known to be able to copy sounds from their environment. Further it has been shown that dolphins produce vocal copies especially in the presence of a certain object that was associated with the original sound. This implies that these objects were meaningful to the dolphins. Is it therefore possible to assess a potential meaningfulness through the dolphins' vocal productions? Can the production of vocal copies serve as indicator for the meaningfulness of the original sound or the context with which this sound was associated?

Methods: We investigated hitherto unknown vocalization of the Planète Sauvage bottlenose dolphins in terms of acoustic parameters (discriminant function analysis) and sound similarity (playback experiment with human subjects).

Results: We found that the unusual dolphin vocalizations were more similar to whale calls than to the dolphins' own whistles in terms of acoustic parameters and sound similarity. The whale calls were part of the soundtrack accompanying the daily public shows. Dolphins were found to produce vocal copies of these sounds during their night time resting periods in the first weeks after the whale sounds were added to the soundtrack. Recordings made before the whale sounds started being broadcast revealed that they had never emitted such sounds before.

Conclusions: Bottlenose dolphins show a separation between auditory memory formation and vocal copy production and perhaps a vocally expressed nocturnal rehearsal of day events. Thus, vocalizations can serve as possible indicators of events or objects that are meaningful to the dolphins.

DO DOLPHINS REHEARSE SHOW-STIMULI WHEN AT REST?
DELAYED MATCHING OF AUDITORY MEMORY

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Abstract

The mechanisms underlying vocal mimicry in animals remain an open question. Delphinidae are able to copy sounds from their environment that are not produced by conspecifics. Usually, these mimicries occur associated with the context in which they were learned. No reports address the question of separation between auditory memory formation and spontaneous vocal copying although the sensory and motor phases of vocal learning are separated in a variety of songbirds. Here we show that captive bottlenose dolphins produce, during their night time resting periods, non-dolphin sounds that they heard during performance shows. Generally, in the middle of the night, these animals produced vocal copies of whale sounds that had been broadcast during daily public shows. As their life history was fully known, we know that these captive dolphins had never had the opportunity to hear whale sounds before then. Moreover, recordings made before the whale sounds started being broadcast revealed that they had never emitted such sounds before. This is to our knowledge the first evidence for a separation between formation of auditory memories and the process of learning to produce calls that match these memories in a marine mammal. One hypothesis is that dolphins may rehearse some special events heard during the daytime and that they then express vocally what could be conceived as a more global memory. These results open the way for broader views on how animals might rehearse life events while resting or maybe dreaming.

Keywords: auditory memory processes; interspecific vocal copying; sensory-motor-phases separation; cetacean acoustic plasticity

1. INTRODUCTION

Dolphins have the ability to copy sounds from their environment other than those produced by conspecifics, like orang-utans or elephants, under captive conditions when mimicries are associated with salient events, such as training or shows (Kelley & Healy 2011; Poole et al. 2005; Richards et al. 1984; Wich et al. 2009). Interspecific copying by cetaceans has been reported under field conditions, seemingly in association with agonistic interactions (May-Collado 2010), social separation (Foote et al. 2006), or other emotionally salient contexts. Earlier anecdotic reports concerning birds mention that vocal mimicry can in some cases emerge and be kept in memory in association with particularly salient events (Armstrong 1960; Frith & Frith 2004), one famous example being Lorenz's (1952) free-living, tame hooded crow (Armstrong 1960) coming back with a broken foot and a never before heard sentence: "Got'im in t'bloomin'trap" (in "Austrian street language").

Examples of separation between auditory memory formation and vocal copying are common in a variety of songbird (e.g. Thorpe 1961) and parrot (Pepperberg 1997) species, when the sensory and motor phases of vocal learning are separated. Songbirds can produce vocal copies totally independently of the context in which they were learned (Hausberger et al. 1991). Similarly, dolphins are capable of associating given sounds with an object or context (Reiss & McCowan 1993; Richards et al. 1984). Hooper et al. (2006) demonstrated that dolphins' imitations can be enhanced by associating sounds with salient events. Here we questioned whether dolphins would produce copies of whale sounds associated with daily shows, a salient event for them.

One intriguing finding is the activation of the same neurons during sleep as while awake in songbirds, which suggests a rehearsal of song during sleep (Dave et al. 2000). Actually, memories of salient events can lead to rehearsal in the form of dreams during sleep both in humans and animals (Cipolli et al. 2004). Animals that have undergone a lesion of their locus coeruleus present motor expressions of their dreams, e.g. hunting in sleeping cats (Jouvet 1979). Vocalizations during sleep are commonly reported, as for instance in horses (Ruckebusch et al. 1970). Speech produced by humans during sleep corresponds to their dream contents (Jouvet 1979). The quality of dreams depends on the type of sleep; more negative-emotional type dreaming occurs during REM (i.e. rapid eye movement) sleep (Stickgold et al. 2001), whereas during non-REM (or day) dreams, the episodic memory

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(memory of an event as a whole) is more involved (Stickgold et al. 2001; Vandekerckhove & Clydts 2010): an "offline model of the world" where events and social interactions are associated in a "vivid and multimodal simulation of real experience" (Revonsuo 2000). Therefore we hypothesized that vocal copies could occur at night during resting or sleeping.

Here we describe the nocturnal production of vocal mimicries by captive bottlenose dolphins (*Tursiops truncatus*) of whale sounds that they only heard during daytime show periods (i.e. whale songs played back to the public through loudspeakers). Our results reveal that delayed production of auditory memories does occur in dolphins, one explanation being that they have a memory of sounds associated with salient events, which would then be produced during rehearsals.

2. MATERIAL & METHODS

2.1. Background

2.1.1. Study group and housing conditions.

Subjects were five captive-born dolphins (2 females, 3 males, from 5 to 25 years old) housed at the "Planète Sauvage" delphinarium (France). They have been in this facility as a group since December 2008 and came from two delphinarium belonging to the same company. In all, this facility covers over 2000m² water surface and contains 8 500 000 L salt water cleaned with ozone (no chlorine). They were feed comprised variety of fish (herring, capelin, sprat, mackerel, and whiting) and squid. The daily ration of 5-10 kg per individual (depending on its size) was given several different times during feeding or training sessions. Training includes medical training (e.g. acceptance of inspection and palpation of all parts of the body or being touched by medical equipment) as well as training for public shows.

2.1.2. Public shows

The dolphins performed exercises during daily public shows (one to four per day, depending on the season). These educative shows were composed of a set of activities (each time performed in a different order so that the dolphins did not become bored) aiming to explain dolphins' biology and behaviour to the

public: demonstration of body features (dorsal and pectoral fins, fluke, blowhole), physical abilities (swimming at maximum speed, jumping), visual abilities (catching thrown balls), sounds (in-air vocalizations). During the shows, a trainer commented the different activities. From the 28 February 2009 on, a 21 minutes soundtrack was broadcast at the beginning of the shows (while the visitors came in and sat down), which included music, sea gulls' calls, dolphins' whistles (their own) and predominantly humpback whales' vocalizations. The playbacks of humpback whale sounds were only broadcast in the current facility and during the period of shows, in total for approximately 2 minutes (a 14-second sequence of 5 whale calls was repeated 8 times during the 21-minute music track), generally 2-3 times a day.

2.1.3. Data collection

The vocalizations were recorded between November 2008 and May 2009 for nine days and eight nights. The recordings were performed using a Nauta SS03-10 hydrophone connected to a Marantz PMD 670 recorder (sample rate: 44.1 kHz; resolution: 16 bit) without the possibility to identify emitters. Observations complied with the current French laws governing animal research.

2.2. Discriminant function analysis

We compared dolphins' vocalizations with the broadcast whale sounds by measuring frequency and time parameters using Raven Pro 1.3. Measurements were then analysed using a stepwise Discriminant function analysis (in SPSS 11.5). Only high quality (i.e. low background noise) "whale-like" productions (WLPs) and randomly chosen whistles were used.

2.3. Human playback experiment

To evaluate dolphin-whale similarities five WLPs (at normal speed and half speed) and five whale sounds were broadcast to 20 human subjects (male and female master and PhD students and scientists working in behavioural biology) that were blind to the study and unfamiliar with cetacean vocalizations. Again only high quality

whistles and WLPs (i.e. low background noise) were chosen from our own recordings. Three humpback whale calls from the Planète Sauvage broadcast were used as well as two additional calls from free-ranging individuals (www.whalesong.net) to see if these calls differed. Dolphins' whistles, WLPs and whale calls were chosen so that they all had approximately the same duration in order to avoid classification based on the length of the sound. Since the WLPs were said to sound like "accelerated" versions of the real whale sounds, we also tested slowed down (factor of 0.5) versions of the WLPs. To ensure that dolphins' WLPs were not classified as different from dolphins' whistles because of this manipulation, the whistles were played back both at normal speed and slowed down. The sounds were equalized (71.8 dB) in sound level using ANA software and a DVM401 Voltcraft decibel meter. A set of five whale sounds, 10 dolphin whistles (five normal speed/five half speed) and 10 dolphin WLPs (five normal speed / five half speed) was randomly broadcast to each subject. After listening to an example of a whale and a dolphin sounds (not included in the testing set), subjects were asked to classify the sounds as a "whale" or "dolphin" sound. Human classifications were compared using a Wilcoxon test with Bonferroni corrections ($P_{corrected} = 0.00\overline{3}$).

3. RESULTS

3.1. General results

Recordings performed between November 2008 and February 2009 (> 80 hours) yielded 2370 vocalizations (2182 whistles, 188 burst-pulsed) from five dolphins. After the broadcast of the soundtrack started, recordings were made between February and May 2009 (40 hours) yielding 876 vocalizations (218 during the day; 658 at night, i.e. 10 p.m. to 06 a.m.). Whereas the vocalizations during the day did not change after the broadcast started, atypical sounds were recorded during the night; these sounds had never been recorded before the broadcast had started. The first atypical sound was recorded after 87 playbacks of the show tape (after 34 days with broadcast). Most remarkable was that 20 of the 25 atypical sounds were recorded between 1 and 3 a.m. (Table 1), which is during early night when the animals were resting, or even potentially sleeping. The five remaining sounds were recorded early morning (6-9 a.m.) while the dolphins were also resting. None of these atypical sounds was ever recorded

during a show, which would suggest immediate mimicry, or during periods of intense activity. Comparisons with the past and present acoustic environment of these animals and these vocalizations revealed that the only close structure was the whale sounds broadcast during the public shows. The life history of these animals was fully known (same company) and these dolphins had had no opportunity to hear such whale sounds at any stage.

Table 2: Acoustic parameters and recording times of dolphins' and humpback whales' vocalizations. Data for wild bottlenose dolphins were taken from Ding et al. (1995) as an example; humpback whale sounds were taken from The Ocean Mammal Institute (http://www.oceanmammalinst.com/songs.html) and The Whalesong Project (http://www.whalesong.net/index.php/the-whalesong-project/sounds/whale-songs). The Planète Sauvage dolphins' whistles were chosen randomly from our own recordings with the aim to match approximately the WLPs ("whale-like" productions) sample size and humpback whale sounds. Acoustic measurements are given as mean ± standard deviation.

Acoustic parameters	Wild bottlenose dolphins' whistles (n = 3449)	Planète Sauvage dolphins' whistles (n = 17)	Planète Sauvage dolphins' WLPs (n = 14)	Humpback whales' sounds (n = 18)
Duration [s]	0.70 ± 0.41	0.72 ± 0.41	1.18 ± 0.73	1.55 ± 0.67
Minimum frequency [Hz]	5450 ± 196	4711 ± 156	397 ± 151	242 ± 104
Maximum frequency [Hz]	11320 ± 318	12224 ± 451	948 ± 436	638 ± 270
Peak frequency [Hz]	-	7651 ± 302	2901 ± 4610	416 ± 178
Number of harmonics	0.33 ± 0.47	1.06 ± 1.03	29.07 ± 13,18	15.50 ± 10.54

Percentage distribution of our five dolphins' whistles and WLPs diel (24 hours) occurrence:

Time	0-3 a.m.	3-6 a.m.	6-9 a.m.	9 a.m. - 6 p.m.	6-0 p.m.
Whistles	7.8 %	1.9 %	12.0 %	65.5 %	12.8 %
WLPs	80.0 %	0.0 %	20.0 %	0.0 %	0.0 %

3.2. Acoustic analysis

These atypical vocalizations clearly stood out from the range of classical descriptions of dolphin whistles' characteristics (Table 1), being characterized by a lower pitch and a larger number of harmonics (Figure 1). The dolphins also produced other low-pitched, namely burst-pulsed vocalizations (Figure 1, 1.(B)), which are not unusual in the dolphins' vocal repertoire (van der Woude 2009; dos Santos et al. 1995; Connor and Smolker 1996). Nevertheless, these "whale-like" productions (WLPs; Figure 1, 2.(A)) clearly differed from their burst-pulsed vocalizations in terms of

noisiness and frequency modulation patterns; they also lasted much longer and were higher pitched.
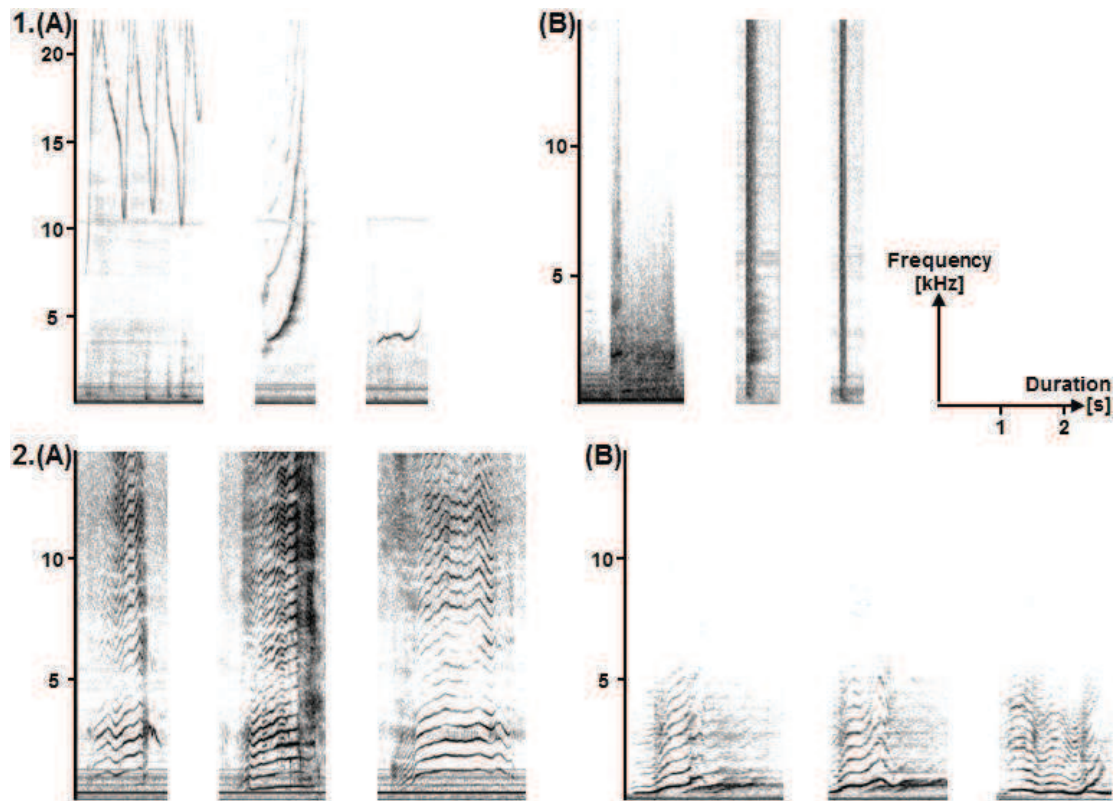
Figure 1: A spectrogram of the Plantète Sauvage dolphins' 1. common vocal repertoire, (A) whistles and (B) burst-pulsed vocalizations, and 2. their atypical (A) whale-like productions (WLPs) and (B) the "model" humpback whales' sounds. FFT: 1(A) 1024; 1(B), 2(A) and 2(B) 2282. The time axes for all spectrograms have been standardized; but the 1(A) frequency axis has been extended.

To ensure that these productions were copies, sounds being broadcast and the dolphins' WLPs were compared both in terms of measurements and by testing a naïve human audience (see 3.3. Human playback experiment). A discriminant function analysis, based on temporal and frequency parameters, clearly separated the "ordinary" dolphin whistles from both WLPs and the "model" whale sounds, while the latter overlapped (Figure 2; percentage of correctly classified cases: dolphins' whistles 100%, dolphins' WLPs 60.0% (40.0% classified as "whale sounds"), humpback whales' sounds 88.9% (11.1% classified as "dolphins' WLPs")).
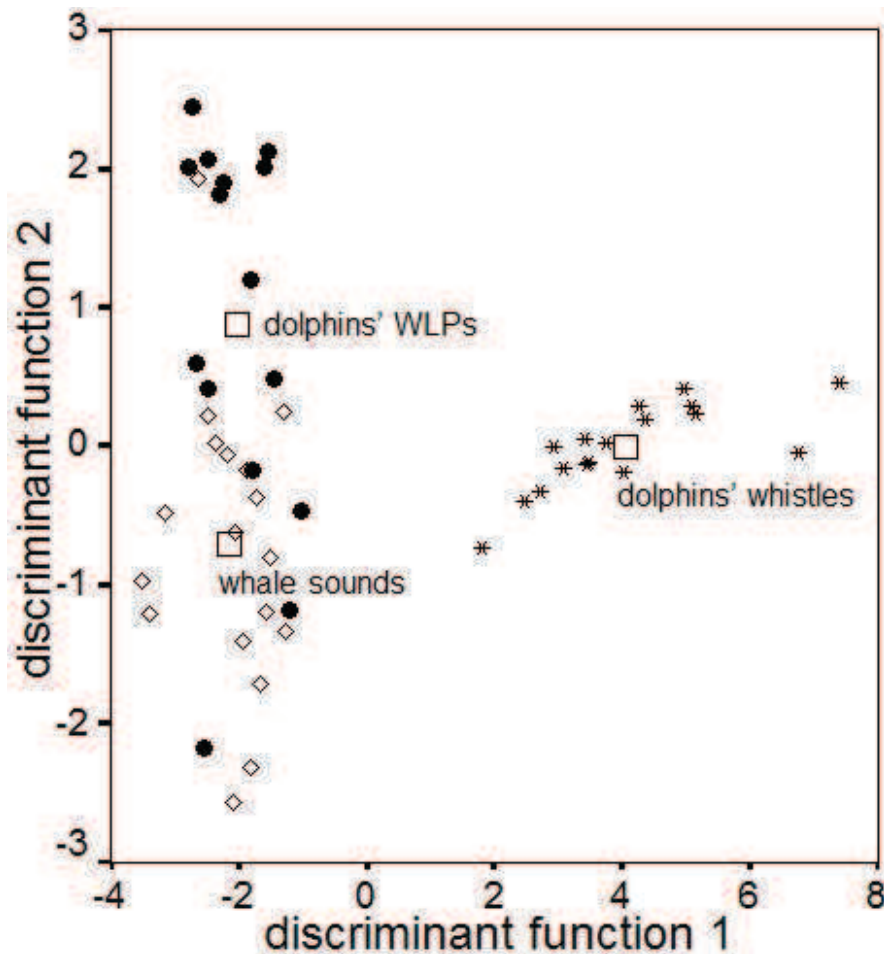
Figure 2: Scatter plot of the Discriminant Function Analysis comparing several acoustic parameters of dolphins' whistles (asterisks), dolphins' WLPs (black dots) and humpback whale sounds (white diamonds). Squares indicate the group means. Discriminant function 1 corresponds to minimum frequency (canonical correlation coefficient = 0.949; Wilks-λ = 0.069; P ≤ 0.001); discriminant function 2 corresponds to number of harmonics (canonical correlation coefficient = 0.551; Wilks-λ = 0.696; P = 0.001).

3.3. Human playback experiment

Human evaluations confirmed these findings. After listening to an example of a humpback whale and a dolphin sound (humpback whale sound from The Ocean Mammal Institute; dolphin sound randomly chosen from our own recordings of this group), they were asked to classify the sounds as being produced by a whale or by a dolphin. While the model whale sounds and ordinary dolphin whistles were clearly identified as such (88-99%), WLPs were often classified as being a whale sound, especially when slowed down (76%) (Figure 3; Wilcoxon test, P ≤ 0.000).

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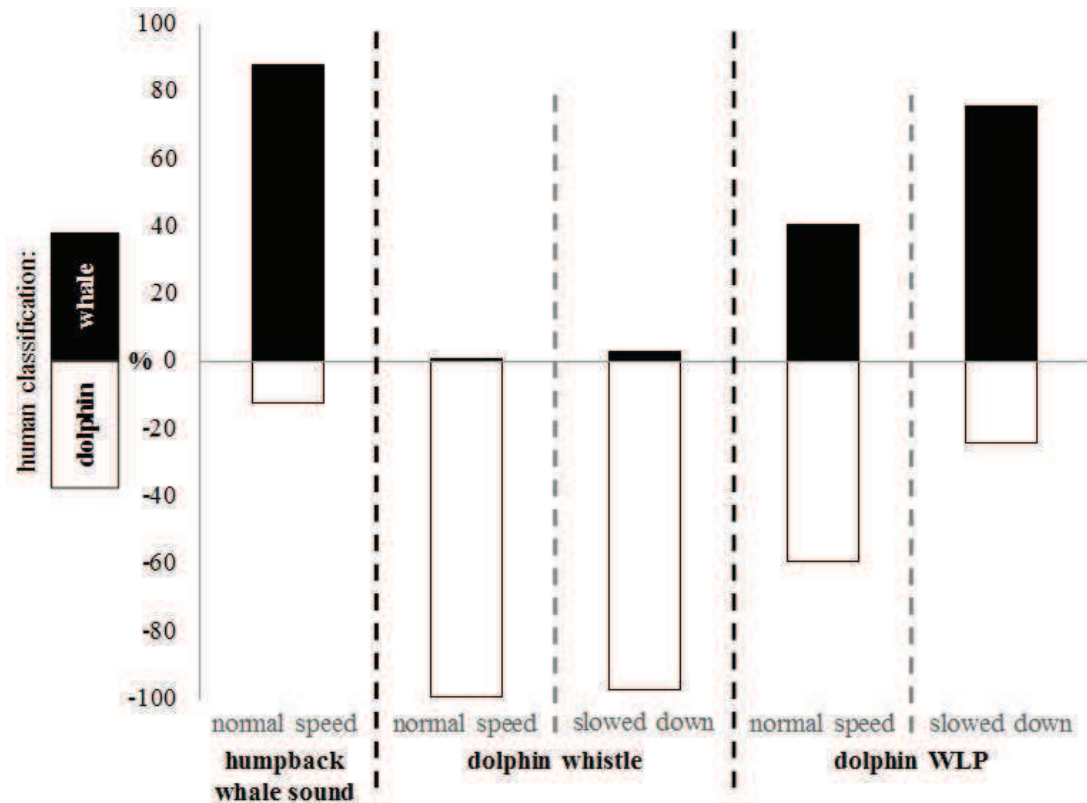
Figure 3: Human evaluation of humpback whale sounds, dolphin whistles and dolphin WLPs broadcast at different speeds. The classification is given in percent. The upper part (black) represents the classification of sounds as being produced by a whale; the lower part (white) represents the classification of sounds as being produced by a dolphin.

4.   DISCUSSION

This study describes an unusually delayed production during the night of mimicries of sounds related to salient events. The fact that these mimicries are produced when the dolphins are resting or sleeping and never when they were active is intriguing, especially as these sounds were only broadcast in the context of daytime shows. Hooper et al. (2006) showed that mimicries are enhanced by association of sounds with objects or events, and that dolphins tend to produce these sounds in the corresponding contexts/activities. Therefore this raises the question of whether these night productions correspond to a form of "rehearsal" of daily shows. None of these vocalizations had ever been recorded before this broadcast was performed and information of the dolphins' life history clearly established that these animals had never had the opportunity to hear whale sounds previously. These mimicries occurred

neither in direct association with the event, nor during interactions with humans and other dolphins. Data concerning both objective measurements of sound parameters and evaluations by humans converge to show that these atypical vocalizations were mimicries of the whale sounds broadcast during shows. Dolphins transposed frequencies as do killer whales (Foote et al. 2006) and a variety of mimicking birds (songbirds: Hausberger et al. 1991; parrots: Cruickshank et al. 1993). There may be some physical constraints, as the preferred range of frequencies for dolphin copying seems to be between 5-10 kHz (Richards et al. 1984). Other authors give examples of low pitched vocalizations emitted by dolphins (Connor & Smolker 1996; dos Santos et al. 1995; van der Woude 2009) and the question of whether these sounds correspond to mimicries has been raised (van der Woude 2009). The sounds produced here clearly differ from these examples in their acoustic structure: WLPs are longer in duration and present more frequency modulations than do "brays" (dos Santos et al. 1995) and "pops" (Connor & Smolker 1996), and their minimum and maximum frequencies are higher than those of "moans" (van der Woude 2009). They also differ from other parts of the dolphin's species specific repertoire (reviewed in Janik 2009).

These mimicries are a further proof that dolphins can learn when adult, as they heard this tape only when adult. The most remarkable aspect though is the delayed production of these mimicries in a quiet context. The "salience" of the event/interaction may have been crucial (Hooper et al. 2006; Tyack & Sayigh 1997). These atypical vocalizations might be episodes of "vocal play" while at rest (Kuczaj & Makecha 2008; Pepperberg 2002), or, given the context, a potential part of a global rehearsal of these salient daytime events. The mimicries occurred only at quiet times, mostly during the night (0-3 a.m.), and outside any kind of social interactions, while obviously resting or sleeping. In captivity, show periods are salient events associated with multisensory stimulations (food reinforcement, vocal orders, public responses…). In addition to the general background (crowd, noise,…) that may be emotionally salient, food reinforcement used by trainers may increase excitation (Innes & McBride 2008) and long term memories (Sankey et al. 2010); positive as well as negative emotional valences could potentially induce increased mimicry and strong memories (Armstrong 1960).

This is to our knowledge the first time that a long separation between hearing an auditory model and copying it has been observed in a marine mammal. One hypothesis

predicts that dolphins, like parrots or songbirds, "practice" outside the "model's" presence (Hausberger et al. 1991). Another hypothesis predicts that these events correspond to rehearsals of a more global memory, as for example in the form of dreams during sleep or "day dreaming" in humans and animals (Cipolli et al. 2004). Reports of potential "dreaming" remain anecdotal in species other than laboratory animals. A pilot study by Lubrano Lavadera (2005) reported that young horses produced adult vocalizations (that they never produced during the day) during REM (i.e. rapid eye movement) sleep. This question is especially intriguing as cetaceans seem to lack typical REM sleep, or may have very short bouts of it (Mukhametov 1995; Shpak et al. 2009). Nevertheless periods of sleep, mostly between 0 and 3 a.m., but also at times during the day, have been described, when the animals are floating or swimming slowly (Lyamin et al. 2008; Sekiguchi & Kohshima 2003). Resting periods are associated with lower whistle production rates (Sekiguchi & Kohshima 2003). Muscle jerks recalling REM sleep have been observed (Lyamin et al. 2008). Whether or not dolphins experience any kind of rehearsal of daytime events during their sleep therefore remains a mystery, although anecdotal reports by trainers suggest that dolphins perform a trained task better in the morning. Improvement of performance is a proved consequence of the rehearsal of memories in human dreams (Aly & Moscovitch 2010).

As individuals and precise behavior could not be identified in this study, only further investigations associating EEG (electroencephalography) recordings, could confirm or infirm our hypothesis that these productions reflect rehearsal of daytime events by dolphins during rest or sleep. Their rarity (1.1% of total production) and timing (mostly at night) may explain that this constitutes the first report of mimicries of sounds heard during special events produced by dolphins in a resting/sleeping context. This finding opens very large perspectives for future investigations on dolphin learning processes and "mental representations".

References

Aly, M. & Moscovitch, M. (2010). The effects of sleep on episodic memory in older and younger adults. Memory 18, 327-334.

Armstrong, E. A. (1960). A Study of Bird Song. Oxford University Press, London.

Cipolli, C., Fagioli, I., Mazzetti, M. & Tuozzi, G. (2004). Incorporation of presleep stimuli into dream contents: evidence for a consolidation effect on declarative knowledge during REM sleep? Journal of Sleep Research 13, 317-326.

Connor, R. C. & Smolker, R. A. (1996). 'Pop' goes the dolphin: a vocalization male bottlenose dolphins produce during consortships. Behaviour 133, 643-662.

Cruickshank, A. J., Gautier, J.-P. & Chappuis, C. (1993). Vocal mimicry in wild African grey parrots *Psittacus erithacus*. IBIS 135, 293-299.

Dave, A. S. & Margoliash, D. (2000). Song replay during sleep and computational rules for sensorimotor vocal learning. Science 290, 812-816.

Ding, W., Würsig, B. & Evans, W. (1995). Comparison of whistles among seven odontocete species. In: Sensory Systems of Aquatic Mammals, edited by Kastelein, R. A., Thomas, J. A. & Nachtigall, P. E., pp. 299-323. De Spil Publishers, Woerden.

dos Santos, M., Ferreira, A. J. & Harzen, S. (1995). Rhythmic sound sequences by aroused bottlenose dolphins in the Sado estuary, Portugal. In: Sensory Systems of Aquatic Mammals, edited by Kastelein, R. A., Thomas, J. A. & Nachtigall, P. E., pp. 325-334. De Spil Publishers, Woerden.

Foote, A. D., Griffin, R. M., Howitt, D., Larsson, L. Miller, P. J. O. & Hoelzel, A. R. (2006). Killer whales are capable of vocal learning. Biology Letters 2, 509-512.

Frith, C. B. & Frith, D. W. (2004). The Bowerbirds. Oxford University Press, London.

Hausberger, M., Jenkins, P. F. & Keene, J. (1991). Species-specificity and mimicry in bird song: are they paradoxes? A reevaluation of song mimicry in the European starling. Behaviour 117, 53-82.

Hooper, S., Reiss, D., Carter, M. & McCowan, B. (2006). Importance of contextual saliency on vocal imitation by bottlenose dolphins. International Journal of Comparative Psychololgy 19, 116-128.

Innes, L. & McBride, S. (2008). Negative versus positive reinforcement: an evaluation of training strategies for rehabilitated horses. Applied Animal Behavior Science 112, 357-368.

Janik, V. M. (2009). Acoustic communication in delphinids. In: Advances in the study of behaviour, Volume 40, edited by Naguib, M. & Janik, V. M., pp. 123-157. Academic Press, Burlington.

Jouvet, M. (1979). What does a cat dream about? Trend in Neuroscience 2, 280-282.

Kelley, L. A. & Healy, S. D. (2011). Vocal mimicry. Current Biology 21, R9-R10.

Kuczaj, S. A. & Makecha, R. (2008). The role of play evolution and ontogeny of contextually flexible communication. In: Evolution of Communicative Flexibility. Complexity, Creativity, and Adaptability in Human and Animal Communication, edited by Oller, D. K. & Griebel, U., pp. 253-277. MIT Press, Cambridge.

Lubrano Lavadera, J. (2005). Etude qualitative des vocalises émises en phase de sommeil paradoxal chez le cheval de Przewalski (*Equus ferus przewalski*). Thesis, Ministère de l'Education Nationale, de la Recherche et la Technologie; Ecole pratique des Hautes Etudes, France.

Lyamin, O. I., Manger, P. R., Ridgway, S. H., Mukhametov, L. M. & Siegel, J. M. (2008). Cetacean sleep: An unusual form of mammalian sleep. Neuroscience and Biobehavioral Reviews 32, 1451-1484.

May-Collado, L. J. (2010). Changes in whistle structure of two dolphin species during interspecific associations. Ethology 116, 1065-1074.

Mukhametov, L. M. (1995). Paradoxical sleep peculiarities in aquatic mammals. Sleep Research 24A, 202.

Pepperberg, I. M. (1997). Social influences on the acquisition of human-based codes in parrots and nonhuman primates. In: Social Influences on Vocal Development, edited by Snowdon, C. T. & Hausberger, M., pp. 157-177, Cambridge University Press, Cambridge.

Pepperberg, I. M. (2002). The Alex Studies: Cognitive and Communicative Abilities of Grey Parrots. Harvard University Press, Cambridge and London.

Poole, J. H., Tyack, P. L., Stoeger-Horwath, A. S. & Watwood, S. (2005). Elephants are capable of vocal learning. Nature 434, 455-456.

Reiss, D. & McCowan, B. (1993). Spontaneous vocal mimicry and production by bottlenose dolphins (*Tursiops truncatus*): Evidence from vocal learning. Journal of Comparative Psychology 107, 301-312.

Revonsuo, A. (2000). The reinterpretation of dreams: An evolutionary hypothesis of the function of dreaming. Behavioral and Brain Sciences 23, 793-1121.

Richards, D. G., Wolz, J. P. & Herman, L. M. (1984). Vocal mimicry of computer generated sounds and vocal labeling of objects by a bottlenosed dolphin, *Tursiops truncatus*. Journal of Comparative Psychology 98, 10-28.

Ruckebusch, Y., Barbey, P. & Guillemot, P. (1970). Les états de sommeil chez le cheval (*Equus caballus*). C.r. Seanc. Soc. Biol. 164, 658-665.

Sankey, C., Richard-Yris M.-A., Leroy, H., Henry, S. & Hausberger, M. (2010). Training experience induces lasting memories of humans in horses, *Equus caballus*. Animal Behaviour 79, 869-875.

Sekiguchi, Y. & Kohshima, S. (2003). Resting behaviors of captive bottlenose dolphins (*Tursiops truncatus*). Physiology & Behavior 79, 643-653.

Shpak, O. V., Lyamin, O. I., Manger, P. R., Siegel, J. M. & Mukhametov, L. M. (2009). States of rest and activity in the Commerson's dolphin *Cephalorhynchus commersonii*. Journal of Evolutionary Biochemistry and Physiology 45, 111-119.

Stickgold, R., Hobson, J. R. & Fosse, M. (2001). Sleep, learning, and dreams: off-line memory reprocessing. Science 294, 1052-1057.

Thorpe, W. H. (1961). Bird-song: the biology of vocal communication and expression in birds. Oxford University Press, Oxford.

Tyack, P. L. & Sayigh, L. S. (1997). Vocal learning in cetaceans. In Social Influences on Vocal Development, edited by Snowdon, C. T. & Hausberger, M., pp. 208-233. Cambridge University Press, Cambridge.

van der Woude, S. E. (2009). Bottlenose dolphins (*Tursiops truncatus*) moan as low in frequency as baleen whales. Journal of the Acoustical Society of America 126, 1552-1562.

Vandekerckhove, M. & Cluydts, R. (2010). The emotional brain and sleep: an intimate relationship. Sleep Medicine Reviews 14, 219-226.

Wich, S. A., Swartz, K. B., Hardus, M. E., Lameira, A. R., Stromberg, E. & Shumaker, R. W. (2009). A case of spontaneous acquisition of a human sound by an orangutan. Primates 50, 56-64.

CHAPTER 4
INVESTIGATIONS ON THE DOLPHINS' SENSITIVITY TO CHEMICAL STIMULI

SUMMARY OF PAPER 3

Questions: Theoretically, a dolphin would simply need to open its mouth to have access to a huge amount of chemical information existent in the surrounding water. However, gustation did not receive much attention by research. As wild and captive dolphins are known to have feeding preferences, we asked whether or not these preferences might be guided by taste. Are dolphins able to discriminate food by its taste?

Methods: We investigated the response of the Planète Sauvage dolphins towards visually and tactually identical ice cubes that differed in taste (herring, salmon, shrimp, and control). Since preferences were tested, we analysed the dolphins' latency to return and beg for another ice cube.

Results: Dolphins took more time to come back after they received ice cubes that tasted like herring or salmon compared to non-fish-tasting ones, an indirect assessment of more exploration of fish-tasting ice cubes.

Conclusions: Bottlenose dolphins responded differently to ice cubes with different tastes. Thus, they seem to be able to discriminate food by its taste. Gustation might be a so far underestimated modality in the dolphin's *Merkwelt*.

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DO DOLPHINS PERCEIVE FLAVOURS? A NOVEL APPROACH TO TEST SPONTANEOUS PREFERENCES

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Abstract

The dolphins' chemosensory world remains poorly understood. Whereas much is known about their acoustic abilities, little knowledge is at hand on other modalities, especially chemoreception. While dolphins live in an environment that is replete with chemical stimuli, there is no consensus on whether and how they do perceive them. Morphological, neuroanatomical, and molecular studies remain dubious on that issue, whereas behavioural and ethoecological data suggest that dolphins may use chemoreception for food selection or socio-sexual interactions. However, very few studies have been performed due to methodological issues. In the present study, we developed a new non-invasive method based on dolphins' liking for ice cubes in order to assess captive dolphins' ability to discriminate chemical stimuli in form of food flavours. Therefore, we offered them visually and tactually similar ice cubes that differed only in terms of flavour. Fish (herring, salmon) and non-fish (shrimp, control) flavours were used to assess these dolphins' potential spontaneous preference for i) fish over non-fish stimuli, and ii) familiar (herring) over non-familiar (salmon) fish stimuli. Ice cubes were distributed on the dolphins' demand and the individual latency to return begging for another one was timed. Dolphins took more time to come back after they received fish-flavoured ice cubes compared to non-fish-flavoured ones, an indirect assessment of more exploration of fish-flavoured ice cubes. These data suggest that dolphins may be able to discriminate food types based only on gustative cues. This method provides an interesting tool for the study of dolphin chemoreception.

Keywords: cetaceans; *Tursiops truncatus*; chemoreception; flavour discrimination

1.   INTRODUCTION

The efficiency of chemoreception in cetaceans is still a debated question. On the one hand, several authors posit that some cetacean species have lost their nasal (Kishida et al. 2007) and oral chemoreception (Jiang et al. 2013) in the course of evolution, as airborne odorants may be considered irrelevant due to their aquatic lifestyle (Thewissen et al. 2011). Firstly, corresponding anatomical structures are rudimentary or absent, at least in adult animals. In the nasal cavity of toothed whales, the cribriform plate of the ethmoid bone and ethmoturbinals are absent (Pihlström 2008). In their oral cavity, no taste buds were found on the tongue or other body areas of various odontocete species (Kuznetzov 1990). However, the number/age of individuals investigated is usually unknown or very limited. Secondly, central structures devoted to olfaction are rudimentary or absent. The main and accessory olfactory tracts are completely absent in toothed whales, and absent or considerably reduced in baleen whales (Oelschläger 2008; Pihlström 2008). Finally, olfactory and taste receptor genes are mostly pseudogenised or entirely absent in Odontoceti (Jiang et al. 2013; Kishida et al. 2007).

On the other hand, numerous studies argue in favour of functional chemoreception in cetaceans. Firstly, chemoreceptive cells were found in the frontal and vestibular sac (close to the blowhole) of harbour porpoises (Behrmann 1989), perhaps enabling some kind of chemical sensation in this species. Moreover, taste buds were found in younger individuals of the same species that were previously described as not having them when investigating adult individuals (Behrmann 1988; Kuznetzov 1990; Yamasaki et al. 1978). Other studies did not describe taste buds but found marginal and vallate papillae on the tongues of dolphins, known to be potential locations of taste buds (Kastelein & Dubbeldam 1990; Werth 2007). Secondly, Odontoceti were found to possess a well-developed olfactory tubercle (Oelschläger & Oelschläger 2009). Finally, go/no-go behavioural tests with trained bottlenose dolphins showed that they can perceive sour, bitter and salty tastes nearly as well as humans (Friedl et al. 1990; Kuznetzov 1990; Nachtigall & Hall 1984).

Taken together, this second set of studies suggests that cetaceans might have, to some extent, access to chemosensory information through the olfactory (Thewissen et al. 2011) and/or taste systems (Pihlström 2008; Watkins & Wartzok 1985). As anatomical, neuroanatomical, and molecular evidence draw unclear conclusions, behavioural studies are

needed. Given the complex but sometimes subtle behaviours displayed by dolphins in response to internal or external stimuli, go/no-go tasks are an elegant way to investigate perceptive abilities; however, they require to train the animals, thus preventing the investigation of dolphins' spontaneous responses. Therefore, the go/no-go paradigm is not suitable for exploring the presence of preferences that are per se spontaneous and cannot be tested in a trained task. Furthermore, it takes time to train the animals what makes other methods that take spontaneous responses into account more attractive as they are easier applicable.

The present study aimed at testing whether bottlenose dolphins display discriminative behavioural responses toward different stimuli presented as fish or non-fish flavours, and as familiar or non-familiar food items. Wild dolphins are indeed reported to display clear feeding selectivity: they tend to prefer fish rather than crustaceans (Spitz et al. 2006) and also high rather than low energy fish (Spitz et al. 2010). One possibility is that dolphins make food choices based on visual or texture differences. Another possibility relates to choices based on taste, odour, or flavour differences (flavour being defined as the perceptual mix between olfaction, gustation, and oro-nasal somesthesis). Thus, we controlled the texture and visual aspects of a set of chemical stimuli in shaping them as coloured and flavoured ice cubes. In these conditions, we predicted that, if bottlenose dolphins have the capacity to detect chemical stimuli, they should behave discriminatively in response to different flavours, along qualitative features involving their source (i.e., fish/non-fish) or along previous exposure to the stimuli (familiar/unfamiliar). In the current study, we aimed at testing potential spontaneous preferences for food flavours in a "naturalistic" setting, i.e., in conditions where dolphins may express their preferences without going through conditioning procedures. Since dolphins are not visible all the time in such conditions, we had to develop an indirect approach to measuring flavour discrimination. Thus, we used the latency of return to the begging spot for ice cubes as a measure of "interest" in the previous ice cube flavour. Since ice cubes are highly attractive, longer latencies to beg again reflected the time spent "exploring" the previous ice cube, and hence were considered as reflecting greater interest in the dolphins. Opportunistic observations of dolphins' behaviour after receiving an ice cube revealed that they tended to spend time "exploring" it in the mouth. Our method used a non-

invasive technique based on the spontaneous begging responses of dolphins toward more or less attractive items bearing biological relevance.

2. MATERIAL & METHODS

2.1. Subjects and facility

In January and February 2012, we studied four captive-born bottlenose dolphins (three males aged 8, 12, and 27 years; one female aged 10 years) that were housed together for more than 3 years in the delphinarium of Planète Sauvage (Port-Saint-Père, France). Overall, the facility covers over 2000 m² water surface and contains 8.500.000 L of salt water cleaned with ozone (without any chlorine). The diet of the dolphins was composed of frozen stored herring, capelin, sprat, mackerel, whiting, and squid. The species composition changed on a daily basis but contained at least three different fish species each day. A daily ration of 5-10 kg per individual (depending on its weight) was given throughout the day during eight feedings (lasting ca. 15 minutes each), the first at 9:00 a.m. and the last at 5:00 p.m. These feedings were conducted by the dolphin trainers, using the food as primary reinforcement for medical training (e.g., acceptance of inspection and palpation of all parts of the body or being touched by medical equipment) as well as training for public shows. Food was given by the trainer directly in the dolphin's mouth.

2.2. Stimuli and procedure

As the matrix to present different food flavours, we used ice cubes, which were equally familiar to all dolphins as they were commonly used as part of environmental enrichment in the delphinarium (1-2 times per week); therefore, all dolphins were accustomed to receive, sense, and ingest odour- and tasteless ice cubes. For the present experiment, ice cubes were produced with herring, salmon, and shrimp flavours (Table 1), originally used for human cooking (salmon/shrimp) or for baiting fish (herring). Herring was familiar to all dolphins through food exposure, whereas salmon and shrimp were not. Semispherical ice cubes (basis diameter: 4 cm; height: 2.5 cm) of 20 mL each were made with plain mineral water (to ensure constant composition; "Volvic" Danone, Paris, France) in which the flavour was diluted.

Table 3: Flavours and concentrations used to produce ice cubes with fish and non-fish flavours. Quantities were chosen in order to obtain a stimulus that resembled as much as possible the quality and intensity of the natural reference products what was assessed by the experimenter through tasting.

	Herring	Salmon	Shrimp
Manufacturer	Biomin Holding Ltd., Herzogenburg, Austria	Patiwizz Ltd., Vieillevigne, France	CBV Aroma, Mülheim an der Ruhr, Germany
Form	powder	liquid	liquid
Quantity of flavour / L	6 g	25 mL	2.7 mL

Flavourless yellow or purple food colourants ("Crazy Colors" Brauns-Heitmann Ltd., Warburg, Germany) were added to homogenize the ice cubes' visual appearance for the dolphins. To prevent any flavour-colour association by the dolphins, the colours were randomly distributed over ice cubes carrying different flavours. Ice cube were frozen at -21.5°C.

Experimental sessions were performed 1-5 times per day, with at least 60 minutes between two experimental sessions and with the largest possible time interval between experimental and feeding session. During one experimental session, (lasting on average 10 minutes (8 ± 2 minutes) one single flavour was tested. We completed all sessions for a given flavour before testing a new flavour.

All dolphins were together in the pool and when they saw the experimenter (D.K.) coming, they immediately and spontaneously approached her standing at the side of the pool. The experimental session started when the experimenter took up her position at the pool (no other person was around the pool) where she was standing with the ice cubes being within reach. The experimenter, who was familiar with all dolphins and could identify each individual without any doubt on the basis of physical differences (e.g., shape of the dorsal fin or colour patterns of the skin), never interacted with the dolphins beside of responding to their begging by giving an ice cube (see below). Although all dolphins were together in the pool, however, the interaction between the dolphins was minimal in front of the experimenter, as rarely more than one individual at a time was present in front of the experimenter. Dolphins were free to participate, meaning that they received ice cubes only when begging, i.e., when clearly opening their rostrum with the head and eyes over the water surface while being oriented to, and less than 1 m away from, the experimenter (Figure 1).

Figure 5: A dolphin begging for an ice cube.

This behaviour was displayed only in this context and was obviously identifiable. After this begging behaviour, the experimenter let the ice cube fall in the open mouth of the dolphin where it landed mostly at the middle of the tongue. Begging latency was timed by the experimenter with a chronometer from the moment a given dolphin received an ice cube (contact with the tongue) to the moment it begged for a new one (as described above). This parameter was the only one independent of the dolphins' position, as other behaviours that occurred between the receipt of an ice cube and the begging of a new one (e.g., playing with the ice cube) were not visible as the dolphins swam around in the pool.

The four stimuli were tested consecutively, i.e. one by one at consecutive days [1. herring (N = 242 ice cubes distributed in total; 13 sessions), 2. salmon (N = 199; 12 sessions), 3. shrimp (N = 206; 12 sessions), 4. control, N = 246; 12 sessions)]. The order of the four stimuli was chosen randomly.

2.3. Data analysis

Statistic calculations were run using R software (version 2.15.0, R Development Core Team, www.r-project.org). Assuming that all dolphins react differently to fish (salmon/herring) vs. non-fish (shrimp/control) items or to familiar (herring/control) vs. unfamiliar (salmon/shrimp) food, we compared begging latencies between different flavours by using a Wald test on a Linear Mixed Model, considering the individual as random factor (R-package: lme4). Data have been log-transformed prior to analyses in order to homogenize the variances. Pairwise comparisons were performed with the contrasts method (correction for multiple testing: false discovery rate; R-package: doBy). As dolphins were free to participate in this experiment, number of ice cubes received differed between individuals and between different tastes. However, this was taken into account by treating individual as random factor in the statistical analysis.

3. RESULTS

The average latency of the four dolphins to beg for another ice cube differed significantly between the distinctly flavoured ice cubes (mixed LM: $\chi^2 = 19.16$; $p = 0.0003$; Table 2). Post-hoc tests indicated that all dolphins took more time to come back after receiving herring- or salmon-flavoured ice cubes than after receiving shrimp-flavoured or control ice cubes (all dyadic comparisons: $5.04 \leq \chi^2 \leq 13.84$; $0.001 \leq p \leq 0.037$; Figure 2).

Table 4: Average latency to beg for another ice cube (in seconds) and number of given ice cubes for the differently flavoured stimuli and for each individual dolphin (mean ± SE; N).

Individual \ Stimulus	herring	salmon	shrimp	control	*overall*
Amtan (♀, 10 years old)	120 ± 23 N = 17	160 ± 32 N = 12	97 ± 33 N = 8	73 ± 17 N = 8	*118 ± 14 N = 45*
Cecil (♂, 27 years old)	30 ± 5 N = 93	30 ± 4 N = 109	24 ± 4 N = 104	16 ± 1 N = 162	*24 ± 2 N = 468*
Mininos (♂, 8 years old)	39 ± 5 N = 86	79 ± 32 N = 8	26 ± 3 N = 9	95 ± 22 N = 18	*49 ± 6 N = 121*
Peos (♂, 12 years old)	67 ± 8 N = 46	43 ± 4 N = 70	38 ± 4 N = 85	42 ± 5 N = 58	*45 ± 3 N = 259*

Both fish-flavoured ice cubes triggered latencies (mean $\pm$ SE: herring 46 ± 4 sec., salmon 44 ± 4 sec.) that did not differ significantly ($\chi^2 = 0.54$; $p = 0.553$); likewise, latencies after non-fish tasting (shrimp 33 ± 3 sec.) and control ice cubes (control 30 ± 3 sec.) did not differ significantly ($\chi^2 = 0.33$; $p = 0.564$). The two familiar flavours (herring and control) elicited different latencies ($\chi^2 = 8.64$; $p = 0.007$); the same was true for the two non-familiar flavours (salmon and shrimp: $\chi^2 = 9.19$; $p = 0.007$).
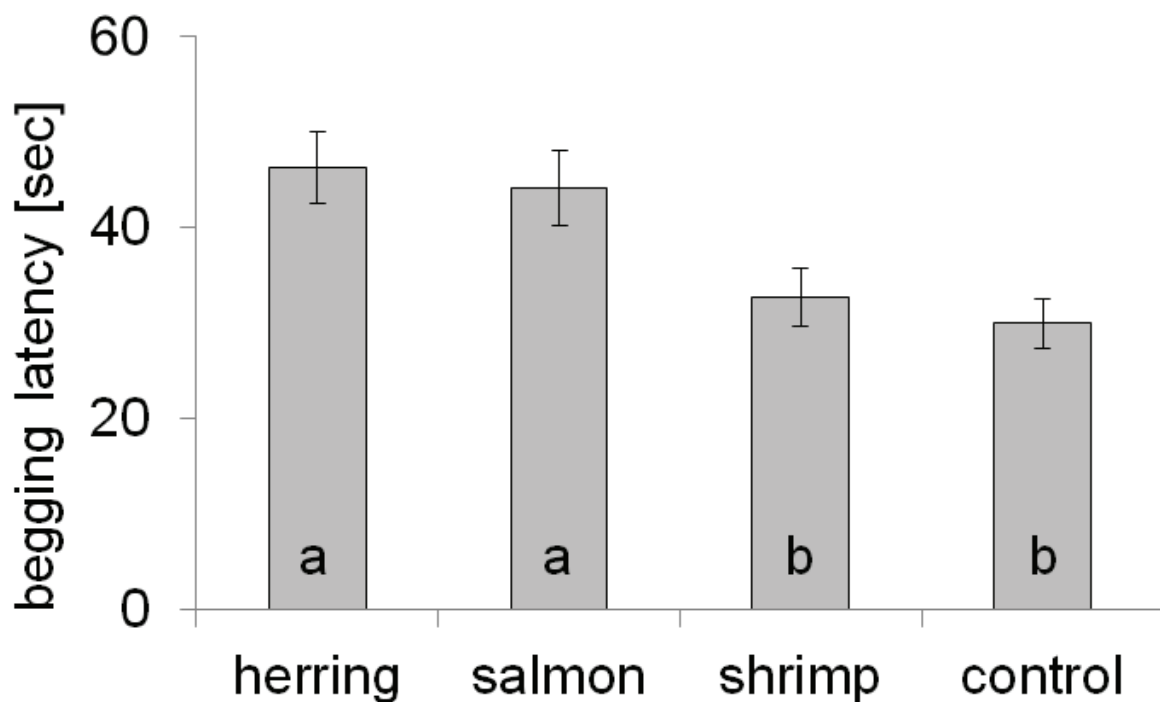
Figure 6: Dolphins' mean ($\pm$ S.E.) latency to come back and request a new ice cube after receiving a herring, salmon, shrimp, or neutral ice cube. Same letters indicate absence of statistical difference (alpha = 0.05).

4.   DISCUSSION

Using an original method to test spontaneous preferences of dolphins for food flavours, it was possible to show that responses of four captive bottlenose dolphins to visually similar stimuli differed dependent on the flavour. Dolphins took more time to beg for a new ice cube after receiving herring/salmon ice cubes compared to shrimp/control ice cubes, indicating that they discriminated between fish and non-fish flavours which triggered a differential attention. Earlier observations suggest that a prolonged latency reflects a longer time spent

"exploring" the flavour by the dolphin. Whether stimuli were familiar (herring/control) or unfamiliar (salmon/shrimp) did not impact their response. Therefore, this study suggests that dolphins are capable to perceive chemical stimuli (Friedl et al. 1990; Kuznetzov 1990; Nachtigall & Hall 1984) and may use this perceptive ability on biologically relevant stimuli.

One factor which may guide food choices of dolphins is energy density. Free-ranging common dolphins do indeed select preferentially high-energy density prey even though they are less abundant (Spitz et al. 2010). In line with this, salmons and herring, the flavours eliciting longer latencies in our study, are about 1.5-2.5 times more energetic than shrimps (National Nutrient Database for Standard Reference). Another factor may be flavour preference that could promote the choice of a certain food. Bottlenose dolphins' diet is primarily composed of fish (94.2 % in stranded dolphins' stomach contents), whereas crustaceans are eaten only occasionally (2.0 %; Spitz et al. 2006), what might be caused, aside from factors such as prey habitat (pelagic/benthic), by a preference for the flavour of fish.

We must acknowledge some limitations to our report. First, social facilitation was not controlled in our setting. However, although all dolphins were always together in the pool, interactions between them were minimal, as rarely more than one individual at a time was present in front of the experimenter. Second, the experimenter was not blind regarding the flavour given to dolphins. Third, we only used non-original (i.e., real fish/shrimp) flavours. Further studies should take these factors into account. Nevertheless, we could demonstrate that the method applied has several advantages because it allows to non-invasively test dolphins' discriminative abilities and is therefore easily applicable and replicable. The responses of the tested bottlenose dolphins to differently flavoured stimuli support the assumption that this species is chemosensitive, thus opening new lines of research on dolphins' sensory world.

References

Behrmann, G. (1988). The peripheral nerve ends in the tongue of the harbour porpoise *Phocoena phocoena* (Linne, 1758). Aquatic Mammals 14, 107-112.

Behrmann, G. (1989). The olfactory regions in the nose of the harbour porpoise *Phocoena phocoena* (Linne, 1758). Aquatic Mammals 15, 130-133.

Friedl, W. A., Nachtigall, P. E., Moore, P. W. B., Chun, N. K. W., Haun, J. E., Hall, R. W. & Richards, J. L. (1990). Taste reception in the Pacific bottlenose dolphin (*Tursiops truncatus gilli*) and the California sea lion (*Zalophus californianus*). In: Sensory abilities of cetaceans, edited by Thomas, J. A. & Kastelein, R. A., pp. 447-454. Plenum Press, New York.

Jiang, P., Josue, J., Li, X., Glaser, D., Li, W., Brand, J. G., Margolskee, R. F., Reed, D. R. & Beauchamp, G. K. (2013). Major taste loss in carnivorous mammals. Proceedings of the National Academy of Science 109, 4956-4961.

Kastelein, R. & Dubbeldam, J. L. (1990). Marginal papillae on the tongue of the harbour porpoise (*Phocoena phocoena*), bottlenose dolphin (*Tursiops truncatus*) and Commerson's dolphin (*Cephalorhynchus commersonii*). Aquatic Mammals 15, 158-170.

Kishida, T., Kubota, S., Shirayama, Y. & Fukami, H. (2007). The olfactory receptor gene repertoire in secondary-adapted marine vertebrates: evidence for reduction of the functional proportion in cetaceans. Biology Letters 3, 428-430.

Kuznetzov, V. B. (1990). Chemical sense of dolphins: quasi-olfaction. In: Sensory abilities of cetaceans, edited by Thomas, J. A. & Kastelein, R. A., pp. 481-503. Plenum Press, New York.

Nachtigall, P. E. & Hall, R. W. (1984). Taste reception in the bottlenose dolphin. Acta Zoologica Fennica 172, 147-148.

National Nutrient Database for Standard Reference. US National Agricultural Library. Available from: http://ndb.nal.usda.gov/.

Oelschläger, H. H. A. (2008). The dolphin brain – a challenge for synthetic neurobiology. Brain Research Bulletin 75, 450-459.

Oelschläger, H. H. A. & Oelschläger, J. S. (2009). Brain. In: Encyclopedia of marine mammals, 2nd edition, edited by Perrin, W. F., Würsig, B. & Thewissen, J. G. M., pp. 134-149. Academic Press: Burlington.

Pihlström, H. (2008). Comparative anatomy and physiology of chemical senses in aquatic mammals. In: Sensory evolution on the threshold: adaptions in secondarily aquatic vertebrates, edited by Thewissen, J. G. M. & Nummela, S., pp. 95-109. University of California Press, Berkeley.

Spitz, J., Rousseau, Y. & Ridoux, V. (2006). Diet overlap between harbour porpoise and bottlenose dolphin: An argument in favour of interference competition for food? Estuarine Coastal Shelf Science 70, 259-270.

Spitz, J., Mourocq, E., Leauté, J.-P., Quéro, J.-C. & Ridoux, V. (2010). Prey selection by the common dolphin: fulfilling high energy requirements with high quality food. Journal of Experimental Marine Biology and Ecology 390, 73-77.

Thewissen, J. G. M., George, J., Rosa, C. & Kishida, T. (2011). Olfaction and brain size in the bowhead whale (*Balaena mysticetus*). Marine Mammal Science 27, 282-294.

Watkins, W. A. & Wartzok, D. (1985). Sensory biophysics of marine mammals. Marine Mammal Science 1, 219-260.

Werth, A. J. (2007). Adaptions of the cetacean hyolingual apparatus for aquatic feeding and thermoregulation. Anatomical Record 290, 546-568.

Yamasaki, F, Komatsu, S. & Kamiya, T. (1978). Taste buds in the pits at the posterior dorsum of the tongue of *Stenella coeruleoalba*. The Scientific Reports of the Whales Research Institute 30, 285-290.

SUMMARY OF PAPER 4

Questions: In cetaceans, both chemical senses (gustation and olfaction) have not received much research attention. Other marine species such as birds and fishes locate their prey even over great distances by using olfactory cues. Therefore we were wondering whether or not dolphins are sensitive to olfactory cues, too. Are dolphins able to perceive food-related odours?

Methods: We investigated the response of the Planète Sauvage dolphins towards two visually identical experimental devices, with one containing fish and the other being empty. As the odour was in air, the number of respirations close to each device was counted and compared between both stimuli (i.e., fish and control).

Results: Dolphins breathed more often close to the device containing fish than close to the empty device. Interestingly, this difference seems to appear not until the fish odour reaches a certain intensity.

Conclusions: Bottlenose dolphins seem to be able to perceive fish using olfactory cues only. Therefore, the dolphin's *Merkwelt* appears to be richer with regard to chemical stimuli than previously suggested.

EVIDENCE FOR OLFACTORY PERCEPTION IN DOLPHINS

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Abstract

Odours are used by different phylogenetic groups of aquatic species. Marine birds as well as fishes locate their prey even over great distances by using olfactory cues. Surprisingly, the debate remains open when it comes to cetaceans. Some anatomists and geneticists doubt that cetaceans can perceive odours. Here, we conducted a behavioural study to test whether or not captive dolphins respond to a biologically relevant smell, the odour of dead fresh fish. We placed an odour source within an opaque barrel at the border of the pool and counted the number of respirations at proximity as an indicator of investigation. Dolphins breathed more often close to the odour source than close to a visually identical empty barrel from the second day on, i.e. when the fish odour was stronger. Our findings suggest that dolphins were able to perceive fish using olfactory cues only, which sheds new light on cetaceans' sensory perception of their environment and foraging abilities.

1.   INTRODUCTION

The knowledge about the chemoreceptive abilities of aquatic species differs between phylogenetic groups. Studies on tube-nosed seabirds (reviewed in Nevitt 2008) have shown that they are able to find their patchily distributed foraging areas in the open ocean over thousands of square kilometres by using odours (Nevitt et al. 1995). Likewise, another marine bird, the African penguin (*Spheniscus demersus*), is attracted by the same odour that procellariiformes use to locate prey, namely dimethyl sulphide (DMS; Wright et al. 2011), which is released by phytoplankton when being grazed by zooplankton or others, thus indicating areas with good foraging grounds (Dacey & Wakeham 1986). Odours can be perceived in water and several marine (Davis et al. 2006; DeBose et al. 2008) and freshwater (Hara 2006) fish species are known to use them as foraging cues. Some fish show a specific behaviour called "sniffing" or "coughing" to drive water inflow into the olfactory sacs, thus increasing the supply for the olfactory epithelium (Nevitt 1991).

Conversely, olfaction has drawn little attention in research on marine mammals. Yet pinnipeds have been shown to be sensitive to food-related odours such as DMS (Kowalewsky et al. 2006) and to use odours to recognize their pubs (Pitcher et al. 2011). However, the presence or absence of chemoreception in cetaceans is still a debated question. Although dolphins are intensively studied, the majority of attention has been paid to their vocal production (reviewed in Janik 2009) and sound perception (reviewed in Mooney et al. 2012). Other senses have been studied only somewhat, if at all. Several authors assume that olfaction is absent in cetaceans based on anatomical and genetic findings. In the nasal cavity of odontocetes the cribriform plate of the ethmoid bone and ethmoturbinals are absent (Pihlström 2008). The main and accessory olfactory tracts are absent in toothed whales, and considerably reduced or absent in baleen whales (Pihlström 2008; Oelschläger 2008). Furthermore, olfactory receptor genes are also highly reduced (pseudogenised) or entirely absent in Odontoceti (Kishida et al. 2007).

In contrast, other studies imply that cetaceans may be capable of olfaction. Chemoreceptor cells were found in the frontal and vestibular sac (close to the blowhole) of harbour porpoises (*Phocoena phocoena*; Behrmann 1989), perhaps enabling some kind of odour sensation. Odontoceti were found to possess a well-developed olfactory tubercle (Oelschläger & Oelschläger 2009). In bowhead whales (*Balaena mysticetus*) a complex

olfactory bulb and olfactory tracts are present and more than half of the olfactory receptor genes are intact, suggesting a functional sense of smell what may enable this species to detect its prey (Thewissen et al. 2011). Taken together, this second set of studies suggests that cetaceans might have, to some extent, access to chemosensory information on airborne odours, but as anatomical and genetic studies draw controversial conclusions, behavioural studies are needed.

Bottlenose dolphins' diet is primarily composed of fish (94.2 % in stranded dolphins' stomach contents; Spitz et al. 2006). Among fish, dolphins prefer high-energy density species (Spitz et al. 2010) and the largest proportion of daily food intake was found to be fat fish (73-93 %; Meynier et al. 2008). Although it is widely accepted that dolphins use their sophisticated echolocation system for prey location (reviewed in Thomas et al. 2004), it may be possible that dolphins also use olfactory cues. We assumed that odours of prey should be interesting for the dolphins and predicted that, if dolphins were capable of perceiving it, they would express some kind of "sniffing" behaviour, i.e. taking more breaths, within the range of the odour source.

2.   MATERIAL & METHODS

2.1. Study subjects and housing conditions

In May and June 2013, we studied six captive-born bottlenose dolphins (*Tursiops truncatus*; four males: aged 5, 8, 14, and 29 years; two females: aged 5 and 12 years) in the delphinarium of Planète Sauvage (Port-Saint-Père, France). The diet of the dolphins was composed of frozen stored squid and fish (herring, capelin, sprat, and whiting) and changed in species composition on a daily basis (containing at least three different fish species each day). A daily ration of 5-10 kg per individual (depending on its weight) was given throughout the day during seven feeding sessions (ca. 15 minutes lasting).

2.2. Data collection

As odour source we used one kilogram of mixed fishes and squids (hereafter referred to as "fish") that were actually destined for feeding the dolphins. Mixing species was done to avoid responses biased by individual preferences. The fish was defrosted during the night preceding the first day of each one of the three experiment

sections (Figure 1a). Then it was placed in an opaque plastic barrel (26 cm high with 20 cm diameter; Figure 1b) that was familiar to the dolphins as it was used in a previous experiment. The perforated barrel was placed without lid directly at the border of the pool, at the same time with a second, identical barrel that served as control (i.e., not containing any fish). Barrels were left for a 10 minute session. Two video cameras (Sony Handycam HDR-XR 155) filmed on of the barrels each. Videos were analysed by an observer who counted the number of respirations for each individual dolphin within a range of 2.5 m around the barrels. Dolphins were identified on the basis of physical differences (e.g., shape of the dorsal fin or colour patterns of the skin).

(a)	Section 1 (22.-24.05.2013)		Section 2 (11.-13.06.2013)		Section 3 (17.-19.06.2013)	
	Position A	*Position B*	*Position A*	*Position B*	*Position A*	*Position B*
1. Day: *midday*	fish	control	fish	control	control	fish
1. Day: *afternoon*	fish	control	control	fish	fish	control
2. Day: *midday*	control	fish	control	fish	fish	control
2. Day: *afternoon*	control	fish	control	fish	control	fish
3. Day: *midday*	control	fish	fish	control	fish	control
3. Day: *afternoon*	fish	control	fish	control	control	fish

Figure 1: Experimental setup: (a) chronological sequence of stimuli presentation; close-up and dimensions of a barrel; (c) outline of the facility (© Planète Sauvage) with the positions of the two experimental barrels (A and B) and the video cameras; black dots indicate the barrel, the grey areas indicate the radius within which the respirations were counted.

The experiment took place in pool 3 (2.2 x 1.8 m; Figure 1c) when the weather was fair. Both barrels were placed each next to a channel that connected to experimental pool with a neighbouring pool and were attached to a pole to prevent them from falling in the pool in case of a wave (Figure 1c). The two barrels were 8 m away from each other (linear distance) and the position for fish/control barrel changed randomly from one session to another.

We conducted two sessions per day, one at midday and another one in the afternoon and each experimental section lasted three days. Three sections were done in total with a new mixture of fish each time, leading to 18 sessions in total over nine days (Figure 1a). During a section the fish was not stored in the fridge but at room temperature in order to intensify the odour.

2.3. Data analysis

Statistical analyses were run using R software (version 2.15.0, R Development Core Team, www.r-project.org). As odour concentration changed on a daily basis due to fish decomposition, we compared the number of respirations between fish and control for each day separately with Wilcoxon tests (N = 6). Therefore we summed up each individual's values obtained during the sessions of the first, the second, and the third days, respectively, of the three experimental sections. Respiration values in the text and figure are given as mean ± standard error.

3. RESULTS

Whereas the number of respirations at the first days did not differ significantly between the barrel containing fish and the control barrel (fish: 6.5 ± 1.6; control: 11.8 ± 3.1; p = 0.0625, V = 20, N = 6), the dolphins breathed more often in the area around the fish-smelling compared to the control both at the second days (fish: 13.5 ± 1.3; control: 5.5 ± 0.5; p = 0.0355, V = 0, N = 6) and even more at the third days (fish: 16.8 ± 1.9; control: 4.8 ± 1.0; p = 0.0313, V = 0, N = 6; Figure 2).
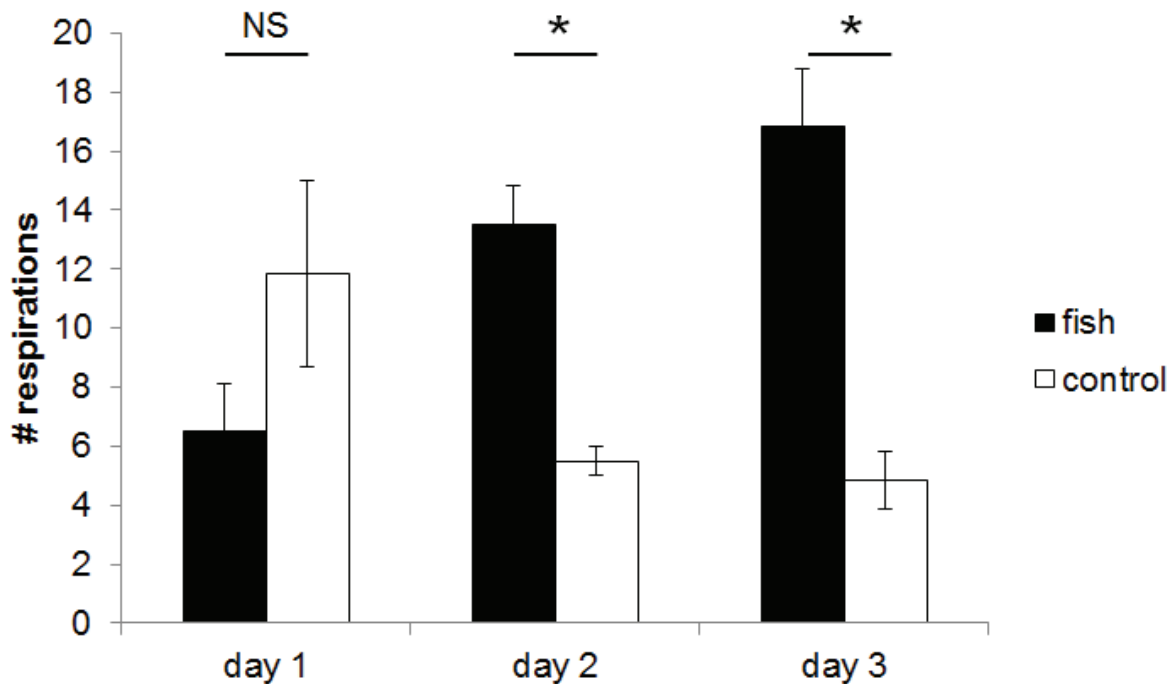
Figure 2: Dolphins' mean (± S.E.) number of respirations in the area around the barrel containing fish compared to the control barrel. Statistical difference is indicated by asterisks (* $p \leq 0.05$; NS = not significant; Wilcoxon tests).

4. DISCUSSION

The response of the six captive bottlenose dolphins to visually identical but differently smelling devices suggests that this species is capable of perceiving odours. The dolphins took more breaths close to the fish-smelling device compared to the control device, wherefore we hypothesize that they are chemosensitive. This is, to our knowledge, the first study on dolphins' spontaneous behavioural responses towards a potentially biologically relevant odour. Other behavioural studies on dolphins' chemoreception are rare. They showed that bottlenose dolphins can detect the flavours sour, bitter, salty, and sweet nearly as well as humans (Friedl et al. 1990; Nachtigall & Hall 1984). Another study going in line with these findings proposed the term "quasi-olfaction" to describe dolphins' chemoreception and suggested that it may be mediated by the trigeminal nerve (Kuznetzov 1990). This nerve is very well developed in dolphins (Oelschläger 2008). In humans, trigeminal perception was shown to be necessary to locate an odour (Kleemann et al. 2009).

That the dolphins did not discriminate between fish-smelling and control device at the first day might be caused by the odour concentration. Perhaps the olfactory sense may not be extremely sensitive in dolphins, especially as the odour was in the air, but requires certain odour strengths that were not yet reached at the first day when the fish was fresh. As the fish odour intensified over time, thus it smelled stronger compared to the first day, dolphins responded to it.

Dolphins may also respond to certain molecules whose concentrations increase progressively in the course of decomposition, such as putrescine, trimethylamine, or other volatile amines (Shakila et al. 2003; Sil et al. 2008). Therefore, the dolphins' response could be explained by an attraction to one or several of the molecules specific to the stage of decomposition at the second and third day. Although dolphins are primarily hunting living prey (Reithaus & Dill 2009) there are some reports that dolphins occasionally feed on already dead prey (Sumpton et al. 2010). Actually, in some areas, populations of dolphins specialize in taking fish baits, sometimes minutes after baiting. One can therefore wonder whether olfactory cues, above other cues, may contribute to fast localization (Sumpton et al. 2010).

Dolphins may also simply have responded to this odour as a novel stimulus (since dolphins living in a delphinarium are exclusively fed fresh frozen-stored fish). In any case, there is certainly room for an adaptive value for this perceptive ability, because living fish, the main prey of dolphins, do indeed emit detectable odours (Hirvonen et al. 2000; Kullmann et al. 2008; McIntosh & Peckarsky 2004). Different aquatic species (fish, crustaceans, as well as insect larvae) respond to the odour of their respective predator fish (Hirvonen et al. 2000; Kullmann et al. 2008; McIntosh & Peckarsky 2004), showing that olfactory cues may play an important role in predator-prey interactions. In conclusion our results suggest that bottlenose dolphins are capable of perceiving odours. Given the fact that this test is easily conducted it may allow to test free-living dolphins, for example by using floating odour sources. To go further towards the idea that dolphins might use olfactory cues to locate prey, their sensitivity for DMS should be investigated. This study provides interesting results on odour perception in dolphins, thus opening new lines of research on cetaceans' chemoreception.

Acknowledgements

References

Behrmann, G. (1989). The olfactory regions in the nose of the harbour porpoise *Phocoena phocoena* (Linne, 1758). Aquatic Mammals 15, 130-133.

Dacey, J. W. H. & Wakeham, S. G. (1986). Oceanic dimethylsulfide: production during zooplankton grazing on phytoplankton. Science 233, 1314-1315.

Davis, M. W., Spencer, M. L. & Ottmar, M. L. (2006). Behavioral responses to food odor in juvenile marine fish: acuity varies with species and fish length. Journal of Experimental Marine Biology and Ecology 328, 1-9.

DeBose, J. L., Lema, S. C. & Nevitt, G. A. (2008). Dimethylsulfoniopropionate as a foraging cue for reef fishes. Science 319, 1356.

Friedl, W. A., Nachtigall, P. E., Moore, P. W. B., Chun, N. K. W., Haun, J. E., Hall, R. W. & Richards, J. L. (1990). Taste reception in the Pacific bottlenose dolphin (*Tursiops truncatus gilli*) and the California sea lion (*Zalophus californianus*). In: Sensory abilities of cetaceans, edited by Thomas J. A. & Kastelein, R. A., pp. 447-454. Plenum Press: New York.

Hara, T. J. (2006). Feeding behaviour in some teleosts is triggered by single amino acids primarily through olfaction. Journal of Fish Biology 68, 810-825.

Hirvonen, H., Ranta, E., Piironen, J., Laurila, A. & Peuhkuri, N. (2000). Behavioral response of naïve Artic charr young to chemical cues from salmonid and non-salmonid fish. Oikos 88, 191-199.

Janik, V. M. (2009). Acoustic communication in delphinids. In: Advances in the study of behaviour, Volume 40, edited by Naguib, M. & Janik, V. M., pp. 123-157. Academic Press, Burlington.

Kishida, T., Kubota, S., Shirayama, Y. & Fukami, H. (2007) The olfactory receptor gene repertoire in secondary-adapted marine vertebrates: evidence for reduction of the functional proportion in cetaceans. Biology Letters 3, 428-430.

Kleemann, A. M., Albrecht, J., Schöpf, V., Haegler, K., Kopietz, R., Hempel, J. M., Linn, J., Flanagin, V. L., Fesl, G. & Wiesmann, M. (2009). Trigeminal perception is necessary to localize odors. Physiology & Behavior 94, 401-405.

Kowalewsky, S., Dambach, M., Mauck, B. & Dehnhardt, G. (2006). High olfactory sensitivity for dimethyl sulphide in harbour seals. Biology Letters 2, 106-109.

Kullmann, H., Thünken, T., Baldauf, S. A., Bakker, T. C. M. & Frommen, J. G. (2008). Fish odour triggers conspecific attraction behaviour in an aquatic invertebrate. Biology Letters 4, 458-460.

Kuznetzov, V. B. (1990). Chemical sense of dolphins: quasi-olfaction. In: Sensory abilities of cetaceans, edited by Thomas, J. A. & Kastelein, R. A., pp. 481-503. Plenum Press, New York.

McIntosh, A. R. & Peckarsky, B. L. (2004). Are mayfly anti-predator responses to fish odour proportional to risk? Archiv für Hydrobiologie 160, 145-151.

Meynier, L., Pusineri, C., Spitz, J., Begoña Santos, M., Pierce, G. J. & Ridoux, V. (2008). Intraspecific dietary variation in the short-beaked common dolphin Delphinus delphis in the Bay of Biscay: importance of fat fish. Marine Ecology Progress Series 354, 277-287.

Mooney, T. A., Yamato, M. & Branstetter, B. K. (2012). Hearing in cetaceans: from natural history to experimental biology. In: Advances in Marine Biology, Vol. 63, edited by Lesser, M., pp. 197-246, Academic Press, London.

Nachtigall, P. E. & Hall, R. W. (1984). Taste reception in the bottlenose dolphin. Acta Zoologica Fennica 172, 147-148.

Nevitt, G. A. (1991). Do fish sniff? A new mechanism of olfactory sampling in pleuronectid flounders. Journal of Experimental Biology 157, 1-18.

Nevitt, G. A. (2008). Sensory ecology on the high seas: investigating the odor world of the procellariiform seabirds. Journal of Experimental Biology 211, 1706-1713.

Nevitt, G. A., Veit, R. R. & Kareiva, P. (1995). Dimethyl sulphide as a foraging cue for Antarctic procellariiform seabirds. Nature 376, 680-682.

Oelschläger, H. H. A. (2008). The dolphin brain – a challenge for synthetic neurobiology. Brain Research Bulletin 75, 450-459.

Oelschläger, H. H. A. & Oelschläger, J. S. (2009). Brain. In: Encyclopedia of marine mammals, 2nd edition, edited by Perrin, W. F., Würsig, B. & Thewissen, J. G. M., pp. 134-149. Academic Press: Burlington.

Pihlström, H. (2008). Comparative anatomy and physiology of chemical senses in aquatic mammals. In: Sensory evolution on the threshold: adaptions in secondarily aquatic vertebrates, edited by Thewissen, J. G. M. & Nummela, S., pp. 95-109. University of California Press, Berkeley.

Pitcher, B. J., Harcourt, R. G., Schaal, B. & Charrier, I. (2011). Social olfaction in marine mammals: wild female Australian sea lions can identify their pup's scent. Biology Letters 7, 60-62.

Reithaus, M. R. & Dill, L. M. (2009). Feeding strategies and tactics. In: Encyclopedia of marine mammals, 2nd edition, edited by Perrin, W. F., Würsig, B. & Thewissen, J. G. M., pp. 414-423. Academic Press: Burlington.

Shakila, R. J., Vijayalakshmi, K. & Jeyasekaran, G. (2003). Changes in histamine and volatile amines in six commercially important species of fish of the Thoothukkudi coast of Tamil Nadu, India stored at ambient temperature. Food Chemistry 82, 347-352.

Sil, S., Joseph, J. & Kumar, K. A. (2008). Changes in biogenic amines during iced and ambient temperature storage of tilapia. Journal of the Science of Food and Agriculture 88, 2208-2212.

Spitz, J., Rousseau, Y. & Ridoux, V. (2006). Diet overlap between harbour porpoise and bottlenose dolphin: An argument in favour of interference competition for food? Estuarine Coastal and Shelf Science 70, 259-270.

Spitz, J., Mourocq, E., Leauté, J.-P., Quéro, J.-C. & Ridoux, V. (2010). Prey selection by the common dolphin: fulfilling high energy requirements with high quality food. Journal of Experimental Marine Biology and Ecology 390, 73-77.

Sumpton, W. D., Lane, B. & Ham, T. (2010). Gear modifications and alternative baits that reduce bait scavenging and minimize by-catch on baited drum-lines used in the Queensland Shark Control Program. Proceedings of the Royal Society of Queensland 116, 23-35.

Thewissen, J. G. M., George, J., Rosa, C. & Kishida, T. (2011). Olfaction and brain size in the bowhead whale (*Balaena mysticetus*). Marine Mammal Science 27, 282-294.

Thomas, J. A., Moss, C. F. & Vater, M. (2004). Echolocation in bats and dolphins. The University of Chicago Press, Chicago and London.

Wright, K. L. B., Pichegru, L. & Ryan, P. G. (2011). Penguins are attracted to dimethyl sulphide at sea. Journal of Experimental Biology 214, 2509-2511.

CHAPTER 5
INVESTIGATIONS ON THE DOLPHINS' SENSITIVITY TO MAGNETIC FIELDS

SUMMARY OF PAPER 5

Questions: Beside the five traditional senses (hearing, sight, touch, taste and smell), the perception of other cues can provide useful information about the environment. One of the less intensively studies senses is magnetoreception. Although some spatial observations and anatomical findings suggest that dolphins (and other cetaceans) may be sensitive to the geomagnetic field, experimental evidence is lacking. Do dolphins possess a magnetic sense? In case they do, will they be attracted to the magnetic stimulus or avoid it instead?

Methods: We tested the response of the Planète Sauvage dolphins towards an experimental device containing a neodymium block that was either magnetized or demagnetized but otherwise identical (form, density). Behaviours analysed included: latency for the first approach, time spent close to the device, latencies for the first rostrum contact and the first body contact, number and duration of rostrum and body contacts.

Results: We found that the dolphins did not differ significantly in latency for the first approach, time spent close to the device, number and duration of rostrum and body contacts. However, they took more time before touching the magnetized device both with the rostrum and with the body.

Conclusions: Bottlenose dolphins respond differently to a magnetized object compared to a visually identical but demagnetized object. It seems that magnetic objects are at least partly repellent for dolphins because they hesitated to touch it. Therefore, this species can be considered as magnetosensitive and magnetic fields have to be added to the list of stimuli that are available for the dolphin to perceive its *Umwelt*.

BEHAVIOURAL EVIDENCE OF MAGNETORECEPTION IN DOLPHINS: A FIRST EXPERIMENTAL REPORT

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Abstract

Magnetoreception, i.e. the perception of a magnetic field, is supposed to play an important role for orientation and navigation in some animals, including both terrestrial and aquatic species. Although some spatial observations of free-ranging cetaceans and anatomical findings led to the assumption that cetaceans may be sensitive to the geomagnetic field, experimental evidence is lacking. Here we tested the spontaneous response of six captive bottlenose dolphins to the presentation of two magnetized and demagnetized devices while they were swimming freely. Dolphins took more time before touching the device when it contained a magnetized neodymium block compared to a control demagnetized block that was identical in form and density. We conclude that the dolphins are able to discriminate the two stimuli on the basis of their magnetic properties, a prerequisite for magnetoreception-based navigation. This finding contributes to the debated question of a magnetic sense in cetaceans that could have function in magnetoreception-based navigation.

1.   INTRODUCTION

The geomagnetic field is a dipole field generated by the Earth's fluid outer iron core (Wiltschko & Wiltschko 1995) providing a consistent source of directional and latitudinal information on the global scale (Winklhofer 2010). Different taxa can detect this magnetic field, although primary magnetoreceptors have not yet been unequivocally identified (Lohmann & Johnson 2000). Birds use geomagnetic cues for navigation, for example during homing and migration (Cadiou & McNaughton 2010). Several insects, e.g. bees and ants, orient around their nests with the aid of the Earth's magnetic field (Wajnberg et al. 2010). Likewise, some amphibians were found to navigate by using geomagnetic cues (e.g. Diego-Rasilla et al. 2008). But also some mammals, e.g. mole rats and bats, are capable of magnetoreception-based orientation (Holland at al. 2006; Marhold et al. 1997).

Not only terrestrial animals rely on geomagnetic information, the same is true for several marine species. The seafloor occurs in distinct bands of positively and negatively magnetized rocks that are symmetrically arranged on opposite sides of the mid-ocean ridges, thus providing potential navigational cues (Walker & Dennis 2005). Magnetoreception-based navigation has been described for crustaceans, fish and turtles (Boles et al. 2003; Kalmijn 1982; Lohmann et al. 2001). Observations of free-ranging cetaceans show some evidence of magnetoreception. Fin whale migration routes (Walker et al. 1992) and live stranding sites of offshore cetaceans (Kirschvink et al. 1986; Klinowska 1985) were found to be correlated with the geomagnetic field.

However, experimental evidence for magnetoreception in cetaceans is lacking. Captive bottlenose dolphins (*Tursiops truncatus*) were exposed to a magnetic field that was introduced into their pool by an induction coil (magnetic field strength unknown) but did not show any spontaneous response (Bauer et al. 1985). Even during a series of conditioning experiments using two-choice discrimination and go/no go designs (magnetic field strength: 3.7×10^{-5} T) the dolphins did not show any indication of a magnetic discrimination (Bauer et al. 1985) However, Bauer et al. (1985) admitted that "experiments that constrain the subject in time and place may be putting significant limits on appropriate orientation". Therefore we conducted an experiment that did neither confine the dolphins spatially to one position as for example during a go/no go experiment nor demand a direct response as it is the case in

conditioning experiments as for example in Bauer et al. (1985), but rather observed their spontaneous reaction towards magnetized and demagnetized devices.

2. METHODS

2.1. Study subjects and housing conditions

In January and February 2013, we studied six captive-born bottlenose dolphins (four males: aged 5, 8, 14, and 29 years; two females: aged 5 and 12 years) in the delphinarium of Planète Sauvage (Port-Saint-Père, France). Daily routine comprised seven training/feeding sessions conducted by the dolphin trainers including medical training (e.g. acceptance of inspection and palpation of all parts of the body or being touched by medical equipment) as well as training for public shows (e.g., jump on command). During this study Planète Sauvage was closed due to winter season therefore no public shows took place at this time.

Overall, this outdoor delphinarium consists of four pools, covering 2000 m² water surface and containing 7.5 million litres salt water. During this study, water temperature ranged from 12.5 to 15.3 °C (mean 14.06 ± 0.13 °C) and salinity from 25.0 to 26.4 % (mean 25.54 ± 0.11 %). The experiment took place in a circular pool (diameter: 20 m; depth: 4.5 m). Animals were free to move in and out during the entire experiment. This pool was chosen as it was symmetrical, providing identical conditions (i.e. pool characteristics such as shape of the pool walls) at every location used to install the experimental device.

2.2. Data collection

We used a neodymium block (length: 10 cm; width: 10 cm; height: 1.5 cm) with a magnetic-field strength of 1.2 T (Ingeniería Magnética Aplicada, S.L., Barcelona, Spain; Figure 1) that was placed in an opaque plastic barrel (diameter: 20 cm; height: 26 cm), which in turn was placed in the water 40 cm from the pool wall at a depth of 50 cm by hanging from a wooden plank (covered with neoprene to avoid injury) to which it was attached with a cord. To allow water inflow, the barrel was perforated with 40 small holes (diameter: 3 mm) and 3 larger holes (diameter: 1 cm; 2 at the bottom to fix the neodymium block inside and 1 in the lid to attach the cord). Together

with the neodymium block a 1 kg plumbum weight was fixed inside the barrel using two plastic cable ties in order to ensure a fast submergence of the device. At the end of a session, the device was removed from the pool. The block remained at the same position in the barrel during all the experiment, so that polarity never changed. As control stimulus we used the exact same (size and density) but demagnetized neodymium block (Ingeniería Magnética Aplicada). During an experimental session, only one device was used, containing either the magnetized or the demagnetized neodymium block, and was installed by a person blind to the content of the barrel.
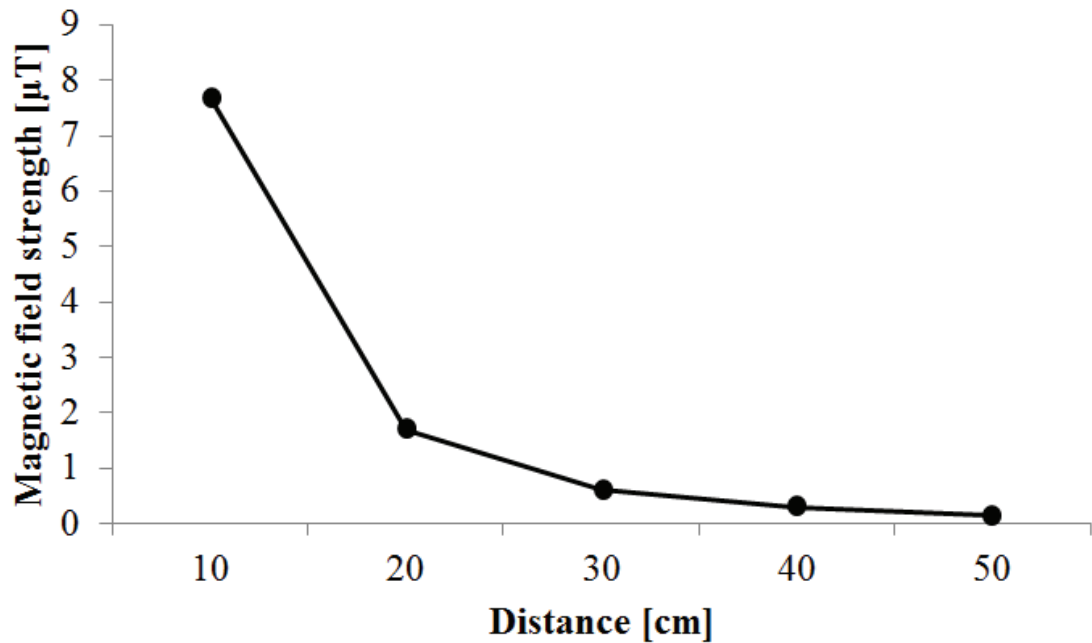
Figure 7: Attenuation of the magnetic field strength in air (provided by the manufacturer Ingeniería Magnética Aplicada, S.L., Barcelona, Spain) with distance from the neodymium block (length: 10 cm; width: 10 cm; height: 1.5 cm; 1.2 T) used in the present study as magnetic stimulus.

As the device was new to the animals, we presented it empty during 51 sessions lasting 15 minutes each without any block inside for habituation on the nine days before the experiment began. Then, we conducted 54 experimental sessions (29 with the magnetized stimulus; 25 with the demagnetized stimulus), presenting the two stimuli in a randomized order. Location of the device at the pool was also changed randomly between three possible positions to avoid any influence of location.

Experimental sessions took place between the training/feeding sessions, resulting in 1 to 6 experimental sessions per day (N = 13 days in total). An experimental session lasted 15 minutes during which the response of the dolphins was filmed by a video camera (Sony Handycam HDR-XR 155) on a tripod behind the device, thus no person was around the pool during the experimental sessions.

Later, the videos were analysed by an observer who was able to identify the dolphins (on the basis of physical differences, e.g. dorsal fin shape) but was blind to the content of the barrel visible in the video. Different behaviours that occurred within a range of 1.5 m around the barrel, defined as the experimental area, were measured or counted for each individual dolphin: latency for the first approach (i.e., entering the experimental area), time spent within the experimental area, latencies for the first rostrum contact and the first body contact (i.e., contact with another part of the body), number and duration of rostrum and body contacts. If an individual did not approach or touch the device during a session, the session's total duration (900 seconds) was used for statistical analysis on latencies.

2.3. Data analysis

Statistical analyses were run using R software (version 2.15.0, R Development Core Team, www.r-project.org). We compared all variables (approach latency, proximity duration, latencies for first rostrum and body contact, number and duration of rostrum and body contacts) between magnet and control sessions with Wilcoxon tests. Therefore we summed up each individual's values obtained during magnet and control sessions, respectively. The sums for the magnet sessions have been corrected to account for the fact that we had more magnet than control sessions. In the text, values present mean ± standard error.

3. RESULTS

Although the dolphins approached the magnetized and demagnetized device with similar latencies (magnet: 9187 ± 2197 sec; control: 9314 ± 1951 sec; $p = 0.6875$, V = 13) and spent similar durations in the presence of both devices (magnet: 657 ± 161 sec; control: 666 ± 176 sec; $p = 0.5625$, V = 14), they took more time before touching the magnetized

device both with the rostrum (magnet: 19929 ± 2080 sec; control: 17415 ± 1484 sec; p = 0.0313, V = 0; Figure 2) and with the body (magnet: 24267 ± 993 sec; control: 20301 ± 1087 sec; p = 0.0313, V = 0; Figure 2). However, neither number of contacts differed between magnetized and demagnetized stimulus (rostrum contacts: magnet: 59 ± 23; control: 85 ± 34; p = 0.2188, V = 17; body contacts: magnet: 6 ± 3; control: 6 ± 3; p = 0.7874, V = 9) nor the duration of contacts (rostrum contacts: magnet: 74 ± 37; control: 96 ± 43; p = 0.3125, V = 16; body contacts: magnet: 10 ± 6; control: 8 ± 4; p = 1, V = 7).
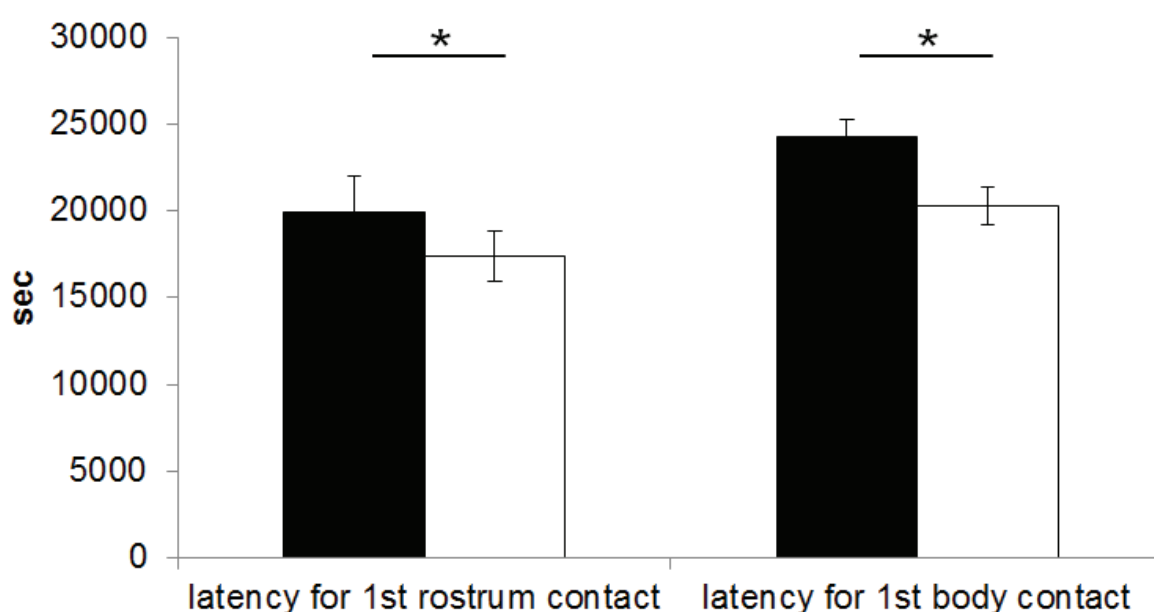
Figure 8: Dolphins latencies [sec] for the first rostrum contact and the first body contact (i.e. other parts of the body) for the magnetized (in black) and demagnetized (in white) device (given is the mean ± SE of the six individuals' sums). Statistical difference is indicated by asterisks (Wilcoxon test; * p ≤ 0.05).

4.   DISCUSSION

The responses of six captive bottlenose dolphins towards visually identical devices that contained either a magnetized or a demagnetized neodymium block suggest that this species is capable of perceiving magnetic fields. The dolphins took more time to touch the device when it contained the magnetized neodymium block compared to the control that was identical in form and density, thus they discriminated between the two stimuli. This is, to our knowledge, the first experimentally obtained behavioural evidence for a sensibility towards magnetic stimuli in cetaceans.

That dolphins can sense magnetic fields was already previously suggested by Stafne & Manger (2004) who observed that captive bottlenose dolphins in the northern hemisphere swim predominantly in counter clockwise direction, while dolphins in the southern hemisphere swim predominantly in clockwise direction. One reason why previous experiments failed to detect a response of the dolphins toward magnetized stimuli might be the magnetic field strength. The magnet used in this study (for details see ESM) created a magnetic field with a strength of approximately 0.150-0.505 T at a distance of 2-5 cm from the magnet, i.e. the minimum and maximum distance between the magnetic block and the border of the barrel. This means, when touching the barrel the magnetic field was roughly 4000-13000 times stronger than the magnetic field used in the conditioning experiments of Bauer et al. (1985). Maybe their magnetic field strength of only 3.7×10^{-5} T was too weak to be detected by the dolphins.

In view of the fact that the Earth's magnetic field is on average 4.5×10^{-5} T strong (Wiltschko & Wiltschko 1995) it seems questionable whether or not dolphins' sensitivity is high enough to perceive and use geomagnetic cues for navigation. However, we did not test dolphins' perception threshold and there are several observations that found a correlation between cetaceans' occurrence and geomagnetic characteristics (Kirschvink et al. 1986; Klinowska 1985; Walker et al. 1992) wherefore this possibility cannot be ruled out.

Another possible function of magnetosensitivity besides navigation might be prey detection. Although living beings do not emit magnetic fields, each muscle movement generates a bioelectrical field. Sharks are known to detect their prey by using the bioelectric fields generated by their prey's movement (Kalmijn 1971). As electric currents create a magnetic field, it may be possible that dolphins use magnetoreception to detect prey via the magnetic field created by the prey's electric impulses. Passive electroreception has been already proposed to be a supplementary sense to echolocation during benthic feeding in dolphins (Czech-Damal et al. 2013).

One possible mechanism to perceive magnetic fields is the presence of ferromagnetic particles, such as magnetite, in the organism's body. These miniature magnets align themselves in the magnetic field and transmit this information through a connection with the central nervous system (Wiltschko & Wiltschko 1995). Magnetite has indeed been found in the dura mater of dolphins, thus suggesting that they are capable of magnetoreception (Bauer

et al. 1985; Zoeger et al. 1981). Cetaceans may have inherited this sensory ability from their ancestors because some of the closely related artiodactyls (Thewissen et al. 2009) are also magnetosensitive. Deer and cattle align their body axes in north-south direction by using the geomagnetic field when grazing and resting (Begall et al. 2008).

Our results suggest that dolphins, and maybe other cetacean species too, possess a magnetic sense. This finding provides new, experimentally obtained evidence that this phylogenetical group should be added to the list of magnetosensitive species, broadening the evolutionary view on magnetoreception.

References

Bauer, G. B., Fuller, M., Perry, A., Dunn, J. R. & Zoeger, J. (1985). Magnetoreception and biomineralization of magnetite in cetaceans. In: Magnetite biomineralization and magnetoreception in organisms: a new biomagnetism, edited by Kirschvink, J. L., Jones, D. S. & MacFadden, B. J., pp 489-507. Plenum Press, New York.

Begall, S., Cerveny, J., Neef, J., Vojtech, O. & Burda, H. (2008). Magnetic alignment in grazing and resting cattle and deer. Proceedings of the National Academy of Science 105, 13451-13455.

Boles, L. C. & Lohmann, K. J. (2003). True navigation and magnetic map in spiny lobsters. Nature 421, 60-63.

Cadiou, H. & McNaughton, P. A. (2010). Avian magnetite-based magnetoreception: a physiologist's perspective. Journal of the Royal Society Interface 7, S193-S205.

Czech-Damal, N. U., Dehnhardt, G., Manger, P. & Hanke, W. (2013). Passive electroreception in aquatic mammals. Journal of Comparative Physiology A 199, 555-563.

Diego-Rasilla, F. J., Luengo, R. M. & Phillips, J. B. (2008). Use of magnetic compass for nocturnal homing orientation in the palmate newt, *Lissotriton helveticus*. Ethology 114, 808-815.

Holland, R. A., Thorup, K., Vonhof, M. J., Cochran, W. W. & Wikelski, M. (2006). Navigation: bat orientation using Earth's magnetic field. Nature 444, 702.

Kalmijn, A. J. (1971). The electric sense of sharks and rays. Journal of Experimental Biology 55, 371-383.

Kalmijn, A. J. (1982). Electric and magnetic field detection in elasmobranch fishes. Science 218, 916-918.

Kirschvink, J. L., Dizon, A. E. & Westphal, J. A. (1986). Evidence from strandings for geomagnetic sensitivity in cetaceans. Journal of Experimental Biology 120, 1-24.

Klinowska, L. (1985). Cetacean live stranding sites relate to geomagnetic topography. Aquatic Mammals 1, 27-32.

Laist, D. W., Knowlton, A. R., Mead, J. G., Collet, A. S. & Podesta, M. (2001). Collisions between ships and whales. Marine Mammal Science 17, 35-75.

Lohmann, K. J. & Johnson, S. (2000). The neurobiology of magnetoreception in vertebrate animals. Trends in Neuroscience 23, 153-159.

Lohmann, K. J., Cain, S. D., Dodge, S. A. & Lohmann, C. M. F. (2001). Regional magnetic fields as navigational markers for sea turtles. Science 294, 364-366.

Marhold, S., Burda, H. & Wiltschko, W. (1997). A magnetic polarity compass for direction finding in a subterranean mammal. Naturwissenschaften 84, 421-423.

O'Connell, C. P., Abel, D. C., Rice, P. H., Stroud, E. M. & Simuro, N. C. (2010). Responses of the southern stingray (*Dasyatis americana*) and the nurse shark (*Ginglymostoma cirratum*) to permanent magnets. Marine and Freshwater Behaviour and Physiology 43, 63-73.

Panigada, S., Pesante, G., Zanardelli, M., Capoulade, F., Gannier, A. & Weinrich, M. T. (2006). Mediterranean fin whales at risk from fatal ship strikes. Marine Pollution Bulletin 52, 1287-1298.

Stafne, G. M. & Manger, P. R. (2004). Predominance of clockwise swimming during rest in southern hemisphere dolphins. Physiology & Behaviour 82, 919-926.

Stoner, A. W. & Kaimmer, S. M. (2008). Reducing elasmobranch bycatch: Laboratory investigation of rare earth metal and magnetic deterrents with spiny dogfish and Pacific halibut. Fisheries Research 92, 162-168.

Thewissen, J. G. M., Cooper, L. N., George, J. C. & Bajpai, S. (2009). From land to water: the origin of whales, dolphins, and porpoises. Evolution: Education & Outreach 2, 272-288.

Wajnberg, E., Acosta-Avalos, D., Alves, O. C., de Oliveira, J. F., Srygley, R. B. & Esquivel, D. M. S. (2010). Magnetoreception in eusocial insects: an update. Journal of the Royal Society Interface 7, S207- S225.

Walker, M. M. & Dennis, T. E. (2005). Role of the magnetic sense in the distribution and abundance of marine animals. Marine Ecology Progress Series 287, 295-307.

Walker, M. M., Kirschvink, J. L., Ahmed, G. & Diction, A. E. (1992). Evidence that fin whales respond to the geomagnetic field during migration. Journal of Experimental Biology 171, 67-78.

Wiltschko, R. & Wiltschko, W. (1995). Magnetic orientation in animals. Springer, Berlin.

Winklhofer, M. (2010). Magnetoreception. Journal of the Royal Society Interface 7, S131-S134.

Zoeger, J., Dunn, J. R. & Fuller, M. (1981). Magnetic material in the head of the common Pacific dolphin. Science 213, 892-894.

CHAPTER 6
DISCUSSION

1.   WHAT THESE FINDINGS TELL US ABOUT THE DOLPHIN'S *UMWELT*

The results obtained during this thesis fill some of the gaps that still exist in the knowledge of the dolphin's *Umwelt* and therefore contribute to a better understanding of this species. With regard to the dolphin's *Merkwelt*, i.e. what dolphins perceive, three modalities can be added to the list of potentially informative cues. As the experiments conducted have shown, dolphins respond to gustatory, olfactory, and magnetic stimuli, suggesting that they are chemo- and magnetosensitive. So far, these modalities have not been considered seriously as potentially functional in dolphins. Concerning the dolphin's *Wirkwelt*, i.e. what dolphins do, their nocturnal activity is more complex than expected with temporally patterned choruses. Moreover, the finding that dolphins emitted vocal copies of sounds heard daily during special events suggests that their vocal productions may serve as potential indicators of events or objects that bear a meaning for the dolphins. The functions of the different sensory modalities in dolphins may be diverse and are hereafter outlined for the senses this thesis has focused on. The word "function" should be used with caution because it implies a goal-directedness. When talking about biological issues this may cause confusion as from the evolutionary point of view, all living creatures are a result of coincidence and benefits. Therefore, the word "function" refers to adaption but not to purpose and is hereafter used with this connotation.

1.1.   Possible functions of audition

Research on the use of vocalizations has been until now traditionally focused on communication (whistles and burst-pulsed sounds) and echolocation (clicks). Acoustic communication signals are often studied with respect to possible functions such as species, group, and individual recognition, group cohesion, social behaviour, or foraging (reviewed in Janik 2009). Dolphins may be able to discriminate heterospecifics by means of their vocalizations (Oswald et al. 2003). Delphinid species such as killer whales that live in stable groups rely on group-specific dialects (Ford & Fisher 1983), while fission-fusion species like bottlenose dolphins identify conspecifics based on their individual-specific whistle contours (Janik et al. 2006). These whistles are probably also used to maintain group cohesion (Janik & Slater 1998). While no context-specificity in whistle type use could be found so far, burst-pulsed sounds seem

to be more frequent during aggressive interactions (e.g. Blomqvist & Amundin 2004; Connor & Smolker 1996) and a certain call type was found to be food-related, probably to manipulate prey (Janik 2000a). Context can influence whistle rate, as whistle rate increases during activities involving excitement such as foraging (Díaz López 2011; Moore & Ridgway 1996) or dispersion of group members for example during socializing (Quick & Janik 2008).

Without questioning the relevance or validity of these research fields, it may be worth extending the research issue by further considering that dolphins' vocalizations may be seen as expressions of some internal process. For example, bottlenose dolphins are thought to encode their level of distress in whistle rate (Caldwell et al. 1990) and alteration of acoustic parameters while keeping the overall frequency modulation pattern constant (Esch et al. 2009). The findings detailed in Chapter 3 suggest that dolphins may express their needs or the attribution of meaning via vocalizations. The observed nocturnal chorusing may be the expression of the need for social cohesion that in turn is manifested in the synchronous behaviours characteristic of resting/sleeping dolphins (Gnone et al. 2001; Goley 1999; Sekiguchi & Kohshima 2003; Würsig et al. 1994). Würsig et al. (1994) described a behaviour in wild spinner dolphins, the so called zig-zag swimming, that occurs in the transition between active and resting state. During this behaviour the dolphins are producing whistle choruses that are suggested to test the other group members' alertness and to strengthen the group cohesion (Würsig et al. 1994). These choruses are thought to be part of a group process of transition from one behavioural state to another to affirm that the group members are synchronous, thus they serve in coordination what is crucial in group-living species (Brownlee & Norris 1994). The chorusing found in the here studied group of captive bottlenose dolphins may serve a similar function, wherefore it provides an indication of the dolphins' inner state. However, we cannot rule out an alternative hypothesis, namely that the increased whistle rate is not functioning in facilitating group behaviour but rather a by-product of high social activity. Other species that are known for their synchronized sleep behaviour such as roosting birds or bats are highly vocal at the roosting sites, what is thought to be a prerequisite to sleep (Adret-Hausberger 1982; Kunz 1982). In European starlings, peaks of vocal activity

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arise before each wave of departure of a group from the roosting site, suggesting a role of vocalization in synchronizing and coordinating departures (Adret-Hausberger 1982; Feare 1984; Hausberger et al. 2008). Therefore it seems possible that dolphins also use vocalizations to synchronize their group behaviour.

Beside overall whistle activity, the production of vocal copies is a very interesting feature of delphinid sound production. The fact that dolphins produce vocal copies predominantly in the presence of a certain object that was previously associated with the original sound (Hooper et al. 2006) implies that the dolphins have attributed a meaning/sense to this object. Thus, the attribution of meaning could be indirectly explorable through the study of dolphins' vocalizations, especially their production of vocal copies. Bottlenose dolphins are known to copy individually distinctive whistles of conspecifics (Janik & Slater 1998; King et al. 2013) and different functions are suggested. It seems possible that dolphins use these copies as referential vocal labels in order to address each other (King & Janik 2013), to confirm the reception of another individual's whistle (Janik & Sayigh 2013), or to locate specific individuals (Watwood et al. 2005). Other mimicking species such as songbirds mostly copy environmental sounds that are frequent and similar to their own (learning mistake model), sounds of predators or aggressive species (Batesian mimicry), or sounds of heterospecific competitors in order to repel them (reviewed in Kelley & Healy 2011).

As stated earlier, most studies deal with diurnal vocal activity, while we presume that the copies of the whale sounds produced at night by the dolphins in Planète Sauvage have been emitted during sleep, as indicated by the time and the overall behavioural state of the group. Therefore it seems possible that the dolphins were maybe "dreaming" of something related to the whale sounds such as the public shows. Indeed, day events are mentally processed during sleep in humans, where presleep stimuli are incorporated into dream contents (Cipolli et al. 2004). This means, that relevant events that happened during the day, are often rehearsed in the form of dreams during sleep or day dreaming. Therefore, these analyses may present an original, indirect way to evaluate which elements of the environment are perceived and relevant (i.e. meaningful) to dolphins. Examples of animals that emit vocalizations during sleep are rare, because not systematically investigated. A maturing male Lowe's guenon

(*Cercopithecus campbelli lowei*) uttered loud calls, which are usually used by mature alpha-males, when he was sleeping (Bertrand in Humphrey 1983). These vocalizations occurred in a stage of the sleep that resembled the dream-intense REM sleep in humans, including rapid eye movements, sporadic movements of hand and feet, irregular respiration, and muscular atony (Bertrand in Humphrey 1983). Similarly, young horses (*Equus ferus przewalski*) have been found to produce vocalizations characteristic for adult conspecifics during REM sleep but never while awake (Lubrano Lavadera 2005). Taken together, vocalizations seem to have the potential to reveal internal processes such as mental processing of experienced environmental stimuli or events.

In addition to this interesting finding of which sound of their environment dolphins copied and the fact that these copies were perhaps emitted while sleeping, the fact that the perception of the auditory template at daytime and the production of the copies at nighttime are separated by several hours is intriguing. Although the sensory and motor phases of vocal learning are separated in a variety of songbird and parrot species (Pepperberg 1997; Thorpe 1961), this separation has not been investigated so far in marine mammals that are also able of vocal learning. The here described separation between auditory memory formation and spontaneous vocal copying in bottlenose dolphins is, to our knowledge, the first report on this phenomenon in a marine mammal. Aside from the hypothesis exposed above that these copies may present rehearsals of a more global memory of events experienced during the daytime, as for example in the form of dreams during sleep in humans (Cipolli et al. 2004), it is also possible that dolphins, like parrots or songbirds, "practice" the production of a newly learned sound outside the "model's" presence (Hausberger et al. 1991). To summarize, the mechanisms underlying vocal copying and therefore vocal learning remain still unclear and require further investigations.

1.2. Possible functions of chemoreception

While dolphins use vocalizations for long-range communication (Janik 2009), short-range communication is also performed via visual and tactile signals such as postures or touch (Connor et al. 2000; Dudzinski 1996; Dudzinski et al. 2012; Paulos et

al. 2008). However, when at close contact communication may be complemented with chemical cues. When dolphins are capable of perceiving different odours/tastes, including urine and faeces (Kuznetzov 1990), it is conceivable that they may use their chemosensory abilities to gain information about conspecifics such as sex, identity, or reproductive state, when engaged in exploratory behaviours such as "genital inspections" (Herzing 1996; Norris & Dohl 1980).

On the other hand, chemoreception may be useful for the dolphins to locate prey or evaluate its quality (e.g. energy content). The results detailed in Chapter 4 indicate that bottlenose dolphins are indeed sensitive to food-related odours and that they can discriminate food flavours. Other marine species such as procellariiform birds also use olfactory cues to locate their patchily distributed prey in the ocean (Nevitt 2008). Furthermore, dolphins were found to select preferentially high-energy density prey species even though they are less abundant (Spitz et al. 2010). It is not clear whether dolphins identify them visually or by means of other modalities. Anyway, chemical information might be very useful in this context. As fish emit species-specific odours (Hirvonen et al. 2000) it seems possible that dolphins could use these cues to locate some prey species.

Several anatomic studies suggested that odontocetes do not possess a functional olfaction (e.g. Pihlström 2008; Oelschläger 2008). The fact that a given species is microsmatic (i.e. has a poorly developed sense of smell) or macrosmatic (i.e. has a well-developed sense of smell) is often based on anatomical characteristics such as the size of the olfactory bulb or the surface of the olfactory epithelium, what led to the conclusion that primates are microsmatic (reviewed in Smith & Bhatnagar 2004). However, there is evidence that some primate species actually have an unexpectedly high olfactory sensitivity, which for some substances is comparable or even better than the sensitivity of macrosmatic species such as rats or dogs (Laska et al. 2000; Laska & Seibt 2002). Therefore, generalizations from anatomical characteristics to actual capacities may have been over-interpreted and should be revised. Small olfactory organs only indicate that a species is not an olfactory specialist but may well have high sensitivity to particular relevant odours (Pihlström et al. 2005; Nummela et al. 2013).

While the findings obtained in this thesis suggest that dolphins are indeed chemosensitive, the perceptual mechanisms remain still unclear as our data do not give information on possible pathways. It seems that bottlenose dolphins possess chemoreceptor cells both in the nasal cavity beyond the blowhole as well as in the oral cavity, but the inner pathway remains unclear as cranial nerve I, which is transmitting the olfactory signal to the central nervous system in terrestrial mammals (Thewissen 2009), seems to vanish during early ontogenesis (Oelschläger & Buhl 1985). However, since taste perception is supposed to be mediated rather by cranial nerve V (Kuznetzov 1990) than by cranial nerve VII as in other mammals, the function of the cranial nerves might be generally different in odontocetes hence comparisons with other mammalian species might be difficult.

1.3. Possible functions of electro-/magnetoreception

Another modality possibly involved in prey detection could be magneto- and/or electroreception. Just as sharks are sensitive to the bioelectric impulses generated by their prey's movements (Kalmijn 1971), dolphins could use the electric currents emitted by the muscles of prey to detect it (Czech-Damal et al. 2012). Although echolocation provides also information about items buried in the sediment (Roitblat et al. 1995), passive electroreception could function as a supplementary sense to echolocation during benthic feeding (Czech-Damal et al. 2013). This feeding style is not uncommon in bottlenose dolphins (Heithaus & Dill 2009; Rossbach & Herzing 1997), so it seems plausible that dolphins developed a sensitivity to electric stimuli. As electric currents create a magnetic field, it may be possible that dolphins also use magnetoreception to detect prey via the magnetic field created by the prey's electric impulses. Our findings show that dolphins are sensitive to a magnetic field. However, whether and how they use this information requires further investigation. So far, the pathway of magnetoreception in general has remained unclear. Different potential receptors have been discussed in the literature, including magnetite-based receptors (Kirschvink et al. 1985), photoreceptors (Liedvogel & Mouritsen 2010; Ritz et al. 2000), and radical-pair reactions (Weaver et al. 2000). According to the theory of induction-based perception, another pathway would be the perception of electric fields

that are generated by the magnetic field (Wiltschko & Wiltschko 1995). Therefore, electroreceptors could be used to indirectly perceive magnetic fields. As Guiana dolphins seem to be capable to perceive electric stimuli via their vibrissal crypts on the rostrum (Czech-Damal et al. 2012), it seems possible that dolphins could use these receptors to indirectly perceive magnetic fields.

Cetaceans may have inherited their magnetoreceptive ability from their ancestors because some of the closely related artiodactyls (Thewissen et al. 2009) are also magnetosensitive. Deer align their body axes in north-south direction and orient their head towards north when grazing and resting (Begall et al. 2008). Magnetic alignment is a spontaneous behavioural expression of magnetoreception that appears particularly in resting animals when body orientation is not controlled by other factors (Wiltschko & Wiltschko 1995) but the function remains unclear. One hypothesis suggests that maintaining a symmetric position to the field lines somehow influences certain physiological processes (Wiltschko & Wiltschko 1995).

Magnetoreception is not limited to a certain phylogenetic group and has been found in other mammals (e.g. bats and some rodents; Deutschlander et al 2003; Holland at al. 2006; Marhold et al. 1997; Oliveriusová et al. 2012), birds (reviewed in Cadiou & McNaughton 2010; Wiltschko & Wiltschko 2002; Wiltschko & Wiltschko 2003), amphibians (Diego-Rasilla et al. 2008; Fischer et al. 2001), insects (Banks & Srygley 2003; Wajnber et al. 2010), lobsters (Boles et al. 2003), fish (Kalmijn 1982; Quinn 1980), and turtles (Lohmann et al. 2001) where this sense is used in navigation and orientation. The common point in all these species is the fact that their habitat does not provide many visual landmarks and/or is three-dimensional hence rather complex. That is true for dense forest vegetation (deer), nocturnal darkness (bats), underground (mole rats), air (bats, birds), and water (fish, turtles). Therefore it does not seem surprising that the habitat of cetaceans might have favoured a sensitivity to magnetic fields.

2.   COMPARING THE *UMWELTEN* OF DOLPHINS AND OTHERS SPECIES

Although evolved from a terrestrial, deer-like ancestor (Thewissen et al. 2009), dolphins are well adapted to their aquatic lifestyle. One could expect that species living in the

same habitat are similarly adapted to the same conditions. Thus, dolphins could be expected to share more similarities with other marine species, such as cuttlefish, than with their closest relatives, such as deer.

Both deer and cuttlefish inhabit visually restricted environments due respectively to dense vegetation, difficult light condition, or turbidity. Nevertheless, or maybe therefore, both species have highly developed visual systems (Alves et al. 2009; Birgersson et al. 2001; Cartron et al. 2013; Mäthger et al. 2013; Shashar et al. 1996; VerCauteren & Pipas 2003). Although dolphins also possess a good vision (Mass & Supin 2009), it does not seem to play a role as important as in deer or cuttlefish. Deer use vision for example to detect predators (D'Angelo et al. 2008; Hodgetts et al. 1998) and remain relatively silent except during the mating seasons (Clutton-Brock 1979). However, dolphins are predators themselves except for occasional attacks by sharks or orcas (Heithaus & Dill 2009; Weller 2009). Consequently, they do not need to remain silent to avoid the attraction of predators, and they can use the advantages of acoustic signals for communication in visually restricted habitats. Cuttlefish on the other hand use their vision to detect prey (Messenger 1989; Shashar et al. 2000). Although dolphins probably use visual cues during prey capture (Heithaus & Dill 2009; Mass & Supin 2009), prey location is primarily facilitated by echolocation (Au 2009; Herzing & dos Santos 2004), again an acoustic modality. Echolocation enables the exploration of distant objects even out of sight and is especially useful while moving fast, something that cuttlefish rarely do as they primarily are ambush predators (Shashar et al. 2000).

Another possible factor favouring acoustic abilities in dolphins is their social life and fission-fusion society. While deer stay close together and in visual contact with other herd members when herding (Geist 2009), dolphins disperse much more while swimming. Given that vision in water is extremely restricted, dolphins loose visual contact quite fast but can stay in acoustic contact even over longer distances. The idea that acoustic communication is favoured in visually restricted habitats has been hypothesized not only for cetaceans (Tyack & Sayigh 1997) but also for forest-living species such as birds or primates (Catchpole & Slater 1997; Marler 1965). Although cuttlefish also have to face the poor visual conditions in water, they did not develop a long-distance communication channel such as acoustics. This is maybe due to their mostly solitary life style where communication with conspecifics is short-range, mainly with visual displays (Boal et al. 1999).

Short-range communication as well as food detection seem to be facilitated by chemical stimuli in both deer and cuttlefish (Boal 1997; Boal & Golden 1999; Lawson et al. 2001; Mary & Balakrishnan 1984; Tixier et al. 1998). Although not intensively investigated until now, chemically mediated communication or prey detection seems possible in dolphins too.

Taken together, the dolphin's *Umwelt* shares similarities with the *Umwelten* of an inhabitant of a similar habitat and a close relative, but does not resemble one more than the other, revealing the importance of phylogeny as well as habitat. According to their specific habitat, mammalian species can be grouped into "sensory types" regarding hearing, vision, and olfaction. As pointed out by Nummela and colleagues (2013), arboreal mammals tend to be more visual than olfactive, in contrast to terrestrial mammals that tend to be more olfactive than visual. Aerial and aquatic mammals seem to use both vision and olfaction equally, although aquatic species are generally considered as less olfactive than terrestrial species. While good vision appears to be correlated with good hearing, there seems to be a trade-off between these two senses and olfaction (Nummela et al. 2013). Interestingly, this study also revealed a tendency that predator and prey species often belong to the same sensory type (e.g. reindeer and wolf, zebra and lion, mice and cat) which might indicate an "arms race" between prey and predator (Nummela et al. 2013). According to this idea, dolphins could be expected to have a similar sensory profile to their prey (fish) and/or their predators (sharks), thus chemo- and magnetoreception might be not that surprising.

3.   RESEARCH PERSPECTIVES

As always in research, one finding raises new questions. For example, to which degree dolphins exploit the here described chemo- and magnetoreceptive abilities needs to be further investigated. It is conceivable that the perception of chemical stimuli might be useful in nutritional and social contexts. To test these questions, experiments are needed that use, for example, food flavours or odours representing different food qualities (e.g. energy content) to test whether or not dolphins are able to use chemical cues to choose high-energy fish, for example sprat (761 ± 102 kJ/100g; average value from the biochemical analyses of fish used as food for the dolphins in Planète Sauvage) over blue whiting (443 ± 71 kJ/100g). Further, dolphins' olfactory sensitivity to dimethyl sulphide (DMS) should be tested with regard to its

relevance for other marine species (e.g. procellariiform birds) that use DMS to locate prey (Kowalewsky et al. 2006; Nevitt et al. 1995; Wright et al. 2011).

Additionally, experiments using dolphins' own body flavours could shed light on questions such as whether or not dolphins are able to discriminate familiar from unfamiliar individuals, males from females, or ovulating from non-ovulating/immature females. Excretions, secretions, or skin could be used as stimuli. While the collection of excretion is relatively difficult as it dissolves quickly in the water and would require an intensive training to earn only very small samples (~1-2 mL of urine at a time), collection of skin samples would be very easy. By gently rubbing the dolphin's skin, for example with a cotton gauze pad, cells from the upper skin layer can be collected, requiring only a minimum of training (personal observation). Different body parts could be tested and should include the urogenital area. Dolphins are often seen "inspecting" this area very closely with their rostrum (personal observation), a behaviour also described for wild dolphins (Herzing 1996; Norris & Dohl 1980).

The role of magnetoreception in dolphins requires further studies too. Experiments with different magnetic field strengths should test the detection threshold in dolphins and investigate whether they elicit avoidance behaviour in dolphins. The possible involvement of dolphins' electroreceptors (Czech-Damal et al. 2012) on magnetoreception could be tested by covering the vibrissal crypts with non-conductive material. Furthermore, the interaction of echolocation and magnetoreception in object location or navigation contexts should be further investigated. Therefore, dolphins' echolocation activity should be recorded in the presence of magnetized stimuli to see whether or not it is influenced by the presence of the magnetic field or its strength.

But even in the intensively studied field of bioacoustics, further investigations are necessary. In order to learn more about how dolphins perceive their environment and which objects/contexts are meaningful to them, a closer study of vocal copy production would be interesting. The same is true for other species known to be capable of vocal copying such as orcas (Foote et al. 2006), elephants (Poole et al. 2005), orang-utans (Wich et al. 2009), parrots (e.g. Cruickshank et al. 1993), and songbirds (e.g. Hausberger et al. 1991). With respect to the mechanisms underlying vocal copying, further investigations are required to

explain findings such as the separation between auditory memory formation and spontaneous vocal copying.

As illustrated by the example of dolphins, the *Umwelt* of a species can be very complex, especially if this species has undergone a drastic environmental change during its phylogeny or ontogeny. With regard to phylogeny, the return of a terrestrial mammal from land to water can be considered a drastic environmental change, which is the case not only for cetaceans. The same is true for pinnipeds, sirenians, otters, some rodents (e.g. beavers), hippopotami, or platypus. Other species experience such changes during their ontogeny, for example if their life cycle is partly aquatic and partly terrestrial. This is the case for several amphibians that undergo a metamorphosis from fully aquatic larvae to semi-aquatic adults, or some insects such as mayflies whose larvae are aquatic but the imago is a flying insect. All these species are potential candidates for interesting studies on *Umwelt*.

4. WHAT THESE FINDINGS TELL US ABOUT RESEARCH

Although it has been intensively studied for decades, many facets of dolphin's biology still remain unknown. Without doubt, this is partly due to the difficulties researchers encounter when studying marine mammals, especially in the field. First, it requires a boat and therefore convenient weather conditions. Second, marine mammals are not easy to locate and once they are found not easy to follow due to their diving capacities. However, the lack of literature about certain topics suggests that these topics have been so far more or less ignored. But why? It seems that most attention has been paid to dolphins' acoustic abilities. Unequivocally, dolphins' acoustic communication system and echolocation abilities are very sophisticated and play a major role in this species' biology. On the other hand, researchers seem to have leaped to the conclusion that other sensory modalities would necessarily not be very well developed and neglected them. This approach is like wearing blinders towards so far not well studied or unstudied modalities. It therefore risks leading to simplified and incomplete knowledge about the whole subject. Dolphins are only one example for this problem, but the same is probably true for other research subjects.

Beside the idealistic concern that a subject might be incompletely studied because some topics are neglected, this approach might also impact conservation and/or management issues. The possibly hasty assumption that for example one modality is by far the most

important for a species can direct conservation issues accordingly. To stay with the example of cetaceans, the fact that many conservation issues deal with anthropogenic noise pollution (Bateson 2007), such as military and seismic survey sonars (Fernandez et al. 2005; Goldbogen et al. 2013; Jepsen et al. 2003; Piantadosi & Thalmann 2004; Risch et al. 2012; Stone & Tasker 2006; Thompson et al. 2013; Tyack et al. 2011), boat noise (Aguilar Soto et al. 2006; Buckstaff 2004; Pirotta et al. 2012), or drilling (Bailey et al. 2010; Richardson et al. 1990; Thomas et al. 1990), is probably at least partly due to research's concentration on cetaceans' acoustic/hearing abilities. Without meaning to deny its importance, maybe these animals also face other potential threads that are unperceived because not yet considered as potentially important. Assuming that dolphins use chemical cues for communication and/or prey detection, these important behavioural tasks could be extremely impaired by chemical pollution that is especially intensive by the coasts (Kakuschke et al. 2010; Williams et al. 2011).

We are facing many conservation problems, especially regarding climate change, and powerful measures need to be implemented as fast as possible. These measures are chosen on the basis of what is known about a given species. But if research rushes to conclusions and provides a simplified and probably incomplete description of a species' biology, these measures are likely to be not as appropriate as they should be. Consequently, it is important that research broadens the view and remains unbiased when studying a topic. Maybe the integration of the Zen concept of Shoshin into science would contribute to a more open-minded research. Cultivating this concept, also known as "beginner's mind", means having an attitude of openness, eagerness, and lack of preconceptions when studying a subject, even when studying at an advanced level, just as a beginner would (Koda 2008; Pant 2010).

"In the beginner's mind there are many possibilities, in the expert's mind there are few"

(Suzuki 1970)

<u>RÉSUMÉ</u>

PLONGER DANS L'*UMWELT* DES DAUPHINS:

PERCEPTION ACOUSTIQUE, GUSTATIVE,

OLFACTIVE ET MAGNÉTIQUE

Résumé

I.   INTRODUCTION

1.   L'*Umwelt* concept de Jakob von Uexküll

En 1909, Jakob von Uexküll a établi un nouveau concept et une nouvelle perspective sur la perception de l'environnement par des êtres vivants : l'*Umwelt* qui signifie « l'univers subjectif » (Chien 2006). En 1934, il a reconnu les animaux comme étant des sujets et non plus des machines guidées uniquement par des réflexes.

L'*Umwelt* d'un sujet est divisé en deux parties formant une entité, le *Merkwelt* et le *Wirkwelt* (von Uexküll 1909). Le *Merkwelt* contient tout ce qu'un sujet perçoit et le *Wirkwelt* tout ce qu'un sujet fait. Pour être perçu par un sujet, l'objet doit avoir une caractéristique (*Merkmal*) correspondant à un récepteur du sujet (von Uexküll 1909). Le stimulus perçu est ensuite traité dans le cerveau qui va lui attribuer un sens. Ce sens peut varier en fonction du contexte ou de l'état interne du sujet. La réaction du sujet face à l'objet va être différente suivant le sens qui lui sera attribué. Cette boucle fermée entre le sujet et l'objet est appelé *Funktionskreis* (von Uexküll 1934).

En raison du rôle crucial des récepteurs et des structures de traitement sensoriel, l'*Umwelt* est déterminé par le plan d'organisation d'une espèce. Ainsi, bien que plusieurs espèces puissent partager le même environnement, chacune va posséder son propre *Umwelt,* correspondant à ses capacités sensorielles spécifiques. En outre, au sein même d'une espèce, les individus ne partagent pas nécessairement le même *Umwelt* en raison des différences morpho-anatomiques, causées par exemple par des défauts génétiques ou d'événements au cours de l'ontogenèse (par exemple, un aveugle et une personne voyante peuvent partager le même environnement, mais pas le même *Umwelt*). Par conséquent, chaque individu a son propre *Umwelt* égocentrique qui est déterminé par le plan d'organisation de l'individu (von Uexküll 1934).

Bien que von Uexküll (1909) admette que les espèces diffèrent par leur expérience basée sur la perception, il insiste sur leur égalité en ce qui concerne leur adaptation. Selon lui, «chaque sujet animal, le simple et le complexe, sont également adaptés à leur environnement; un animal simple a un *Umwelt* simple, un animal complexe un *Umwelt* complexe", et aucune espèce ne peut donc être considérée comme supérieure à une autre (von Uexküll 1934).

2. Que sait-on de l'*Umwelt* des dauphins?

La famille odontocète des Delphinidae comprend les espèces de cétacés les plus étudiées, c'est pourquoi ils présentent un modèle approprié pour la description de leur *Umwelt*. L'analyse du monde du dauphin doit commencer par un examen de l'information sensorielle qui leur est disponible. Les dauphins sont connus pour leurs capacités acoustiques et leur système de communication est très bien étudié (revue dans Janik 2009). L'ouïe est donc considérée comme la modalité sensorielle la plus importante (par exemple Thewissen 2009) puisqu'elle est impliquée non seulement dans la communication, mais aussi dans la navigation et la localisation des proies (par exemple Mooney et al. 2012). Par conséquence, la majorité des études portent sur des questions liées à l'audition, la production sonore, l'écholocation et la communication. D'autres modalités sensorielles sont considérées comme moins importantes (par exemple Marriott et al. 2013) et sont donc peu ou pas étudiées pour cause de compromis entre les modalités (Nummela et al. 2013). La capacité à percevoir les stimuli chimiques est très controversée car des études anatomiques, moléculaires et comportementales mènent à des conclusions peu claires et parfois contradictoires (Friedl et al. 1990; Jiang et al. 2013; Kishida et al. 2007; Kuznetzov 1990; Nachtigall & Hall 1984; Oelschläger 2008; Pihlström 2008). De même, l'électro- et la magnetoréception n'ont pas été intensivement étudiées, mais certaines observations indiquent une fonctionnalité possible de ces modalités chez les dauphins (Czech-Damal et al. 2012; Zoeger et al. 1981).

3. Questions ouvertes sur l'*Umwelt* des dauphins

L'objectif de cette thèse est de contribuer à une meilleure compréhension de l'*Umwelt* du dauphin en comblant certaines des lacunes dans les connaissances. Jusqu'à présent, l'*Umwelt* du dauphin n'a été qu'en partie décrite, les différentes études ont principalement été menées sur l'audition, la vision et la perception sensitive. Dans ces domaines, l'*Umwelt* du dauphin est donc relativement bien compris.

Certains des sens sont temporellement indépendants, ce qui signifie qu'ils sont fonctionnels à tout moment de la journée, contrairement à la vue qui est limitée à la journée. A cause de cette restriction visuelle l'utilisation de signaux acoustiques est

favorisée et les vocalisations pourraient différer entre la nuit et le jour. Cependant, la plupart des études sur le comportement vocal dauphins ont été effectuées de jour. Contrairement à la plupart des mammifères, les cétacés, en raison de leur sommeil uni-hémisphérique, n'ont pas un rythme d'activité diurne (Lyamin et al. 2008). La nuit ne peut donc pas être considérée comme une période d'inactivité, mais doit être considérée comme une partie aussi importante de l'*Umwelt* du dauphin que le jour. Puisqu'ils ne passent pas la nuit à dormir, les dauphins peuvent être engagés dans différentes activités ou comportements sociaux au cours de cette période. Compte tenu du fait qu'ils sont des animaux très vocaux, il semble probable que ces activités soient médiées par des vocalisations. En outre, la nuit est le seul moment sans intervention humaine pour les dauphins en captivité, présentant ainsi un moment particulier où ils pourraient exprimer des comportements correspondant plus à leurs processus internes. Par conséquent, une étude plus approfondie de l'activité vocale nocturne des dauphins est nécessaire afin de compléter nos connaissances sur l'*Umwelt* du dauphin. Ce questionnement a mené à un premier manuscrit : « *Presleep chorusing in captive bottlenose dolphins* ».

Concernant la capacité des dauphins à copier des sons de leur environnement, la question demeure ouverte : Pourquoi imitent-ils certains sons plutôt que d'autres ? Il a été démontré que les dauphins produisent des imitations vocales en particulier en présence de certains objets préalablement associés au son original (Hooper et al. 2006). Cela implique que ces objets étaient significatifs pour les dauphins. Cela nous a conduit à nous demander si la production d'imitations vocales peut être révélateur de la significativité du son d'origine ou de l'objet/du contexte dans lequel le son a été émis (Article 2). Ce questionnement a mené à un second manuscrit : « *Do dolphins rehearse show-stimuli when at rest? Delayed matching of auditory memory* ».

Le second aspect de l'*Umwelt* du dauphin concerne les capacités de perception des différentes modalités. Comme la revue de littérature l'a révélé, le gout, l'odorat, et la magnetoréception, bien qu'ils soient des sens potentiellement fonctionnels, n'ont pas été beaucoup étudiés. Par conséquent, il existe un manque d'informations sur leur éventuelle pertinence pour la perception par le dauphin, de son *Umwelt*. Les dauphins sont entourés d'une énorme quantité d'informations chimiques, exploitées par d'autres

espèces marines (Hirvonen et al. 2000; Nevitt et al. 1995; Wright et al. 2011). Nous avons donc voulu savoir dans quelle mesure le dauphin est capable d'utiliser ces informations chimiques présentes dans l'environnement. Des préférences alimentaires ayant été rapportées chez cette espèce (Spitz et al. 2010), nous nous sommes demandé dans quelle mesure elles pouvaient être guidées par le gout. Ce questionnement a mené à un troisième manuscrit : « *Do dolphins perceive flavours? A novel approach to test spontaneous preferences* ». En outre, chez d'autres espèces marines, il a été montré que la localisation des proies est médiée par des signaux olfactifs. Nous avons donc voulu savoir si les dauphins étaient également capables de percevoir les odeurs liées à l'alimentation : « Evidence for olfactory perception in dolphins ».

Outre les cinq sens traditionnels (ouïe, vue, toucher, goût et odorat), la perception d'autres indices peuvent également fournir des informations utiles sur l'environnement. L'un de ces sens moins étudiés est la magnétoréception. Malgré certaines observations spatiales et constatations anatomiques suggérant que les dauphins (et autres cétacés) sont sensibles au champ magnétique terrestre (Kirschvink et al. 1986; Klinowska 1985; Walker et al. 1992), il n'existe aucune preuve expérimentale de cette sensibilité. Nous avons donc voulu savoir si les dauphins possèdent réellement une capacité de magnéto-réception : « *Behavioural evidence of magnetoreception in dolphins: a first experimental report* ».

II. MÉTHODOLOGIE

1. Sujets et site d'étude

Nous avons étudié un groupe de dauphins nés en captivité dans le delphinarium de "Planète Sauvage" (Port-Saint-Père, France). Le groupe étudié a toujours été composé de mâles et de femelles non apparentés d'âge variable, mais la composition a évolué au cours de la thèse (taille du groupe: 4-7; Figures 1 et 2; Tableau 1). L'installation est entièrement extérieure et est composée de quatre piscines d'une surface totale de 2000 m² et contenant 7,5 millions de litres d'eau salée (Figure 3).

Tous les dauphins ont été entrainés à un âge précoce à l'aide d'un renforcement positif (conditionnement opérant), du poisson étant utilisé comme renforçateur primaire. Pour les dauphins, une journée type dure de 8 à 19 heure. Elle comprend sept

sessions de formation/d'alimentation et   jusqu'à quatre spectacles publics (selon la saison). Les sessions de formation durent environ 15 minutes et les spectacles environ 30 minutes. Les sessions d'entrainement incluent une partie dédiée à l'acceptation de soins vétérinaires (inspection et palpation de toutes les parties du corps, être touché par un équipement médical) et une partie dédiée à la formation pour les spectacles (par exemple, sauter sur commande). Durant les périodes de temps libre entre deux sessions d'entrainement, des jouets (par exemple tapis de mousse, balle) et des jets d'eau sont mis à la disposition des dauphins, qui restaient cependant libres de faire ce qu'ils voulaient.

Le régime alimentaire des dauphins était principalement composé de poissons (hareng, capelan, sprat, maquereau, merlan) et de calmar congelés. La qualité des aliments est contrôlée régulièrement par des analyses biochimiques réalisées par un laboratoire indépendant. La composition des repas changeait quotidiennement, les dauphins ayant accès à 3 espèces de poisson différentes chaque jour. Les dauphins recevaient quotidiennement entre 5 et10 kg de poisson par individu (selon la taille) distribués tout au long de la journée pendant les sessions de formation / d'alimentation.

2.   **Collecte des données**

2.1. **Enregistrements acoustiques**

Le comportement acoustique des dauphins à Planète Sauvage a été l'objet d'une étude précédente (stage de master 2, Briseño Jaramillo 2009). Une partie des enregistrements, réalisés au cours de huit nuits (entre 18:00 et 06:00) en Avril et Mai 2009 et qui n'avaient pas été utilisés dans l'étude précédente ont servi de base de données pour les résultats présentés ici. Les vocalisations des dauphins ont été enregistrées en semi continu à l'aide de deux hydrophones Nauta SS03-10 placés sur deux côtés opposés de la piscine 1. Ces hydrophones étaient reliés à un enregistreur Marantz PMD 670 (fréquence d'échantillonnage 44.1 kHz; résolution: 16 bit; réponse en fréquence: 15-20000 Hz ± 3dB) lui-même connecté à un ordinateur Dell 390 où les sons ont été enregistrés en utilisant le logiciel ANA (Richard et al. 1991). En parallèle des enregistrements acoustiques, un

observateur placé à côté de la piscine 1 comptait le nombre de respirations (respirations audibles).

2.2. Chémoréception

2.2.1. Gout

L'étude sur le gout a été menée en collaboration avec le Pr Benoist Schaal (Centre des Sciences du Goût, UMR CNRS-Université de Bourgogne 6265). En Janvier et Février 2012, nous avons testé la capacité des dauphins à percevoir les saveurs. Pour cela, nous avons utilisé des glaçons qui présentent une matrice appropriée pour la présentation de saveur. En effet, ils sont faciles à produire avec des saveurs différentes, sont visuellement et tactilement identiques, et très attractifs pour les dauphins. Trois saveurs différentes ont été utilisées : hareng (242 sessions de 10 minutes), saumon (199 sessions) et crevette (206 sessions). Pour le témoin nous avons utilisé des glaçons sans saveur, seulement de l'eau (246 sessions).

2.2.2. Olfaction

L'étude sur l'olfaction a été menée en collaboration avec Aurélie Célérier et Silvia Campagna (Centre d'écologie fonctionnelle et évolutive, UMR CNRS-Université de Montpellier 5175). En Mai et Juin 2013, nous avons testé la capacité des dauphins à percevoir une odeur. Pour cela, nous avons placé un baril en plastique opaque de chaque côté de la piscine Dans un des deux barils, nous avons placé du poisson, tandis que le second baril restait vide (témoin ; Figure 4). La position des deux barils (témoin/contenant le poisson) était changée de manière aléatoire. Au cours des séances de test, les dauphins étaient filmés (Sony Handycam HDR-XR 155) pour éviter toute interaction avec l'expérimentateur. Nous avons effectué 18 sessions (durée : 10 minutes).

2.3. Magnétoréception

En Janvier et Février 2013, nous avons testé la capacité des dauphins à percevoir un champ magnétique. Pour cela, les barils en plastique utilisés au cours de l'expérience sur l'olfaction ont été réutilisés. Cette fois, un bloc de

néodyme a été placé dans chacun des barils. L'un des blocs était magnétisé tandis que l'autre ne l'était pas. L'ensemble du dispositif a ensuite été mis à l'eau. (Figure 5). Les séances ont été filmées avec une caméra vidéo (Sony Handycam HDR-XR 155) sur un trépied. Nous avons effectué 29 sessions (durée : 15 minutes) avec le bloc magnétisé et 25 sessions avec le bloc démagnétisé.

3.   Analyse des données

À l'exception des enregistrements acoustiques, toutes les données étaient disponibles au niveau individuel. Différents tests statistiques paramétriques et non paramétriques ont été utilisés pour l'analyse des données. Tous les tests ont été réalisés à l'aide du logiciel R (version 2.15.0, R Development Core Team, www.r-project.org).

3.1.   Enregistrements acoustiques

Les sifflements ont d'abord été classés visuellement en catégories sur la base des modulations de fréquence. Le nombre de sifflements de chaque catégorie a été compté par tranche de 2h (18:00-20:00, 20:00-22:00, 22:00-00:00, 00:00-02:00, 02:00-04:00, et 04:00-06:00) afin de déterminer le taux de sifflement pour chaque catégorie et chaque tranche horaire. Nous avons ensuite comparé les taux de sifflement entre les différentes tranches horaires (chi²-tests) et entre les différentes catégories (GLM). Nous avons également comparé ces taux entre les différentes catégories de sifflement pour chaque tranche horaire et inversement (G-tests).

Nous avons ensuite étudié l'organisation temporelle des séquences vocales, soit une série de sifflements consécutifs du même type au moyen de répétabilité de sifflement (indiquée par un index de séquence de sifflement, WSI) et d'intervalle inter-sifflement (IWI). Les WSI et IWI ont été comparés entre les périodes pour chaque catégorie de sifflement. Pour les WSI, un G-test non paramétrique a été utilisé, tandis que les données concernant les IWI ont permis l'utilisation d'un GLM paramétrique.

L'analyse des enregistrements acoustiques, a permis de mettre en évidence, en plus des sifflements, des sons inhabituels qui n'avaient jamais été enregistrés précédemment chez ces dauphins. Ces sons inhabituels semblaient se rapprocher

plus des vocalisations de baleine (diffusés au cours des spectacles) qu'on sons émis traditionnellement par les dauphins. Afin d'évaluer cette première impression, nous avons utilisé une analyse de fonction discriminante sur plusieurs paramètres de fréquence et de temps. Nous avons également effectué une expérience de lecture avec des sujets humains et la classification des sons (dauphin ou baleine) obtenue a été comparée à l'aide de tests de Wilcoxon.

3.2. Chémoréception

3.2.1. Gout

Les observations préliminaires ont permis de mettre en évidence le fait que les dauphins pouvaient rester proches de l'expérimentateur, mais pouvaient également s'éloigner jusqu'à être hors de vue. Nous avons donc utilisé le temps de latence nécessaire au dauphin pour revenir près de l'expérimentateur et demander un autre glaçon comme mesure de l'intérêt que les animaux portaient aux glaçons proposés Les latences de demande ont été comparées entre les différentes saveurs à l'aide de LMM en ajoutant l'identité de l'individu comme facteur aléatoire.

3.2.2. Olfaction

Le mode de respiration influence la perception des odorants (Saslow 2002). Nous avons donc choisi de prendre en compte le nombre de respiration dans un périmètre de 2,5 m autour des barils comme une mesure de perception des odeurs par les dauphins. Le nombre de respirations autour du baril contenant le poisson et autour du baril témoins a été fait à l'aide de tests de Wilcoxon.

3.3. Magnéto-réception

Afin de déterminer dans quelle mesure les dauphins percevaient le stimulus magnétique, nous avons comparé : la latence de première approche (entrer dans un périmètre de 1,5m autour du baril), le temps passé dans la zone proximale (périmètre de 1,5m), la latence de premier contact avec le rostre et la latence de premier contact avec le corps, le nombre et la durée de ces différents contacts entre le baril témoin et le baril contenant le stimulus magnétique à l'aide de tests de Wilcoxon.

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III.   L'*UMWELT* NOCTURNE DES DAUPHINS: PLUS RICHE QUE PRÉVU

Résumé de l'article 1:

"Presleep chorusing in captive bottlenose dolphins (*Tursiops truncatus*)"

Questions: Du point de vue humain, l'*Umwelt* diffère entre le jour et la nuit en raison d'un rythme d'activité circadien (i.e. être éveillé pendant la journée et dormir pendant la nuit). Les cétacés sont connus pour avoir un autre type de sommeil (uni-hémispheric contrairement au sommeil bi-hémispheric), c'est pourquoi leur rythme d'activité n'est pas aussi strictement attaché à l'alternance jour/nuit. Pourtant, la nuit est une période particulière (obscurité, calme). Toutefois, on en sait peu sur l'*Umwelt* nocturne des dauphins. Est-ce qu'il y a une activité nocturne, mesurable par le biais de l'activité vocale?

Méthodologie: Nous avons étudié le taux de sifflement nocturne des dauphins de Planète Sauvage. En outre, le sommeil chez les dauphins étant entre-autres caractérisé par un taux de respiration faible, nous avons utilisé le taux de respiration comme indicateur de l'activité physique.

Résultats: Nous avons constaté que la production vocale des dauphins a suivi une tendance temporelle avec deux pics d'activité de sifflement intense (20 h et minuit), qui ont été suivies par une forte baisse d'activité vocale et une diminution du taux de respiration, ressemblant au chorus pré-sommeil chez d'autres espèces.

Conclusions: Le modèle d'activité nocturne des grands dauphins suggère une alternance entre des phases actives et des phases plus calmes. Bien qu'il y ait probablement des phases de repos et de sommeil l'activité vocale indique un rythme d'activité plus complexe qu'une simple alternance jour/nuit probablement à cause du sommeil uni-hémispherique. Ainsi, l'*Umwelt* nocturne des dauphins peut être considéré comme plus riche que prévu.

Résumé de l'article 2:

"Do dolphins rehearse show-stimuli when at rest? Delayed matching of auditory memory"

Questions: Les dauphins sont connus pour savoir imiter les sons de leur environnement. En outre, il a été démontré que les dauphins produisent des imitations vocales en particulier en présence de certains objets ayant été associés avec le son d'origine. Cela implique que ces objets sont devenus significatifs pour les dauphins. Est-il donc possible d'évaluer la significativité potentielle d'un objet à partir des productions vocales des dauphins? La production d'imitation vocale peut-elle servir d'indicateur de la significativité du son d'origine ou du contexte dans lequel le son a été émis?

Méthodologie: Nous avons étudié des patterns de vocalisation inhabituels des dauphins de Planète Sauvage en utilisant des paramètres acoustiques (analyse de fonction discriminante) et la similitude sonore (expérience de lecture avec des sujets humains).

Résultats: Nous avons constaté que les vocalisations inhabituelles des dauphins ressemblaient plus à des vocalisations de baleines qu'aux sifflements des dauphins à la fois en termes de paramètres acoustiques et en ce qui concerne l'évaluation sonore par des humains. Les vocalisations de baleines font partie de la bande sonore qui accompagne les spectacles publics quotidiens. Les premières imitations des vocalisations de baleine ont été enregistrées au cours des périodes de repos nocturnes des dauphins les premières semaines qui ont suivi l'ajout des vocalisations de baleine dans la bande son des spectacles. L'analyse des enregistrements effectués avant l'ajout des vocalisations de baleine ont montré que les imitations n'avaient jamais été émises.

Conclusions: Cette étude montre qu'il y a une séparation temporelle entre la formation de la mémoire auditive et la production d'une imitation vocale chez le dauphin. Il existe peut-être également une répétition vocale nocturne des évènements pertinents de la journée. Ainsi, les imitations vocales peuvent servir d'indicateurs d'événements ou d'objets potentiellement pertinents pour les dauphins.

IV. INVESTIGATIONS DE LA SENSITIVIÉ DES DAUPHINS CONCERNANT DES STIMULI CHIMIQUES

Résumé de l'article 3:

"Do dolphins perceive flavours? A novel approach to test spontaneous preferences"

Questions: En théorie, les dauphins ont juste besoin d'ouvrir la bouche pour avoir accès à une énorme quantité d'informations chimiques présentes dans l'eau qui les entoure. Cependant, peu de scientifiques se sont intéressés à l'étude du gout chez cette espèce. Comme les dauphins sauvages et en captivité sont connus pour avoir des préférences alimentaires, nous nous sommes demandé si ces préférences pouvaient être guidées par le goût. Les dauphins sont-ils capables de discriminer la nourriture par son goût?

Méthodologie: Nous avons étudié les réponses des dauphins de Planète Sauvage en présence de glaçons visuellement et tactilement identiques mais différant en goût (hareng, saumon, crevettes et contrôle). Comme les préférences ont été testées, nous avons comparé la latence des dauphins à revenir et demander un autre glaçon en fonctions de la saveur.

Résultats: La latence des dauphins à revenir et demander un autre glaçon après avoir reçu un glaçon parfumé au hareng ou au saumon était plus longue que lorsqu'ils recevaient un glaçon parfumé à la crevette ou un glaçon sans arôme.

Conclusions: Les dauphins ont répondu différemment aux glaçons en fonction des différents gouts. Ainsi, ils semblent être en mesure de distinguer la nourriture par son goût. Le gout pourrait donc être une modalité jusqu'ici sous-estimé dans le *Merkwelt* du dauphin.

Résumé de l'article 4:

"Evidence for olfactory perception in dolphins"

Questions: Chez les cétacés, la gustation et l'olfaction sont deux sens chimiques qui ont été très peu étudiés. Certaines espèces 'oiseaux marins et de poissons sont capables de localiser leurs proies sur de grandes distances en utilisant les signaux olfactifs. Nous nous sommes donc demandé si les dauphins sont également sensibles aux signaux olfactifs. Les dauphins sont-ils en mesure de percevoir les odeurs liées à l'alimentation?

Méthodologie: Nous avons étudié la réponse des dauphins de Planète Sauvage envers deux dispositifs expérimentaux visuellement identiques, l'un contenant un poisson l'autre étant vide. Le nombre de respirations à proximité de chaque dispositif a été compté et comparé.

Résultats: Les dauphins respirent plus souvent à proximité du dispositif contenant le poisson qu'à proximité du dispositif vide. Fait intéressant, cette différence ne semble apparaître qu'à partir du moment où l'odeur de poisson atteint une certaine intensité.

Conclusions: Les dauphins semblent être en mesure de percevoir l'odeur du poisson en utilisant seulement les signaux olfactifs. Par conséquent, le *Merkwelt* du dauphin semble être plus riche à l'égard des stimuli chimiques que ce qui était suggéré précédemment.

V. INVESTIGATIONS DE LA SENSITIVIÉ DES DAUPHINS CONCERNANT D'UN CHAMP MAGNÉTIQUE

Résumé de l'article 5:

"Behavioural evidence of magnetoreception in dolphins: a first experimental report"

Questions: Outre les cinq sens traditionnels (ouïe, vue, toucher, goût et odorat), la perception d'autres indices peut fournir des informations utiles sur l'environnement. L'un des moins étudiés est la magnéto-réception. Bien que certaines observations spatiales et constatations anatomiques suggèrent que les dauphins (et autres cétacés) peuvent être sensibles au champ magnétique terrestre, il n'en existe aucune preuve expérimentale. Les dauphins possèdent-ils un sens magnétique? Dans ce cas sont-ils attirés ou repoussés par la stimulation magnétique?

Méthodologie: Nous avons testé la réponse des dauphins de Planète Sauvage à un dispositif expérimental contenant un bloc de néodyme identique en forme et en densité, ayant été magnétisé ou démagnétisé. Nous avons ensuite analysé les comportements suivants: temps de latence pour la première approche, temps passé à proximité de l'appareil, latences de premier contact avec le rostre / avec le corps, nombre et durée des contacts avec le rostre / le corps.

Résultats: La latence de première approche, le temps passé à proximité du périphérique, le nombre et la durée des contacts avec le rostre ou le corps ne diffèrent pas significativement entre le stimulus magnétisé et le stimulus démagnétisé. Cependant, les dauphins ont mis plus de temps à toucher le dispositif magnétisé à la fois avec le rostre et avec le corps.

Conclusions: Les dauphins réagissent différemment à un objet magnétisé et à un objet démagnétisé. Il semble que les objets magnétisés sont au moins partiellement répulsifs pour les dauphins qui mettent plus de temps à le toucher. Par conséquence, cette espèce peut être considérée comme capable de percevoir des champs magnétiques et les champs magnétiques doivent être ajoutés à la liste des stimuli qu'il peut détecter dans son *Umwelt*.

VI. **DISCUSSION**

1. **QU'EST CE QUE CES RÉSULTATS NOUS DISENT SUR L'*UMWELT* DES DAUPHINS?**

Les résultats obtenus au cours de cette thèse permettent de combler certaines des lacunes qui subsistent dans la connaissance de l'*Umwelt* du dauphin et contribuent ainsi à une meilleure compréhension de cette espèce. En ce qui concerne le *Merkwelt* du dauphin, à savoir ce que les dauphins perçoivent de leur environnement, trois modalités peuvent être ajoutées à la liste des indices potentiellement informatifs. Comme nos expériences l'ont montré, les dauphins répondent aux stimuli gustatifs, olfactifs et magnétique, ce qui suggère qu'ils sont capables de percevoir des stimuli chimiques et magnétiques. Jusqu'ici, ces modalités n'avaient pas été considérées sérieusement comme potentiellement fonctionnelles chez les dauphins. Concernant le *Wirkwelt* du dauphin, à savoir ce que les dauphins font, leur activité nocturne est plus complexe que ce qui était suggéré avec des patterns temporels. En outre, nous avons mis en évidence le fait que les dauphins sont capables d'effectuer des imitations vocales de sons entendus lors d'événements spéciaux laissant à penser que leurs productions vocales peuvent servir d'indicateurs potentiels d'événements ou d'objets pertinents. Les rôles des différentes modalités sensorielles chez les dauphins peuvent être nombreux et nous avons détaillé ci-dessous ceux des modalités sur lesquelles cette thèse s'est concentrée.

1.1. Fonctions possibles de l'audition

La recherche sur l'utilisation des vocalisations a été jusqu'à présent majoritairement axée sur la communication (sifflements et bruits d'éclatement pulsés) et l'écholocation (clicks). Les signaux de communication acoustiques sont souvent étudiés en ce qui concerne d'éventuelles fonctions telles que la reconnaissance de l'espèce, du groupe ou de l'individu, la cohésion du groupe, le comportement social, ou la recherche de nourriture (revue dans Janik 2009). Sans remettre en cause la pertinence ou la validité de ces domaines de recherche, il peut être utile d'élargir la question en considérant que les vocalisations des dauphins peuvent être vues comme l'expression d'un processus interne. Par exemple, les grands dauphins sont connus pour encoder le niveau de détresse dans le taux de sifflement (Caldwell et al. 1990) et la modification des paramètres

acoustiques tout en gardant la structure globale de modulation de fréquence constante (Esch et al. 2009). Les résultats détaillés dans le chapitre 3 suggèrent que les dauphins peuvent exprimer leurs besoins par des vocalisations ou leur attribuer un sens. Le chorus nocturne observée peut être l'expression de la nécessité d'une cohésion sociale qui se manifeste dans les comportements synchrones caractéristiques de repos / sommeil des dauphins (Gnone et al, 2001; Goley 1999; Sekiguchi & Kohshima 2003; Würsig et al. 1994). Würsig et al. (1994) ont décrit un comportement chez les dauphins à long bec sauvages, que l'on appelle « natation en zig-zag », qui se produit pendant la transition entre l'état actif et le repos. Lorsqu'ils expriment ce comportement, les dauphins produisent des chorus de sifflements qui semblent avoir pour rôle de tester la vigilance des autres membres du groupe et de renforcer la cohésion du groupe (Würsig et al. 1994). Il semble que ces chorus fassent partie d'un processus de transition au niveau du groupe d'un état comportemental à un autre afin d'assurer une synchronisation et donc une coordination entre les membres du groupe ce qui est essentiel pour les espèces vivant en groupe (Brownlee & Norris 1994). Le chorus mis en évidence dans le groupe de grands dauphins étudié ici en captivité peut remplir une fonction similaire puisqu'il donne une indication de l'état intérieur des dauphins. D'autres espèces également connues pour leur comportement de sommeil synchronisé, comme les oiseaux ou les chauves-souris, sont très vocaux sur les aires de repos, ce qui semble être un pré-requis pour initier le sommeil (Adret-Hausberger 1982; Kunz 1982).

En dehors de la production de sifflements, l'imitation vocale est une caractéristique très intéressante de la production sonore des delphinidés. Le fait que les dauphins produisent des imitations vocales particulièrement en présence de certains objets ayant été associés à son original (Hooper et al. 2006) implique que les dauphins ont attribué une signification ou un sens à cet objet. Ainsi, l'attribution de sens pourrait être indirectement explorée à travers l'étude des vocalisations des dauphins, en particulier leur production d'imitations vocales. Les grands dauphins sont connus pour imiter les sifflements individuels de leurs congénères (Janik & Slater 1998; King et al 2013) et différentes fonctions sont

proposées. Il est possible que les dauphins utilisent ces imitations comme des référentiels vocaux afin d'identifier le destinataire de leur message (King & Janik 2013), pour confirmer la réception du sifflement d'un individu (Janik & Sayigh 2013), ou encore pour localiser des individus précis (Watwood et al. 2005).

Comme indiqué précédemment, la plupart des études portent sur l'activité vocale diurne. Cependant, notre étude laisse penser que les imitations des vocalisations de baleine sont produites dans la nuit par les dauphins de Planète Sauvage et ont été émises pendant leur sommeil. Il semble donc possible que les dauphins aient « rêvé » d'un événement lié aux sons de la baleine (i.e. les spectacles publics). En effet, les événements d'une journée sont mentalement traités pendant le sommeil chez les humains, et les stimuli pré-sommeil sont incorporés dans le contenu du rêve (Cipolli et al. 2004). Cela signifie que les événements pertinents qui se sont produits au cours de la journée, sont souvent répétés sous forme de rêves pendant le sommeil ou le repos. Par conséquent, l'analyse de ces productions vocales inhabituelles pendant le sommeil des dauphins peut-être une manière originale, indirecte d'évaluer les éléments de l'environnement qui sont perçus comme particulièrement pertinents / significatifs pour les dauphins.

En plus de cette conclusion intéressante selon laquelle les dauphins imitent les sons de leur environnement et ceci probablement pendant leur phase de sommeil, la séparation temporelle entre la perception du modèle auditif (pendant la journée) et la production des imitations (au cours de la nuit) sont séparés de plusieurs heures est intrigante. Bien que les phases motrices et sensorielles de l'apprentissage vocal soient séparées chez une variété d'oiseaux chanteurs et d'espèces de perroquets (Pepperberg 1997; Thorpe 1961), cette séparation n'a pas été étudiée jusqu'à présent chez les mammifères marins qui sont également capables d'apprentissage vocal. La séparation décrite ici entre la formation de la mémoire auditive et la production d'imitation vocale spontanée chez les grands dauphins est, à notre connaissance, le premier rapport sur ce phénomène chez un mammifère marin. En dehors de l'hypothèse exposée ci-dessus que les imitations vocales pourraient être des répétitions d'événements vécus au cours de la

journée, par exemple sous forme de rêves pendant le sommeil chez les humains (Cipolli et al. 2004), il est également possible que les dauphins, comme les perroquets ou certains oiseaux chanteurs, « s'exercent » à la production d'un son nouvellement appris en dehors de la présence du « modèle » (Hausberger et al. 1991). Pour résumer, les mécanismes sous-jacents à l'imitation et à l'apprentissage vocal restent méconnus et nécessitent des investigations complémentaires.

1.2. Fonctions possibles de la chémoréception

Lorsque deux individus sont spatialement proches, la communication peut être complétée par des signaux chimiques. Si les dauphins sont capables de percevoir différentes odeurs / goûts, y compris l'urine et les fèces (Kuznetsov 1990), il est concevable qu'ils puissent utiliser leurs capacités chimiosensorielles pour obtenir des informations sur leurs congénères, comme le sexe, l'identité ou le statut reproducteur, lorsqu'ils effectuent des explorations au niveau des zones génitales (Herzing 1996; Norris & Dohl 1980).

D'autre part, la chimio-réception peut être utile aux dauphins lorsqu'ils cherchent à localiser leurs proies ou à évaluer leur qualité (par exemple la teneur en énergie). En effet, les résultats détaillés dans le chapitre 4 indiquent que les dauphins sont sensibles aux odeurs liées à l'alimentation et qu'ils peuvent distinguer les saveurs des aliments. D'autres espèces marines comme les oiseaux procellariiformes utilisent également les signaux olfactifs pour repérer leurs proies inégalement répartie dans l'océan (Nevitt 2008). En outre, il a été montré que les dauphins choisissent préférentiellement des proies de haute densité énergétique, même si elles sont moins abondantes (Spitz et al. 2010). Les modalités sensorielles utilisées par les dauphins pour identifier la valeur énergétique de leur proie ne sont pas clairement identifiées. Quoi qu'il en soit, l'information chimique pourrait être très utile dans ce contexte. Comme les poissons émettent des odeurs spécifiques (Hirvonen et al. 2000), il semble possible que les dauphins utilisent ces indices pour localiser certaines proies.

Plusieurs études anatomiques suggèrent que l'olfaction des odontocètes n'est pas fonctionnelle (par exemple, Pihlström 2008; Oelschläger 2008). Cependant, il est

possible les conclusions faites à partir de caractéristiques anatomiques aient été sur-interprétées et que leur généralisation aux capacités sensorielles réelles des individus doivent être révisées. Les petits organes olfactifs peuvent simplement indiquer que l'olfaction n'est pas un des sens principaux de l'espèce mais les individus peuvent néanmoins très bien avoir une sensibilité élevée à odeurs particulières pertinentes (Pihlström et al 2005; Nummela et al 2013).

Bien que les résultats obtenus dans cette thèse suggèrent que les dauphins sont en effet capables de percevoir des stimuli chimiques, les mécanismes perceptifs restent peu clairs dans la mesure ou nos données ne permettent pas d'identifier les voies de communications utilisées. Il semble que les dauphins possèdent des récepteurs chimiosensoriels à la fois dans la cavité nasale au-delà de l'évent ainsi que dans la cavité buccale, mais les voies internes restent à étudier.

1.3. Fonctions possibles de l'électro-/magnétoréception

Une autre modalité éventuellement impliqués dans la détection des proies pourrait être la magnéto et/ou l'électro-réception. Tout comme les requins sont sensibles aux impulsions bioélectriques générés par les mouvements de leurs proies (Kalmijn 1971), les dauphins pourraient utiliser les courants électriques émis par les muscles de leurs proies (Czech-Damal et al. 2012). Bien que l'écholocation fournisse également des informations sur les objets enfouis dans les sédiments (Roitblat et al. 1995), l'électro-réception passive pourrait fonctionner comme un sens supplémentaire à l'écholocation lors de l'alimentation benthique (Czech-Damal et al. 2013). Ce style d'alimentation n'est pas rare chez les grands dauphins (Heithaus & Dill 2009; Rossbach & Herzing 1997), il semble donc plausible que les dauphins aient développé une sensibilité à des stimuli électriques. Comme les courants électriques créent un champ magnétique, il est possible que les dauphins utilisent également la magnéto-réception afin de détecter ses proies via le champ magnétique créé par des impulsions électriques de leurs muscles. Si nos résultats montrent que les dauphins sont sensibles et peuvent détecter les champs magnétiques savoir si et comment ils utilisent cette information requière une étude plus approfondie. Jusqu'à présent, la voie interne utilisées pour la magnéto-réception sont peu connues. Une voie possible serait la

perception des champs électriques qui sont générés par le champ magnétique (Wiltschko & Wiltschko 1995). Par conséquent, les électro-récepteurs pourraient être utilisés pour percevoir indirectement les champs magnétiques. Comme les dauphins de Guyane semblent être capables de percevoir des stimuli électriques via leurs vibrisses sur le rostre (Czech-Damal et al. 2012), il est possible que les dauphins utilisent ces récepteurs pour percevoir indirectement les champs magnétiques.

2. QU'EST CE QUE CES RÉSULTATS NOUS DISENT SUR LA RECHERCHE

Bien que cette espèce ait été intensivement étudiée pendant des décennies, de nombreux aspects de la biologie des dauphins restent encore inconnus. Ceci est sans aucun doute dû en partie aux difficultés rencontrées lors de l'étude des mammifères marins, en particulier en conditions naturelles. Cependant, le manque de littérature sur certains sujets suggère que ces sujets ont été jusqu'à présent plus ou moins négligés. Mais pourquoi ? Il semble que l'essentiel des recherches se soient concentrées sur les capacités acoustiques des dauphins. Il est indiscutable que le système de communication acoustique et les capacités d'écholocation des dauphins sont très sophistiqués et jouent un rôle majeur dans la biologie de cette espèce. D'autre part, les chercheurs semblent avoir conclus que les autres modalités sensorielles sont nécessairement sous-développées et les ont donc négligées. Cette approche revient à porter des œillères et mène à une connaissance simplifiée et incomplète de l'espèce. Les dauphins ne sont qu'un exemple de ce problème, mais il est probable que la même chose soit vraie pour d'autres sujets d'étude.

En plus de cette vision purement idéaliste (fait qu'un sujet ne soit qu'incomplètement connu car des aspects entiers de sa biologie ont été négligés), cette approche peut également influer sur les questions de conservation et / ou de gestion. L'hypothèse hâtive que telle ou telle modalité est de loin la plus importante pour une espèce peut orienter et biaiser les mesures de conservation et de gestion. En effet, peut-être que ces animaux sont également confrontés à d'autres contraintes passées inaperçues car considérées comme peu importantes.

Si la recherche mène à des conclusions précipitées, la description de la biologie de l'espèce sera probablement simplifiée et incomplète. Par conséquence, il est important que les chercheurs élargissent leur champ d'investigation et restent impartiaux lors de l'étude d'un sujet. Peut-être que l'intégration du concept zen de Shoshin (1970) en sciences contribuerait à une recherche plus ouverte. Cultiver ce concept, également connu sous le terme "l'esprit du débutant", c'est-à-dire garder l'esprit ouvert, l'ardeur et l'absence de préjugés lors de l'étude d'un sujet, tout comme le ferait un débutant, même à un niveau avancé d'étude, permettrait de conserver une recherche plus ouverte (Koda 2008; Pant 2010).

ANNEX
VOCAL SHARING AND INDIVIDUAL SPECIFICITY
IN THE VOCAL REPERTOIRE OF ORCAS

VOCAL SHARING AND INDIVIDUAL ACOUSTIC DISTINCTIVENESS WITHIN A GROUP OF CAPTIVE ORCAS (*ORCINUS ORCA*)

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Abstract

Among vocal learners, some animal species are known to develop individually distinctive vocalizations, and others clearly learn to produce group signatures. The optimal vocal sharing hypothesis suggests that vocal divergence and convergence are not compulsorily exclusive and both can be found at different levels in a given species. Being individually recognizable is socially important even in species sharing vocal badges. Acoustic divergence is not systematically controlled as it can simply be due to interindividual morphological differences. We tested that hypothesis in a species known to learn their family vocal dialect socially: the orca (*Orcinus orca*). We identified 13 different call types, including some shared by all group members, some shared only by 2 or 3 individuals, and others particular to 1 individual. Sharing was higher between males than between females. Three of our 4 orcas each produced a unique call type, which was preferably emitted. The call types shared by all orcas still presented individual acoustic distinctiveness that could, to some degree, be explained by morphological differences. We found evidence for strong similarities between some of the call types of our captive orcas and the call types of their ancestors, which are Canadian and Icelandic free-ranging orcas. Our findings suggest that captive orcas use a complex vocal repertoire enabling each individual to produce sounds that are similar to some of their partners', which might be used as social badges to advertise their preferential bonds, as well as individual-specific calls. Our findings open new lines of research concerning the functional value of a balanced "diverging – converging" vocal system.

Keywords: vocal communication; call repertoire; vocal sharing; individual specificity; cetaceans

1. INTRODUCTION

Some species are capable of vocal learning, that is, they are able to entirely modify the acoustic structure of their vocalizations on the basis of auditory input and feedback (Janik & Slater 2000). This ability enables animals to either converge or diverge vocally with their group mates, two social strategies that at first might appear exclusive. Whereas some species seem to rely mainly on individually distinctive calls encoding the caller's identity (e.g., dolphins: Caldwell & Caldwell 1965), other species instead produce calls that are similar to all (e.g., bats: Boughman 1998) or to some (e.g., starlings: Hausberger et al. 1995) group members advertising social preferences. On the one hand, being auditorily identifiable is socially relevant so that receivers are able to adjust their behavioural response to the identity of the interacting partner that is often out of sight (e.g., elephants: Soltis et al. 2005). On the other hand, sharing a vocal badge with others facilitates social bonding and consolidates group cohesion (e.g., budgerigars: Hile et al. 2000). Resident orcas fall into this latter category. They live in matrilineal groups, which often gather and form pods (Bigg et al. 1990). Each pod possesses a dialect composed of pod-specific calls (Ford & Fisher 1983). Thus, all members of a pod use the same repertoire of discrete calls (Ford 1989). One or more pods that share parts of their dialect constitute an acoustic clan (Ford 1991; Yurk et al. 2002). Similar dialects indicate similar ancestry (Barrett-Lennard 2000). Dialects and acoustic clans are also known in another cetacean, the sperm whale (Rendell & Whitehead 2003; Weilgart & Whitehead 1997). But both vocal convergence and divergence can be found in a given species. In their vocal repertoires, dolphins and starlings, for instance, also possess vocalizations that are, respectively, mimicries of others' calls (Tyack 2000; Tyack 2008) and individually distinctive (Gentner & Hulse 1998). In captive bottlenose dolphins, whistles that are shared as well as individually specific are described (McCowan & Reiss 1995). The social context of call emission (Janik 2000) as well as the social status of the caller (Sayigh et al. 2007) determines the level of vocal convergence and divergence in this species.

Producing individually distinctive sounds is not always controlled by the caller. In animal vocal and nonvocal learners, interindividual acoustic differences can simply be due to morphological constraints. For instance, in primates and horses, a large body size predicts a long vocal tract able to produce low-pitched sounds and a large lung capacity allowing more

flexibility in call duration (Ey et al. 2007; Lemasson et al. 2009). Likewise, body size is negatively correlated with fundamental frequency in human males (Evans et al. 2006). In addition, body size is also negatively correlated with echolocation signal frequency in some bats (Stoffberg et al. 2011) and with amplitude in some songbirds (Brumm 2009). Individually distinctive voices are commonly found in a large range of taxa (e.g., nonhuman primates: Lemasson et al. 2008; Snowdon & Cleveland 1980; ground squirrels: McCowan & Hooper 2002; marmots: Blumstein & Munos 2005; dogs: Yin & McCowan 2004; sheep: Sèbe et al. 2007; sea lions: Charrier et al. 2009). Morphology plays a crucial role in species forming large groups (e.g., penguins: Jouventin et al. 1999) or living in visually restricted habitats (e.g., forest monkeys: Price et al. 2009) that have difficulties in localizing group mates or dependent young (e.g., bats: Knörnschild & von Helversen 2008). Despite those strong morphological constraints, some animals known as nonvocal learners, such as nonhuman primates, can still modify to some extent the detailed acoustic structure of their calls and increase the level of vocal convergence or divergence with others. However, not all call types in, for example, a monkey repertoire are equally flexible (Lemasson & Hausberger 2011). Moreover, the context of emission determines the pattern of variability. The fact that vocal convergence and divergence can appear in the same species was demonstrated recently by different studies in forest guenons. In Campbell's monkeys, vocal sharing appeared to be important after a sudden change in the group composition, whereas individualism was favored after several months of social stability (Lemasson & Hausberger 2004). In Diana monkeys, females converge vocally during vocal interactions with other females and diverge when calling while traveling in a habitat with poor visibility (Candiotti et al. 2012).

Based on the previously mentioned examples taken from pure vocal learners as well as from nonvocal learners with some ability in acoustic flexibility, it appears that, as predicted by the *optimal vocal sharing hypothesis* (Snowdon & Hausberger 1997), interindividual vocal divergence and convergence are not compulsorily exclusive. This hypothesis envisages that the vocalizations of species, for which vocal sharing plays a crucial social role, should still present a minimum of individual distinctiveness to ensure identification of the caller. Individuals with a plastic acoustic system can notably increase and/or decrease the level of vocal convergence/divergence according to the situation, within the limits imposed by their morphoanatomy. Therefore, we investigated whether the optimal vocal sharing hypothesis

could also apply to captive orcas, a species considered capable of vocal learning (Foote et al. 2006). To our knowledge, orcas are known to produce only shared dialects. As they sometimes travel in areas with reduced luminosity and form complex social societies (Bigg et al. 1990), we hypothesized that individual distinctiveness could be found in their repertoires. As the repertoire of a given orca usually includes several call types (Ford & Fisher 1983), we suspected that this diversity could be obtained in two different ways. First, an orca's vocal repertoire can contain both shared and nonshared vocalizations. Second, acoustic parameters of shared vocalizations can differ between individuals, possibly due to morphological differences.

2. MATERIAL & METHODS

2.1. Subjects

Underwater vocalizations of two male (Keto: 14 years old; Tekoa: 9 years old) and two female (Kohana: 7 years old; Skyla: 5 years old) orcas (*Orcinus orca*) were recorded in the captive facility of Loro Parque (Tenerife, Spain) between February and May 2009. They belonged to the second generation of orcas that were born under human care and descended from Icelandic (Keto, Tekoa, Kohana, and Skyla), Canadian resident (Keto and Skyla), and transient (Tekoa) orcas (for relatedness and details of morphology see Table 1). All subjects came from SeaWorld parks in the United States (males from San Antonio, Texas; females from Orlando, Florida) before they were brought together in Loro Parque in February 2006. The orcas' Loro Parque facility consisted of three connected pools (with more than 21 million liters; Figure 1). However, as the three pools were being alternated because of maintenance, orcas could use only two pools simultaneously during this study. Public presentations and training sessions occurred five times a day and corresponded to feeding times. The diet primarily comprised herring and capelin. In addition, other fish such as hake, salmon, sardine, and mackerel were used as positive reinforcement. The average daily rations ranged from 80 kg (Skyla) to 120 kg (Keto). Periodically, body size and weight were measured by the orcas' trainers with tape and scales.

Table 1: History, relationships, and morphology of our subjects. The origin of wild-caught orcas (Canada, Iceland) is given in parentheses after their name. Paternal grandparents are unknown because the fathers were wild-caught. SW = SeaWorld facility. Previous contact = periods when subjects were in the same facility before they came to Loro Parque in 2006. Body lengths (i.e., the total length from tip of snout to tip of fluke) were measured on November 27, 2008 (Keto) and April 16, 2009 (Tekoa, Kohana, and Skyla); body weights were measured on May 20, 2009.

	Keto (♂)	Tekoa (♂)	Kohana (♀)	Skyla (♀)
Date of birth	17.06.1995	08.11.2000	03.05.2002	35
Mother	Kalina	Taima	Takara	Kalina
Father	Kotar (Iceland)	Tilikum (Iceland)	Tilikum (Iceland)	Tilikum (Iceland)
Maternal grandparents	Katina (Iceland), Winston (Canada)	Gudrun (Iceland), Kanduke (Canada)	Kasatka (Iceland), Kotar (Iceland)	Katina (Iceland), Winston (Canada)
Blood	75 % Icelandic, 25 % Canadian southern resident	75 % Icelandic, 25 % Canadian transient	100 % Icelandic	75 % Icelandic, 25 % Canadian southern resident
Time spent with mother	first 45 months of life	first 41 months of life	first 45 months of life	first 24 months of life
Time spent with father	-	first 41 months of life	22 months (from 2 to 4 years old)	first 24 months of life
Previous contact with current group members	with Tekoa: 22 months in SW Texas (from 9 to 11 years old)	with Skyla: 2 months in SW Florida (when 3 years old); with Keto: 22 months in SW Texas (from 3 to 5 years old)	with Skyla: 22 months in SW Florida (from 2 to 4 years old)	with Tekoa: first 2 months of life in SW Florida; with Kohana: first 22 months of life in SW Florida
Body length (m)	5.43	4.82	4.56	4.08
Body weight (kg)	6115	3425	3265	2265

ⅰ

Pool	Max. Depth [m]	Max. Width [m]	Max. Length [m]
(1) Holding Pool	8.1	30.5	44.8
(2) Holding Pool	8.1	20.5	36.5
(3) Med Pool	4.2	7.1	12.4
(4) Main Pool	24.5	24.5	50.5
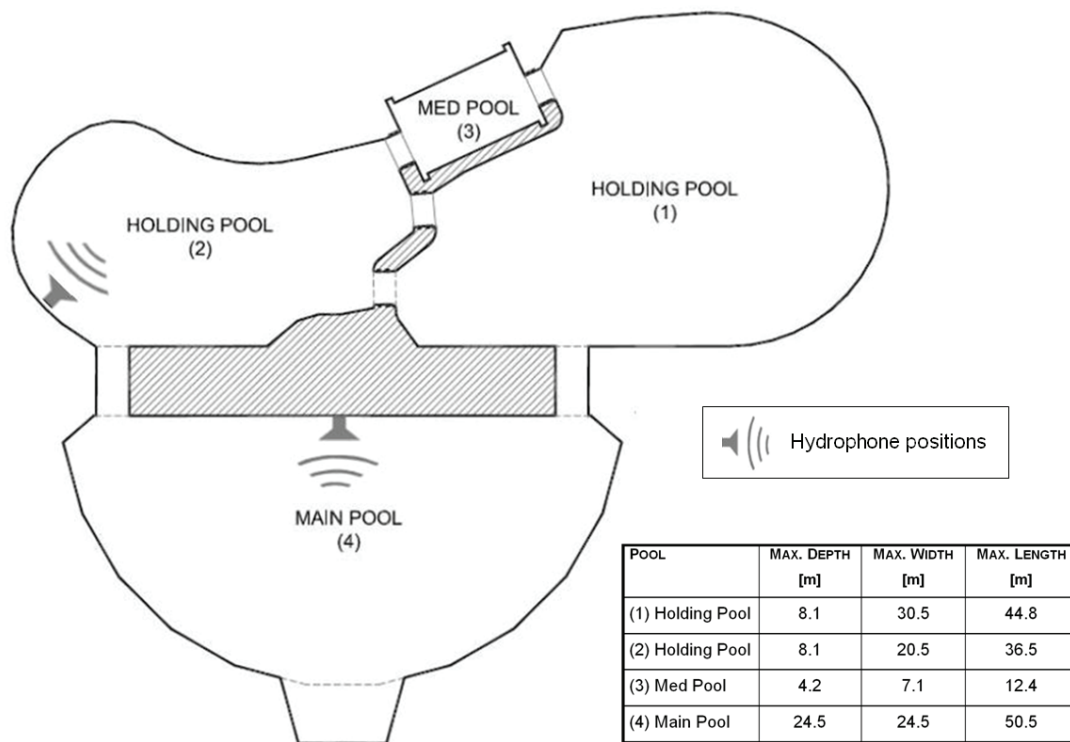
Figure 1: Diagram of the orcas' facility including pool dimensions and hydrophone positions. The hydrophone in the main pool (4) was used for recording group repertoire data; both hydrophones were used to allocate the recorded sounds to an individual when the orcas had access only to holding pool (2) and the main pool (4).

2.2. Data collection

2.2.1. Group repertoire

During February and March 2009, underwater sounds were recorded using hydrophones (ITC-6050C International Transducer Corporation, Santa Barbara, CA) built into the walls of the pools and connected to a computer (sample rate 200 kHz, frequency response 20–75000 Hz, resolution 16 bits). A homemade detection software (Luke et al. 2010) extracted single sound events automatically in real time and recorded them as separate sound files without any possibility of identifying callers. These data were used here to assess the general vocal repertoire of the group (i.e., to identify the call types used by these orcas). Total recording time was 450 min, enabling a collection of 686 sounds uttered at various times of the day distributed randomly (235 min between 6 a.m. and 2 p.m., 85 min between 2 p.m. and 10 p.m., 130 min between 10 p.m. and 6 a.m.).

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2.2.2. Individual repertoires

During April and May 2009, the vocalizations recorded with the same equipment could be confidently ascribed to one given individual. During recordings, trainers were absent and all orcas had free access to two connected pools. Sounds were recorded simultaneously with two built-in hydrophones (one per pool). With the aid of a localization algorithm, developed by J. P. Luke especially for this purpose, the vocalizations could be allocated to the pool in which the sender was located. Every time one orca was alone in one pool, vocalizations that were produced at that time in that pool could be opportunistically and confidently assigned to this individual. Orcas were determined to be alone in one pool by a human observer (DK).

Thirty sessions were recorded on 16 different days (one to three recording sessions per day). The recording sessions occurred at all possible times: in the morning (9-10 a.m.; n = 4), at midday (11 a.m. to 1 p.m.; n = 11), in the afternoon (2-4 p.m.; n = 10), and in the evening (5-7 p.m.; n = 5). Total recording time during which one orca was alone in one pool was 504 min, enabling the collection of 842 calls. Orcas were entirely free to move and separations of individuals occurred spontaneously and voluntarily.

2.3. Data analysis

We collected 1528 vocalizations with sufficient quality (well audible and visible in the spectrograms and therefore usable for categorization) during group repertoire and individual repertoire recordings. A large majority of the vocalizations (97.4 %) were pulsed calls (Ford 1989). The other vocalizations were whistles (Thomsen et al. 2001), which, because of their rarity, were not included in the present analysis. Calls consisted mainly of discrete (i.e., stereotyped in overall frequency contour; Ford 1989) acoustic structures (74.1 %; individual n values are given in Table 2). The remaining quarter of so-called variable calls (Ford 1989) were excluded from our analyses, following Foote et al. (2008).

Table 2: Vocalization recordings: distribution of discrete and variable pulsed calls as well as whistles of our subjects (total number, N, and percentage, %). Recording time when the emitter individual could be identified is given in parentheses with the name.

	Keto (135 min)		Tekoa (216 min)		Kohana (73 min)		Skyla (80 min)	
	N	**%**	**N**	**%**	**N**	**%**	**N**	**%**
Discrete calls	524	92.4	86	53.8	44	69.8	41	78.8
Variable calls	40	7.1	70	43.8	17	27.0	9	17.3
Whistles	3	0.5	4	2.5	2	3.2	2	3.8

Spectrograms of discrete calls were generated using a fast Fourier transform length of 4096 samples, a 90 % overlap and a Hann window function, with Signal software (Version 4.02.04). As a first step, aiming to classify call types, we asked 10 naïve (inexperienced in bioacoustics) people to classify spectrogram similarities visually (method classically used in cetacean studies; e.g., Sayigh et al. 2007). Each of these naïve helpers was given a random selection of 220 spectrograms (with standardized axes), which were numbered randomly. The helpers were asked to assemble the spectrograms on the basis of overall contour. They did not receive any advice concerning either the expected number of call types or the number of individual orcas. A percentage for each pair of calls was calculated representing the proportion of helpers who sorted these calls into the same call type. This concordance between helpers (i.e., their level of agreement concerning the allocation of two given calls to the same call type) was used as the basis for the classification. The matrix resulting from this human classification was analysed using a hierarchical cluster analysis (method: Ward; measure of distance: square of Euclidean distance) by SPSS for Windows (Version 16.0) to identify the call types classified by the helpers. To determine the number of call types (i.e., the number of clusters), we used the elbow method (Backhaus et al. 2005), in which the squared Euclidean distances are plotted against the clusters obtained in the stepwise division of the calls. As a second step, the experienced coauthors conducted a deeper investigation based on visual and auditory inspection to identify potential call subtypes within some of the call types.

To confirm the validity of this detailed classification, we analysed several acoustic measurements of all the discrete calls (n = 1103). The following parameters were measured using the fundamental frequency: duration, start and end frequency,

minimum and maximum frequency, bandwidth (difference between minimum and maximum frequency), and maximum peak frequency. All calls consisted of a low-frequency component (LFC; for details see, e.g., Miller & Bain 2000) ranging between 333 and 1941 Hz (average minimum frequency: 663 Hz; average maximum frequency: 1041 Hz). Some calls were composed of an LFC and an additional high-frequency component (HFC), ranging between 1427 and 10821 Hz (average minimum frequency: 3390 Hz; average maximum frequency: 5805 Hz); the HFC appeared in the spectrogram as a "whistle-like" frequency contour overlapping the LFC as it is independently modulated (Miller et al. 2007) but clearly distinguishable from the harmonics of the LFC. In these cases, the entire vocalization and both elements were measured independently. If a call consisted of a two-part LFC (i.e., it had a visible and audible gap that lasted less than 0.4 s), the entire LFC and both parts were measured separately as well as the gap between the parts (Figure 2 illustrates the different parts for the most frequent call type C31, a two-part call with HFC; Figure 3 also indicates LFC and HFC for all call types described for this group).
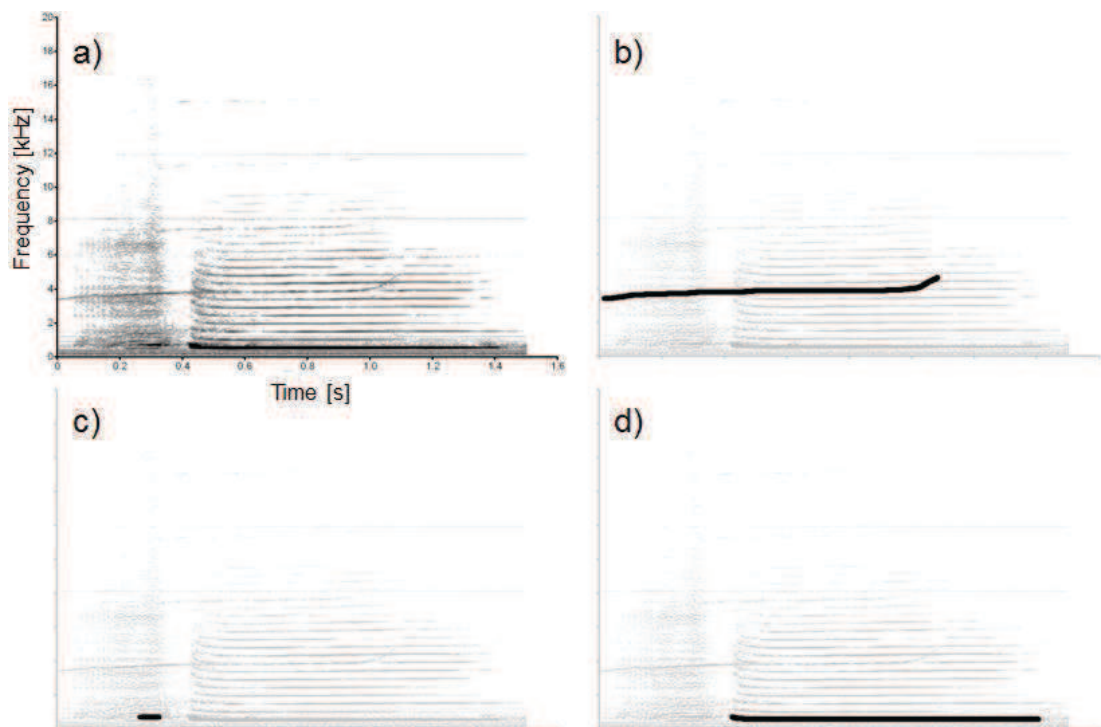
Figure 2: a) Spectrogram of the most common call type, C31 (FFT: 4096; window type: Hann), a two-part call with HFC (high-frequency component). b-d) The same spectrogram highlighting b) the high-frequency component (HFC), c) the first low-frequency component (LFCa), and d) the second low-frequency component (LFCb).

Afterward, a stepwise discriminant function analysis (DFA) was performed by SPSS to identify factors important for the classification using all measured acoustic parameters (except bandwidth because this parameter is dependent on minimum and maximum frequency). The vocalizations were divided into the following groups: one-part calls without HFC, one-part calls with HFC, two-part calls without HFC, and two-part calls with HFC. Each group was analysed separately. Beforehand, the normal distribution and homogeneity of variances of the data were analysed. First, a DFA was performed only with data that met these assumptions. As these results did not differ significantly from those obtained for DFA with the whole data set (i.e., including data that did not meet the assumptions), we believe that the results containing all data are relevant. Therefore, all data were included in the present analyses. After the classification of all calls, a cumulative discovery curve of the call types found was plotted to investigate whether a plateau was reached; this plateau can be seen as an indicator of how complete the recorded repertoire was (Samarra et al. 2010).

As a third step, we calculated the percentage of each call type emitted by each subject. G tests then compared individual call repertoires. DFA revealed differences between individuals of shared call types' acoustic parameters. Furthermore, Spearman correlations evaluated relationships between acoustic parameters and morphology of emitters for the call types shared by all individuals. As body length and body weight are significantly correlated with age (for each, Spearman $r_s = 1.00$, $p = 0.01$), we investigated correlations between acoustic parameters and age.

As a last step, we compared the call types identified here visually with call types of free-ranging orcas in British Columbia, Canada (Ford 1987), and in eastern Iceland (Moore et al. 1988), that is, from where our subjects' ancestors originated. When available, we also compared acoustic parameters.

3. RESULTS

3.1. Call classification

The call repertoire of our orca group appeared to be composed of 13 stereotyped acoustic structures (see Figure 3 and Table 3).
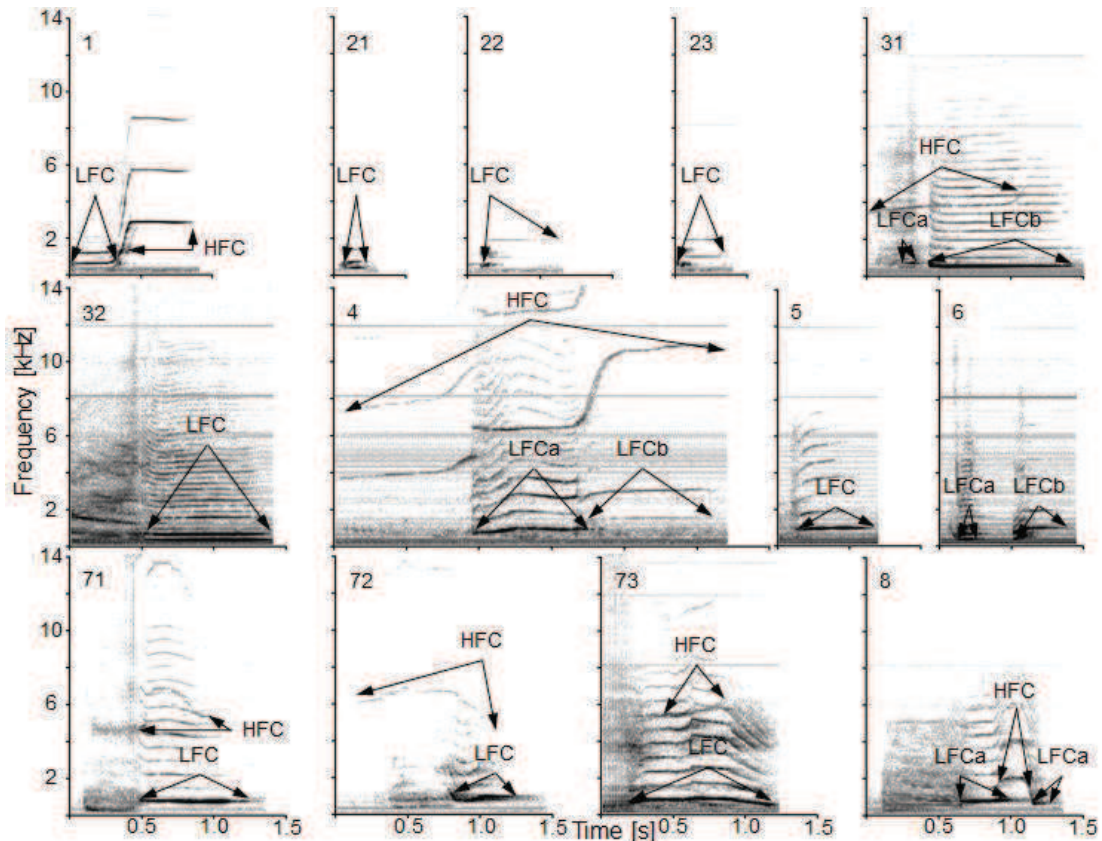
Figure 3: Spectrograms (scales standardized; FFT: 4096; window type: Hann) of all call types emitted by the Loro Parque's orcas. LFC: low-frequency component; two-part vocalizations: LFCa: first part, LFCb: second part; HFC: high-frequency component. Arrows indicate the start and end of the corresponding element.

Following the hierarchical cluster analysis and the elbow method, based on the judgment of naïve people, eight call types (named C1 to C8) could be identified. Call types were classified according to their acoustic structure, that is, the overall frequency modulation pattern, consisting of one or two LFC parts, with or without an HFC. A more detailed investigation led us to subdivide three of these call types into two (C3) or three (C2 and C7) subtypes (named CX1 to CX3, with X being the call type number). C21 is shorter in duration and generally lower in frequency than the two other subtypes, whereas C23 is generally higher pitched than C22. Acoustic patterns differ between C31 and C32, whereas C31 is a two-part call containing an HFC, C32 is a one-part call without HFC and is lower pitched. LFCs of C72 are shorter than those of C71 and C73 and their frequency modulations differ. The LFC of C73 is longer in duration, with a higher maximum frequency, although in general the frequency is lower than that of C71.

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Table 3: Acoustic parameters measured for all call types (given as mean ± SD). LFC: low-frequency component of a one-part call; LFCa: first low-frequency component of a two-part call; LFCb: second low-frequency component of a two-part call; LFCc = complete low-frequency component of a two-part call; HFC: high-frequency component.

Call Type	N	Part	Duration (s)	Start frequency (Hz)	End frequency (Hz)	Minimum frequency (Hz)	Maximum frequency (Hz)	Bandwidth (Hz)	Maximum peak frequency (Hz)	Interval between parts (s)
C1	143	LFC	0.206 ± 0.060	854 ± 198	1037 ± 227	763 ± 197	1098 ± 217	334 ± 89	1304 ± 1200	-
		HFC	0.373 ± 0.169	1721 ± 611	2953 ± 219	1661 ± 630	3096 ± 240	1435 ± 516	2327 ± 1454	-
C21	84	LFC	0.111 ± 0.020	476 ± 147	500 ± 146	361 ± 128	602 ± 144	241 ± 48	481 ± 136	-
C22	64	LFC	0.270 ± 0.122	881 ± 218	1099 ± 338	805 ± 218	1194 ± 328	390 ± 185	970 ± 397	-
C23	20	LFC	0.276 ± 0.069	1789 ± 232	1855 ± 153	1724 ± 205	1941 ± 163	217 ± 73	1688 ± 419	-
C31	295	LFCa	0.162 ± 0.066	589 ± 224	579 ± 217	497 ± 202	689 ± 234	191 ± 57	595 ± 218	-
		LFCb	0.862 ± 0.064	549 ± 80	508 ± 67	379 ± 64	644 ± 73	265 ± 47	469 ± 65	-
		LFCc	1.068 ± 0.156	587 ± 221	511 ± 68	368 ± 60	745 ± 199	377 ± 173	478 ± 62	0.060 ± 0.035
		HFC	0.655 ± 0.188	3332 ± 319	4298 ± 902	3228 ± 298	4336 ± 885	1108 ± 778	1523 ± 1573	-
C32	177	LFC	0.719 ± 0.153	479 ± 197	462 ± 153	333 ± 160	557 ± 194	224 ± 56	469 ± 427	-
C4	44	LFCa	0.750 ± 0.187	862 ± 105	1140 ± 97	689 ± 60	1195 ± 80	506 ± 88	929 ± 48	-
		LFCb	0.561 ± 0.232	1586 ± 147	1527 ± 65	1404 ± 90	1682 ± 93	278 ± 96	1263 ± 880	-
		LFCc	1.284 ± 0.241	870 ± 115	1517 ± 60	688 ± 59	1682 ± 92	995 ± 103	942 ± 69	-0.028 ± 0.037
		HFC	1.494 ± 0.484	3755 ± 303	10585 ± 996	3701 ± 307	10821 ± 1136	7121 ± 1159	1181 ± 1028	-
C5	142	LFC	0.512 ± 0.105	910 ± 81	993 ± 30	811 ± 53	1095 ± 40	284 ± 55	1036 ± 570	-
C6	55	LFCa	0.134 ± 0.032	598 ± 104	630 ± 112	483 ± 110	723 ± 110	240 ± 51	565 ± 140	-
		LFCb	0.384 ± 0.175	837 ± 252	1011 ± 227	761 ± 255	1141 ± 230	379 ± 144	714 ± 281	-
		LFCc	0.785 ± 0.152	595 ± 99	1028 ± 261	473 ± 108	1160 ± 257	687 ± 260	632 ± 202	0.267 ± 0.054
C71	25	LFC	0.601 ± 0.064	823 ± 61	732 ± 25	624 ± 17	883 ± 38	259 ± 38	732 ± 17	-
		HFC	0.605 ± 0.205	4346 ± 255	5778 ± 495	4298 ± 265	6434 ± 615	2137 ± 661	727 ± 14	-
C72	4	LFC	0.410 ± 0.007	1004 ± 101	1042 ± 76	627 ± 33	1119 ± 67	492 ± 53	745 ± 25	-
		HFC	0.605 ± 0.343	6528 ± 1710	5128 ± 160	4942 ± 369	7577 ± 677	2634 ± 691	734 ± 30	-
C73	29	LFC	0.795 ± 0.196	691 ± 111	599 ± 139	466 ± 81	902 ± 125	436 ± 139	719 ± 603	-
		HFC	0.449 ± 0.142	4567 ± 770	5899 ± 779	4471 ± 768	5922 ± 732	1451 ± 805	762 ± 720	-
C8	21	LFCa	0.288 ± 0.107	837 ± 82	815 ± 80	659 ± 86	977 ± 82	318 ± 57	769 ± 86	-
		LFCb	0.073 ± 0.022	742 ± 103	614 ± 104	512 ± 91	855 ± 113	343 ± 133	596 ± 78	-
		LFCc	0.554 ± 0.108	831 ± 89	619 ± 108	502 ± 86	981 ± 65	479 ± 113	758 ± 66	0.190 ± 0.056
		HFC	0.384 ± 0.103	1582 ± 337	1781 ± 330	1427 ± 317	2448 ± 336	1021 ± 282	752 ± 73	-

A DFA based on acoustic measurements confirmed the pertinence of our classification into 13 stereotyped acoustic structures. The percentage of correctly classified calls was higher than expected by chance (> 95 % in all comparisons; see Figure 4 and Table 4). The cumulative discovery curve of the call types corresponding to the repertoire of this group reached its plateau at 13 call types after around 100 calls analysed (see Figure 5).
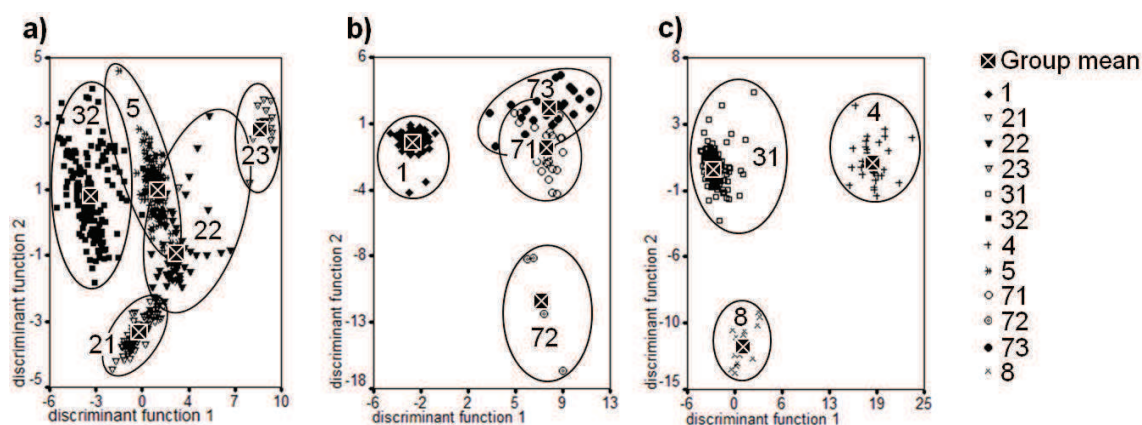
Figure 4: Scatter plot of the Discriminant Function Analyses comparing several acoustic parameters of different call types emitted by the Loro Parque's orcas. Each small symbol represents a call; type of symbol varies with call type. Black squares (with white border and cross): group means. a) One-part calls: discriminant function 1 is correlated to minimum frequency; discriminant function 2 is correlated to duration. b) One-part calls with HFC (high-frequency component): discriminant function 1 is correlated to maximum frequency of HFC; discriminant function 2 is correlated to end frequency of HFC. c) Two-part calls with HFC: discriminant function 1 is correlated to minimum frequency of LFCb (second low-frequency component of a two-part call); discriminant function 2 is correlated to minimum frequency of HFC. As call type C6 is the only call type belonging to the two-part-call group, it is not represented within a scatter plot.
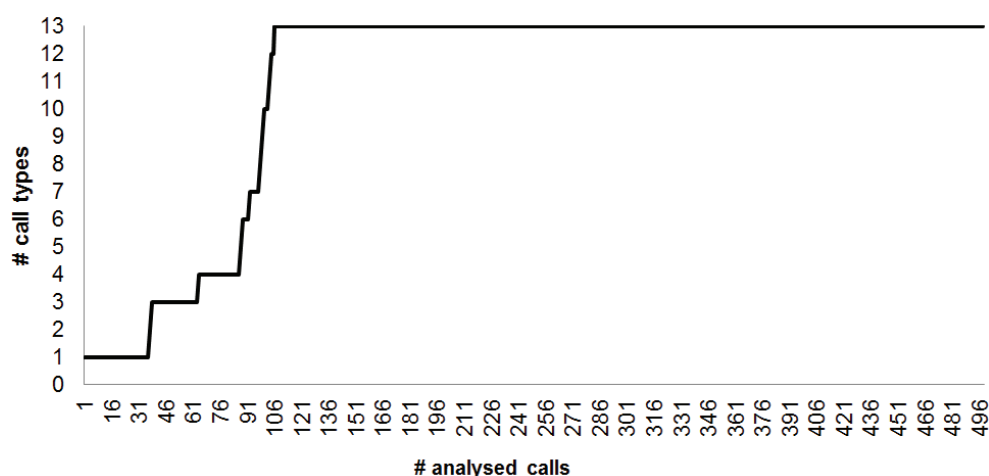
Figure 5: Cumulative discovery curve of all call types.

Table 4: Discriminant Function Analyses of call types. LFC: low-frequency component; LFCb: second low-frequency component of a two-part call; HFC: high-frequency component. Call types were analyses in groups according to their structure: one-part calls, one-part calls with HFC, and two-part calls with HFC. The two-part-calls group contained only one call type, C6, therefore it is not represented. For corresponding scatter plots see Figure 4.

	Call types					
	One-part calls: C21, C22, C23, C32, C5 (N = 487)		**One-part calls with HFC: C1, C71, C72, C73 (N = 201)**		**Two-part calls with HFC: C31, C4, C8 (N = 360)**	
Discriminant function	df 1	df 2	df 1	df 2	df 1	df 2
Canonical correlation coefficient	0.945	0.863	0.979	0.882	0.989	0.032
Wilks-λ	0.020	0.182	0.005	0.118	0.003	0.131
P	≤ 0.001	≤ 0.001	≤ 0.001	≤ 0.001	≤ 0.001	≤ 0.001
Standardized canonical correlation coefficient	1.839	0.816	0.711	1.517	1.177	1.667
Correlated variable (coefficient of correlation)	Minimum frequency LFC (0.722)	Duration LFC (0.861)	Maximum frequency HFC (0.678)	End frequency HFC (-0.129)	Minimum frequency LFCb (0.717)	Minimum frequency HFC (0.505)
Correctly classified (%)	95.8		96.5		100	

3.2. Individual call repertoires and call rates

Individual call repertoires presented important variations (number of calls with identified individual: 695; see Table 5). Twelve of the 13 call types (i.e., excluding C23) identified in the group analysis could be identified in the individual analyses. Four of the 12 call types were shared by all four orcas (C1, C31, C32, and C5). Two call types (C21 and C22) were shared only by the two males, whereas females did not have their own call structure. Nevertheless, each female individually shared one additional call type with both males (Kohana C4, Skyla C6). The degree of sharing was higher between males (eight call types) than between females (four call types). In addition, four call types were individual-specific; in other words, they were produced by only one particular individual (Tekoa C71 and C72; Kohana C8; Skyla C73). Only Keto, who presented the highest call rate, did not emit his own particular call (see Table 5).

It is interesting that each individual used one call structure preferentially, which for Tekoa, Kohana, and Skyla was their individual-specific call (G test per column, Table 5). We also found individual preferences for six of the eight shared call types, preferentially uttered by males (G test per row; Keto C31 and C32; Tekoa C21, C22, C4, and C6).

Table 5: Individual call repertoires (in percentage for each subject). Call rate: number of calls uttered per min. Values in bold: call type emitted preferentially (G test per column, P ≤ 0.0001). Underlined values: shared call type used most frequently (G test per row, P ≤ 0.0001, except two values: * P ≤ 0.05).

Call Type	♂ Keto[a] (call rate 3.88)	♂ Tekoa[b] (call rate: 0.40)	♀ Kohana[b] (call rate: 0.60)	♀ Skyla[a,b] (call rate 0.51)
C1 (N = 66)	9.9	7.0	11.4	7.3
C21 (N = 54)	8.4	11.6	-	-
C22 (N = 54)	8.4	11.6	-	-
C31 (N = 194)	**33.8**	4.7	20.5	9.8
C32 (N = 131)	23.1	7.0	6.8	2.4
C4 (N = 12)	1.1	4.7 *	4.5 *	-
C5 (N = 68)	11.5	2.3	9.1	4.9
C6 (N = 37)	3.8	17.4	-	4.9
C71 (N = 25)	-	**29.1**	-	-
C72 (N = 4)	-	4.7	-	-
C73 (N = 29)	-	-	-	**70.7**
C8 (N = 21)	-	-	**47.7**	-

[a] Same mother. [b] Same father.

3.3. Individual differences in acoustic parameters

Individual acoustic distinctiveness could be detected significantly for the four call types shared by all orcas (C1, C31, C32, and C5; DFA: correctly classified > 89 % for all call types; see Table 6). Some individual differences could be explained by morphological differences as body length and weight continued to increase with age (see Table 7). The end frequency of C1 (HFC part) was significantly higher the younger (and thus, smaller and lighter) the individual. Also, the bandwidth of C32 was significantly wider the younger the individual. Duration of C5 was negatively correlated with age.

Table 6: Discriminant Function Analyses of shared call types. Values are given for discriminant function 1, which was in all cases sufficient to discriminate individuals. LFC: low-frequency component; HFC: high-frequency component. For each individual the value (mean ± standard deviation) for the acoustic parameter correlated with the discriminant function 1 is given; in brackets: number of calls (N) and percentage of correctly classified calls (%).

	C1 (N = 66)	C31 (N = 171)	C32 (N = 127)	C5 (N = 67)
Canonical correlation coefficient	0.853	0.893	0.372	0.688
Wilks-λ	0.240	0.085	0.861	0.526
P	≤ 0.001	≤ 0.001	≤ 0.001	≤ 0.001
Standardized canonical correlation coefficient	0.647	1.369	1.000	1.000
Correlated variable (coefficient of correlation)	Duration HFC (0.852)	Maximum frequency HFC (0.687)	Start frequency LFC (1.000)	Minimum frequency LFC (1.000)
Keto	239 ± 74 ms (N = 52 98.1%)	4000 ± 282 Hz (N = 159 98.1%)	409 ± 86 Hz (N = 117 96.6%)	768 ± 28 Hz (N = 59 98.3%)
Tekoa	447 ± 87 ms (N = 6 77.8%)	4604 ± 253 Hz (N = 2 100%)	499 ± 123 Hz (N = 6 16.7%)	870 ± 36 Hz (N = 2 50.0%)
Kohana	486 ± 73 ms (N = 5 100%)	5755 ± 757 Hz (N = 6 66.7%)	495 ± 141 Hz (N = 3 0.0%)	838 ± 39 Hz (N = 4 50.0%)
Skyla	546 ± 65 ms (N = 3 100%)	5818 ± 128 Hz (N = 4 100%)	716 Hz (N = 1 0.0%)	857 ± 54 Hz (N = 2 0.0%)
Correctly classified (%)	95.7	97.1	89.8	91.0

Table 7: Correlation between different acoustic parameters and age of the calling individual (Spearman's coefficient of correlation r_s and P); bold values = significant correlations. LFC = low-frequency component; HFC = high-frequency component. Call types C32 and C5 do not contain a HFC.

Variable	C1		C31		C32		C5	
	r_s	p	r_s	p	r_s	p	r_s	p
LFC								
Duration	0.20	0.80	-0.40	0.60	-0.80	0.20	**-0.95**	**0.05**
Start frequency	0.20	0.80	0.20	0.80	-0.80	0.20	-0.40	0.60
End frequency	0.80	0.20	-0.40	0.60	0.80	0.20	-0.80	0.20
Bandwidth	-0.80	0.20	-0.40	0.60	**-1.00**	**0.00**	0.40	0.60
Peak frequency	-0.80	0.20	-0.40	0.60	-0.80	0.20	-0.80	0.20
HFC								
Duration	-0.40	0.60	-0.20	0.80				
Start frequency	-0.80	0.20	-0.80	0.20				
End frequency	**-1.00**	**0.00**	-0.20	0.80				
Bandwidth	0.40	0.60	-0.80	0.20				
Peak frequency	-0.20	0.80	-0.20	0.80				

3.4. Comparison with free-ranging orcas

Some of the call types described in this study showed similarities with call types of Canadian and Icelandic free-ranging orcas, that is, the ancestors of our subjects (see Figure 6). The C1s we recorded resemble the frequency contour of N7i that is part of the northern resident orcas' repertoire. Their average durations are similar: 579 ms (total duration of C1, LFC and HFC; n = 147) and 570 ms (N7i; n = 27). The C8s we recorded resemble the frequency contour of S44 (southern residents' repertoire). Their average durations are similar: 554 ms (C8; n 14) and 447 ms (S44 without part 1; n = 29). C5 presents similarities with the frequency contour of I7 that is part of the eastern Icelandic orcas' repertoire. According to the spectrogram, their pulse rates differ slightly. C6 resembles the frequency contour of I19 to some extent. However, the duration of I19 is clearly longer than in C6. It is interesting that all our orcas produced calls with structures resembling those of both Canadian and Icelandic orcas.

4. DISCUSSION

The vocal repertoire data we collected for four captive orcas support the *optimal vocal sharing hypothesis* proposed by Snowdon and Hausberger (1997). Vocal sharing as well as individual acoustic distinctiveness could be identified when looking both at the call repertoire compositions and the acoustic parameters of the shared call types. Our data analyses involved only four captive orcas and, therefore, must be interpreted and compared with data for orcas in their natural habitat with caution. Nevertheless, we believe the results we obtained are important because studies investigating the individual vocal repertoires of orcas are rare. It is indeed very difficult to identify emitters and their corresponding behaviour in the wild. Moreover, the basic characteristics of the repertoires we describe here agree with those found for wild resident orcas as they contain the same types of vocalizations (clicks, whistles, as well as variable and discrete calls) in similar proportions with a majority of discrete calls (Thomsen 1999). Also, the total repertoire size of the test group recorded (N = 13) is within the range of repertoire sizes reported for wild groups of orcas (7-17 calls per pod; Ford & Fisher 1983).
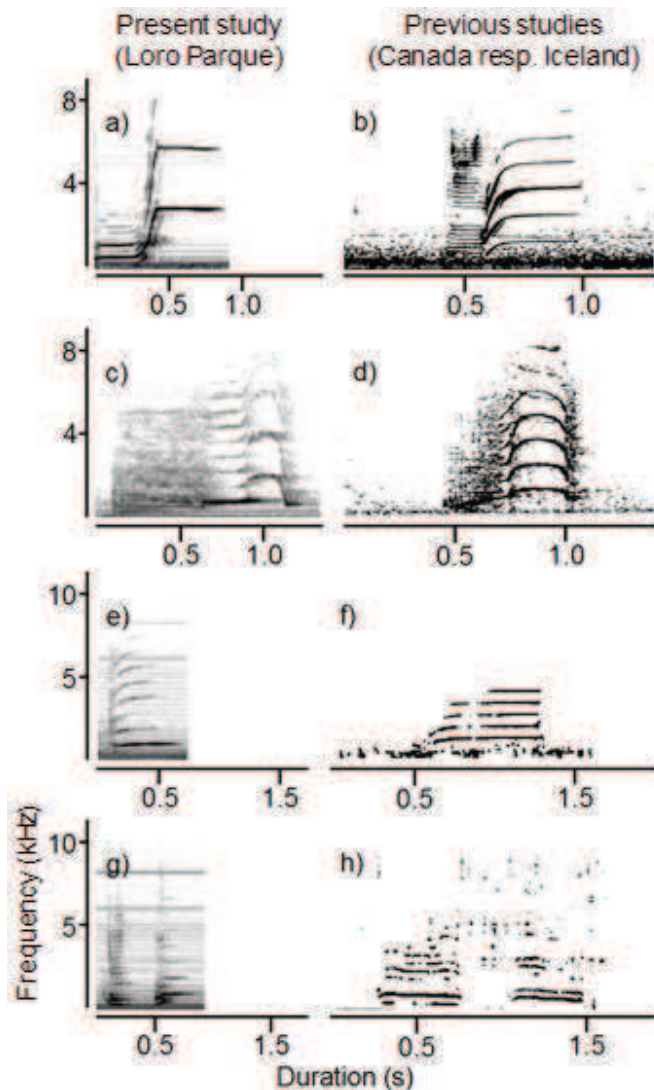
Figure 6: Comparison between Loro Parque (left spectrograms) and British Columbian, Canadian, or eastern Icelandic (right spectrograms; modified from Ford, 1987 and Moore et al., 1988) call types: a) C1, b) Ford's N7i, c) C8, d) Ford's S44, e) C5, f) Moore's I7, g) C6, h) Moore's I19.

Vocal resemblance seems to have played a key role in structuring our captive orcas' vocal repertoires as most of the call types identified were shared by at least two individuals. The present study shows that the establishment of a group dialect does not seem to be the unique rule as several call types were shared by only two or three individuals. Rather than genetic proximity or past life history, sex appears to be a determining key factor to explain vocal-sharing patterns. In particular, our two males presented the highest degree of sharing, including some exclusive call types, a fact that cannot be explained by their past life history:

First, the males do not have the same parents from which they could learn the same calls; second, both males and females had spent the same amount of time together before they came to the current facility (see Table 1). These findings are supported by Crance (2008), who reported that captive male orcas showed higher call matching and stronger convergence of their vocal repertoires than the females, which kept their repertoires stable. Overall, the repertoire similarity was contingent on social association: The more often two individuals associate, the more similar their repertoires are (Crance 2008). For instance, wild bottlenose dolphin males forming coalitions engage in vocal sharing (Watwood et al. 2004) and whistle convergence (Smolker & Pepper 1999).

Our group was formed 3 years before the study started and half of the call types were shared by the four subjects. Because no prior recordings were available of these four individuals before they were placed together in this facility or of their parents or previous pool mates, it was not possible for us to reconstruct their vocal ontogeny. We cannot totally rule out the possibility that the four orcas shared the corresponding call types even before they were placed together in the current facility by learning them from other individuals and not from one another. Even if they did, the fact that they were still using them is interesting and indicates the social relevance of these shared call types. However, an argument can be made to support vocal learning as the underlying mechanism as learning is known to be the major factor behind acoustical development in this species (Riesch et al. 2005). Orcas are capable of vocal learning in less than 3 years, as a young isolated orca learned to produce sea lions' calls in less than 2 years (Foote et al. 2006). Similarly, captive bottlenose dolphins learned to mimic humpback whale calls within 2 months (Kremers et al. 2011). Also, Watwood et al. (2004) suggested that delphinids (adult male bottlenose dolphins) would be able to modify their vocalizations as a consequence of changing social relationships.

It is interesting that, although orcas are definitively capable of acoustic plasticity, as individuals involved in a vocal interaction acoustically match one another's sounds (Miller et al. 2004), some of the sounds used by our captive orcas resembled call types recorded in the wild in the 1980s. Thus, some call types of the Icelandic and Canadian ancestors might have been passed from generation to generation in captivity. This would also suggest that orca acoustics are based on a "sustainable" system conserving the same acoustic structures for a long time when there is no need to create new ones. Here, the blood origin (Icelandic vs.

Canadian) of our orcas did not explain the degree of similarity with wild structures. Unexpectedly, the call type found in Loro Parque (C8) similar to a call type from the southern resident orcas' repertoire (S44) was uniquely emitted by Kohana. However, she is not even distantly related to a member of the southern resident community, but to the Icelandic population. A possible way to explain why Kohana emitted a call similar to one of the southern residents could be vocal learning. Because her mother, Takara, had spent several years with a member of the southern resident community, Takara could possibly have learned vocalizations from him and passed them to Kohana. Likewise, the northern resident orcas' call type (N7i) similar to the C1 described here could have been learned by Tekoa and Kohana from another individual that, in turn, learned it from a northern resident orca. Keto and Skyla might have learned this call type directly, as they spent, respectively, 13 and 23 months with a member of the northern resident community in a previous facility. There is some long-term evidence showing that acoustic structures can be preserved or slightly modified with time (orcas: Deecke et al. 2000; dolphins: Sayigh et al. 2007). Ford (1991) reported that repertoires of wild orcas can persist with little change for more than 25 years.

Besides vocal sharing, individual acoustic distinctiveness was also important in our captive group. We found that three of the four studied orcas displayed their own call type. This was not due to a recording bias as the subject with the highest call rate emitted no individual-specific calls (Keto). The fact that the individual-specific calls were the sounds emitted preferentially implies their socially relevant function. Nevertheless, we cannot exclude the possibility that, to identify emitters, we had to record sounds uttered in social isolation, which might have led us to overestimate the rate of individual-specific calls. Likewise, the rate of wild orcas' individual-specific calls might have been underestimated. Therefore, this debate may be resolved only after more studies are performed that compare wild and captive individuals. These individual-specific calls could possibly be actually group-specific calls of the families that the individuals belong to or originate from. A group-specific dialect is thought to convey group identity and affiliation (Ford 1991) and may play a function in kin recognition (Deecke 1998). A clarification concerning this matter would require analysing the whole population of orcas that they had met previously during their life.

Apart from the individual-specific call types, we found acoustic differences in the call types shared by all individuals, supporting previous findings that individual orcas producing

the same call type can be discriminated by computer methods (Brown et al; 2010; Gaetz et al. 1993; Nousek et al. 2006). Although we did not perform the playback experiments that would be necessary to confirm the biological relevance of this degree of variability, it is likely that animals can perceive these acoustic differences and identify callers even for shared call types. As a first approach, Filatova et al. (2011) demonstrated that orcas react differently to playbacks of calls from their own and from other pods. Captive bottlenose dolphins produce a shared whistle type (McCowan & Reiss 1997) that contains subtle variations in contour, called signature information (McCowan & Reiss 2001).

Individual differences in vocalizations might be due to morphological constraints. This effect was described for cetaceans, as species with different constitution produce different frequencies (Wang et al. 1995). Evidence suggests a linear relationship between body size and vocalization wavelength in cetaceans (Matthews et al. 1999). We found that the heavier, the larger, and the older our orcas were, the lower pitched their voices were; this certainly reflects morphoanatomical maturational changes common in many species (Fletcher et al. 1992). Because both males were heavier, larger, and older than both females, sex might also influence vocalizations, as in wild orcas (Miller et al. 2007).

Different interpretations of our present findings are possible; we outline them below with regard to the mechanisms that might underlie the vocal development. First, orcas could learn their vocal repertoire at a young age from their family members and thereafter it would remain stable lifelong. Accordingly, the existence of shared call types could only be explained by a common ancestor from whom the individuals learned this call type at a young age. The individual-specific call types described here would in fact be group-specific calls shared with group members not present in the current facility. However, if this were true, individuals born from the same mother and growing up with her for at least 2 years (Keto and Skyla) should share more call types than the other subjects, a fact not supported by our recordings. Second, orcas may be capable of learning new vocalizations not only at a young age but also throughout their lifetime. Thus, their repertoire could change, as reported by previous authors (Foote et al. 2006; Hooper et al. 2006; Watwood et al. 2004). If this were true, the present results could be interpreted in terms of vocal convergence and vocal divergence. This study opens new lines of research regarding the contextual importance of diverging versus converging vocally and the likelihood of this also happening in the wild,

given the fact that free-ranging killer whale acoustic structures seem relatively stable in the wild (Ford 1991).

These two processes might be part of a necessary adaptation to a changing social environment when group compositions change. It is often stressed in the literature that social changes, like the one imposed by captive care, trigger vocal changes (Brown & Farabaugh 1997; Lemasson & Hausberger 2004; Snowdon & Elowson 1999). Unlike free-living orcas, captive orcas are often moved from one facility to another; thus, the group composition in which a given individual lives changes. This situation does not resemble the social stability of wild orca groups, which is thought to be one of the major factors behind group-specific repertoires (e.g., Ford 1991; Ford & Fisher 1983; Yurk et al. 2002). In contrast, species living in less stable groups produce more individual-specific vocalizations, for instance, bottlenose dolphins that live in fission–fusion societies (e.g., Janik & Slater 1998). According to this hypothesis, orcas that live in unstable social environments, as in captivity, might adapt their repertoire and produce not only group-specific but also individual-specific vocalizations. We know from dolphin studies that the mother has a strong impact on the acoustic structuration of juveniles' repertoire (Sayigh et al. 1990). Our orcas had been separated from their parents at an early age, compared with what is found in the wild, where they remain in their natal pod even after independence, and this might have also played a role here. Why orca groups display so many different call types in their repertoire has long been a matter of vivid debate. Some investigations have failed to provide evidence that contextual differences might explain the coexistence of several call structures in a given individual with different referential functions (Ford 1989). Nevertheless, authors agree that discrete calls primarily function as contact signals (Ford 1989). Here, we suggest that the functional significance of having several calls might be to open opportunities for a given individual to advertise vocally either the group to which it belongs or its social preference as well as its individual identity.

Acknowledgements

References

Backhaus, K., Erichson, B., Plinke, W. & Weiber, R. (2005). Multivariate Analysemethoden. Eine anwendungsorientierte Einführung. Springer, Berlin.

Barrett-Lennard, L. G. (2000). Population structure and mating patterns of killer whales (*Orcinus orca*) as revealed by DNA analysis. PhD dissertation, Department of Zoology, University of British Columbia.

Bigg, M. A., Olesiuk, P. F., Ellis, G. M., Ford, J. K. B. & Balcomb, K. C. (1990). Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Report of the International Whaling Commission Special Issue 12, 383-405.

Blumstein, D. T. & Munos, O. (2005). Individual, age and sex-specific information is contained in yellow-bellied marmot alarm calls. Animal Behaviour 69, 353-361.

Boughman, J. W. (1998). Vocal learning by greater spear-nosed bats. Proceedings of the Royal Society B 265, 227-233.

Brown, E. D. & Farabaugh, S. M. (1997). What birds with complex social relationships can tell us about vocal learning: vocal sharing in avian groups. In: Social influences on vocal development, edited by Snowdon, C. T. & Hausberger, M., pp. 98-127. Cambridge University Press, Cambridge.

Brown, J. C., Smaragdis, P. & Nousek-McGregor, A. (2010). Automatic identification of individual killer whales. Journal of the Acoustical Society of America 128, EL93-EL98.

Brumm, H. (2009). Song amplitude and body size in birds. Behavioral Ecology and Sociobiology 63, 1157-1165.

Caldwell, M. C. & Caldwell, D. K. (1965). Individualized whistle contours in bottlenose dolphins (*Tursiops truncatus*). Nature 207, 434-435.

Candiotti, A., Zuberbühler, K. & Lemasson, A. (2012). Convergence and divergence in Diana monkey vocalizations. Biology Letters (published online 11.01.2012). doi: 10.1098/rsbl.2011.1182.

Charrier, I., Pitcher, B. J. & Harcourt, R. G. (2009). Vocal recognition of mothers by Australian sea lion pups: individual signature and environmental constraints. Animal Behaviour 78, 1127-1134.

Crance, J. L. (2008). Changes in killer whale, *Orcinus orca*, stereotyped call repertoires as a function of time and social association. MSc thesis, Department of Marine Science, University of San Diego, CA.

Crockford, C., Herbinger, I., Vigilant, L. & Boesch, C. (2004). Wild chimpanzees produce group-specific calls: a case for vocal learning? Ethology 110, 221-243.

Deecke, V. B. (1998). Stability and change of killer whale (*Orcinus orca*) dialects. MSc thesis, Department of Zoology, University of British Columbia.

Deecke, V. B., Ford, J. K. B. & Spong, P. (2000). Dialect change in resident killer whales: Implications for vocal learning and cultural transmission. Animal Behaviour 60, 629-638.

Evans, S., Neave, N. & Wakelin, D. (2006). Relationships between vocal characteristics and body size and shape in human males: An evolutionary explanation for a deep male voice. Biological Psychology 72, 160-163.

Ey, E., Pfefferle, D. & Fischer, J. (2007). Do age- and sex-related variations reliably reflect body size in non-human primate vocalizations? Primates 48, 253-267.

Filatova, O. A., Fedutin, I. D., Burdin, A. M. & Hoyt, E. (2011). Responses of Kamchatkan fish-eating killer whales to playbacks of conspecific calls. Marine Mammal Science 27, E26-E42.

Fletcher, N. H. (1992). Acoustic systems in biology. Oxford University Press, Oxford.

Foote, A. D., Griffin, R. M., Howitt, D., Larsson, L., Miller, P. J. O. & Hoelzel, A. R. (2006). Killer whales are capable of vocal learning. Biology Letters 2, 509-512.

Foote, A. D., Osborne, R. W. & Hoelzel, A. R. (2008). Temporal and contextual patterns of killer whale (*Orcinus orca*) call type production. Ethology 114, 599-606.

Ford, J. K. B. (1987). A catalogue of underwater calls produced by killer whales (*Orcinus orca*) in British Columbia. Canadian Data Report of Fisheries and Aquatic Sciences 633.

Ford, J. K. B. (1989). Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. Canandian Journal of Zoology 67, 727-745.

Ford, J. K. B. (1991). Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. Canadian Journal of Zoology 69, 1454-1483.

Ford, J. K. B. & Fisher, H. D. (1983). Group specific dialects of killer whales (*Orcinus orca*) in British Columbia. In: Communication and behavior of whales: AAAS Selected Symposia Series 76, edited by Payne, R., pp. 129-161. Westview Press, Boulder.

Gaetz, W., Jantzen, K., Weinberg, H., Spong, P. & Symonds, H. (1993). A neural network method for recognition of individual *Orcinus orca* based on their acoustic behaviour: phase 1. OCEANS'93. Engineering in Harmony with Oceans. Proceedings, 1455-1457.

Gentner, T. Q. & Hulse, S. H. (1998). Perceptual mechanisms for individual vocal recognition in European starlings, *Sturnus vulgaris*. Animal Behaviour 56, 579-594.

Hausberger, M., Richard-Yris, M.-A., Henry, L., Lepage, L. & Schmidt, I. (1995). Song sharing reflects the social organization in a captive group of European starling (*Sturnus vulgaris*). Journal of Comparative Psychology 109, 222-241.

Hile, A. G., Plummer, T. K. & Striedter, G. F. (2000). Male vocal imitation produces call convergence during pair bonding in budgerigars, *Melopsittacus undulatus*. Animal Behaviour 59, 1209-1218.

Janik, V. M. (2000). Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). Science 289, 1355-1357

Janik, V. M. & Slater, P. J. B. (1998). Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. Animal Behaviour 56, 829-838.

Janik, V. M. & Slater, P. J. B. (2000). The different roles of social learning in vocal communication. Animal Behaviour 60, 1-11.

Jouventin, P., Aubin, T. & Lengagne, T. (1999). Finding a parent in a king penguin colony: the acoustic system of individual recognition. Animal Behaviour 57, 1175-1183.

Knörnschild, M. & von Helversen, O. (2008). Nonmutual vocal mother-pup recognition in the greater sac-winged bat. Animal Behaviour 76, 1001-1009.

Kremers, D., Briseño Jaramillo, M., Böye, M., Lemasson, A. & Hausberger, M. (2011). Do dolphins rehearse show-stimuli when at rest? Delayed matching of auditory memory. Frontiers in Comparative Psycholog, 2, 386.

Lemasson, A. & Hausberger, M. (2004). Patterns of vocal sharing and social dynamics in a captive group of Campbell's monkeys (*Cercopithecus campbelli campbelli*). Journal of Comparative Psychology 118, 347-359.

Lemasson, A. & Hausberger, M. (2011). Acoustic variability and social significance of calls in female Campbell's monkeys (*Cercopithecus campbelli campbelli*). Journal of the Acoustical Society of America 129, 3341-3352.

Lemasson, A., Palombit, R. A. & Jubin, R. (2008). Friendships between males and lactating females in a free-ranging group of olive baboons (*Papio hamadryas anubis*): evidence from playback experiments. Behavioral Ecology and Sociobiology 62, 1027-1035.

Lemasson, A., Boutin, A., Boivin, S., Blois-Heulin, C. & Hausberger, M. (2009). Horse (*Equus caballus*) whinnies: a source of social information. Animal Cognition 12, 693-704.

Luke, J. P., Marichal-Hernández, J. G., Rosa, F. & Almunia, J. (2010). Real time automatic detection of *Orcinus orca* vocalizations in a controlled environment. Applied Acoustics 71, 771-776.

Matthews, J. N., Rendell, L. E., Gordon, J. C. D. & MacDonald, D. W. (1999). A review of frequency and time parameters of cetacean tonal calls. Bioacoustics 10, 47-71.

McCowan, B. & Hooper, S. L. (2002). Individual acoustic variation in Belding's ground squirrel alarm chirps in the High Sierra Nevada. Journal of the Acoustical Society of America 111, 1157-1160.

McCowan, B. & Reiss, D. (1995). Quantitative comparison of whistle repertoires from captive adult bottlenose dolphins (Delphinidae, *Tursiops truncatus*): A re-evaluation of the signature whistle hypothesis. Ethology 100, 194-209.

McCowan, B. & Reiss, D. (1997). Vocal learning in captive bottlenose dolphins: a comparison to humans and nonhuman animals. Social influences on vocal development, edited by Snowdon, C. T. & Hausberger, M., pp. 178-207. Cambridge University Press, Cambridge.

McCowan, B. & Reiss, D. (2001). The fallacy of 'signature whistles' in bottlenose dolphins: a comparative perspective of 'signature information' in animal vocalizations. Animal Behaviour 62, 1151-1162.

Miller, P. J. O. & Bain, D. E. (2000). Within-pod variation in the sound production of a pod of killer whales, *Orcinus orca*. Animal Behaviour 60, 617-628.

Miller, P. J. O., Shapiro, A. D., Tyack, P. L. & Solow, A. R. (2004). Call-type matching in vocal exchanges of free-ranging resident killer whales, *Orcinus orca*. Animal Behaviour 67, 1099-1107.

Miller, P. J. O., Samarra, F. I. P. & Perthuison, A. (2007). Caller sex and orientation influence spectral characteristics of "two-voice" stereotyped calls produced by free-ranging killer whales. Journal of the Acoustical Society of America 121, 3932-3937.

Moore, S. E., Francine, J. K., Bowles, A. E. & Ford, J. K. B. (1988). Analysis of calls of killer whales, *Orcinus orca*, from Iceland and Norway. Rit Fiskideildar 11, 225-250.

Nousek, A. E., Slater, P. J. B., Wang, C. & Miller, P. J. O. (2006). The influence of social affiliation on individual vocal signatures of northern resident killer whales (*Orcinus orca*). Biology Letters 2; 481-484.

Price, T., Arnold, K., Zuberbühler, K. & Semple, S. (2009). Pyow but not hack calls of the male putty-nosed monkey (*Cercopithcus nictitans*) convey information about caller identity. Behaviour 146, 871-888.

Rendell, L. E. & Whitehead, H. (2003). Comparing repertoires of sperm whale codas: a multiple methods approach. Bioacoustics 14, 61-81.

Riesch, R., Ford, J. K. B. & Thomsen, F. (2005). Stability and group specificity in stereotyped whistles in resident killer whales, *Orcinus orca*, off British Columbia. Animal Behaviour 71, 79-91.

Samarra, F. I. P., Duc, A. V. & Miller, P. J. O. (2010). Identification of Morgan's discrete stereotyped call repertoire and matching to sounds recorded from wild North Atlantic killer whales. Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews.

Sayigh, L. S., Tyack, P. L., Wells, R. S. & Scott, M. D. (1990) Signature whistles of free-ranging bottlenose dolphins *Tursiops truncatus*: stability and mother-offspring comparisons. Behavioral Ecology and Sociobiology 26, 247-260.

Sayigh, L. S., Esch, H. C., Wells, R. S. & Janik, V. M. (2007). Facts about signature whistles of bottlenose dolphins, *Tursiops truncatus*. Animal Behaviour 74, 1631-1642.

Sèbe, F., Nowak, R., Poindron, P. & Aubin, T. (2007). Establishment of vocal communication and discrimination between ewes and their lamb in the first two days after parturition. Developmental Psychobiology 49, 375-386.

Smolker, R. & Pepper, J. W. (1999). Whistle convergence among allied male bottlenose dolphins (Delphinidae, *Tursiops sp.*). Ethology 105, 595-618.

Snowdon, C. T. & Cleveland, J. (1980). Individual recognition of contact calls in pygmy marmosets. Animal Behaviour 28, 717-727.

Snowdon, C. T. & Elowson, A. M. (1999). Pygmy marmosets modify call structure when paired. Ethology 105, 893-908.

Snowdon, C. T. & Hausberger, M. (1997). Social influences on vocal development. Cambridge University Press, Cambridge.

Soltis, J., Leong, K. & Savage, A. (2005). African elephant vocal communication. I. antiphonal calling behaviour among affiliated females. Animal Behaviour 70; 579-587.

Stoffberg, S., Jacobs, D. S. & Matthee, C. A. (2011). The divergence of echolocation frequency in horseshoe bats: moth hearing, body size or habitat? Journal of Mammalian Evolution 18, 117-129.

Thomsen, F. (1999). Eine Untersuchung der akustischen Signale des Schwertwals (*Orcinus orca*) aus den Gewässern um Vancouver Island, British Kolumbien. PhD dissertation, Department of Zoology, University of Hamburg.

Thomsen, F., Franck, D. & Ford, J. K. B. (2001). Characteristics of whistles from the acoustic repertoire of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. Journal of the Acoustical Society of America 109, 1240-1246.

Tyack, P. L. (2000). Functional aspects of cetacean communication. In: Cetacean societies – Field studies of dolphins and whales, edited by Mann, J, Conner, R. C., Tyack, P. L. & Whitehead, H., pp. 270-307. The University of Chicago Press, Chicago.

Tyack, P. L. (2008). Convergence of calls as animals form social bonds, active compensation for noisy communication channels, and the evolution of vocal learning in mammals. Journal of the Acoustical Society of America 122, 319-331.

Wang, D., Würsig, B. & Evans, W. E. (1995). Comparison of whistles among seven odontocete species. In: Sensory systems of aquatic mammals, edited by Kastelein, R. A., Thomas, J. A. & Nachtigall, P. E., pp. 299-323. DeSpil, Woerden.

Watwood, S. L., Tyack, P. L. & Wells, R. S. (2004). Whistle sharing in paired male bottlenose dolphins, *Tursiops truncatus*. Behavioral Ecology and Sociobiology 55, 531-543.

Weilgart, L. & Whitehead, H. (1997). Group-specific dialects and geographical variation in coda repertoire in south Pacific sperm whales. Behavioral Ecology and Sociobiology 40, 277-285.

Yin, S. & McCowan, B. (2004). Barking in domestic dogs: context specificity and individual identification. Animal Behaviour 68, 343-355.

Yurk, H., Barrett-Lennard, L. G., Ford, J. K. B. & Matkin, C. O. (2002). Cultural transmission within maternal lineages: vocal clans in resident killer whales in southern Alaska. Animal Behaviour 63, 1103-1119.

<u>BIBLIOGRAPHY</u>

Bibliography

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Abramson, J. Z., Hernández-Lloreda, V., Call, J. & Colmenares, F. (2013). Experimental evidence for action imitation in killer whales (*Orcinus orca*). Animal Cognition 16, 11-22.

Acevedo-Gutiérrez, A. & Stienessen, S. C. (2004). Bottlenose dolphins (*Tursiops truncatus*) increase number of whistles when feeding. Aquatic Mammals, 30, 357-362.

Adret-Hausberger, M. (1982). Social influences on the whistled songs of starlings. Behavioral Ecology and Sociobiology, 11, 241-246.

Adret-Hausberger, M. (1989). The species-repertoire of whistled songs in the European starling: species-specific characteristics and variability. Bioacoustics, 2, 137-162.

Aguilar Soto, N., Johnson, M., Madsen, P. T., Tyack, P. L., Bocconcelli, A. & Borsani, J. F. (2006). Does intense ship noise disturb foraging in deep-diving Cuvier's beaked whales (*Ziphius cavirostris*)?. Marine Mammal Science 22, 690-699.

Alves, C., Boal, J. G. & Dickel, L. (2009). Short-distance navigation in cephalopods: a review and synthesis. Cognitive Processing 9, 239-247.

Aly, M. & Moscovitch, M. (2010). The effects of sleep on episodic memory in older and younger adults. Memory 18, 327-334.

Ansorge, V., Hammerschmidt, K. & Todt, D. (1992). Communal roosting and formation of sleeping clusters in Barbary macaques (*Macaca sylvanus*). American Journal of Primatology, 28, 271-280.

Armstrong, E. A. (1960). A Study of Bird Song. Oxford University Press, London.

Atem, A. C. G. & Monteiro-Filho, E. L. A. (2006). Nocturnal activity of the estuarian dolphin (*Sotalia guianensis*) in the region of Cananéia, São Paulo State, Brazil. Aquatic Mammals, 32, 236-241.

Au, W. W. L. (2009). Echolocation. In: Encyclopedia of marine mammals, 2nd edition, edited by Perrin, W. F., Würsig, B. & Thewissen, J. G. M., pp. 348-357. Academic Press, Burlington.

Au, W. W. L. & Hastings, M. C. (2008). Principles of marine bioacoustics. Springer, New York.

Au, W. W. L., Mobley, J., Burgess, W.C. & Lammers, M. O. (2000). Seasonal and diurnal trends of chorusing humpback whales wintering in waters off western Maui. Marine Mammal Science, 16, 530-544.

Azevedo, F. A., Oliveira, A. M., Dalla Rosa, L. & Lailson-Brito, J. (2007). Characteristics of whistles from resident bottlenose dolphins (*Tursiops truncatus*) in southern Brazil. Journal of the Acoustical Society of America 121, 2978-2983.

Bailey, H., Senior, B., Simmons, D., Rusin, J., Picken, G. & Thompson, P. M. (2010). Assessing underwater noise levels during pile-driving at an offshore windfarm and its potential effects on marine mammals. Marine Pollution Bulletin 60, 888-897.

Banks, A. N. & Srygley, R. B. (2003). Orientation by magnetic field in leaf-cutter ants, *Atta colombica* (Hymenoptera: Formicidae). Ethology 109, 835-846.

Bannister, J. L. (2009). Baleen whales (mysticetes). In: Encyclopedia of marine mammals, 2nd edition, edited by Perrin, W. F., Würsig, B. & Thewissen, J. G. M., pp. 80-89. Academic Press, Burlington.

Bateson, M. (2007). Environmental noise and decision making possible implications of increases in anthropogenic noise for information processing in marine mammals. International Journal of Comparative Psychology 20, 169-178.

Bauer, G. B., Fuller, M., Perry, A., Dunn, J. R. & Zoeger, J. (1985). Magnetoreception and biomineralization of magnetite in cetaceans. In: Magnetite biomineralization and magnetoreception in organisms: a new biomagnetism, edited by Kirschvink, J. L., Jones, D. S. & MacFadden, B. J., pp 489-507. Plenum Press, New York.

Bazúa-Duran, M. C. & Au, W. W. L. (2002). The whistles of Hawaiian spinner dolphins. Journal of the Acoustical Society of America 112, 3064-3072.

Begall, S., Cerveny, J., Neef, J., Vojtech, O. & Burda, H. (2008). Magnetic alignment in grazing and resting cattle and deer. Proceedings of the National Academy of Science USA 105, 13451-13455.

Behrmann, G. (1988). The peripheral nerve ends in the tongue of the harbour porpoise *Phocoena phocoena* (Linne, 1758). Aquatic Mammals 14, 107-112.

Behrmann, G. (1989). The olfactory regions in the nose of the harbour porpoise *Phocoena phocoena* (Linne, 1758). Aquatic Mammals 15, 130-133.

Bender, C. E., Herzing, D. L. & Bjorklund, D. F. (2009). Evidence of teaching in Atlantic spotted dolphins (*Stenella frontalis*) by mother dolphins foraging in the presence of their calves. Animal Cognition 12, 43-53.

Birgersson, B., Alm, U. & Forkman, B. (2001). Colour vision in fallow deer: a behavioural study. Animal Behaviour 61, 367-371.

Black, J. M. (1988). Preflight signalling in swans: a mechanism for group cohesion and flock formation. Ethology 79, 143-157.

Blomqvist, C., Mello, I. & Amundin, M. (2004). High-frequency burst-pulse sounds in agonistic/aggressive interactions in bottlenose dolphins, *Tursiops truncatus*. In: Echolocation in bats and dolphins, edited by Thomas, J. A., Moss, C. F. & Vater, M., pp. 425-431. University Of Chicago Press, Chicago.

Boal, J. G. (1997). Female choice of males in cuttlefish (Mollusca, Cephalopoda). Behaviour 134, 975-988.

Boal, J. G. & Golden, D. K. (1999). Distance chemoreception in the common cuttlefish, *Sepia officinalis* (Mollusca, Cephalopoda). Journal of Experimental Marine Biology and Ecology 235, 307-317.

Boal, J. G., Hylton, R. A., Gonzalez, S. A. & Hanlon, R. T. (1999). Effects of crowding on the social behavior of cuttlefish (*Sepia officinalis*). Contemporary Topics in Laboratory Animal Science 38, 49-55.

Boinski, S. & Campbell, A. F. (1995). Use of trill vocalizations to coordinate troop movement among white-faced capuchins: a second field test. Behaviour 132, 875-901.

Boles, L. C. & Lohmann, K. J. (2003). True navigation and magnetic map in spiny lobsters. Nature 421, 60-63.

Bojanowski, E. (2002). Vocal behaviour in bottlenose dolphins (*Tursiops truncatus*): Ontogeny and contextual use in specific interactions. Dissertation, Freie Universität Berlin, Germany.

Boucher, Y. Simons, C. T., Faurion, A., Azérad, J. & Carstens, E. (2003). Trigeminal modulation of gustatory neurons in the nucleus of the solitary tract. Brain Research 973, 265-274.

Brownlee, S. M. & Norris, K. S. (1994). The acoustic domain. In: The Hawaiian spinner dolphin, edited by Norris, K. S., Würsig, B., Wells, R. S. & Würsig, M., pp. 161-187. University of California Press, Berkeley and Los Angeles.

Bryden, M. M. & Molyneux, G. S. (1986). U1trastrucrure of encapsulated mechanoreceptor organs in the region of the nares. In: Research on dolphins, edited by Bryden, M. M. & Harrison, R., pp. 99-107. Clarendon Press, Oxford.

Buckstaff, K. C. (2004). Effects of watercraft noise on the acoustic behaviour of bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. Marine Mammal Science 20, 709-725.

Budelmann, B. U. & Bleckmann, H. (1988). A lateral line analogue in cephalopods: water waves generate microphonic potentials, in the epidermal head lines of *Sepia* and *Lolliguncula*. Journal of Comparative Physiology A 164, 1-5.

Burt, J. M. & Vehrencamp, S. L. (2005). Dawn chorus as an interactive communication network. In: Animal communication networks, edited by McGregor, P. K., pp. 320-343. Cambridge University Press, Cambridge.

Cadiou, H. & McNaughton, P. A. (2010). Avian magnetite-based magnetoreception: a physiologist's perspective. Journal of the Royal Society Interface 7, S193-S205.

Caldwell, M. C. & Caldwell, D. K. (1965). Individualized whistle contours in bottlenose dolphins (*Tursiops truncatus*). Nature 207, 434-435.

Caldwell, M. C. & Caldwell, D. K. (1967). Intraspecific transfer of information via the pulsed sound in captive odontocete cetaceans. In: Animal sonar systems: biology and bionics, edited by Bullock, R. G. pp. 879-936. Laboratoire Physiologie Acoustique, Jouy-en-Josas.

Caldwell, M. C., Caldwell, D. K.. & Tyack, P. L. (1990). Review of the signature-whistle-hypothesis for the Atlantic bottlenose dolphin. In: The bottlenose dolphin, edited by Leatherwood, S. & Reeves, R. R., pp. 199-234. Academic Press, San Diego.

Catchpole, C. K. & Slater, P. J. (1995). Bird song: biological themes and variations. Press Syndicate University of Cambridge, Cambridge.

Cartron, L., Josef, N., Lerner, A., McCusker, S. D., Darmaillacq, A.-S., Dickel, L. & Shashar, N. (2013). Polarization vision can improve object detection in turbid waters by cuttlefish. Journal of Experimental Marine Biology and Ecology 447, 80-85.

Charlton, B. D., Reby, D. & McComb, K. (2007). Female perception of size-related formant shifts in red deer, *Cervus elaphus*. Animal Behaviour 74, 707-714.

Chien, J.-P. (2006). Of animals and men: a study of Umwelt in Uexküll, Cassirer, and Heidegger. Concentric: Literary and Cultural Studies 32, 57-79.

Cipolli, C., Fagioli, I., Mazzetti, M. & Tuozzi, G. (2004). Incorporation of presleep stimuli into dream contents: evidence for a consolidation effect on declarative knowledge during REM sleep? Journal of Sleep Research 13, 317-326.

Clutton-Brock, T. H. & Albon, S. D. (1979). The roaring of red deer and the evolution of honest advertising. Behaviour 69, 145-170.

Connor, R. C. (2007). Dolphin social intelligence: complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. Philosophical Transactions of the Royal Society B 362, 587-602.

Connor, R. C. & Smolker, R. A. (1996). 'Pop' goes the dolphin: a vocalization male bottlenose dolphins produce during consortships. Behaviour 133, 643-662.

Connor, R. C., Smolker, R. A. & Richards, A. F. (1992). Two levels of alliance formation among male bottlenose dolphins (*Tursiops sp.*). Proceedings of the National Academy of Sciences 89, 987-990.

Connor, R. C., Richards, A. F., Smolker, R. A. & Mann J. (1996). Patterns of female attractiveness in Indian Ocean bottlenose dolphins. Behaviour 133, 37-69.

Connor, R. C., Wells, R. S., Mann, J. & Read, A. J. (2000). The bottlenose dolphin: social relationships in a fission-fusion society. In: Cetacean societies: field studies of dolphins and whales, edited by Mann, J., Connor, R. C., Tyack, P. L. & Whitehead, H., pp. 91-126. The University of Chicago Press, Chicago.

Cranford, T. W. (2000). In search of impulse sound sources in odontocetes. In: Hearing by whales and dolphins, edited by Au, W. W. L., Popper, A. N. & Fay, R. R., pp. 109-155. Springer, New York.

Cruickshank, A. J., Gautier, J.-P. & Chappuis, C. (1993). Vocal mimicry in wild African grey parrots *Psittacus erithacus*. IBIS 135, 293-299.

Czech-Damal, N. U., Liebschner, A., Miersch, L., Klauer, G., Hanke, F. D., Marshall, C., Dehnhardt, G. & Hanke, W. (2012). Electroreception in the Guiana dolphin (*Sotalia guianensis*). Proceedings of the Royal Society B 279, 663-668.

Czech-Damal, N. U., Dehnhardt, G., Manger, P. & Hanke, W. (2013). Passive electroreception in aquatic mammals. Journal of Comparative Physiology A 199, 555-563.

Dacey, J. W. H. & Wakeham, S. G. (1986). Oceanic dimethylsulfide: production during zooplankton grazing on phytoplankton. Science 233, 1314-1315.

D'Angelo, G. J., Glasser, A., Wendt, M., Williams, G. A., Osborn, D. A., Gallagher, G. R., Warren, R. J., Miller, K. V. & Pardue, M. T. (2008). Visual specialization of an herbivore prey species, the white-tailed deer. Canadian Journal of Zoology 86, 735-743.

Darmaillacq, A.-S., Dickel, L., Chichery, P.-P., Agin, V. & Chichery, R. (2004). Rapid taste aversion learning in adult cuttlefish, *Sepia officinalis*. Animal Behaviour 68, 1291-1298.

Dave, A. S. & Margoliash, D. (2000). Song replay during sleep and computational rules for sensorimotor vocal learning. Science 290, 812-816.

Davis, M. W., Spencer, M. L. & Ottmar, M. L. (2006). Behavioral responses to food odor in juvenile marine fish: acuity varies with species and fish length. Journal of Experimental Marine Biology and Ecology 328, 1-9.

Dawson, W. W. (1980). The cetacean eye. In: Cetacean Behavior: mechanisms and functions, edited by Herman, L. M., pp. 54-99. Wiley Interscience, New York.

DeBose, J. L., Lema, S. C. & Nevitt, G. A. (2008). Dimethylsulfoniopropionate as a foraging cue for reef fishes. Science 319, 1356.

Delfour, F. (2010). Marine mammals enact individual worlds. International Journal of Comparative Psychology 23, 792-810.

Deutschlander, M. E., Freake, M. J., Borland, C., Phillips, J. B., Madden, R. C., Anderson, L. E. & Wilson, B. W. (2003). Learned magnetic compass orientation by the Siberian hamster, *Phodopus sungorus*. Animal Behaviour 65, 779-786.

Díaz López, B. (2011). Whistle characteristics in free-ranging bottlenose dolphins (*Tursiops truncatus*) in the Mediterranean Sea: influence of behaviour. Mammalian Biology 76, 180-189.

Díaz López, B. & Shirai, J. A. B. (2009). Mediterranean common bottlenose dolphin's repertoire and communication use. In: Dolphins: anatomy, behavior, and threats, edited by Pearce, A. G. & Correa, L. M., pp. 129-148. Nova Science Publishers, Inc., New York.

Diego-Rasilla, F. J., Luengo, R. M. & Phillips, J. B. (2008). Use of magnetic compass for nocturnal homing orientation in the palmate newt, *Lissotriton helveticus*. Ethology 114, 808-815.

Ding, W., Würsig, B. & Evans, W. (1995). Comparison of whistles among seven odontocete species. In: Sensory Systems of Aquatic Mammals, edited by Kastelein, R. A., Thomas, J. A. & Nachtigall, P. E., pp. 299-323. De Spil Publishers, Woerden.

Dormer, K. J. (1979). Mechanism of sound production and air recycling in delphinids: cineradiographic evidence. Journal of the Acoustic Society of America 65, 229-239.

dos Santos, M., Ferreira, A. J. & Harzen, S. (1995). Rhythmic sound sequences by aroused bottlenose dolphins in the Sado estuary, Portugal. In: Sensory Systems of Aquatic Mammals, edited by Kastelein, R. A., Thomas, J. A. & Nachtigall, P. E., pp. 325-334. De Spil Publishers, Woerden.

dos Santos, M. E., Louro, S., Couchinho, M. & Brito, C. (2005). Whistles of bottlenose dolphins (*Tursiops truncatus*) in the Sado estuary, Portugal: characteristics, production rates, and long-term contour stability. Aquatic Mammals 31, 453-462.

Dral, A. D. G. (1977). On the retinal anatomy of cetacea. In: Functional anatomy of marine mammals, Volume 3, edited by Harrison, R. J., pp. 86-87. Academic Press, London.

Dudzinski, K. M. (1996). Communication and behavior in the Atlantic spotted dolphins (*Stanella frontalis*): Relationship between vocal and behavioral activities. Dissertation, Texas A & M University, United States of America.

Dudzinski, K. M., Melillo-Sweeting, J. G., Melillo-Sweeting; K., Seay, B., Levengood, A. & Kuczaj, S. A. (2012). Tactile contact exchanges between dolphins: self-rubbing versus inter-individual contact in three species from three geographies. International Journal of Comparative Psychology 25, 21-43.

Dudzinski, K. M., Thomas, J. A. & Gregg, J. D. (2009a). Communication in marine mammals. In: Encyclopedia of marine mammals, 2nd edition, edited by Perrin, W. F., Würsig, B. & Thewissen, J. G. M., pp. 260-269. Academic Press, Burlington.

Dudzinski, K. M., Gregg, J. D., Ribic, C. A. & Kuczaj, S. A. (2009b). A comparison of pectoral fin contact between two different wild dolphin populations. Behavioural Processes 80, 182-190.

Dudzinski, K. M., Gregg, J. D., Paulos, R. D. & Kuczaj, S. A. (2010). A comparison of pectoral fin contact behaviour for three distinct dolphin populations. Behavioural Processes 84, 559-567.

Dusenbery, D. B. (1992). Sensory ecology: how organisms acquire and respond to information. W. H. Freeman and Company, New York.

Esch, H. C., Sayigh, L. S., Blum, J. E. & Wells, R. S. (2009). Whistles as potential indicators of stress in bottlenose dolphins (*Tursiops truncatus*). Journal of Mammalogy 90, 638-650.

Feare, C. J. (1984). The starling. Oxford University Press, Oxford.

Fernández, A., Edwards, J. F., Rodríguez, F., Espinosa de los Monteros, A., Herráez, P., Castro, P., Jaber, J. R., Martín, V. & Arbelo, M. (2005). "Gas and fat embolic syndrome" involving a mass stranding of beaked whales (Family Ziphiidae) exposed to anthropogenic sonar signals. Veterinary Pathology 42, 446-457.

Ferrando, T., Caresano, F., Ferrando, S., Gallus, L., Wurty, M. & Tagliafierro, G. (2010). The tongue morphology and lingual gland histochemistry of Ligurian Sea odontocetes. Marine Mammal Science 26, 588-601.

Fischer, J. H., Freake, M. J., Borland, S. C. & Phillips, J. B. (2001). Evidence for the use of magnetic map information by an amphibian. Animal Behaviour 62, 1-10.

Foote, A. D., Griffin, R. M., Howitt, D., Larsson, L. Miller, P. J. O. & Hoelzel, A. R. (2006). Killer whales are capable of vocal learning. Biology Letters 2, 509-512.

Ford, J. K. B. (1984). Call traditions and dialects of killer whales (*Orcinus orca*) in British Columbia. Dissertation, University of British Columbia, Canada.

Ford, J. K. B. (1989). Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. Canandian Journal of Zoology 67, 727-745.

Ford, J. K. B. (1991). Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. Canadian Journal of Zoology 69, 1454-1483.

Ford, J. K. B. (2009). Killer whale: *Orcinus orca*. In: Encyclopedia of marine mammals, 2nd edition, edited by Perrin, W. F., Würsig, B. & Thewissen, J. G. M., pp. 650-657. Academic Press, Burlington.

Ford, J. K. B. & Fisher, H. D. (1983). Group specific dialects of killer whales (*Orcinus orca*) in British Columbia. In: Communication and behavior of whales: AAAS Selected Symposia Series 76, edited by Payne, R., pp. 129-161. Westview Press, Boulder.

Friedl, W. A., Nachtigall, P. E., Moore, P. W. B., Chun, N. K. W., Haun, J. E., Hall, R. W. & Richards, J. L. (1990). Taste reception in the Pacific bottlenose dolphin (*Tursiops truncatus gilli*) and the California sea lion (*Zalophus californianus*). In: Sensory abilities of cetaceans, edited by Thomas, J. A. & Kastelein, R. A., pp. 447-454. Plenum Press, New York.

Frith, C. B. & Frith, D. W. (2004). The Bowerbirds. Oxford University Press, London.

Galdikas, B. M. F. (1983). The orangutan long call and snag crashing at Tanjung Puting Reserve. Primates 24, 371-384.

Gannon, D. P., Barros, N. B., Nowacek, D. P., Read, A. J., Waples, D. M. & Wells, R. S. (2005). Prey detection by bottlenose dolphins (*Tursiops truncatus*): an experimental test of the passive listening hypothesis. Animal Behaviour 69, 709-720.

Gatesy, J., Geisler, J. H., Chang, J., Buell, C., Berta, A., Meredith, R. W., Springer, M. S. & McGowen, M. R. (2013). A phylogenetic blueprint for a modern whale. Molecular Phylogenetics and Evolution 66, 479-506.

Geissmann, T. & Mutschler, T. (2006). Diurnal distribution of loud calls in sympatric wild indris (Indri indri) and ruffed lemurs (*Varecia variegata*): implications for call functions. Primates 47, 393-396.

Geist, V. (2009). Deer. In : Encyclopedia of mammals, 2nd edition, edited by: MacDonald, D., pp. 504-519. Oxford University Press, Oxford.

Gnone, G., Benoldi, C., Bonsignori, B. & Fogani, P. (2001). Observations of rest in captive bottlenose dolphins. Aquatic Mammals 27, 29-33.

Goldbogen, J. A., Southall, B. L., DeRuiter, S. L., Calambokidis, J., Friedlaender, A. S., Hazen, E. L., Falcone, E. A., Schorr, G. S., Douglas, A., Moretti, D. J., Kyburg, C., McKenna, M. F. & Tyack, P. L. (2013). Blue whales respond to simulated mid-frequency military sonar. Proceedings of the Royal Society B, published online July 2013. doi 10.1098/rspb.2013.0657

Goley, P. D. (1999). Behavioral aspects of sleep in Pacific white-sided dolphins (*Lagenorhynchus obliquidens*, Gill 1865). Marine Mammal Science 15, 1054-1064.

Goold, J. C. (2000). A diel pattern in vocal activity of short-beaked common dolphins, *Delphinus delphis*. Marine Mammal Science 16, 240-244.

Guibé, M., Boal, J. G. & Dickel, L. (2010). Early exposure to odors changes later visual prey preferences in cuttlefish. Developmental Psychobiology 52, 833-837.

Hagelin, J. C., Straley, J. M., Nielson, L. B. & Szabo, A. (2012). Baleen whales and tubenose seabirds—a colossal chemosensory convergence? Presented at the 34th Association for Chemoreception Sciences, Huntington Beach, California. April 25-28

Hammerschmidt, K., Ansorge, V., Fischer, J. & Todt, D. (1994). Dusk calling in barbary macaques (*Macaca sylvanus*): demand for social shelter. American Journal of Primatology 32, 277-289.

Hara, T. J. (1994). Olfaction and gustation in fish: an overview. Acta Physiologica Scandinavica 152, 207-217.

Hara, T. J. (2006). Feeding behaviour in some teleosts is triggered by single amino acids primarily through olfaction. Journal of Fish Biology 68, 810-825.

Hausberger, M., Jenkins, P. F. & Keene, J. (1991). Species-specificity and mimicry in bird song: are they paradoxes? A reevaluation of song mimicry in the European starling. Behaviour 117, 53-82.

Hausberger, M., Bigot, E. & Clergeau, P. (2008). Dialect use in large assemblies: a study in European starlings *Sturnus vulgaris* roosts. Journal of Avian Biology 39, 672-682.

Heithaus, M. R. & Dill, L. M. (2009). Feeding strategies and tactics. In: Encyclopedia of marine mammals, 2nd edition, edited by Perrin, W. F., Würsig, B. & Thewissen, J. G. M., pp. 414-423. Academic Press, Burlington.

Hemilä, S. & Reuter, T. (2008). The physics and biology of olfaction and taste. In: Sensory evolution on the threshold: adaption in secondarily aquatic mammals, edited by Thewissen, J. G. M. & Nummela, S., pp. 29-33. University of California Press, Berkeley and Los Angeles.

Henwood, K. & Fabrick, A. (1979). A quantitative analysis of the dawn chorus: temporal selection for communicatory optimization. American Naturalist 114, 260-274.

Herman, L. M., Peacock, M. F., Yunker, M. P. & Madsen C. J. (1975). Bottlenosed dolphin: double-slit pupil yields equivalent aerial and underwater diurnal acuity. Science 189, 650-652.

Herzing, D. L. (1996). Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins, *Stenella frontalis* and bottlenose dolphins, *Tursiops truncatus*. Aquatic Mammals 22, 61-79.

Herzing, D. L. & dos Santos, M. E. (2004). Functional aspects of echolocation in dolphins. Echolocation in bats and dolphins, edited by Thomas, J. A., Moss, C. F. & Vater, M., pp. 386-392. University Of Chicago Press, Chicago.

Hirvonen, H., Ranta, E., Piironen, J., Laurila, A. & Peuhkuri, N. (2000). Behavioral response of naïve Artic charr young to chemical cues from salmonid and non-salmonid fish. Oikos 88, 191-199.

Hodgetts, B. V. , Waas, J. R. & Matthews, L. R. (1998). The effects of visual and auditory disturbance on the behaviour of red deer (*Cervus eluphus*) at pasture with and without shelter. Applied Animal Behaviour Science 55, 337-351.

Holland, R. A., Thorup, K., Vonhof, M. J., Cochran, W. W. & Wikelski, M. (2006). Navigation: bat orientation using Earth's magnetic field. Nature 444, 702.

Hooper, S., Reiss, D., Carter, M. & McCowan, B. (2006). Importance of contextual saliency on vocal imitation by bottlenose dolphins. International Journal of Comparative Psychololgy 19, 116-128.

Houser, D. S. & Finneran, J. J. (2006). A comparison of underwater hearing sensitivity in bottlenose dolphins (*Tursiops truncatus*) determined by electrophysiological and behavioral methods. Journal of the Acoustical Society of America 120, 1713-1722.

Humphrey, N. (1983). Consciousness regained: chapters in the development of mind. Oxford University Press, Oxford.

Bibliography

Innes, L. & McBride, S. (2008). Negative versus positive reinforcement: an evaluation of training strategies for rehabilitated horses. Applied Animal Behavior Science 112, 357-368.

James, W. (1962). Principles of psychology (original was published 1890). Dover, New York.

Janik, V. M. (2000a). Food-related bray calls in wild bottlenose dolphins (*Tursiops truncatus*). Proceedings of the Royal Society B 267, 923-927.

Janik, V. M (2000b). Source levels and estimated active space of bottlenose dolphins (*Tursiops truncatus*) whistles in the Moray Firth, Scotland. Journal of Comparative Physiology A 186, 673-680.

Janik, V. M. (2000c). Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). Science 289, 1355-1357.

Janik, V. M. (2009). Acoustic communication in delphinids. In: Advances in the study of behaviour, Volume 40, edited by Naguib, M. & Janik, V. M., pp. 123-157. Academic Press, Burlington.

Janik, V. M. & Sayigh, L. S. (2013). Communication in bottlenose dolphins: 50 years of signature whistle research. Journal of Comparative Physiology A 199, 479-489.

Janik, V. M. & Slater, P. J. B. (1998). Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. Animal Behaviour 56, 829-838.

Janik, V. M. & Slater, P. J. B. (2000). The different roles of social learning in vocal communication. Animal Behaviour 60, 1-11.

Janik, V. M., Sayigh, L. S. & Wells, R. S. (2006). Signature whistle contour shape conveys identity information to bottlenose dolphins. Proceedings of the National Academy of Science 103, 8293-8297.

Janik, V. M., King, S. L., Sayigh, L. S. & Wells, R. S. (2013). Identifying signature whistles from recordings of groups of unrestrained bottlenose dolphins (*Tursiops truncatus*). Marine Mammal Science 29, 109-122.

Jensen, A.-L. M., Delfour, F. & Carter, T. (2013) Anticipatory behavior in captive bottlenose dolphins (*Tursiops truncatus*): a preliminary study. Zoo Biology 32, 436-444.

Jepson, P. D., Arbelo, M., Deaville, R., Patterson, I. A. P., Castro, P., Baker, J. R., Degollada, E., Ross, H. M., Herráez, P., Pocknell, A. M., Rodríguez, F., Howie, F. E., Espinosa, A., Reid, R. J., Jaber, J. R., Martin, V., Cunningham, A. A., & Fernández, A. (2003). Gas-bubble lesions in stranded cetaceans. Nature 425, 575-576.

Jiang, P., Josue, J., Li, X., Glaser, D., Li, W., Brand, J. G., Margolskee, R. F., Reed, D. R. & Beauchamp, G. K. (2013). Major taste loss in carnivorous mammals. Proceedings of the National Academy of Science 109, 4956-4961.

Jones, G. J. & Sayigh, L. S. (2002). Geographic variation in rates of vocal production of free-ranging bottlenose dolphins. Marine Mammal Science 18, 374-393.

Jouvet, M. (1979). What does a cat dream about? Trend in Neuroscience 2, 280-282.

Kakuschke, A., Valentine-Thon, E., Griesel, S., Gandrass, J., Perez Luzardo, O., Dominguez Boada, L., Zumbado Peña, M., Almeida González, M., Grebe, M., Pröfrock, D., Erbsloeh, H. B., Kramer, K., Fonfara, S. & Prange, A. (2010). First health and pollution study on harbor seals (*Phoca vitulina*) living in the German Elbe estuary. Marine Mollution Bulletin 60, 2079-2086.

Kalmijn, A. J. (1971). The electric sense of sharks and rays. Journal of Experimental Biology 55, 371-383.

Kalmijn, A. J. (1982). Electric and magnetic field detection in elasmobranch fishes. Science 218, 916-918.

Kastelein, R. & Dubbeldam, J. L. (1990). Marginal papillae on the tongue of the harbour porpoise (*Phocoena phocoena*), bottlenose dolphin (*Tursiops truncatus*) and

Commerson's dolphin (*Cephalorhynchus commersonii*). Aquatic Mammals 15, 158-170.

Kelley, L. A. & Healy, S. D. (2011). Vocal mimicry. Current Biology 21, R9-R10.

Kelman, E. J., Osorio, D. & Baddeley, R. J. (2008). A review of cuttlefish camouflage and object recognition and evidence for depth perception. Journal of Experimental Biology 211, 1757-1763.

King, S. L. & Janik, V. M. (2013). Bottlenose dolphins can use learned vocal labels to address each other. Proceedings of the National Academy of Science 110, 13216-13221.

King S. L., Sayigh, L. S., Wells, R. S., Fellner, W. & Janik, V. M. (2013). Vocal copying of individually distinctive signature whistles in bottlenose dolphins. Proceedings of the Royal Society London B 280, 20130053.

Kirschvink, J. L., Jones, D. S. & McFadden, B. J. (1985). Magnetite biomineralization and magnetoreception in organisms: a new biomagnetism. Plenum Press, New York.

Kirschvink, J. L., Dizon, A. E. & Westphal, J. A. (1986). Evidence from strandings for geomagnetic sensitivity in cetaceans. Journal of Experimental Biology 120, 1-24.

Kishida, T., Kubota, S., Shirayama, Y. & Fukami, H. (2007). The olfactory receptor gene repertoire in secondary-adapted marine vertebrates: evidence for reduction of the functional proportion in cetaceans. Biology Letters 3, 428-430.

Kleemann, A. M., Albrecht, J., Schöpf, V., Haegler, K., Kopietz, R., Hempel, J. M., Linn, J., Flanagin, V. L., Fesl, G. & Wiesmann, M. (2009). Trigeminal perception is necessary to localize odors. Physiology & Behavior 94, 401-405.

Klinowska, L. (1985). Cetacean live stranding sites relate to geomagnetic topography. Aquatic Mammals 1, 27-32.

Koda, K. (2008). Sacred path of Reiki: healing as a spiritual discipline. Llewellyn, Woodbury.

Kolchin, S. P. & Bel'kovich, V. M. (1973). Tactile sensitivity in *Delphinus delphis*. Zoologichesky ZhurnaI 52, 620-622.

Komak, S., Boal, J. G., Dickel, L. & Budelmann, B. U. (2005). Behavioural responses of juvenile cuttlefish (*Sepia officinalis*) to local water movements. Marine and Freshwater Behaviour and Physiology 38, 117-125.

Kowalewsky, S., Dambach, M., Mauck, B. & Dehnhardt, G. (2006). High olfactory sensitivity for dimethyl sulphide in harbour seals. Biology Letters 2, 106-109.

Kremers, D., Briseño Jaramillo, M., Böye, M., Lemasson, A. & Hausberger, M. (2011). Do dolphins rehearse show-stimuli when at rest? Delayed matching of auditory memory. Frontiers in Psychology 2, 386.

Kuczaj, S. A. & Makecha, R. (2008). The role of play evolution and ontogeny of contextually flexible communication. In: Evolution of Communicative Flexibility. Complexity, Creativity, and Adaptability in Human and Animal Communication, edited by Oller, D. K. & Griebel, U., pp. 253-277. MIT Press, Cambridge.

Kuczaj, S. A., Makecha, R. N., Trone, M., Paulos, R. D. & Ramos, J. A. (2006). The role of peers in cultural transmission and cultural innovation: evidence from dolphin calves. International Journal of Comparative Psychology 19, 223-240.

Kullmann, H., Thünken, T., Baldauf, S. A., Bakker, T. C. M. & Frommen, J. G. (2008). Fish odour triggers conspecific attraction behaviour in an aquatic invertebrate. Biology Letters 4, 458-460.

Kunz, T. H. (1982). Roosting ecology of bats. In: Ecology of bats, edited by Kunz, T. H., pp. 1-55. Plenum Publishing Corporation, New York.

Kuznetzov, V. B. (1990). Chemical sense of dolphins: quasi-olfaction. In: Sensory abilities of cetaceans, edited by Thomas, J. A. & Kastelein, R. A., pp. 481-503. Plenum Press, New York.

Laist, D. W., Knowlton, A. R., Mead, J. G., Collet, A. S. & Podesta, M. (2001). Collisions between ships and whales. Marine Mammal Science 17, 35-75.

Lammers, M. O. & Au, W. W. L. (2003). Directionality in the whistles of Hawaiian spinner dolphins (*Stenella longirostris*): a signal feature to cue direction of movement? Marine Mammal Science 19, 249-264.

Laska, M. & Seibt, A. (2002). Olfactory sensitivity for aliphatic alcohols in squirrel monkeys and pigtail macaques. Journal of Experimental Biology 205, 1633-1643.

Laska, M., Seibt, A. & Weber, A. (2000). 'Microsmatic' primates revisited: olfactory sensitivity in the squirrel monkey. Chemical Senses 25, 47-53.

Lawson, R. E., Putman, R. J. & Fielding, A. H. (2001). Chemical communication in Eurasian deer (Cervidae): do individual odours also code for attributes? Journal of Zoology 253, 91-99.

LeDuc, R. (2009). Delphinids: overview. In: Encyclopedia of marine mammals, 2nd edition, edited by Perrin, W. F., Würsig, B. & Thewissen, J. G. M., pp. 298-302. Academic Press, Burlington.

Lemasson, A. & Hausberger, M. (2011). Acoustic variability and social significance of calls in female Campbell's monkeys (*Cercopithecus campbelli campbelli*). Bioacoustics 129, 3341-3352.

Liedvogel, M. & Mouritsen, H. (2010). Cryptochromes, a potential magnetoreceptor: what do we know and what do we want to know? Journal of the Royal Society Interface 7, S147-S162.

Lohmann, K. J. & Johnson, S. (2000). The neurobiology of magnetoreception in vertebrate animals. Trends in Neuroscience 23, 153-159.

Lohmann, K. J., Cain, S. D., Dodge, S. A. & Lohmann, C. M. F. (2001). Regional magnetic fields as navigational markers for sea turtles. Science 294, 364-366.

Lubrano Lavadera, J. (2005). Etude qualitative des vocalises émises en phase de sommeil paradoxal chez le cheval de Przewalski (*Equus ferus przewalski*). Thesis, Ministère de l'Education Nationale, de la Recherche et la Technologie; Ecole pratique des Hautes Etudes, France.

Lyamin, O. I., Manger, P. R., Ridgway, S. H., Mukhametov, L. M. & Siegel, J. M. (2008). Cetacean sleep: an unusual form of mammalian sleep. Neuroscience and Biobehavioral Reviews 32, 1451-1484.

Madsen, C. J. & Herman, L. M. (1980). Social and ecological correlates of cetacean vision and visual appearance. In: Cetacean Behavior: mechanisms and functions, edited by Herman, L. M., pp. 101-148. Wiley Interscience, New York.

Madsen, P. T. & Surlykke, A. (2013). Functional convergence in bat and toothed whale biosonar. Physiology 28, 276-283.

Mäthger, L. M., Barbosa, A., Miner, S. & Hanlon, R. T. (2006). Color blindness and contrast perception in cuttlefish (*Sepia officinalis*) determined by a visual sensorimotor assay. Vision research 46, 1746-1753.

Mäthger, L. M., Hanlon, R. T., Håkansson, J. & Nilsson, D.-E. (2013). The W-shaped pupil in cuttlefish (*Sepia officinalis*): Functions for improving horizontal vision. Vision Research 83, 19-24.

Mann, J., Connor, R. C., Tyack, P. L. & Whitehead, H. (2000). Cetacean societies: field studies of dolphins and whales. The University of Chicago Press, Chicago.

Marhold, S., Burda, H. & Wiltschko, W. (1997). A magnetic polarity compass for direction finding in a subterranean mammal. Naturwissenschaften 84, 421-423.

Marler, P. (1965). Communication in monkeys and apes. In: Primate behavior, edited by DeVore, I., pp. 1-52. Holt, New York.

Marriott, S., Cowan, E., Cohen, J. & Hallock, R. M. (2013). Somatosensation, echolocation, and underwater sniffing: adaptions allow mammals without traditional olfactory capabilities to forage for food underwater. Zoological Science 30, 69-75.

Marshall, N. J. & Messenger, J. B. (1996). Colour-blind camouflage. Nature 382, 408-409.

Mary, E. & Balakrishnan, M. (1984). A study on olfactory communication signals in sambar deer, *Cervus unicolor*. Proceedings of the Indian Academy of Science (Animal Science) 93, 71-76.

Mass, A. M. & Supin, A. Y. (2009). Vision. In: Encyclopedia of marine mammals, 2nd edition, edited by Perrin, W. F., Würsig, B. & Thewissen, J. G. M., pp. 1200-1211. Academic Press, Burlington.

May-Collado, L. J. (2010). Changes in whistle structure of two dolphin species during interspecific associations. Ethology 116, 1065-1074.

May-Collado, L. J. & Wartzok, D. (2008). A comparison of bottlenose dolphin whistles in the Atlantic Ocean: factors promoting whistle variation. Journal of Mammalogy 89, 1229-1240.

McComb, K. (1987). Roaring by red deer stags advances oestrus in hinds. Nature 330, 684-649.

McCowan, B. & Reiss, D. (1995). Quantitative comparison of whistle repertoires from captive adult bottlenose dolphins (Delphinidae, *Tursiops truncatus*): A re-evaluation of the signature whistle hypothesis. Ethology 100, 194-209.

McCowan, B. & Reiss, D. (1997). Vocal learning in captive bottlenose dolphins: a comparison to humans and nonhuman animals. In: Social influences on vocal development, edited by Snowdon, C. T. & Hausberger, M., pp. 178-207. Cambridge University Press, Cambridge.

McIntosh, A. R. & Peckarsky, B. L. (2004). Are mayfly anti-predator responses to fish odour proportional to risk? Archiv für Hydrobiologie 160, 145-151.

Messenger, J. B. (1968). The visual attack of the cuttlefish, *Sepia officinalis*. Animal Behaviour 16, 342-357.

Meynier, L., Pusineri, C., Spitz, J., Begoña Santos, M., Pierce, G. J. & Ridoux, V. (2008). Intraspecific dietary variation in the short-beaked common dolphin Delphinus delphis in the Bay of Biscay: importance of fat fish. Marine Ecology Progress Series 354, 277-287.

Miller, K. V., Jemiolo, B., Gassett, J. W., Jelinek, I., Wiesler, D. & Novotny, M. (1998). Putative chemical signals from white-tailed deer (*Odocoileus virginianus*): social and seasonal effects on urinary volatile excretion in males. Journal of Chemical Ecology 24, 673-683.

Milton, K. (1980). The foraging strategy of howler monkeys. Columbia University Press, New York.

Mobley, J. R. & Helweg, D. A. (1990). Visual ecology and cognition in cetaceans. In: Sensory abilities of cetaceans, edited by Thomas, J. A. & Kastelein, R. A., pp. 519-536. Plenum Press, New York.

Morisaka, T. & Connor, R. C. (2007). Predation by killer whales (*Orcinus orca*) and the evolution of whistle loss and narrow-band high frequency clicks in odontocetes. Journal of Evolutionary Biology 20, 1439-58.

Morisaka, T., Shinohara, M. & Taki, M. (2005). Underwater sounds produced by neonatal bottlenose dolphins (*Tursiops truncatus*) I.: Acoustic characteristics. Aquatic Mammals 311 248-257.

Mooney, T. A., Yamato, M. & Branstetter, B. K. (2012). Hearing in cetaceans: from natural history to experimental biology. In: Advances in Marine Biology, Vol. 63, edited by Lesser, M., pp. 197-246, Academic Press, London.

Moore, S. E. & Ridgway, S. H. (1996). Patterns of dolphin sound production and ovulation. Aquatic Mammals 22, 175-184.

Mukhametov, L. M. (1995). Paradoxical sleep peculiarities in aquatic mammals. Sleep Research 24A, 202.

Munger, L. M., Wiggins, S. M., Moore, S. E. & Hildebrand, J. A. (2008). North Pacific right whale (*Eubalaena japonica*) seasonal and diel calling patterns from long-term acoustic recordings in the southeastern Bering Sea, 2000–2006. Marine Mammal Science 24, 795-814.

Murray, R. W. (1960). Electrical sensitivity of the ampullae of Lorenzini. Nature 187, 957.

Nachtigall, P. E. & Hall, R. W. (1984). Taste reception in the bottlenose dolphin. Acta Zoologica Fennica 172, 147-148.

Nevitt, G. A. (1991). Do fish sniff? A new mechanism of olfactory sampling in pleuronectid flounders. Journal of Experimental Biology 157, 1-18.

Nevitt, G. A. (2008). Sensory ecology on the high seas: investigating the odor world of the procellariiform seabirds. Journal of Experimental Biology 211, 1706-1713.

Nevitt, G. A., Veit, R. R. & Kareiva, P. (1995). Dimethyl sulphide as a foraging cue for Antarctic procellariiform seabirds. Nature 376, 680-682.

Norris, K. S. (1991). Dolphin days: the life and times of the spinner dolphin. W; W. Norton, New York.

Norris, K. S. & Dohl, T. P. (1980). Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. Fishery Bullertin 77, 821-849.

Norris, K. S., Würsig, B., Wells, R. S. & Würsig, M. (1994). The Hawaiian spinner dolphin. University of California Press, Berkeley and Los Angeles.

Notarbartolo di Sciara, G. & Gordon, J. (1997). Bioacoustics: A tool for the conservation of cetaceans in the Mediterranean Sea. Marine Freshwater Behaviour and Physiology 30, 125-146.

Nummela, S. (2009). Hearing. In: Encyclopedia of marine mammals, 2nd edition, edited by Perrin, W. F., Würsig, B. & Thewissen, J. G. M., pp. 553-562. Academic Press, Burlington.

Nummela, S., Pihlström, H., Puolamäki, K., Fortelius, M., Hemilä, S. & Reuter, T. (2013). Exploring the mammalian sensory space: co-operations and trade-offs among senses. Journal of Comparative Physiology A, published online September 2013. doi 10.1007/s00359-013-0846-2.

O'Connell, C. P., Abel, D. C., Rice, P. H., Stroud, E. M. & Simuro, N. C. (2010). Responses of the southern stingray (*Dasyatis americana*) and the nurse shark (*Ginglymostoma cirratum*) to permanent magnets. Marine and Freshwater Behaviour and Physiology 43, 63-73.

Oelschläger, H. H. A. (2008). The dolphin brain – a challenge for synthetic neurobiology. Brain Research Bulletin 75, 450-459.

Oelschläger, H. H. A. & Buhl, E. H. (1985). Development and rudimentation of the peripheral olfactory system in the harbor porpoise, *Phocoena phocoena* (Mammalia: Cetacea). Journal of Morphology 184, 351–360.

Oelschläger, H. H. A. & Oelschläger, J. S. (2009). Brain. In: Encyclopedia of marine mammals, 2nd edition, edited by Perrin, W. F., Würsig, B. & Thewissen, J. G. M., pp. 134-149. Academic Press, Burlington.

Oliveriusová, L., Němec, P., Králová, Z. & Sedlácek, F. (2012). Magnetic compass orientation in two strictly subterranean rodents: learned or species-specific innate directional preference? Journal of Experimental Biology 215, 3649-3654.

Oswald, J. N., Barlow, J. & Norris, T. F. (2003). Acoustic identification of nine delphinid species in the eastern tropical Pacific ocean. Marine Mammal Science 19, 20-37.

Ouattara, K., Lemasson, A. & Zuberbühler, K. (2009). Campbell's monkeys concatenate vocalizations into context-specific call sequences. Proceedings of the National Academy of Science 106, 22026-22031.

Panigada, S., Pesante, G., Zanardelli, M., Capoulade, F., Gannier, A. & Weinrich, M. T. (2006). Mediterranean fin whales at risk from fatal ship strikes. Marine Pollution Bulletin 52, 1287-1298.

Pant, A. (2010). Fire up the learner within: the art of self-directed learning. Timeless Lifeskills Ltd., London.

Paulos, R. D., Dudzinski, K. & Kuczaj, S. A. (2008). The role of touch in select social interactions of Atlantic spotted dolphin (*Stenella frontalis*) and Indo-Pacific bottlenose dolphin (*Tursiops aduncus*). Journal of Ethology 26, 153-164.

Pepperberg, I. M. (1997). Social influences on the acquisition of human-based codes in parrots and nonhuman primates. In: Social Influences on Vocal Development, edited by Snowdon, C. T. & Hausberger, M., pp. 157-177, Cambridge University Press, Cambridge.

Pepperberg, I. M. (2002). The Alex Studies: Cognitive and Communicative Abilities of Grey Parrots. Harvard University Press, Cambridge and London.

Perez, J. M., Dawson, W. W. & Landau, D. (1972). Retinal anatomy of the bottlenose dolphin (*Tursiops truncatus*). Cetology 11, 1-11.

Perrin, W. F. & Reilly, S. B. (1984). Reproductive parameters of dolphins and small whales of the family Delphinidae. In: Reproduction in whales, dolphins, and porpoises, edited by Perrin, W. F., Brownell, R. L. & DeMaster, D. P., pp. 97-133. Reports of the International Whaling Commission 6, Cambridge.

Pfeiffer, D. C., Wang, A., Nicolas, J. & Pfeiffer C. J. (2001). Lingual ultrastructure of the long-finned pilot whale (*Globicephala melas*). Anatomy, Histology and Embryology 30, 359-365.

Piantadosi, C. A. & Thalmann, E. D. (2004). Pathology: whales, sonar and decompression sickness. Nature 428, 716-717.

Pihlström, H. (2008). Comparative anatomy and physiology of chemical senses in aquatic mammals. In: Sensory evolution on the threshold: adaptions in secondarily aquatic vertebrates, edited by Thewissen, J. G. M. & Nummela, S., pp. 95-109. University of California Press, Berkeley.

Pihlström, H., Fortelius, M., Hemilä, S., Forsman, R. & Reuter, T. (2005). Scaling of mammalian ethmoid bones can predict olfactory organ size and performance. Proceedings of the Royal Society B 272, 957-962.

Pirotta, E., Milor, R., Quick, N., Moretti, D., Di Marzio, N., Tyack, P. L., Boyd, I. & Hastie, G. (2012). Vessel noise affects beaked whale behavior: results of a dedicated acoustic response study. PLoS ONE 7, e42535.

Pitcher, B. J., Harcourt, R. G., Schaal, B. & Charrier, I. (2011). Social olfaction in marine mammals: wild female Australian sea lions can identify their pup's scent. Biology Letters 7, 60-62.

Pivari, D. & Rosso, S. (2005). Whistles of small groups of *Sotalia fluviatilis* during foraging behavior in southeastern Brazil. Journal of the Acoustical Society of America 118, 2725-2731.

Poole, J. H., Tyack, P. L., Stoeger-Horwath, A. S. & Watwood, S. (2005). Elephants are capable of vocal learning. Nature 434, 455-456.

Powell, B. A. (1966). Periodicity of vocal activity of captive Atlantic bottlenose dolphin: *Tursiops truncatus*. Bulletin Southern California Academy of Sciences 65, 237-244.

Purves, D., Augustine, G. J., Fitzpatrick, D., Katz, L. C., LaMantia, S., McNamara, J. O. & Williams, S. M. (2001). Neuroscience, 2nd edition. Sinauer Ass., Sunderland.

Quick, N. J. & Janik, V. M. (2008). Whistle rates of wild bottlenose dolphins (*Tursiops truncatus*): influences of group size and behavior. Journal of Comparative Psychology 122, 305-311.

Bibliography

Quinn, T. P. (1980). Evidence for celestial and magnetic compass orientation in lake migrating sockeye salmon fry. Journal of Comparative Physiology 137, 243-248.

Quintana-Rizzo, E., Mann, D. A. & Wells, R. S. (2006). Estimated communication range of social sounds used by bottlenose dolphins (*Tursiops truncatus*). Journal of the Acoustic Society of America 120, 1671-1683.

Ralston, J. V. & Herman, L. M. (1995). Perception and generalization of frequency contours by a bottlenose dolphin (*Tursiops truncatus*). Journal of Comparative Psychology 109, 268-277.

Reby, D. & McComb, K. (2003). Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. Animal Behaviour 65, 519-530.

Reby, D., Charlton, B. D., Locatelli, Y. & McComb, K. (2010). Oestrous red deer hinds prefer male roars with higher fundamental frequencies. Proceedings of the Royal Society B 277, 2747-2753.

Reiss, D. & McCowan, B. (1993). Spontaneous vocal mimicry and production by bottlenose dolphins (*Tursiops truncatus*): Evidence from vocal learning. Journal of Comparative Psychology 107, 301-312.

Reithaus, M. R. & Dill, L. M. (2009). Feeding strategies and tactics. In: Encyclopedia of marine mammals, 2nd edition, edited by Perrin, W. F., Würsig, B. & Thewissen, J. G. M., pp. 414-423. Academic Press, Burlington.

Revonsuo, A. (2000). The reinterpretation of dreams: An evolutionary hypothesis of the function of dreaming. Behavioral and Brain Sciences 23, 793-1121.

Richards, D. G., Wolz, J. P. & Herman, L. M. (1984). Vocal mimicry of computer generated sounds and vocal labeling of objects by a bottlenosed dolphin, *Tursiops truncatus*. Journal of Comparative Psychology 98, 10-28.

Richardson, W. J., Würsig, B. & Greene, C. R. (1990). Reactions of bowhead whales, *Balaena mysticetus*, to drilling and dredging noise in the Canadian Beaufort Sea. Marine Environmental Research 29, 135-160.

Ridgway, S. H. (2002). Asymmetry and symmetry in brain waves from dolphin left and right hemispheres: some observations after anesthesia, during quiescent hanging behaviour, and during visual obstruction. Brain, Behavior and Evolution 60, 265-274.

Ridgway, S. H. & Carder, D. A. (1990). Tactile sensitivity, somatosensory responses, skin vibrations, and the skin surface ridges of the bottlenose dolphin, *Tursiops truncatus*. In: Sensory abilities of cetaceans, edited by Thomas, J. A. & Kastelein, R. A., pp. 163-179. Plenum Press, New York.

Risch, D., Corkerin, P. J., Ellison, W. T. & von Parijs, S. M. (2012). Changes in humpback whale song occurrence in response to an acoustic Ssource 200 km away. PLoS ONE 7, e29741.

Ritz, T., Ahmad, M., Mouritsen, H., Wiltschko, R. & Wiltschko, W. (2010). Photoreceptor-based magnetoreception: optimal design of receptor molecules, cells, and neuronal processing. Journal of the Royal Society Interface 7, S135-S146.

Roitblat, H. L., Au, W. W. L., Nachtigall, P. E., Shizumura, R. & Moons , G. (1995). Sonar recognition of targets embedded in sediment. Neural Networks 8, 1263-1273.

Romagny, S., Darmaillacq, A.-S., Guibé, M., Bellanger, C. & Dickel, L. (2012). Feel, smell and see in an egg: emergence of perception and learning in an immature invertebrate, the cuttlefish embryo. Journal of Experimental Biology 215, 4125-4130.

Rossbach, K. A. & Herzing, D. L. (1997). Underwater observations of benthic-feeding bottlenose dolphins (*Tursiops truncatus*) near Grand Bahama Island, Bahamas. Marine Mammal Science 13, 498-504.

Rossi-Santos, M. R. & Wedekin, L. L. (2006). Evidence of bottom contact behavior by estuarine dolphins (*Sotalia guianensis*) on the eastern coast of Brazil. Aquatic Mammals 32, 140-144.

Ruckebusch, Y., Barbey, P. & Guillemot, P. (1970). Les états de sommeil chez le cheval (*Equus caballus*). C.r. Seanc. Soc. Biol. 164, 658-665.

Sakai, M., Hishii, T., Takeda, S. & Kohshima, S. (2006). Flipper rubbing behaviors in wild bottlenose dolphins (*Tursiops aduncus*). Marine Mammal Science 22, 966-978.

Sankey, C., Richard-Yris M.-A., Leroy, H., Henry, S. & Hausberger, M. (2010). Training experience induces lasting memories of humans in horses, *Equus caballus*. Animal Behaviour 79, 869-875.

Saslow, C. A. (2002). Understanding the perceptual world of horses. Applied Animal Behaviour Science 78, 209-224.

Schel, A. M. & Zuberbühler, K. (2012). Dawn chorusing in guereza colobus monkeys. Behavioral Ecology and Sociobiology 66, 361-373.

Schultz, K. W. & Corkeron, P. J. (1994). Interspecific differences in whistles produced by inshore dolphins in Moreton Bay, Queensland, Australia. Canadian Journal of Zoology 72, 1061-1068.

Schultz, K. W., Cato, D. H., Corkeron, P. J. & Bryden, M. M. (1995). Low frequency narrow-band sounds produced by bottlenose dolphins. Marine Mammal Science 11, 503-509.

Sekiguchi, Y. & Kohshima, S. (2003). Resting behaviors of captive bottlenose dolphins (*Tursiops truncatus*). Physiology and Behavior 79, 643-653.

Shakila, R. J., Vijayalakshmi, K. & Jeyasekaran, G. (2003). Changes in histamine and volatile amines in six commercially important species of fish of the Thoothukkudi coast of Tamil Nadu, India stored at ambient temperature. Food Chemistry 82, 347-352.

Shashar, N., Rutledge, P. S. & Cronin, T. W. (1996). Polarization vision in cuttlefish: a concealed communication channel? Journal of Experimental Biology 199, 2077-2084.

Shashar, N., Hagan, R., Boal, J. G. & Hanlon, R. T. (2000). Cuttlefish use polarization sensitivity in predation on silvery fish. Vision Research 40, 71-75.

Shpak, O. V., Lyamin, O. I., Manger, P. R., Siegel, J. M. & Mukhametov, L. M. (2009). States of rest and activity in the Commerson's dolphin *Cephalorhynchus commersonii*. Journal of Evolutionary Biochemistry and Physiology 45, 111-119.

Sil, S., Joseph, J. & Kumar, K. A. (2008). Changes in biogenic amines during iced and ambient temperature storage of tilapia. Journal of the Science of Food and Agriculture 88, 2208-2212.

Smith, T. D. & Bhatnagar, K. P. (2004). Microsmatic primates: reconsidering how and when size matters. Anatomical Record 279B, 24-31.

Smith, T. G., Aubin, D. J. S. & Hammill M. O. (1992). Rubbing behaviour of belugas, *Delphinapterus leucas*, in a high Arctic estuary. Canadian Journal of Zoology 70, 2405-2409.

Smolker, R. A., Richards, A. F., Connor, R. C. & Pepper, J. W. (1992). Sex differences in patterns of association among Indian Ocean bottlenose dolphins. Behaviour 123, 38-69.

Souza, M. L. S., Freitas, C. F., Domingos, M.-A. O., Nunes-Tavares, N., Hasson-Voloch, A., Nasciutti, L. E. & Silva, L.-C. F. (2007). Identification and distribution of chondroitin sulfate in the three electric organs of the electric eel, *Electrophorus electricus* (L.). Comparative Biochemistry and Physiology Part B 146, 227-233.

Spitz, J., Rousseau, Y. & Ridoux, V. (2006). Diet overlap between harbour porpoise and bottlenose dolphin: An argument in favour of interference competition for food? Estuarine Coastal Shelf Science 70, 259-270.

Spitz, J., Mourocq, E., Leauté, J.-P., Quéro, J.-C. & Ridoux, V. (2010). Prey selection by the common dolphin: fulfilling high energy requirements with high quality food. Journal of Experimental Marine Biology and Ecology 390, 73-77.

Stafford, K. M., Moore, S. E., Berchok, C. L., Wiig, Ø., Lydersen, C., Hansen, E., Kalmbach, D. & Kovacs, K. M. (2012). Spitsbergen's endangered bowhead whales sing through the polar night. Endangered Species Research 18, 95-103.

Stafne, G. M. & Manger, P. R. (2004). Predominance of clockwise swimming during rest in southern hemisphere dolphins. Physiology & Behaviour 82, 919-926.

Staicer, C. A., Spector, D. A. & Horn, A. G. (1996). The dawn chorus and other diel patterns in acoustic signaling. In: Ecology and evolution of acoustic communication in birds, edited by Kroodsma, D. E. & Miller, E. H., pp. 426-453. Cornell University Press, Ithaca.

Stickgold, R., Hobson, J. R. & Fosse, M. (2001). Sleep, learning, and dreams: off-line memory reprocessing. Science 294, 1052-1057.

Stone, C. J. & Tasker, M. L. (2006). The effects of seismic airguns on cetaceans in UK waters. Journal of Cetacean Research and Management 8, 255-263.

Stoner, A. W. & Kaimmer, S. M. (2008). Reducing elasmobranch bycatch: Laboratory investigation of rare earth metal and magnetic deterrents with spiny dogfish and Pacific halibut. Fisheries Research 92, 162-168.

Sumpton, W. D., Lane, B. & Ham, T. (2010). Gear modifications and alternative baits that reduce bait scavenging and minimize by-catch on baited drum-lines used in the Queensland Shark Control Program. Proceedings of the Royal Society of Queensland 116, 23-35.

Suzuki, S. (1970). Zen min, beginner's mind. Weatherhill, London.

Tamaki, N., Morisaka, T. & Taki, M. (2006). Does body contact contribute towards repairing relationships? The association between flipper-rubbing and aggressive behavior in captive bottlenose dolphins. Behavioural Processes 73, 209-215.

Thewissen, J. G. M. (2009). Sensory biology: overview. In: Encyclopedia of marine mammals, 2nd edition, edited by Perrin, W. F., Würsig, B. & Thewissen, J. G. M., pp. 1003-1005. Academic Press, Burlington.

Thewissen, J. G. M., Cooper, L. N., George, J. C. & Bajpai, S. (2009). From land to water: the origin of whales, dolphins, and porpoises. Evolution: Education & Outreach 2, 272-288.

Thewissen, J. G. M., George, J., Rosa, C. & Kishida, T. (2011). Olfaction and brain size in the bowhead whale (*Balaena mysticetus*). Marine Mammal Science 27, 282-294.

Therrien, S. C., Thomas, J. A., Therrien, R. E. & Stacey, R. (2012). Time of day and social change affect underwater sound production by bottlenose dolphins (*Tursiops truncatus*) at the Brookfield Zoo. Aquatic Mammals 38, 65-75.$

Thomas, J. A., Kastelein, R. A. & Awbrey, F. T. (1990). Behavior and blood catecholamines of captive belugas during playbacks of noise from an oil drilling platform. Zoo Biology 9, 393-402.

Thomas, J. A., Moss, C. F. & Vater, M. (2004). Echolocation in bats and dolphins. The University of Chicago Press, Chicago and London.

Thompson, R. K. R. & Herman, L. M. (1975). Underwater frequency discrimination in the bottlenosed dolphin (1-140 khz) and the human (1-8 khz). Journal of the Acoustic Society of America 57, 943-948.

Thompson, P. M., Brookes, K. L., Graham, I. M., Barton, T. R., Needham, K., Bradbury, G. & Merchant, N. D. (2013). Short-term disturbance by a commercial two-dimensional seismic survey does not lead to long-term displacement of harbour porpoises. Proceedings of the Royal Society B, published online October 2013. doi 10.1098/rspb.2013.2001.

Thorpe, W. H. (1961). Bird-song: the biology of vocal communication and expression in birds. Oxford University Press, Oxford.

Tixier, H., Maizeret, C., Duncan, P., Bertrand, R., Poirel, C. & Roger, M. (1998). Development of feeding selectivity in roe deer. Behavioural Processes 43, 33-42.

Tyack, P. L. (2000). Functional aspects of cetacean communication. In: Cetacean societies: field studies of dolphins and whales, edited by Mann, J., Connor, R. C., Tyack, P. L. & Whitehead, H., pp. 270-307. The University of Chicago Press, Chicago.

Tyack, P. L. & Sayigh, L. S. (1997). Vocal learning in cetaceans. In Social Influences on Vocal Development, edited by Snowdon, C. T. & Hausberger, M., pp. 208-233. Cambridge University Press, Cambridge.

Tyack, P. L., Zimmer, W. M. X., Moretti, D., Southall, B. L., Claridge, D. E., Durban, J. W., Clark, C. K., D'Amico, A., DiMarzio, N., Jarvis, S., McCarthy, E., Morrissey, R., Ward, J. & Boyd, I. L. (2011). Beaked whales respond to simulated and actual Navy sonar. PLoS ONE 6, e17009.

Urian, K. W., Duffield, D. A., Read, A. J., Wells, R. S. & Shell, E. D. (1996). Seasonality of reproduction in bottlenose dolphins, *Tursiops truncatus*. Journal of Mammalogy 77, 394-403.

van der Woude, S. E. (2009). Bottlenose dolphins (*Tursiops truncatus*) moan as low in frequency as baleen whales. Journal of the Acoustical Society of America 126, 1552-1562.

Vandekerckhove, M. & Cluydts, R. (2010). The emotional brain and sleep: an intimate relationship. Sleep Medicine Reviews 14, 219-226.

Varanasi, U. & Malins, D. C. (1971). Unique lipids of the porpoise *Tursiops gilli*: Differences in triacyl glycerols and wax esters of acoustic (mandibular canal and melon) and blubber tissues. Biochemica et Biophysica Acta: Lipids and Lipid Metabolism 231, 415-418.

VerCauteren, K. C. & Pipas, M. J. (2003). A review of color vision in white-tailed deer. USDA National Wildlife Research Center - Staff Publications. Paper 284.

von Uexküll, J. (1909). Umwelt und Innenwelt der Tiere. Springer, Berlin.

von Uexküll, J. (1934). Streifzüge durch die Umwelten von Tieren und Menschen: ein Bilderbuch unsichtbarer Welten. Springer, Berlin.

Wajnberg, E., Acosta-Avalos, D., Alves, O. C., de Oliveira, J. F., Srygley, R. B. & Esquivel, D. M. S. (2010). Magnetoreception in eusocial insects: an update. Journal of the Royal Society Interface 7, S207- S225.

Walker, M. M. & Dennis, T. E. (2005). Role of the magnetic sense in the distribution and abundance of marine animals. Marine Ecology Progress Series 287, 295-307.

Walker, M. M., Kirschvink, J. L., Ahmed, G. & Diction, A. E. (1992). Evidence that fin whales respond to the geomagnetic field during migration. Journal of Experimental Biology 171, 67-78.

Warne-Reese, J. B. (1997). Ice treats take on a different mold. The Shape of Enrichment 6, 6.

Wartzok, D. & Ketten, D. R. (1999). Marine mammal sensory systems. In: Biology of marine mammals, edited by Reynolds, J. & Rommel S., pp. 117-175. Smithsonian Institution Press, Washington.

Watkins, W. A. & Wartzok, D. (1985). Sensory biophysics of marine mammals. Marine Mammal Science 1, 219-260.

Watwood, S. L., Owen, E. C. G., Tyack, P. L. & Wells, R. S. (2005). Signature whistle use by temporarily restrained and free-swimming bottlenose dolphins, *Tursiops truncatus*. Animal Behaviour 69, 1373-1386.

Weaver, J., Vaughan, T. & Astumian, R. (2000). Biological sensing of small field differences by magnetically sensitive chemical reactions. Nature 405, 707-709.

Weller, D. W. (2009) Predation on marine mammals. In: Encyclopedia of marine mammals, 2nd edition, edited by Perrin, W. F., Würsig, B. & Thewissen, J. G. M., pp. 923-932. Academic Press, Burlington.

Wells, R. S. & Scott, M. D. (2009). Common bottlenose dolphin, Tursiops truncatus. In: Encyclopedia of marine mammals, 2nd edition, edited by Perrin, W. F., Würsig, B. & Thewissen, J. G. M., pp. 249-255. Academic Press, Burlington.

Wells, R. S., Scott, M. D. & Irvine, A. B. (1987). The social structure of free-ranging bottlenose dolphins. In: Current mammalogy, Volume 1, edited by Genoways, H., pp. 247-305. Plenum Press, New York.

Werth, A. J. (2007). Adaptions of the cetacean hyolingual apparatus for aquatic feeding and thermoregulation. Anatomical Record 290, 546-568.

Whitehead, H. & Weilgart, L. (1991). Patterns of visually observable behaviour and vocalizations in groups of female sperm whales. Behaviour 118, 275-296.

Whitehead, H., Rendell, L., Osborne, R. W. & Würsig, B. (2004). Culture and conservation of non-humans with reference to whales and dolphins: review and new directions. Biological Conservation 118, 205-218.

Wich, S. A., Swartz, K. B., Hardus, M. E., Lameira, A. R., Stromberg, E. & Shumaker, R. W. (2009). A case of spontaneous acquisition of a human sound by an orangutan. Primates 50, 56-64.

Willams, R., Ashe, E. & O'Hara, P. D. (2011). Marine mammals and debris in coastal waters of British Columbia, Canada. Marine Pollution Bulletin 62, 1303-1316.

Wiltschko, R. & Wiltschko, W. (1995). Magnetic orientation in animals. Springer, Berlin.

Wiltschko, W. & Wiltschko, R. (2002). Magnetic compass orientation in birds and its physiological basis. Naturwissenschaften, 89, 445- 452.

Wiltschko, R. & Wiltschko, W. (2003). Avian navigation: from historical to modern concepts. Animal Behaviour 65, 257-272.

Winklhofer, M. (2010). Magnetoreception. Journal of the Royal Society Interface 7, S131-S134.

Wright, K. L. B., Pichegru, L. & Ryan, P. G. (2011). Penguins are attracted to dimethyl sulphide at sea. Journal of Experimental Biology 214, 2509-2511.

Würsig, B. (1986). Delphinid foraging strategies. In: Dolphin cognition and behaviour: a comparative approach, edited by Schusterman, R. J., Thomas, J. A. & Wood, F. G., pp. 347-360. Lawrence Earlbaum Associates, London.

Würsig, B., Wells, R. S., Norris, K. S. & Würsig, M. (1994). A spinner dolphin's day. In: The Hawaiian spinner dolphin, edited by Norris, K. S., Würsig, B., Wells, R. S. & Würsig, M., pp. 65-102. University of California Press, Berkeley and Los Angeles.

Xitco, M. J., Groy, J. D. & Kuczaj, S. A. (2001). Spontaneous pointing by bottlenose dolphins (*Tursiops truncatus*). Animal Cognition 4, 115-123.

Yamasaki, F, Komatsu, S. & Kamiya, T. (1978). Taste buds in the pits at the posterior dorsum of the tongue of *Stenella coeruleoalba*. The Scientific Reports of the Whales Research Institute 30, 285-290.

Yoshida, Y., Morisaka, T., Sakai, M., Iwasaki, M., Wakabayashi, I., Seko, A., Kasamatu, M., Fukuzawa, H., Akamatu, T. & Kohshima, S. (2010). Acoustic behavior of captive Commerso's dolphins. Do they use the pulse sounds for communication? Presentation at the 15th Kyoto University International Symposium, Nagoya.

Yuen, M. M. L., Nachtigall, P. E., Breese, M. & Vlachos, S. A. (2007). The perception of complex tones by a false killer whale (*Pseudorca crassidens*). Journal of the Acoustic Society of America 121, 1768-1774.

Yurk, H., Barrett-Lennard, L. G., Ford, J. K. B. & Matkin, C. O. (2002). Cultural transmission within maternal lineages: vocal clans in resident killer whales in southern Alaska. Animal Behaviour 63, 1103-1119.

Zoeger, J., Dunn, J. R. & Fuller, M. (1981). Magnetic material in the head of the common Pacific dolphin. Science 213, 892-894.

ABSTRACT

The *Umwelt* concept of Jakob von Uexküll considers animals as subjects that inhabit their own subjective universe which is determined by the animal's sensory perception and cognitive abilities. Dolphins present an interesting species to investigate its *Umwelt* because cetaceans underwent a drastic change in lifestyle in the course of evolution because these mammals returned from a terrestrial life back into the water. Although bottlenose dolphins are intensively studied there are still many knowledge gaps. Here we studied some aspects of the dolphins' *Umwelt* by asking: (1) how their nocturnal acoustic *Umwelt* is arranged; (2) what the production of vocal copies can tell us about the dolphins' perception of their environment; (3) whether they are able to perceive tastes (4) or odours; (5) whether they are sensitive to magnetic stimuli. We found that the dolphins' nocturnal *Umwelt* was characterized by a temporally patterned vocal activity that also included vocal copies of sounds that the dolphins had heard during the day. This is a striking separation between auditory memory formation and vocal copy production and the copies might be a vocally expressed nocturnal rehearsal of day events. Thus, vocalizations can serve as possible indicators of events or objects that are meaningful to the dolphins. Regarding dolphins' perceptive abilities, we found that they were sensitive to both gustatory and olfactory food-related stimuli. They might use this ability to locate and/or evaluate prey. Further, dolphins responded to a magnetic stimulus, suggesting that they are magnetosensitive, what could be useful for navigation. So far, chemo- and magnetoreception have not been considered seriously as potentially functional in dolphins. The results obtained during this thesis fill some of the gaps that still exist in the knowledge of the dolphin's *Umwelt* and therefore contribute to a better understanding of this species. Moreover, they illustrate that even already intensively studied species may still hold important facets of their biology to reveal and that research should broaden the view and remain unbiased when studying a topic.

RÉSUMÉ

Le concept d'*Umwelt* de Jakob von Uexküll considère les animaux comme des sujets qui habitent leur propre univers subjectif qui est déterminé par la perception sensorielle de l'animal et ses capacités cognitives. Le dauphin apparait être une espèce intéressante pour étudier l'*Umwelt*, car les cétacés ont subi un changement radical de mode de vie au cours de l'évolution. Ces mammifères sont passés d'une vie terrestre à une vie aquatique. Bien que les grands dauphins soient intensivement étudiés, des recherches sur leur perception sensorielle sont encore nécessaires. Ici, nous avons étudié certains aspects de l'*Umwelt* des dauphins en nous interrogeant sur: (1) l'organisation de leur *Umwelt* acoustique nocturne ; (2) ce que la production de copies vocales par les dauphins peut nous dire sur leur perception de leur environnement ; (3) s'ils sont capables de percevoir des goûts (4) ou des odeurs ; (5) s'ils sont sensibles aux stimuli magnétiques. Nous avons constaté que l'*Umwelt* nocturne des dauphins a été caractérisé par une activité vocale avec des patterns temporels qui comprenaient également des copies vocales des sons que les dauphins avaient entendus au cours de la journée. Il s'agit d'une nette séparation entre la formation de la mémoire auditive et la production de copies vocales. Les copies pourraient être des répétitions nocturnes vocalement exprimées des événements de la journée. Ainsi, les vocalisations peuvent servir d'indicateurs d'événements ou d'objets qui ont un sens pour les dauphins. En ce qui concerne les capacités perceptives des dauphins, nous avons constaté qu'ils étaient sensibles aux stimuli liés à l'alimentation à la fois sur les plans gustatif et olfactif. Ils peuvent utiliser cette capacité pour localiser et / ou évaluer la nature de leur proie. En outre, les dauphins ont répondu à un stimulus magnétique, ce qui suggère qu'ils sont magnétosensibles, cela pourrait être utile pour la navigation. Jusqu'à présent, la chimio- et la magnétoréception n'ont pas été considérées sérieusement comme potentiellement fonctionnelles chez les dauphins. Les résultats obtenus au cours de cette thèse ont permis de combler certaines des lacunes qui subsistaient dans la connaissance de l'*Umwelt* du dauphin et contribuent ainsi à une meilleure compréhension de cette espèce. En outre, ils montrent que des aspects importants de la biologie d'espèces pourtant intensivement étudiées peuvent être encore méconnus. Cela nous rappelle l'importance de garder une grande ouverture d'esprit lorsque l'on étudie un sujet.