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Léo Papet

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Localisation des sons chez les crocodiliens
(Sound localisation in crocodilians)

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List of abbreviations

ABR	Auditory Brainstem Response
dB	Decibel
DPR	Dome Pressure Receptors
GLMM	Generalised Linear Mixed Models
HRTF	Head-Related Transfer Function
ICE	Internally Coupled Ears
ILD	Interaural Level Differences
ISO	Integumentary Sensory Organ
ITD	Interaural Time Differences
LMM	Linear Mixed Models
MAA	Minimum Audible Angle
SRM	Spatial Release from Masking
SNR	Signal-to-Noise Ratio

PART I

General introduction



Crocodylians

Terminology

This project is entitled "Sound localisation in crocodylians", and first, we need to explicit what does the term "crocodylians" refer to. In their book about the "Biology and evolution of crocodylians" (Grigg et al., 2015), Grigg and Kirshner defined the term "crocodylians" as referring to all species of the clade Crocodylia, including all the surviving species and all the extinct species of this clade. They justified their use of "crocodylians" rather than "crocodylians" by the fact that this term is unambiguous in the evolution context. They also make the hypothesis that the physiology, ecology and behaviour described in the still living crocodylians may be generalised to the extinct species of Crocodylia. Stevenson did agree with the definition proposed by Grigg and Kirschner (Stevenson, 2019). He insists in the relevance of the term "crocodylians" when studying the evolution of the order Crocodylia and in particular in phylogenetics. In this project, we focused on the physiological and behavioural aspects of several, still living, species of crocodylians. Thus, and based on the usual denomination encountered in the literature entering in the scope of this project, we made the choice to generalise our results, when it seemed relevant, to all "**crocodylians**".

Archosaurs

With dinosaurs (including birds) and pterosaurs, crocodylians form the the order of Archosaurs (figure 1). In the early Triassic (252 Millions of years ago), a wide variety of reptiles occupied both land and water and Archosaurs were the most abundant (Grigg et al., 2015; Stevenson, 2019). A wide variety of groups of Crurotarsi was present in the late Triassic, including the Crocodylomorpha from which the Crocodyliformes derived. In the Jurassic, Mesoeucrocodylia gathered a wide diversity of Crocodyliformes evolving in the oceans, on land or in a semi-aquatic environment. Eusachians are the only Mesoeucrocodylians surviving the Cretaceous-Paleogene extinction (with Sebecida). Eusuchia were all supposed to be adapted to an aquatic or semi-aquatic environment in the early Cretaceous (145 Millions years ago). Eusuchia are included in Crocodylia as, consequently, the three families of crocodylians still living: Crocodylidae, Alligatoridae and Gavialidae.

One major point when studying crocodylians is that they remain the most closely-related (still living) species to birds (Grigg et al., 2015; Stevenson, 2019). Comparatively to the acoustic behaviours of birds (particularly vocal birds) which are subject of interest since decades, only a few studies were conducted about the acoustic world of crocodylians. Compiling information from studying birds and crocodylians is primordial to increase our knowledge extinct close-related species, like dinosaurs for example

(Vergne et al., 2009). Describing the acoustic communication in crocodilians and birds produces essential inputs to the hypotheses about the use of acoustic features in extinct species (Vergne et al., 2009).

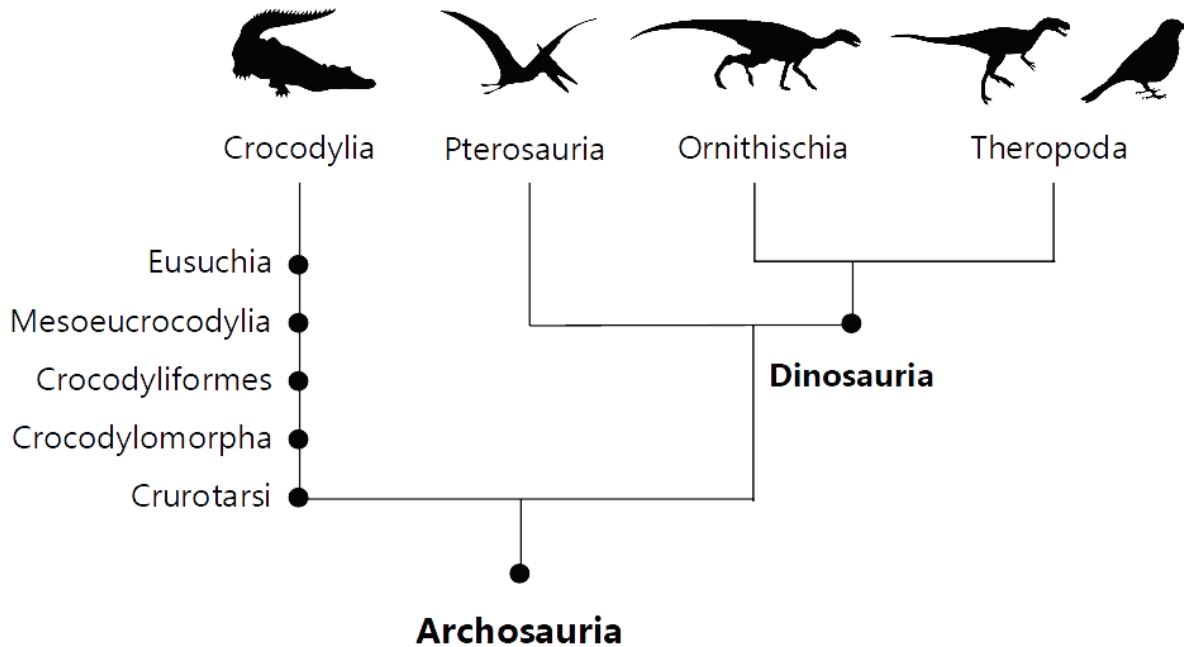


Figure 1 – Simplified cladogram of Archosauria order (based on: Vergne et al., 2009; Grigg et al., 2015; Stevenson, 2019).

Actual crocodilians

The Crocodile Specialist Group (CSG) of the International Union for Conservation of Nature (IUCN) identifies 24 different species of Crocodilians (iucnscg.org - *Crocodilian Species* 2019) highlighting the recent recognition of the West African Crocodile *Crocodylus suchus* (Hekkala et al., 2011; Shirley et al., 2014). Furthermore, the CSG emphasises that the *Osteolaemus tetraspis* will be split into three different new species: *Osteolaemus tetraspis*, *Osteolaemus osborni* and *Osteolaemus sp. nov.* (Eaton, 2010). Furthermore, recent works suggest that *Mecistops cataphractus* population will be divided into *Mecistops leptorhynchus* (Central Africa) and *Mecistops cataphractus* (West Africa, Shirley et al., 2014; Shirley et al., 2018). More recently, Colin Stevenson recognised 27 species of Crocodilians and expected from the works in progress about South American caimans an increase of species in the next years (Stevenson, 2019).

Modern Crocodilians are divided in three distinct families: the *Crocodylidae*, the *Alligatoridae* and the *Gavialidae* represented by only one species: the Gharial (*Gavialis gangeticus*). The classification of Tomistoma (*Tomistoma schlegelii*) is open for debate. Based on its morphology, it is often placed within *Crocodylidae* but genetic studies suggest that it may be placed within *Gavialidae*. If not including Tomistoma, 14 different

species form the *Crocodylidae*. They may be encountered in Central America, Africa, Australia and in South-East Asia From India to New Guinea. The *Alligatoridae* include 8 species of alligators (*Alligatorinae*) and caimans (*Caimaninae*). They mainly occupy in America except for the Chinese alligators (*Alligator sinensis*) which are centred in East-China.

Crocodylians show common features but also several differences between species. They are all able to evolve in both terrestrial and aquatic environments and their opportunistic behaviour often offers them a position the apex predators in their habitat. However, they may vary greatly in size going from only 1.2 meters in Dwarf caimans (*Paleosuchus palpebrosus*) to an impressive 5 meters in Saltwater crocodiles (*Crocodylus porosus*). Maybe the most noticeable difference remains the size of the snout going from very short (Broad-snouted caiman *Caiman latirostris*) to very long and narrow (Gharial *Gavialis gangeticus*, Erickson et al., 2012). If Crocodylians' diet remains opportunistic, the narrow-snouted species consume more fish and amphibians and small birds or mammals (Erickson et al., 2012). All crocodylians lay their eggs in nests but, where some species use to build a nest with surrounding vegetation, others dig a hole directly in the ground. Furthermore, some species prefer to remain near a freshwater place such as a river or a pond whereas Saltwater crocodiles rather occupy the deltas of the rivers, evolving in brackish water and they are able to hunt in salt waters.

Sensory skills

The accuracy of crocodylians' sensory skill did allow them to access their apex predator position. They show an excellent vision in air, a very good sense of smell, a high developed audition and an extraordinary use of mechanoreceptors. These senses give crocodiles a wide range of sensory inputs ensuring them to continuously probe their environment.

Vision

The eyes of the Crocodylians are situated on top of the head in order to give them visual information when they hunt even when the main part of their body is immersed (Picture 2). A double eyelids ensure the protection of the eyes being closed when resting or just before starting an attack. When diving, an extra horizontal eyelid called nictitating membrane slides in front of the eye to protect it. This membrane is semi transparent and degrades the visual acuity by making impossible the eye to focus underwater (Fleishman et al., 1988). Each eye covers a field of vision of 130 °and Crocodylians experience a binocular vision in the axis of the snout of about 25 °allowing a three dimensional estimation of space. The retina reveals a high concentration of photoreceptors organised in streaks (Nagloo et al., 2016, whereas in humans, for example, it is punctual). This particular organisation ensures a two dimensional clear field of vision in the azimuthal

plane without the need to focus (Nagloo et al., 2016). The regulation of the amount of light entering in the eye is ensured by a vertical slit pupil (Walls, 1942). Crocodilians experience a good perception of colours thanks to four types of cones (Sillman et al., 1991). To improve night vision, the crocodilians' eye is equipped with a tapetum lucidum (like in nocturnal birds or even in some mammals and fishes; Grigg et al., 2015; Dieterich, 1978). This feature makes the eyes of the Crocodilians shining when flashing it in dark environment. This is commonly used to count them and even for tracking their movements -the experiments conducted in open-air captivity presented in the following are based on the tracking of the eyes. To the best of our knowledge, no behavioural studies were conducted on the visual abilities in Crocodilians.

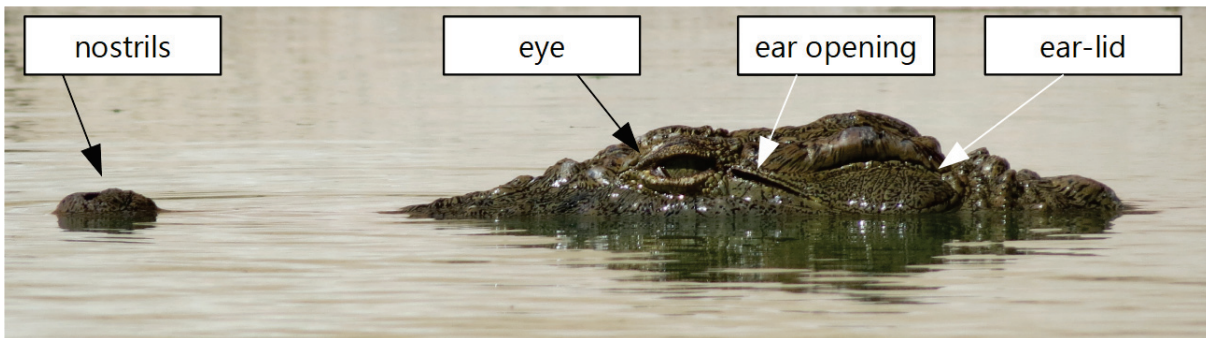


Figure 2 – Illustration of the natural position at the air-water interface in which only eyes, ear-openings and nostrils are emerged. The animal on the picture is an adult Nile crocodile (*Crocodylus niloticus*) from Crocoparc Agadir, Morocco.

Smell

At the end of the snout, Crocodilians have nostrils on the nasal "button" (Picture 2). These nostrils may be opened or fully closed when going underwater, to avoid the water goes in. One external signal to detect when Crocodilians are looking for olfactory cues is the increase of the gular pumping rhythm. The sense of smell was identified to be relevant when looking for food (Scott et al., 1990; Chabrolles et al., 2017) and they are able to learn olfactory signals even before hatching (Sneddon et al., 2001). Two different glands (mandibular and paracloacal) may play a role in social interactions (Johnsen et al., 1982) during mating or before nesting but the actual role of these glands is not yet strongly identified.

Mechanoreception

Besides vision, audition and sense of smell previously detailed, Crocodilians experience the use of other sensory channels. One of the most impressive one is the use of mechanical inputs giving information about water movements when being in water. On their

body, crocodylians reveal the presence of mechanoreceptors called Integumentary Sensory Organs (ISOs; Soares, 2002). These sensors, also called Dome Pressure Receptors (DPR) are present mainly on the jaws of the Alligatoridae whereas there are spread on the whole body of Crocodylidae. Thanks to DPR, crocodylians are sensitive to water movements and are able to detect the origin of water droplet or an air stream on the water surface (Soares, 2002; Soares, 2007; Grap et al., 2015). One observation made on a spectacled caiman fishing with success in total darkness illustrates how efficient may be those mechanoreceptors.

Audition

The ears are situated just behind the eyes on top of the head. letting only their openings above the water surface when the animal is in water (Figure 2). They are protected by a the squamosal bone from the cranial platform which can be very prominent in certain species (such as *Paleosuchus palpebrosus* and *Paleosuchus trigonatus*). The eardrum is situated in a small cavity under the ear-lid which is articulated by two muscles (Saunders et al., 2000). Just before diving, the ear-lid is closed to avoid the water comes in direct contact of the eardrum, capturing a bubble of air. The effect of this bubble was examined but seems to not impact the underwater audition of the animal (Wever et al., 1957; Higgs et al., 2002). When surfacing, it is common to see the ear-lids flapping in order to remove the water from the opening of the ear. The tympanic membrane is linked to an only ossicle, the columella, ensuring the transmission from the external ear to the inner ear. The structure of the inner ear is similar to the one known in tetrapods and very close to the one observed in birds (Grigg et al., 2015; Vergne et al., 2009). The cochlear apparatus of crocodylians contains the basilar papilla, which is composed of two types of hair cells, a feature encountered in mammals and in archosaurs (Gleich et al., 2000).

One feature encountered in Crocodylians is that both ears are internally connected by an air pathway through the skull called interaural canal. The presence of Internally Coupled Ears (ICE) is encountered in birds, and in several amphibians and lizards (Carr et al., 2016; Christensen-Dalsgaard et al., 2011; Kettler et al., 2016; Moiseff et al., 1981; Larsen et al., 2016; Hemmen et al., 2016). In small animals with small heads, this interaural canal is known to improve sound localisation abilities by increasing the acoustic cues based on time delays (ITD; Christensen-Dalsgaard et al., 2011; Vedurmudi et al., 2016) even if it remains only a vestige in some birds (Moiseff et al., 1981). In crocodylians, the interaural canal has for an effect to slightly increase the delay between the contra- and ipsilateral ears (Bierman et al., 2014; Carr et al., 2016). The audition abilities of crocodylians are detailed below.

Acoustic communication

Vocal repertoire

Crocodylians show a common vocal repertoire between all the species (Britton, 2001). From inside the eggs, crocodylians emit hatching calls. These calls are used to synchronise the hatch between the siblings (D. S. Lee, 1968) and stimulate the female which will help the hatchlings to leave their eggs. (Vergne et al., 2012; Vergne et al., 2009; Deraniyagala, 1939). Once hatched, the juvenile crocodylians form a group and its cohesion is ensured by contact calls. These calls are emitted when the group is moving (Vergne et al., 2009) and when they are feeding (Campbell, 1973). If a juvenile detects a danger, it will use distress calls causing a protection behaviour from the mother (Vergne et al., 2009; Britton, 2001; Romero, 1983; Gorzula, 1978). Finally, juvenile individuals may use hisses (broadband and vocalisations) as a threatening signal. This vocalisation is often coupled with an inflation of the body by blowing up their lungs. Vergne et al. demonstrated that hatchlings calls weakly carry the information of identity in Nile crocodiles (Vergne et al., 2006a).

The adults vocalise less frequently than juveniles but they keep the use of acoustic vocalisations in several contexts. During courtships or when they need to defend their territory, adult crocodylians may use bellows. This call is very low frequency and induce sometimes waves at the water surface. During the incubation of the eggs, the females stay around their nest. If their nest is in danger, they emit hisses to reject the potential predator. When the hatch occurred, females use "growls" to reinforce the cohesion of its youngs to induce a common movement for example (Vergne et al., 2009). Finally, other types of calls were observed but neither their acoustic structure nor their effects were well described. Garrick and Lang (Garrick et al., 1977) reported "coughlike" calls and infrasonic vibrations during courtship, Wang et al. identified "moos" inducing an escape behaviour of the surrounding congeners (Wang et al., 2007). More recently, Jailabdeen et al. reported the production of underwater "pops" in gharials. These short bursts seem to be used during breeding and hatching (Jailabdeen et al., 2019). Besides these vocal signalling, Crocodylians also slap their head and jaw on the water surface in social interactions (Dinets, 2011).

Sound perception

The sound perception of crocodylians was measured on different species using several techniques (review by Vergne et al.; Vergne et al., 2009). The first studies conducted in spectacled caiman (*Caiman crocodilus*), American alligator (*Alligator mississippiensis*) and American crocodile (*Crocodylus acutus*) evidenced a U-shaped audiogram between 100 and 3000 Hz with a maximum of sensitivity centred around 1000 Hz (figure 3; Wever, 1971; Wever et al., 1957). This U-shaped audiogram, which is really close to the ones

observed in birds (figure 3; Vergne et al., 2009; Higgs et al., 2002; Brittan-Powell et al., 2002), was confirmed by measuring the Auditory Brainstem Response (ABR) in spectacled caiman and in American alligator (Klinke et al., 1980; Manley, 1970; Bierman et al., 2015) and by characterising the transfer function of the middle ear in spectacled caiman (Saunders et al., 2000). Because of the amphibious life of crocodylians, the question of their audition underwater was treated by Higgs et al. studying American alligators (figure 3; Higgs et al., 2002). The underwater audiogram was narrower than in air ([100, 2000] Hz). In their study, Higgs et al. did focus on the effect of the closed ear-lid and of the air bubble trapped between the ear-lid and the eardrum (Higgs et al., 2002). They highlighted that no effect of these features was impacting the underwater audiogram even if Wever et al. showed that, in air, closing the ear-lid reduced the audition thresholds of 10 to 12 dB (Wever, 1971). Based on these results, Higgs et al. emitted the hypothesis that bone conduction may compensate the attenuation effect of the ear-lid to ensure a relevant good hearing performances (Higgs et al., 2002). Bone conduction may also occur in air and increase audition performances (to a lesser extent than in water because air is much less dense than water).

All the audiograms measured in crocodylians showed a maximum of sensitivity around 1000 Hz. Higgs et al. evidenced that the maximum of sensitivity of the audiograms measured on American alligator and matched with the maximum of energy contained in a hatchling call (Higgs et al., 2002). This was explained by vibrometry laser measurements conducted on the eardrum of young American alligators (Bierman et al., 2014). The tympanic membrane's maximal movements were measured around 1000 Hz, due to the stiffness of the eardrum itself, tuned to the hatchling calls.

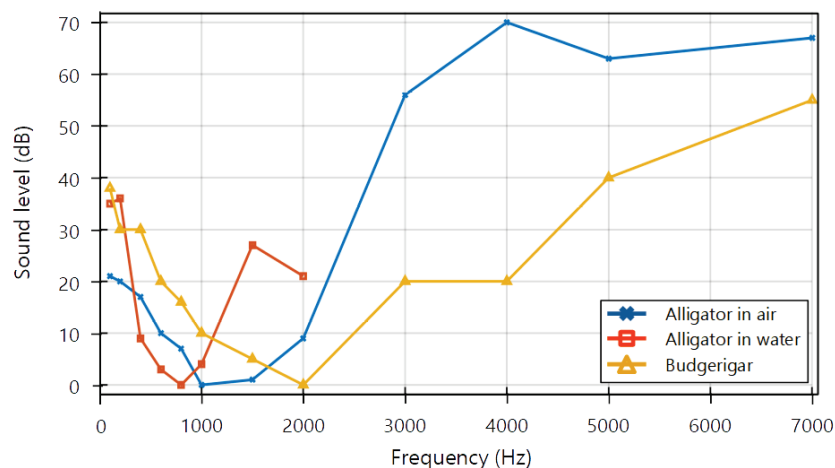


Figure 3 – Audiograms redrawn from Higgs et al., 2002 and Brittan-Powell et al., 2002. The blue and orange lines represent the audiograms measured on an American Alligator in water (blue) and in the air (orange). The yellow line represents the audiogram measured on a budgerigar. All the data were normalised by their minimum value to help the comparison.

Sound localisation

Sound perception gives a wide variety of information to probe the environment, find food (hunting) and to social interact with congeners. Acoustic environment may be very complex due to a wide variety of sound sources and sound localisation appears as a very efficient strategy to analyse the surrounding, continuous soundscapes.

Sound localisation cues

Sound localisation is based on the use of different external acoustic cues. The ability to localise a sound source depends on its temporal and frequential features on the one hand and on its position in the acoustic environment surrounding the subject on the other hand. Classically, these cues are divided in two categories based on the use of one or two ears: respectively the monaural and binaural cues.

Monaural cues

When an acoustic source emits a sound around a subject, the acoustic wave experienced some modifications due to the propagation medium itself before arriving to the eardrums of the subject. Considering a simple environment (no reflection on the walls nor non-linear effect), those modifications are due to the external morphology of the subject and mainly to the external ear when existing (figure 4). Therefore, the spectral components of the acoustic wave measured at the eardrum will differ from those measured at the sound source. Then, the head of the subject can be considered as a filter and the characterisation of this filter is called the Head-Related Transfer Functions (HRTF). Considering a sound source at the position \vec{r} and tuned at the frequency f , the HRTF may be computed as:

$$H_e(f, \vec{r}) = \frac{S_e(f, \vec{r})}{S(f)} \quad (1)$$

with $H_e(f, \vec{r})$ the Head-Related Transfer Function at the ear e (left or right). $S_e(f, \vec{r})$ represents the spectrum of the signal measured at the ear e and $S(f)$ is the emitted signal (at the sound source position).

Even if these cues are monaural because they are available at one ear independently from the other one, they may differ between the left and right ears of the subject for different sound source positions ($s_L(t)$ and $s_R(t)$ on the figure 4). HRTF can be estimated by playing a broadband signal (white noise, sine sweep or Maximum Length Signal) at different positions around the considered subject and recording the acoustic signals inside the ears of the subject. HRTF are useful to localise the origin of a sound when the power spectrums measured near the eardrum evidence notches depending on the position of the sound source. Using this approach Keller et al. measured the HRTF of 12 barn owls (*Tyto*

alba Keller et al., 1998). Derived from the HRTF, the Directional Transfer Functions (DTFs) correspond to the directional component of the HRTF. Koka et al. measured this cues in 9 chinchillas (*Chinchilla lanigera*) and evidenced potentially relevant notches between 6 and 18 kHz (Koka et al., 2011). Instead of placing a microphone near the eardrum, the HRTF may be estimated using simulations based on three-dimensional modelling as in dolphins *Delphinus delphinus* in phyllostomid bat *Phyllostomus discolor* or humans (Aroyan, 2001; De Mey et al., 2008; Otani et al., 2006). More recently, Rébillat et al. measured the HRTF on a stuffed cat and obtained very similar results using a model of the cat’s body, based on simple photographs of the animals (Rebillat et al., 2014). In crocodylians, Bierman et al. did measure the DTF of American alligators (*Alligator mississippiensis*) suggesting monaural cues for frequencies higher than 2000 Hz (Bierman et al., 2014).

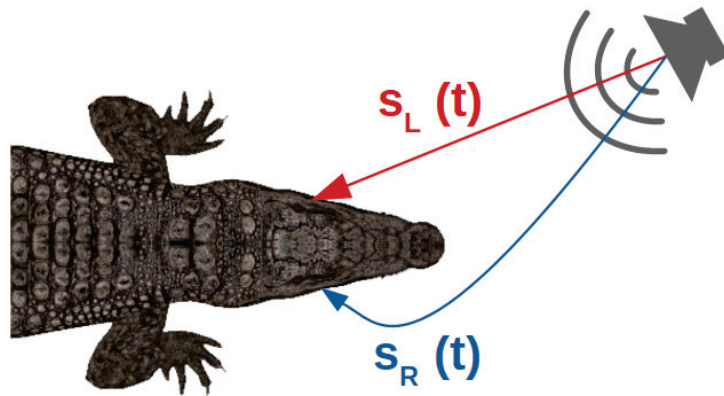


Figure 4 – Illustration of the Head-Related Transfer Function (HRTF); $s_L(t)$ represents the acoustic wave arriving at the left ear and $s_R(t)$ represents the acoustic wave arriving at the right ear.

Binaural cues

Binaural cues are based on the confrontation of the acoustic signals arriving at both the right and left ears. When considering the external morphology of a subject as a filter, they can be computed from the left and right Head-Related Impulse Response (HRIR) in the temporal domain.

Interaural Level Differences

Considering a sound coming from the right side of the head, the sound intensity measured next to the right ear will be higher than the sound intensity measured close to the left ear. This phenomenon induces binaural cues called Interaural Level Differences (ILD, figure 5). This is due to the acoustic shadow effect of the head, in which the head may attenuate the sound intensity differently for right and left ears depending on the position of the sound source in space. ILD are frequency dependent and appear efficient when the wavelength of the acoustic wave is lower than the dimensions of the head, i.e. in

high frequencies, relatively to the head of the animal (Rayleigh, 1909). ILD are relevant when estimating the azimuth of the sound source and, in animals showing asymmetrical ears, as the barn owl, ILD are used to code the elevation of a sound source (Carr et al., 2015; Knudsen et al., 1979). The maximum ILD measured using both vibrometry and ABR revealed a maximum ILD of 4 dB in the American alligator for frequencies higher than 2 kHz (Bierman et al., 2014).

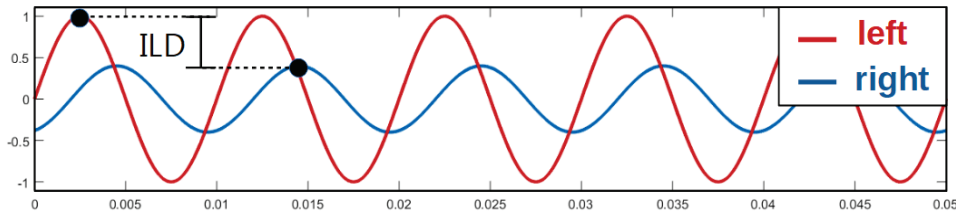


Figure 5 – Illustration of the Interaural Level Differences (ILD).

Interaural Time Differences

If we consider again a source coming from the right of the head, the acoustic wave will arrive first to the right ear and, in second time, to the left ear. The time delay between the right and left ears constitutes a cue on the sound source position called Interaural Time Differences (ITD, figure 6). The delay coded through ITD is not only the onset delay but also the phase difference between both left and right sounds. The coding of the phase difference between two different acoustic signals coming to the ears is ensured by neurons specialised in detecting coincidence (Jeffress model; Jeffress, 1948). The timing between left and right ears acoustic signals are coded through phase-locked spikes. The interaural phase difference is coded by neurons acting as coincidence detectors in the nucleus laminaris (Carr, 2010; Carr et al., 2009). These neurons show their maximal activity when both left and right signals arrive simultaneously. In other words, each laminaris neuron is tuned for a specific ITD value cancelling the delays between both input signals (Carr, 2010). In barn owls for example, these neurons are then spatially organised in topographic maps in which the location of maximal neuronal activity is linked to the azimuthal position of the sound stimulus (Carr, 2010; Carr et al., 2015). This system shows its limits when the delay between both signals is decreasing i.e. when the frequency increases. When frequency is too high for the model, a lack a phase locking happens and the relevance of ITD dramatically decreases. In American alligator, Carr et al. demonstrated that ITD is well coded until 1000 Hz (Carr et al., 2009). Thus, strong evidence of a ITD maps were shown in American alligator (Kettler et al., 2016).

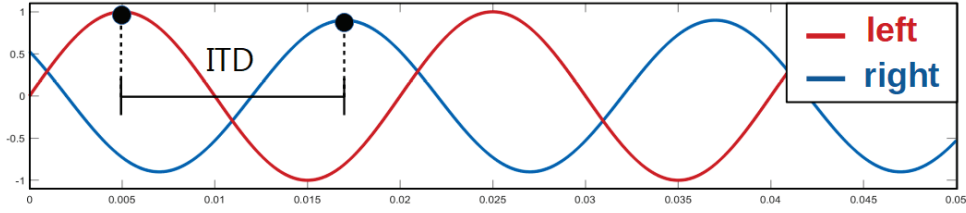


Figure 6 – Illustration of the Interaural Time Differences (ITD).

Duplex theory

Even if it is not the case in all animals, the use of both ITD and ILD is a efficient strategy to estimate the location of a sound source in space. However, Rayleigh highlighted in his duplex theory the fact that ILD are more adapted in high frequencies whereas ITD are more relevant in low frequency range (Rayleigh, 1909). Indeed, in the low frequency range (especially when the wavelength is larger than the head dimensions) the head of the animal may not impact the acoustic propagation and the resulting shadow effect tend to be negligible. In this situation, ILD are not relevant to localise a sound source in space. ITD is then more adapted to code the position of a low frequency sound source.

In the duplex theory, ILD and ITD cues are overlapping to ensure good sound localisation in a wide frequency range. In humans for example, sound localisation is ensured by ITD for frequencies up to 1000 Hz and ILD are predominant for frequencies higher than 2000 Hz, ensuring an overlapping area between 1000 and 2000 Hz in which sound localisation is founded on both cues (Middlebrooks et al., 1991). The central frequency of this overlap is called "frequency of ambiguity" (Rayleigh, 1909). Below the frequency of ambiguity, ITD are predominant whereas for frequencies higher than the frequency of ambiguity, mainly ILD are available.

In order to test the use of ILD and/or ITD, sound stimulations are broadcast above and below the frequency of ambiguity. The method is commonly used to demonstrate the use of both ILD and ITD in sound localisation tasks (R. Heffner et al., 2015; Wesolek et al., 2010; Koay et al., 1998). Interestingly, some species use only one of the classical binaural cues. Indeed, cattle, horse and pig estimate the location of a sound source only based on ITD cues (R. Heffner et al., 1992b; H. Heffner et al., 1984; R. Heffner et al., 1989) whereas the Norway rat *Rattus norvegicus*, big brown bats *Eptesicus fuscus* or new-world frugivorous bats *Artibeus jamaicensis* are using only ILD (Wesolek et al., 2010; Koay et al., 1998; R. Heffner et al., 2001). Besides, in some species such as the common vampire bats *Desmodus rotundus*, both ITD and ILD are used respectively in the low frequency and high frequency regions but no overlapping of these cues were evidenced (R. Heffner et al., 2015).

Spatial Release from Masking

Animals are constantly experiencing complex sound scenes composed by a wide variety of sound sources in their environment. Some sound sources are relevant when ensuring an acoustic communication between individuals, foraging or mating. On the contrary, some sound sources are not relevant and may be considered as noise sources. In particularly noisy environments, the sound localisation performances may be dramatically damaged. One strategy used by a wide range of animals to impair this problem is the Spatial Release from Masking (SRM; Saberi et al., 1991; Litovsky, 2012). The concept of SRM may be explained by simplifying the problem to only one source of interest (target) and one noise source (mask) as illustrated on the figure 7). When both the mask and the target sources are situated at the same position (co-localised condition, figure 7), the acoustic detection of the target may appear difficult because the noise will mask the target signal. When both sound sources are spatially separated one from each other (separated condition of figure 7), the detection performances will be improved. The improve of detection abilities by spatially separating the target source from the mask (compared to the situation where both sources are co-localised) is the effect of the SRM.

Even if SRM has been investigated for thirty years, it was studied in different species. In humans, a sound source spatially separated from a mask source (in azimuth and elevation) was significantly easier to detect compared to the situation where both sources are co-located (Saberi et al., 1991). In mammals, the use of SRM was demonstrated in ferrets *Mustela putorius* (Hine et al., 1994), cats (Wakeford et al., 1974), big brown bats *Eptesicus fuscus* (Sümer et al., 2009) and in pinnipeds, in air, such as in harbour seal *Phoca vitulina*, and sea lion *Zalophus californianus* (Holt et al., 2007). SRM remains a very needed strategy in birds and more specifically in songbirds. It was evidenced in budgerigars (*Melopsittacus undulatus*) when detecting pure tones in a broadband noise (Dent, 1997) and in zebra finches *Taeniopygia guttata* and budgerigars when detecting bird songs in a masking chorus (Dent et al., 2009). In amphibians, the Cope's gray treefrog (*Hyla chrysoscelis*) use SRM and in particular when they need to localise a conspecific call in a chorus-shaped noise (Caldwell et al., 2016; Bee et al., 2008; Nityananda et al., 2012).

SRM was demonstrated in two cricket species (*Paroecanthus podagrosus* and *Diatrypa sp.*) while testing them with conspecific calls masked by a natural rainforest ambient noise (Schmidt et al., 2011). However, if the use of SRM may appear universal, it was recently demonstrated that in *Ormia ochracea*, an insect known for its strong accuracy in localisation tasks (Mason et al., 2001), increasing the spatial separation between the target source from the mask did not affect the detection scores (N. Lee et al., 2017).

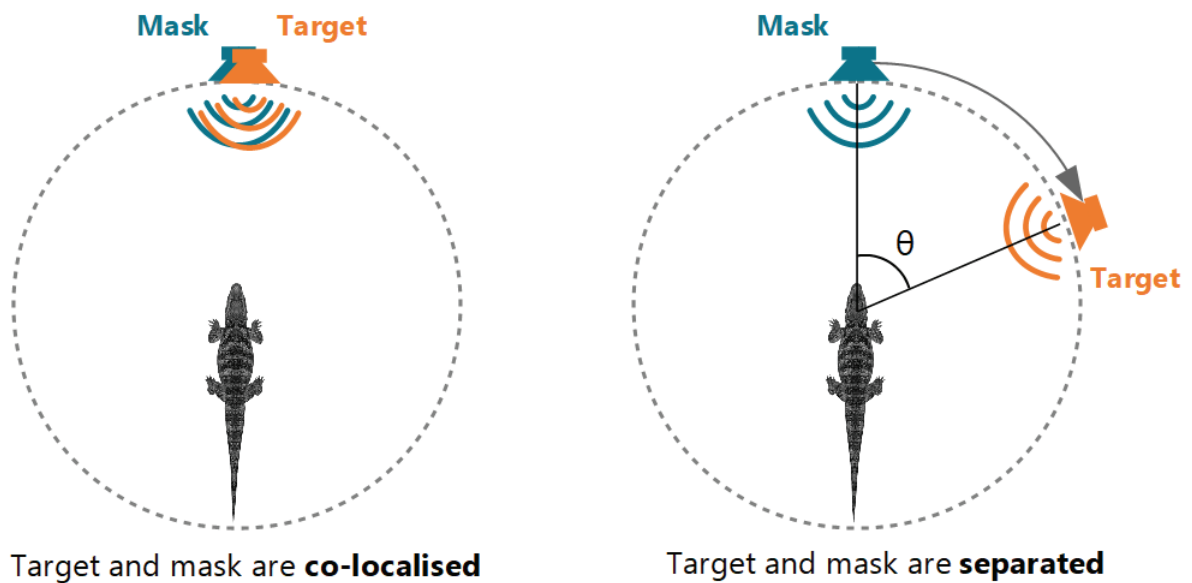


Figure 7 – Schematic representation of two situations unfavourable (left) and favourable (right) for Spatial Release from Masking.

Sound localisation abilities

The Barn owl (*Tyto alba*) may be the most studied model species when working on sound localisation. Thanks to the feathers organisation on its face, this nocturnal owl is known to be very accurate when estimating a sound position in the azimuthal plane, a feature very useful when hunting (Payne, 1971; Konishi, 1973). Another interesting feature of the barn owl is the asymmetry of its ears, each one at different height. This physiological characteristic gives the owl information on the elevation of the sound source of interest by the classical azimuthal binaural cues (Knudsen et al., 1979). The middle ears of Barn owls are linked by an interaural canal, but its implication in sound localisation is controversial: the interaural canal may play a role in the directionality of the eardrum in the low frequencies (Kettler et al., 2016) but its impact remain too weak to modify consequently sound localisation abilities (Moiseff et al., 1981). In other birds, sound localisation performances vary substantially across species. While the Marsh hawk (*Circus cyaneus hudsonius*) shows an angle of resolution of 2° (Rice, 1982), smaller non-hunter birds as the canary *Serinus canarius*, budgerigar *Melopsittacus undulatus* and zebra finch *Poephila guttata* show weak abilities in locating sound sources in space (75% Minimum Audible Angles of 27, 29 and 101° respectively (Park et al., 1991).

In mammals, sound localisation may be very accurate as well as some species show very poor faculties in locating sound sources in space. The most precise sound localisation abilities were measured in elephants, dolphins and humans which are able to discriminate two different sources when their separated by 1° (R. Heffner et al., 1988a; R. Heffner et al., 1982; Renaud et al., 1975). Pinnipeds (northern elephant seal *Mirounga*

angustirostris, harbor seal *Phoca vitulina* and California sea lion *Zalophus californianus*) localise precisely pure tones in air (MAA = [3.6, 4.7]°; Holt et al., 2004) and in water (harbor seals' MAA = 2.5°; Byl et al., 2016). Terrestrial mammals as Old world monkey (*Macaca*), cat, opossum, pig, dog or ferret show errors lower than 10 °when estimating the position of a sound source (Brown et al., 1978; R. Heffner et al., 1988a; Ravizza et al., 1972; R. Heffner et al., 1989; Kavanagh et al., 1987). This localisation error is larger in horse, cow or gerbil (*Meriones unguiculatus*) MAAs between 25 and 30 °(H. Heffner et al., 1984; R. Heffner et al., 1992b; R. Heffner et al., 1988b). Finally, sound localisation tests were led on different subterranean species such as in naked mole rat (*Heterocephalus glaber*) and blind mole rats (*Spalax ehrenbergi*) highlighting very poor abilities in locating sound sources (R. S. Heffner et al., 1993; R. Heffner et al., 1992a). This result is directly in line with their behaviour: those species use to mainly move in tunnels and need to localise sounds only in one dimension to ensure a front-rear discrimination (R. Heffner et al., 2016).

Behavioural approaches about sound localisation in insects remain challenging and only a few of studies were conducted in this group. However, Wytttenbach and Hoy were able to measured a MAA of 11.25°in crickets (*Teleogryllus oceanicus*) using a habituation-dishabituation procedure and (Wytttenbach et al., 1997). Mason et al. demonstrated how impressively accurate can be the *Ormia ochracea* when localising sounds showing a MAA equal to 2° (Mason et al., 2001). Moreover, it was demonstrated in lesser wax moths (*Achroia grisella*) that the females are approaching males call with a particular angle in the aim of increasing their sound localisation cues (Reid et al., 2016). The diversity of hearing apparatus let think to a wide range of sound localisation strategies which still have to be characterised (Robert, 2005).

In amphibians, sound localisation is needed to find a sexual partner when calling, sometimes forming choruses. Frogs show relatively good sound localisation abilities with an MAA of 11.8° in *Hyla cinerea*, and of 19° in *Hyla versicolor* (Bee et al., 2016; Klump et al., 2004; Jorgensen et al., 1991). It is interesting to note that some frogs, such as *Odorrana tormota* are very accurate (MAA = 0.7°) in localising ultrasonic signals (Shen et al., 2008).

Concerning crocodylians, Beach reported several observations about the ability of an American alligator (*Alligator mississippiensis*) "not only to hear but to localise sound" when playing different sound stimuli (Beach, 1944). More recently, Bierman et al. succeeded in conditioning two juvenile American alligators to test them in sound localisation tasks (Bierman et al., 2015). This study demonstrated that the alligators were able to detect the signal (movement induced by the playback) and to swim toward the emitting loudspeaker (Bierman et al., 2015). Underwater, Dinets evidenced that American alligators are moving toward the origin of an immersed sound source suggesting that sound localisation may occur in water (Dinets, 2013b).

Interaction between sound and visual localisation

Heffner and Heffner displayed a theory on the interaction between visual and acoustic acuities in localising a source in space (R. Heffner et al., 1992c). This study suggested that sound localisation is commonly used to orient the visual cues in order to scrutinise what did caused the sound. This hypothesis is supported by the fact that for short stimuli (in time), the acoustic cues appear more efficient and induce a more rapid reaction of the animal than the visual channel (Whittington et al., 1981).

Classically, the visual channel is characterised by the spatial distribution of the photoreceptors on the retina. A lot of vertebrates as cats, dogs or least weasels (Belleville et al., 1986; R. Heffner et al., 1992c) show a narrow field of best vision because of a punctual fovea (i.e. the highest density of ganglion cells in the retina forms a small rounded area; R. Heffner et al., 1992c). This feature induces the need to orient the visual cues to examine precisely the stimulus of interest. Besides, in other species such as cows, pigs, gerbils or horses (R. Heffner et al., 1992c; Baker et al., 1983; Hebel, 1976) the retinal topography does not reveal a punctual fovea but it is rather organised in visual streaks. This characteristic has the advantage to give a clear image on a two-dimensional area, offering a wide field of vision without needing to move the head.

In their study (R. Heffner et al., 1992c), Heffner and Heffner compared the acoustic and visual abilities of several mammal species and highlighted the correlation between both modalities. Their main conclusion was that mammals with a fovea experience better sound localisation performances than mammals with visual streaks. Indeed, because the animals with visual streaks do not need to focus on a specific point in the azimuthal plane, the information provided by sound localisation appear less relevant than in animals showing a punctual fovea.

A recent anatomical study (Nagloo et al., 2016) revealed that the visual system of crocodylians is adapted to their amphibious, two-dimensional environment. Indeed, when analysing the retina of several Saltwater crocodiles (*Crocodylus porosus*) and Freshwater crocodiles (*Crocodylus johnstoni*), Nagloo et al. evidenced the presence of a visual streak in the naso-temporal axis (Nagloo et al., 2016). This result follows the idea of an adaptation of the visual apparatus to the position at the interface. Because crocodylians show both visual streaks and developed sense of hearing, studying their ability to localise sounds remains a question of interest. On one hand, the theory displayed by Heffner and Heffner on the interaction between acoustical and visual performances (R. Heffner et al., 1992c) may suggest poor sound localisation abilities in crocodylians because of their visual characteristics. On the other hand, their hearing abilities and their apex predator position would rather implies high precision in sound localisation tasks.

PART II

General methods



Laboratory experiments

All the behavioural experiments conducted in laboratory conditions took place in the ENES lab of the Université Jean Monnet in Saint-Étienne. All the animals kept in the dedicated area of the laboratory were under the responsibility of Nicolas Boyer who is certified skilled in managing all species of Crocodylians. The ENES lab was, during all the time of the experiments, referenced under the agreement number n° D 42-218-0901.

Animal subjects

During this PhD program, we had the chance to work with four different species of Crocodylians lent by several zoological structures. Two Nile crocodiles *Crocodylus niloticus* were from "La ferme aux crocodiles" (Pierrelatte, France). These subjects were included in the experiments conducted in the lab presented in part 5 and in part 6. "Planète crocodiles" (Civaux, France) allowed us to work with one Chinese alligator *Alligator sinensis*, two broad-snouted caimans *Caiman latirostris* and two Nile crocodiles. One of the broad-snouted caimans and one of the Nile crocodiles were included in the experiments presented in part 4. Finally, we had the opportunity to work with eight Cuvier's dwarf caimans (*Paleosuchus palpebrosus*) from the Parc zoologique de Paris (Vincennes, France). During the period of this PhD, only conditioning experiments were conducted on those individuals.

Enclosures

All the animals were kept at the ENES laboratory (Saint-Étienne, France) under the laboratory ethic agreement (n° D 42-218-0901) and the certificate of capacity of Nicolas Boyer which includes all Crocodylians species. The enclosures were designed to give the animals all the necessary parameters for their well-being. In each enclosure, the ambient temperature was constant at 29°C, a UV-light ensure a hot spot at 32°C and the water was always slightly fresher than the air to allow the animals to cool down their body temperature (around 26°). Depending on the age and the size of the animals, they were raised in a tank or in a dedicated area (figure 1.1). The food intake, the development and health, were assessed continuously. Based on these parameters, it was possible to isolated some specific individuals if necessary (low food intake, aggressive behaviour) to ensure their well development. All the enclosures were designed to be easily modulated.

The mobility of the animals in their dedicated area was increased right after changing the organisation of their environment. This had the advantage to reduce the habituation time in the experimental area or any other new environment.

Using video recordings, we observed that all individuals were more active during night time. To use this characteristic behaviour, the day-night alternation was shifted in order to ensure a night time from midnight to noon and a day time from noon to midnight. This allowed us to run the experiments during the end of the night times.

The animals were fed between one and three times a week (depending on their size). They were given insects (grasshoppers, crickets), mice (foetus, pup, adult specimens), fish and occasionally chicken meat. Because crocodylians are able to spend weeks and even months without eating, the food intake was precisely monitored to ensure at least one feeding time a week. This rhythm allowed us to conduct conditioning experiments and to feed the animals as a reward from the conditioning task. The same type of food reward was used during the experiments conducted in the lab.

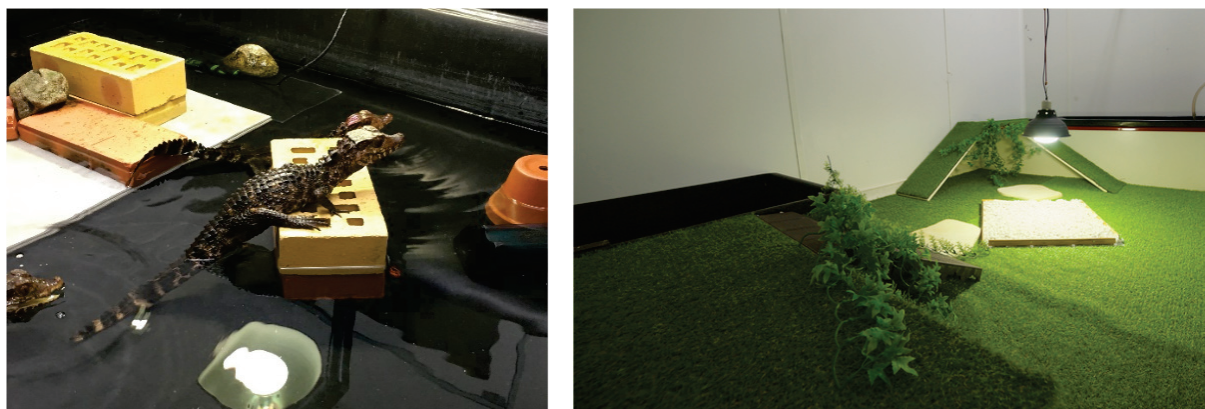


Figure 1.1 – Examples of two different kinds of enclosures used in the ENES laboratory to maintain the animals: tanks (left) and dedicated area (right).

Conditioning

To test sound localisation abilities and more generally acoustic perception in animals, a classical approach is the Go/No-Go method. This suggests a conditioning of the subjects prior to the experiments. Once trained, the analysis of the behaviour of the animal is associated to a positive or a negative response. In our case, the objective was to test sound localization performances of crocodiles. Thus, we trained them to come nearby a loudspeaker when a specific signal was played and they were fed when the sound was detected and localised.

Procedure

The conditioning process was progressive until it was strong enough to use the animals in an experimental procedure. To reduce the stress and to make the conditioning possible, the first step was to habituate the animals to the human presence. All the people included in the project were asked to visit the animals' area as often as possible. Once the animals were not afraid of humans, the second step was to feed the crocodilians using feeding tongs. This step was the most complicated (especially with the Cuvier's dwarf caimans) because it is opposite to the feeding behaviour of crocodilians which consists in hunting from a hide. Once the first individuals started to eat, the conditioned signal (details in part 5 and 6) was played back simultaneously with the presentation of the food. From this step, the conditioning procedure was more linear to the final level. The animals were progressively attracted to the loudspeaker position and the food presentation was gradually delayed. The final level of the conditioning was reached when the crocodiles approached the loudspeaker as a response of playing back the signal (Table 1.1). Once this level was reached, the conditioning of the animals were reinforced at every feeding time.

Progressive habituation to human presence, manipulation and new environments

It was necessary to anticipate the fact that crocodilians are easily stressed to ensure valid investigations about their cognitive abilities. For example, in the experiment 4, the animals were supposed to stay immobile during a full session of around 30 minutes duration. Because anaesthesia is not well documented in crocodilians and in reptiles in general and could be dangerous for the animals, it was not a conceivable option. Consequently, the animals had to be immobile on a plate during the testing session while being awake. To allow that condition, the animals were positioned on the restraint plate while their behaviour was monitored. Every times the animals showed a sign of stress, they were brought back to their enclosures. After several weeks of training, the individuals stayed calm without showing any external sign of stress (escape behaviour, pupil dilatation, rapid gular pumping).

In the experiments 5 and 6, the animals were tested in a dedicated experimental area. Once the conditioned was considered strong enough, the animals were placed in the experimental pool. Before starting the regular testing, they were let several times in this new environment for a complete 24 hours cycle during which they were fed. The first time they stayed immobile for a long moment before showing exploring behaviours. After several habituation sessions, this freezing phase was progressively reduced and the experimental testing were conducted. Before each testing session, it was necessary to let the crocodile alone in the pool after the capture without any playback. The time of this

session varied from 2 hours at the beginning to 10 minutes when the animals were used to this environment.

Table 1.1 – Detailed behavioural score considered in the conditioning procedure. The 6th level of the learning is the final step of the conditioning procedure.

Score	Behaviour
0	Refusal to take food
1	Food eaten out of sight
2	Food eaten in the presence of the experimenter
3	Food presented with forceps eaten
4	Movement to the forceps to eat
5	Attraction to the speaker emitting target for eating
6	Movement to the active speaker when playing the target

General comments

The general conditioning procedure was designed at the beginning of this project and a lot of parameters were adapted based on the observations made during the conditioning was conducted. Increasing the number of cues linked to the feeding times does accelerate the second step (i.e. food intake while it is delivered using feeding tongs). Indeed, if the feeding times are regular and surrounded by constant visual and acoustic stimuli, it has for an effect to increase the global motivation of the animals. For example, some individuals firstly associated the food intake with the presence of the loudspeaker in the area and they showed higher conditioning scored more rapidly. Initially, the training were done in the experimental area, after capturing the individuals and a period of habituation (of several hours). To increase the conditioning performances, the first steps may be done in the animals enclosures. The exploration of the experimental area can be done after the animals showed a strong conditioning behaviour.

The number of individuals may improve the conditioning performances. Indeed, we had the chance to work with 6 Cuvier's dwarf caimans from the same hatch. Because they grew more slowly than the others from the group, 3 individuals were alternately isolated from the group (blue, yellow and red individuals on the figure 1.2). The conditioning of the juvenile caimans seemed more rapid when they were included in the group than when they were isolated even if the conditioning procedure was identical in both conditions (figure 1.2). One individual was kept isolated since the second conditioning session to ensure a regular food intake (red individual on the figure 1.2). The performances of this individual were slower compared to others. Based on these observations, the learning process may be increased within a group, because of imitating behaviour. If one caiman approached from the playing loudspeaker, others caimans followed and the group approached together the loudspeaker until being rewarded. When being reintro-

duced to into the group, the previously isolated caimans' performances were dramatically increased (blue and yellow individuals on figure 1.2). The learning curves presented in figure 1.2 show a global decrease after session 75. This is due to aggressive behaviours of some individuals on others, suggesting a hierarchical organisation of the group.

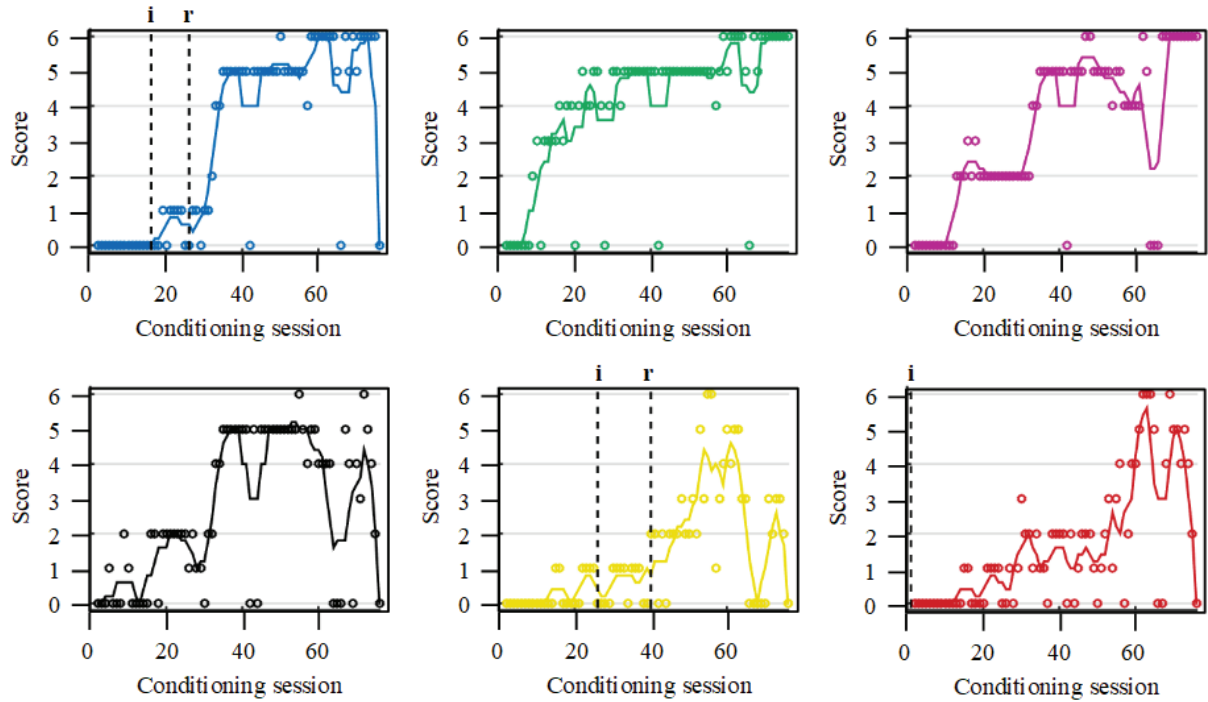


Figure 1.2 – Learning curves of 6 juveniles Cuvier's dwarf caimans (*Paleosuchus palpebrosus*) during their conditioning sessions. The circles represent the score attributed after each conditioning session. The solid lines correspond to a simple smoothing of the data points. The score considered in ordinate is detailed in table 1.1. The vertical dashed lines represent an isolation of an individual from the group (letter "i") or a reintroduction in the main group (letter "r").

Experimental apparatus

Design

All the experiments conducted in the ENES laboratory took place in an acoustic booth (TipTopWood, dimensions = $1.8 \times 2.3 \times 2.2$ meters) with foam covering the walls and ceiling (figure 1.3). This ensured a quiet environment in which the acoustic reflections are limited. A pool was installed inside this chamber as in figure 1.3. The testing apparatus was designed to elicit the use of the acoustic channel in the tested subject. The experiments were led in the artificial late night for the animals (i.e. before noon). Because the chamber can be completely closed, the animal was in the complete dark (except from the infrared light of the camera fixed on the ceiling). To avoid an habituation of the animal,

the loudspeakers were moved between each testing session. To limit a visual localisation of the loudspeakers, a lure loudspeaker may be placed in the experiment 6. All the loudspeakers (lure included) were surmounted by a system containing food rewards. These olfactory information give a cue on the position of the loudspeakers but as the reward was given only when the subject chose the active loudspeaker, it did not interfere with the sound localization tasks.

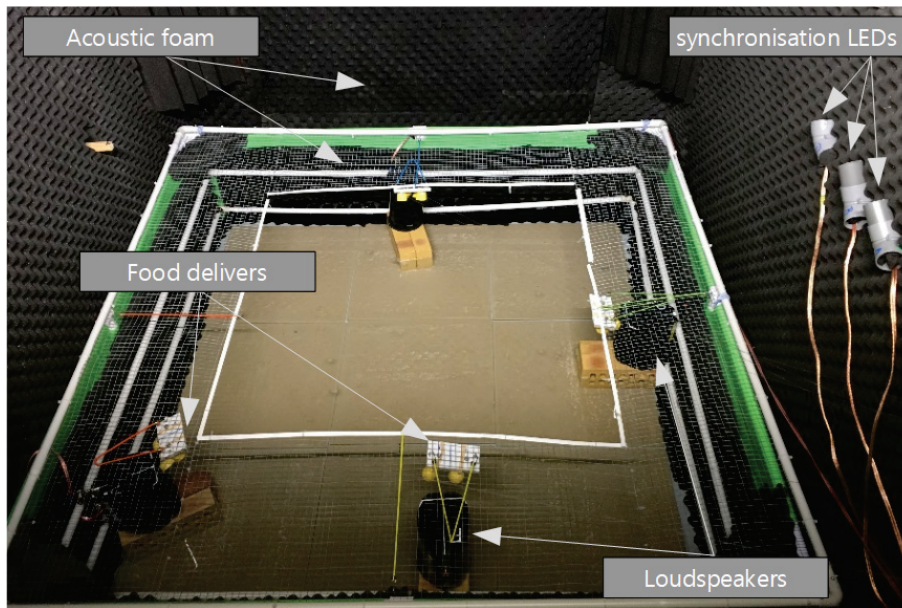


Figure 1.3 – Experimental apparatus designed at the laboratory.

Food rewards

In the wild, crocodylians may spend several weeks (more rarely several months) without any food intake. In captivity, we fed them one to three times a week with small portions of food to ensure their well development. During the testing periods, the only food given to the animals included in the experiments were the rewards obtained in the experiment once a week (except when an individual showed an injury or did not eat within the past week). The food rewards had to be sufficient to motivate the animal in participating in the experiments but it had to be small to allow several stimuli in one session. Each reward was about 5 to 10 g of meat. The reward system had to be silent (to avoid an additional cue and ensure accurate negative answers) but it must be efficient to deliver the food reward quickly after the animal's response. If no reward was given after a positive response it can impact the quality of the conditioning and the subjects' motivation and compromise the following tests.

Open-air captivity



Two different experimental sessions were conducted in Crocoparc Agadir, in Morocco. Only one experiment is detailed in the chapter 6 because it was not possible to treat the results obtained during the first session. The experiments were conducted on young Nile crocodiles (*Crocodylus niloticus*) in a large dedicated experimental pond, outside. All the experiments ran in this set-up consisted in playing back juveniles calls to an isolated individual. The experiments were filmed using infra-red cameras to post-analyse the behaviour reactions of the subject.

Acoustic propagation

The experimental pond in which were conducted the experiments presented in part 6 was around 40 m^2 with maximum dimensions of 6×7 m. We used remote controlled loudspeakers (FoxPro Fusion) to play back all the stimuli. These loudspeakers were directive and induced a non homogeneous acoustic propagation on the area of the pond. In the experiment 6, one of the main parameter of interest was the Sound to Noise Ratio (i.e. the difference of intensity levels induced by two different loudspeakers). Because of the strong variability of the sound intensity level in the pond surface area, we had to characterise and to compensate this phenomenon in order to compute valid Sound to Noise Ratios.

To characterise the sound propagation in the pond area, the sound level was mapped on a regular grid (resolution: 1×1 m) using a Zoom H4n recorder (figure 2.1). Two different loudspeakers placed on the bank (turned towards the length and the width of the pond) played alternatively the same white noise at the same output level. At each point of the grid, the sound level was measured and it was possible to map the evolution of the sound intensity on the surface of the pond (figure 2.1).

From these measurements, a two dimensional model of propagation was designed in order to predict the sound intensity level at every point of the pond from every point on the bank (cf. in part 6 figure 6.8). We characterise the decrease of the sound level intensity (in dB) according to the logarithm of the distance to each loudspeaker. Considering a relative 2D space with the playing loudspeaker as the origin, the sound level intensity (and thus the SNR) was calculated for each position of the crocodile (triangles and squares of the figures 6.8, part 6).

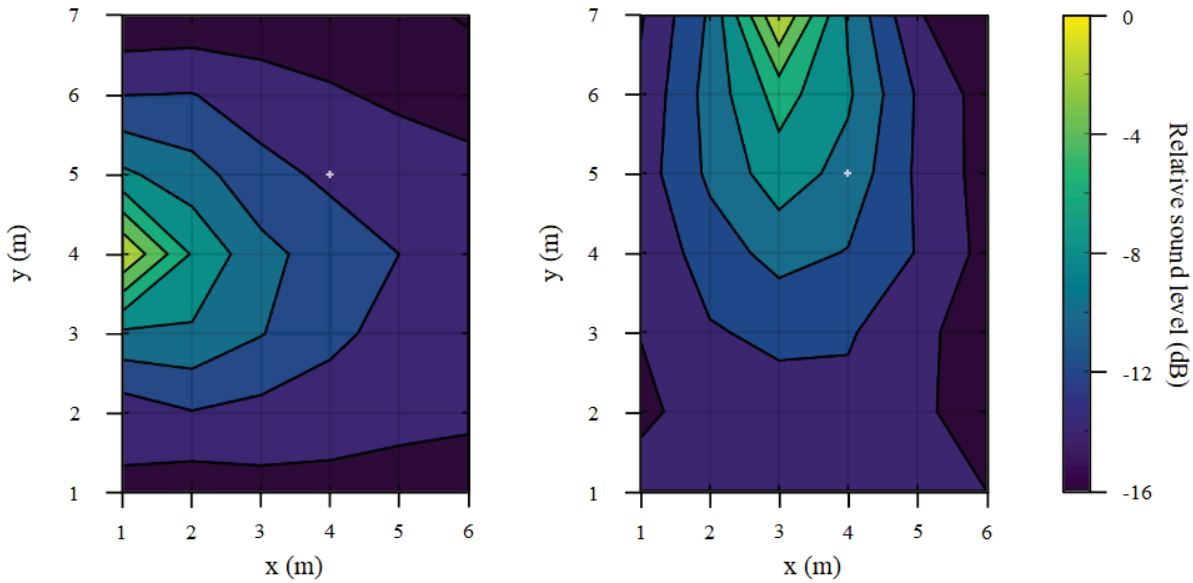


Figure 2.1 – Acoustic propagation measured in the experimental pond. The loudspeakers were placed on the bank in (1, 4) (left) and in (3, 7) (right). The sound level measured at the position of the sound source positions is 0 dB.

Image calibration

All experiments conducted in open-air captivity conditions were filmed to allow post-analyses. The video recordings were impacted by two different parameters: the lens distortion and the perspective of the global image, both deforming the image (left panels of the figure 2.2). To increase the angle of view and to cover a larger area, a method classically used by the manufacturers is the use of a deforming lens (fisheye) inducing a distortion of the image. The position of the camera in relation to the image plan also induced a deformation of the image due to the perspective. Because the experiments presented in the chapter 6 were based on the use of precise spatial parameters (positions of the animal and of the loudspeakers), the deformation of the image had to be compensated to ensure the validity of the resulting data.

Because the lens distortion is intrinsic to the camera itself, the calibration consisted in filming a regular grid pattern and identifying regular distributions on the image (using Kinovea software). The perspective deformation was compensated by filming a rectangle pattern on the surface of interest (i.e. in our case: the surface of the experimental pond). Once this calibration made, it was possible to associate two different point of views to cover the full experimental area (right panel of figure 2.2).

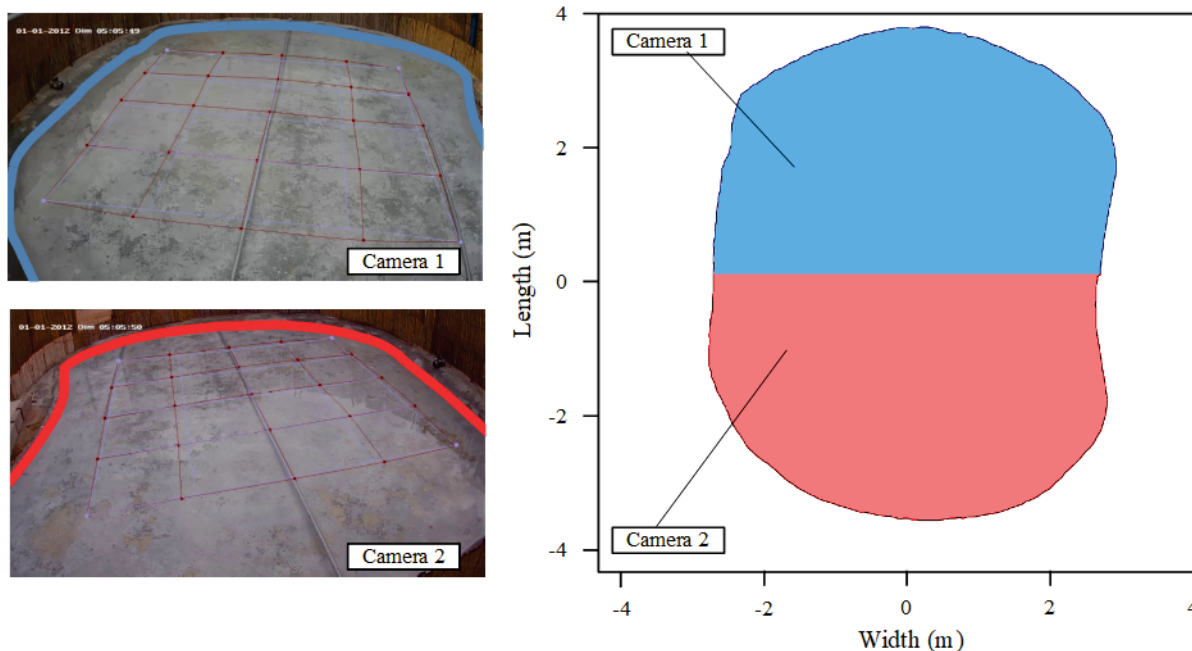


Figure 2.2 – Reconstruction of the shape of the experimental area using two different camera angles (left). The lens distortion and the deformation due to the perspective were compensated in order to obtain the 2D projection of the pond (right).

Experiments in adult individuals

In Crocoparc Agadir (Morocco), we had the opportunity to lead some experiments on adult Nile crocodiles. The testing procedures were as close as possible to those used to test the juveniles. Because introducing an object in the crocodiles environment attracted all the individuals without emitting any sound, we had to habituate them to the presence of the loudspeakers. We first placed the loudspeakers on the bank using a rope as illustrated in figure 2.3. Once the crocodiles habituated, we played back hatchling calls (natural or filtered as in parts 5 and 6).

Because of the high density of individuals, the results obtained on adults were not exploitable. Indeed, it was not possible to clearly identify individual responses from one crocodile from the others. Several animals were attracted by the sound source by mimicking each other. Another difficulty encountered was the habituation phenomenon to the playbacks. If it was possible to attract some individuals two or three times using hatchling calls, the motivation dramatically decreased after 3 stimuli were broadcast (until inducing no reaction at all). However, these playback sessions confirmed the biological relevance of our stimuli in adult specimens. One particular trial attracted several individuals until a female showed a really strong reaction, surrounding the loudspeaker with her tail and opposing her body to the other individuals.



Figure 2.3 – Example of two adult Nile crocodiles approaching the loudspeaker after a playback experiment (picture taken in Crocoparc Agadir, Morocco).



We conducted a fieldwork in the Brazilian Pantanal, in partnership with Zilca Campos from EMBRAPA (www.embrapa.br), between April and May 2019. The experimental area was around Nhumirim Ranch which is one of the experimental bases of the EMBRAPA, in Mato Grosso do Sul, Brazil (cf. Chapter 6). The experiments were conducted on Yacare caimans (*Caiman yacare*), on the lakes surrounding the ranch, inside a protected area.

Acoustic signals and propagation

Distress calls

The first step of the field work conducted in Brazil was to record distress calls of Yacare caimans (*Caiman yacare*) to play them back to females to test their use of Spatial Release from Masking (cf. Chapter 6). The situations of the nests were determined by the team of Zilca Campos (Luis Alberto Rondon and Denis Celin Tilcara from EMBRAPA) and the hatchings happened two to four weeks before the experiments began. We recorded three different hatchlings from the same brood. They were captured by hand and did vocalise right after. We recorded their vocalisations for 2 to 3 minutes before releasing the individual in the pond next their mother. The acoustic structure appeared similar to the vocalisations recorded in other species (figure 3.1; Vergne et al., 2006a; Vergne et al., 2009; Vergne et al., 2012). Indeed, the spectrographic representations highlighted a complex modulation in frequency and the maximum of energy was centred between 1 and 2 kHz.

Female and hatchlings reactions

The experiments were conducted on females surrounded by their own youngs. When playing back the distress calls to elicit a response from the female, the juveniles present around the females occasionally emitted back distress calls. This behaviour may allow them to pass the information carried by the original signal (a potential predator for example) to the other young individuals of the group. More unexpectedly, several tested females did vocalise after playing back juveniles' distress calls. These vocalisations sounds like “grunts” (Vergne et al., 2009) and we had the opportunity to record a few of them

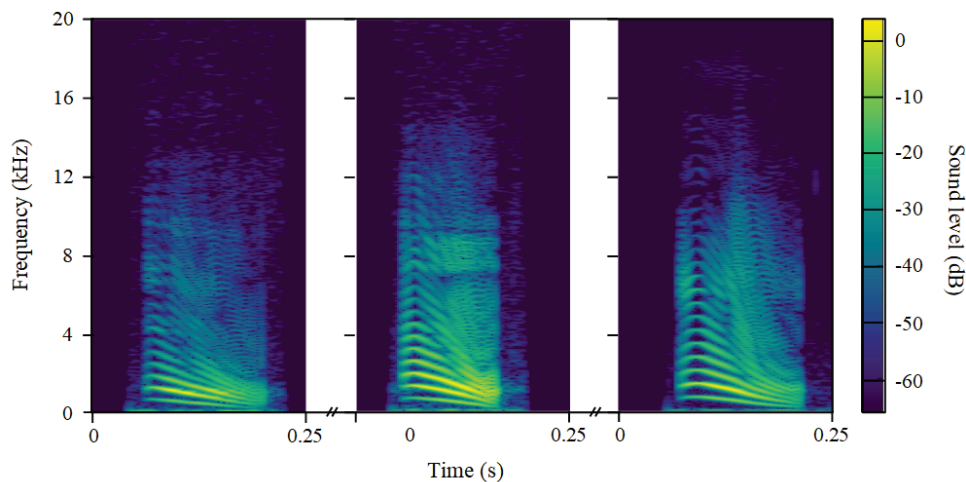


Figure 3.1 – Spectrographic representations of distress calls recorded on three different hatchlings (Yacare caimans) in Pantanal, Brazil.

(figure 3.2). These grunts may be emitted only once or in sequences of variable numbers. The recordings turned out to be quiet noisy in low frequencies and more precise acoustic analyses are needed to describe these vocalisations. We observed that these vocalisations were emitted as a response of distress vocalisations from several juveniles and had the consequence to end the juveniles' calls.

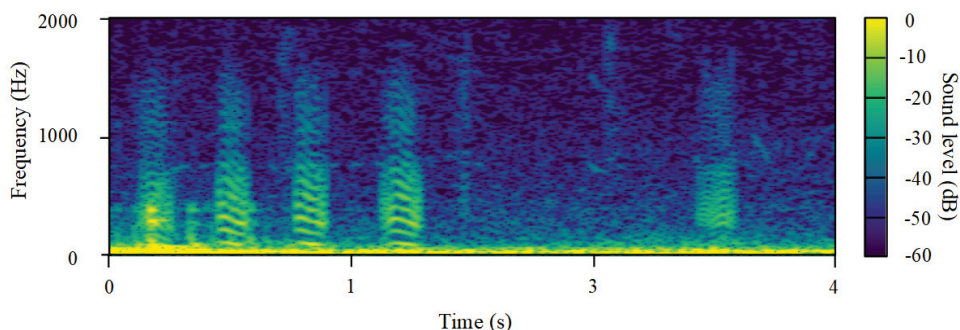


Figure 3.2 – Spectrogram representation of grunt emitted by a female Yacare caiman surrounded by her youngs recorded in Pantanal, Brazil.

Acoustic propagation

During the day, the Yacare caimans evolved mainly in water covered with two types of vegetation: long grass and dense concentration of *Salviniaceae* as illustrated on figure 3.3. By broadcasting a white noise through a FoxPro Fusion loudspeaker and recording the signal at several distances (Zoom H4n recorder), the evolution of the sound level was computed relatively to the position at 1m from the recorder (cf. figure 3.3). The sound level intensity dramatically decreased with distance (-33 dB after 1 m of propagation) in both types of vegetation. The same experiments was conducted by broadcasting the

juveniles' calls and recording them at several distances from the loudspeaker. The spectrographic representations displayed on the figure 3.3 illustrates the degradation of the signal when propagating in this natural environment (when background noise was weak: 41 dB(A)).

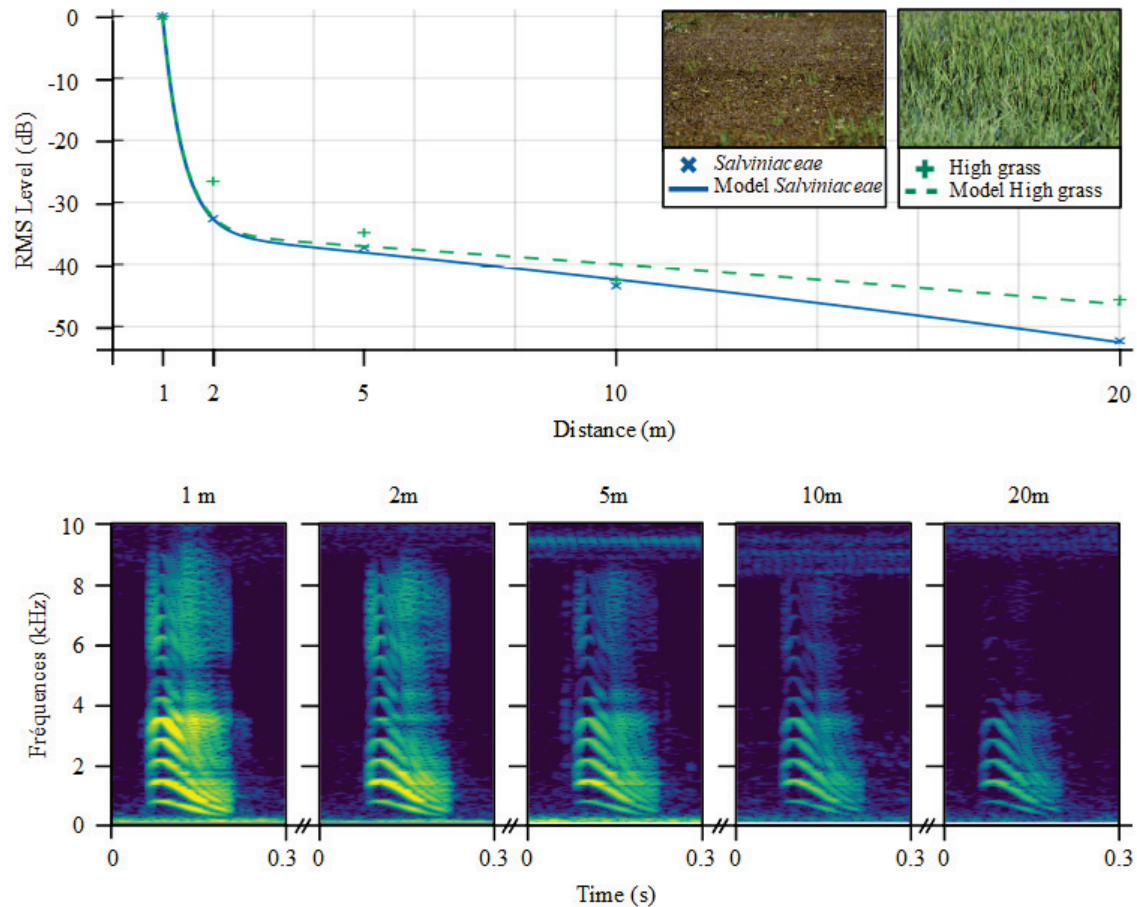


Figure 3.3 – Acoustic propagation in the field. Top panel: Spatial decrease of the sound level above the water surface covered by *Salviniaaceae*. The crosses represent the measured sound levels and the lines were the fitted exponential models. Bottom panel: Spectrographic representation of a young *Yacare caiman*'s distress call recorded at different distances from the sound source.

PART III

Results



Influence of head morphology and natural postures on sound localisation cues in crocodilians

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All the data used in this study are available on the open-source platform Zenodo under the DOI [10.5281/zenodo.2572624](https://doi.org/10.5281/zenodo.2572624).

Graphical abstract

Does the external morphology induce sound localization cues?
Are these cues relevant in natural postures ?

Crocodylians are known to have an acute sense of hearing useful in hunting situations and in acoustic communication. Because sound localisation is primordial to support social interactions and hunting, we measure sound localisation cues induced by the external morphology in two natural positions.

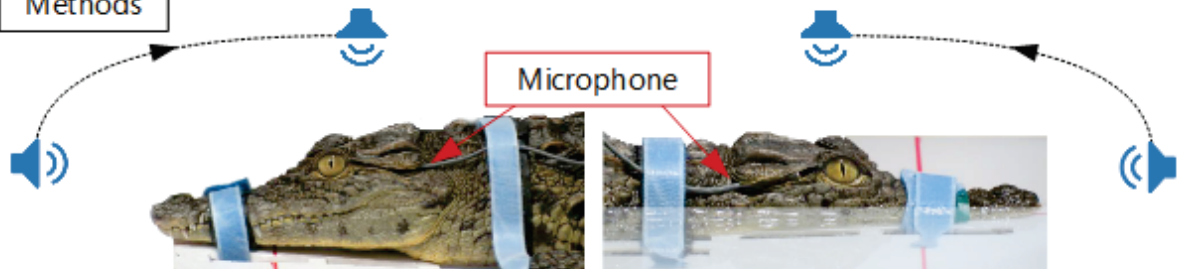


On the ground

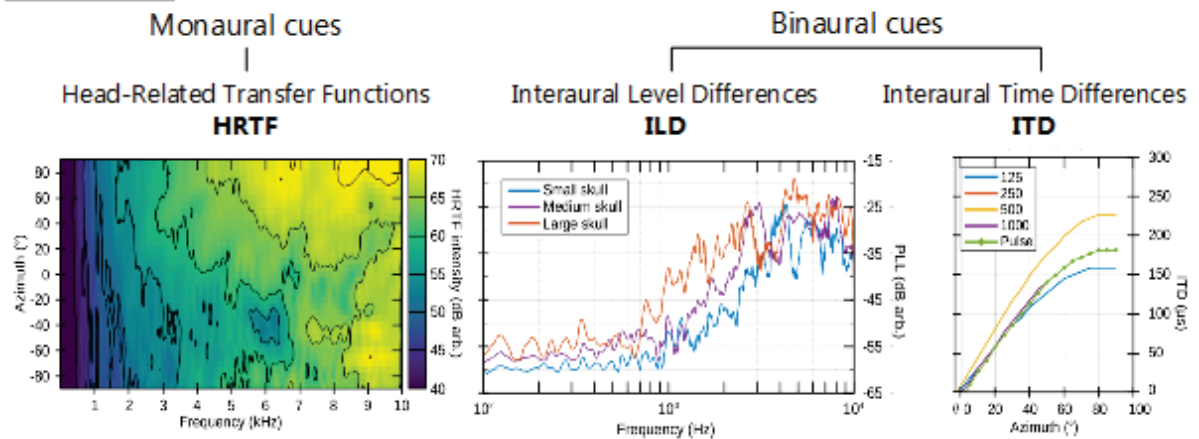


At the interface

Methods



Results



Conclusions

The external morphology induces monaural cues (HRTF) showing strong variations potentially relevant for sound localisation, particularly in high frequencies. The measured binaural cues (ILD and ITD) are influenced by the size of the head. ITD are relevant up to 1000 Hz and ILD are relevant for higher frequencies (>1500 Hz). All sound localisation cues are preserved at the air-water interface, suggesting an adaptation to this particular position, even when only a small part of the head is emerged.

Abstract

As top predators, crocodilians have an acute sense of hearing useful for their social life and for probing their environment in hunting situations. Although previous studies suggest that crocodilians are able to localise the position of a sound source, how they do this remains largely unknown. In this study, we measured the potential monaural sound localisation cues (Head-Related Transfer Functions: HRTFs) on alive animals and skulls in two situations, both mimicking natural positions: basking on the land and cruising at the interface between air and water. Binaural cues were also estimated by measuring the Interaural Level Differences (ILDs) and the Interaural Time Differences (ITDs). In both conditions, HRTF measurements show large spectral variations (> 10 dB) for high frequencies, depending on the azimuthal angle. These localisation cues are influenced by head size and by the internal coupling of the ears. ITDs give reliable information regarding sound-source position for low frequencies, while ILDs are more suitable for frequencies higher than 1.5 kHz. Our results support the hypothesis that crocodilian head morphology is adapted to acquire reliable localisation cues from sound sources when outside the water, but also when only a small part of their head is above the air-water interface.

4.1 Introduction

As top predators, crocodylians have developed fascinating sensory skills: accurate vision in air (Sillman et al., 1991; Nagloo et al., 2016), highly developed olfaction (Scott et al., 1990; Weldon et al., 1993), precise abilities to detect water vibrations (Fleishman et al., 1989; Leitch et al., 2012; Grap et al., 2015), and an acute sense of hearing (Wever, 1971; Higgs et al., 2002). Experimental studies, as well as field observations, have demonstrated that the auditory modality is of primary importance for both their social life (e.g. during mating and mother-offspring interactions) and hunting success (Vergne et al., 2006a; Vergne et al., 2012). Although it is known that crocodylians hear sounds over a broad frequency range (from around 300 Hz up to 8 kHz, with a peak in audiogram around 1 kHz; Wever, 1971; Higgs et al., 2002), and while the functional anatomy of the ear of these archosaurs is similar in many respects to that of birds (Vergne et al., 2009), we have little knowledge on many aspects of their hearing biology. Thus, while some observations have brought evidence for directional hearing in crocodylians, suggesting the existence of specialised adaptations (Beach, 1944; Dinets, 2013a; Bierman et al., 2015), how they localise sound sources in their environment remains poorly described.

In birds and mammals including humans, sound-source localisation relies on Interaural Time Differences (ITDs: a sound from the left will arrive at the left ear first) and Interaural Level Differences (ILDs: a sound from the left will be louder in the left ear due to the shadowing effect of the head). Moreover, monaural spectral cues are induced by the filtering effect of the head: Head-Related Transfer Functions (HRTFs) result from sounds experiencing spectral modifications during their propagation through and around the head, providing different spectral cues when arriving from different azimuths and elevations (Middlebrooks et al., 1990). The detection of sounds and the perception of localisation cues are often reinforced by some anatomical particularities such as the external ears of mammals (De Mey et al., 2008), and ruff feathers and asymmetrical ears of the barn owl (Keller et al., 1998). Remarkably, the hearing apparatus of crocodylians includes a well-developed external ear formed by horny, prominent bone overhanging a muscular ear-lid that protects the eardrum (Montefeltro et al., 2016; Manley, 2017; Bierman et al., 2015), suggesting a functional role in directional hearing.

Previous studies showed that some directional information is encoded in the auditory nerve of juvenile American alligators *Alligator mississippiensis*. These data support the hypothesis that the acoustic coupling of middle-ear air cavities - an anatomical particularity found in both birds and crocodylians - could enhance localisation abilities (Bierman et al., 2014). By combining results from passive acoustic experiments and measurements of auditory brainstem response to sounds in young alligators, Bierman et al. suggested that HRTFs do not entirely account for the level of directional sensitivity in auditory nerve activity. However this requires further consideration and the current study will fo-

cus on larger animals (alive and skulls), in natural positions in water, and on an extended frequency range.

The main characteristic of crocodilian biology is their amphibious way of life. These animals spend most of their active time at the interface between air and water while they mostly come on land to regulate their internal temperature by basking motionless in the sun (Grigg et al., 2015). In water, the upper part of the head -with the nostrils, eyes and ears- appears above the waterline (figure 4.1a, b). The acoustic environment of crocodilians may be strongly influenced by this position, as air and water show different sound-propagation properties. As water acts as a reflective surface, it should contribute to the properties of sound waves arriving at the eardrums.

In the present paper, we investigate the acoustic localisation cues available to crocodilians, paying specific attention to the effect of the air-water interface, and its interaction with head morphology and head size. We hypothesise that localisation cues generated by interactions between sound waves and the head morphology still exist when the animal is at the interface of air and water, in spite of having most of its body concealed underwater. It is worth to note that the presence of such cues does not necessarily induce the behavioural use of the cues by the animals. Using microphones positioned within the ears, we recorded sounds emitted by a source set up at different azimuths from the animal's head axis. We then measured HRTFs, which characterise the transfer function of the spatial acoustic filter created by the head and body of the animal. This method has commonly been used in humans and other species (e.g. in mammals Rebillat et al., 2014; Koka et al., 2011, in alligators Bierman et al., 2014 and in birds Keller et al., 1998). As HRTFs are related to the complex absorption and reflection pattern of acoustical waveforms by the head and body, we compared HRTFs obtained with the crocodile positioned at the interface of air and water with those obtained with the animal's whole body outside water. We further estimated the potential influence of species-specific head shape on HRTFs by performing the experiment on individuals from two different species: the Nile crocodile *Crocodylus niloticus* and the broad-snouted caiman *Caiman latirostris*. To assess the impact of head size, we measured HRTFs on three skulls of different rostral snout lengths: 6.9 cm, 16.5 cm and 22.7 cm, corresponding respectively to a juvenile, a young and subadult Nile crocodile. Beside HRTF monaural cues, the binaural cues ITDs (Interaural Time Differences) and ILDs (Interaural Level Differences) are also well known to facilitate sound-source localisation. We computed ITDs by comparing the waves' arrival time between the two ears, and ILDs by calculating the difference of sound pressure level measured at the right and left ears. Overall, our results may suggest that the shape of the crocodilian head induces both monaural (HRTF) and binaural (ITD, ILD) sound localisation cues even when the head is mostly concealed in water.

4.2 Material and methods

4.2.1 Experimental models

We assessed acoustic localisation cues on two living animals (see pictures on figure 4.2) and three skulls (see pictures on figure 4.3). The animals were one broad-snouted caiman *Caiman latirostris* (rostral snout length: 4.4 cm, 2 years old) and one Nile crocodile *Crocodylus niloticus* (rostral snout length: 6.9 cm, 2 years old), provided by the zoo Planète Crocodiles (Civaux, France). Both individuals were accommodated in the ENES lab in dedicated areas. These species show strong differences in head morphology (Erickson et al.; Erickson et al., 2012) that are well-illustrated by the rostral proportion: *C. latirostris* has the broadest snout, whereas the rostral proportion of *C. niloticus* is just above the average of the 23 crocodylian species. In addition, we measured monaural and binaural cues on three skulls of Nile crocodiles (rostral snout length from 6.9 cm, 16.5 cm and 22.7 cm).

Animal condition

A critical point with the living individuals was to prevent movements while minimising stress during HRTF measurements. Three months prior to the experiment, both animals were habituated to remain motionless on a board for 30 minutes. The animal position was further secured by straps. This procedure allowed avoiding anaesthesia, which is difficult to master in crocodylians and could have been a survival risk (Grigg et al., 2015). During the experiments, we (NB) continuously assessed the stress level of the animal by observing its pupillary dilatation and behaviour (escape attempts). During the weeks following the experiments, the condition of both animals was carefully monitored in terms of growth parameters and behaviour (e.g. food intake), and the animals behaved similarly to the time before testing.

Signal acquisition for HRTFs measurements

We measured HRTFs in two conditions mimicking biologically relevant situations (figure 4.1):

1) 'land condition': The animal was placed on a board lying on the land of a semi-anechoic room (LVA-INSA Lyon: background noise level = 20 ± 1 dB SPL; reverberation time = 0.1 ± 0.1 s), mimicking a position frequently used by crocodylians when basking (figure 4.1a, c and e). The ground of the semi-anechoic room can be considered as perfectly reflective to acoustic waves.

2) 'Interface condition': The animal was placed in water, with its nostrils, eyes and ears just above the waterline (figure 4.1b, d, f). This condition mimicked the natural position of an animal in water, e.g. when cruising, ambushing prey or protecting its young. In this position, the water surface was also considered to be fully reverberant, thanks to the short distance between the acoustic source and the microphones.

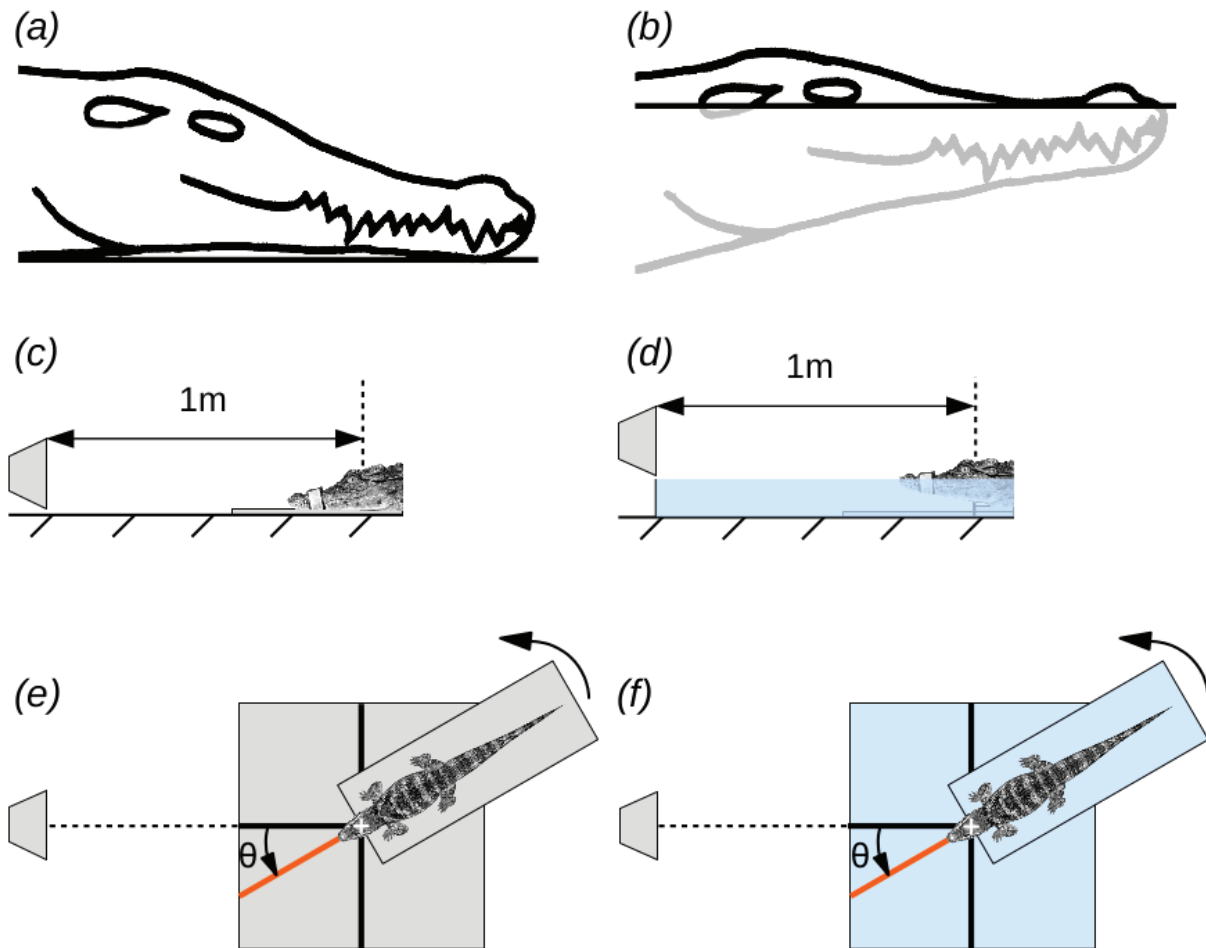


Figure 4.1 – Experimental set-up used to measure HRTF localisation cues. Two natural postures of crocodylians considered in the present study: (a) on the land and (b) at the interface between air and water. Cross-section and top view of the set-up in the land condition (c) and (e), and at the interface (d) and (f).

Under both conditions, the sound source (loudspeaker) was positioned 1 meter from the centre of the head of the animal (defined as the point equidistant between the two ears, see figure 4.1), with 0° elevation. A rotation of the animal's body along its antero-posterior axis enabled measurements of HRTFs in a 2D plane between -90 and $+90^\circ$ in 5° increments. The sound-emitting equipment was composed of a sound card (Presonus, Audiobox 44-VSL) connected via an amplifier (Yamaha, AX-397) to the loudspeaker (AudioPro loudspeaker, Bravo Allroom Sat). The loudspeaker was hung just above the ground or the waterline to avoid acoustic coupling with the ground or the water. The

centre of the medium loudspeaker membrane was placed at the same height as the microphones that were inside the ears.

The experiments were always performed with the ears out of the water. We placed one microphone (Knowles, FG-23329-P07) inside the cavity of each ear, behind the ear-lid and close to, but without touching, the tympanic membrane. This allowed simultaneous recording of the sounds arriving at both right and left ears. The recording equipment was composed of both left and right microphones connected to the input channels of the sound card (sampling frequency = 44.1 kHz).

The emitted signal was a logarithmic sine sweep (frequency range = 20-10000 Hz; duration = 5 s; intensity level = 80 ± 0.5 dB SPL). The frequency range was chosen to mostly cover the hearing range of crocodylians, which is mainly centred on 1-2 kHz (Wever, 1971; Higgs et al., 2002). For analysis purposes, we used a Matlab code to synchronise in time the source signal with the two recorded microphonic signals.

Prior each measurement, we calibrated the broadcast signals in the absence of any animal, with both microphones placed at the virtual centre of the crocodile's head. This calibration was a necessary step to take into account the properties of the sound-producing and recording equipment ('transfer function' due to material gains, frequency responses, etc.) in HRTFs measurements. Recorded signals were averaged ($n=10$) and used as a reference to compensate for this transfer function.

In addition to HRTF calculations, we measured Interaural Time Differences (ITDs) and Interaural Level Differences (ILDs) using the out-of-water set-up. First, we sent an impulse signal (pulse) to estimate the broadband ITD. We then broadcast 500 ms pure tones at 125, 250, 500 and 1000 Hz. Since Carr et al. (Carr et al., 2009) demonstrated that in alligators ITDs are not coded in the auditory nerve for frequencies over 1 kHz, we chose to consider only frequencies below 1 kHz. The ITD corresponds to the value of τ maximising the cross correlation between left and right ears $\int_{-\infty}^{+\infty} s_L(t)s_R^*(t - \tau)dt$, where t is the time and τ is the time delay between left and right microphonic signals ($s_L(t)$ and $s_R(t)$, respectively). Assuming symmetry of the head, ITDs were normalised to the 0° value. Directly from HRTF measurements and because of the assumption of symmetry to the normal incidence, the ILD can be calculated for a given frequency and azimuth as:

$$ILD(f, \theta) = H(f, \theta) - H(f, -\theta), \quad (4.1)$$

where f is the frequency, θ the azimuth of the sound source and $H(f, \theta)$ the Head-Related Transfer Function.

Signal processing

To avoid clipping, we applied a Hanning ramp (501 points) at the onset and at the end of recorded microphonic signals, and normalised all recorded signals by the root-mean square amplitude of the normal incidence signal (left and right channels independently). The spectrum of the recorded microphonic signals (R) within the ear can be expressed as a linear combination of frequency (f), sound source azimuth (θ), elevation (ϕ) and microphone position (\vec{x}), such as:

$$R(f, \theta, \phi, \vec{x}) = S(f) \times H(f, \theta, \phi) \times \mu(f, \vec{x}), \quad (4.2)$$

where $S(f)$ is the calibration signal, $H(f)$ is the Head-Related Transfer Function and $\mu(f, \vec{x})$ is the contribution of the microphone position (adapted from Middlebrooks et al., 1990).

In our experiments, elevation was maintained at 0° . HRTFs thus depend only on the sound source azimuth and the sound frequency. One caveat concerns the in-ear position of the microphones: as they were placed under the (opaque) ear-lids, their position could not be perfectly assessed and could be slightly different between left and right ears. We took into account this potential issue by performing two methodological steps. First, the position of the microphone was carefully controlled to be as reliable as possible. Second, we used a normalisation method adapted from that developed by Middlebrooks (Middlebrooks et al., 1990) to reduce the effect of microphone position in the human ear canal when measuring HRTF. Briefly speaking, the measured microphonic signal was normalised by the average of all microphonic signals ($\mu(f, \vec{x})$), depending only on the frequency and the position of the microphone. The HRTF was then supposed to depend only on the frequency and the azimuth of the sound source, as follows:

$$H(f, \theta) = \frac{R(f, \theta, \vec{x})}{S(f) \times \mu(f, \vec{x})}, \text{ with: } \mu(f, \vec{x}) = \frac{1}{S(f) \times N} \sum_{i=1}^N R_i(f, \theta_i, \vec{x}), \quad (4.3)$$

where N is the number of microphonic signals.

To limit the error in HRTF estimations, we considered in this study each head as symmetrical and thus averaged the HRTFs simultaneously measured in the right and left ears. To limit discontinuities in HRTF measurements along angular and frequential axes, we applied a smoothing procedure based on a two-dimensional floating Gaussian window normalised in amplitude with a 5 points width in azimuth and a logarithmically varying width in frequency (3 Hz at $f = 20$ Hz and 1 kHz at $f = 10$ kHz).

Finally, we calculated a Potential localisation Level (PLL) based on HRTF and ILD

as follows:

$$PLL_H(f) = 20 \times \log_{10}\left(\frac{1}{N_\theta} \sum_{\theta=-90}^{90} \left| \frac{\partial H(f, \theta)}{\partial \theta} \right| \right), \quad (4.4)$$

and,

$$PLL_{ILD}(f) = 20 \times \log_{10}\left(\frac{1}{N_\theta} \sum_{\theta=-90}^{90} \left| \frac{\partial ILD(f, \theta)}{\partial \theta} \right| \right), \quad (4.5)$$

with N_θ is the number of azimuth positions (in here θ varies between -90° and 90° with a step of 5° , so: $N_\theta = 37$). $PLL_H(f)$ and $PLL_{ILD}(f)$ are expressed in *dB*. The PLLs are computed to facilitate the comparison of HRTFs and ILDs between the different conditions. Classically, sound localisation cues are considered efficient when varying monotonously according to the azimuth of the sound source. For each frequency, the PLL corresponds to the average of the variation of $H(f, \theta)$ or $ILD(f, \theta)$ according to θ in *dB*. So, the Potential localisation Level is a cumulative measurement of variations of monaural cues across azimuth and a high PLL indicates a strong variation of the considered cue with the position of the source.

4.3 Results

HRTF cues in land- and air-water interface conditions

The HRTFs measured in the awake animals in both land- and interface conditions are displayed in figure 4.2 (panels a-d). The HRTF intensity level is coded by an arbitrary coloured *dB* scale (from -12 to 8 *dB* arb., with contour lines representing 5 *dB* intervals), and expressed as both a function of frequency (20 - 10000 Hz) and of the sound-source azimuth (-90° - $+90^\circ$). Positive (resp. negative) values of HRTF intensity level induce an amplification (resp. attenuation) of the acoustic field due to the presence of the head of the animal compared to the calibration situation (i.e. with no animal). Positive azimuth angles correspond to sounds recorded from the ipsilateral side, i.e. from the side of the sound source, whereas negative azimuths correspond to the contralateral side, i.e. sounds recorded in the 'acoustic shadow' of the head.

In both land- and air-water interface conditions, HRTFs showed similar complex patterns of sound pressure level variations, with high dynamics (20 *dB*) depending both on sound-source incidence and sound frequency (figure 4.2a-d). This intensity pattern varied depending on the side: for azimuths smaller than 0° (contra-aural side), the sound level measured near the ear-drum is negative whereas it appears mainly positive (i.e. amplified) for incidences larger than 0° (ipsilateral side). This main result indicates that the angular position of the sound source influences the spectral cues perceived at the

ears' level, suggesting that HRTFs could support sound source localisation in both the land- and air-water interface conditions. The difference in sound-pressure levels between the ears due to the position of the sound source was, however, mainly present for frequencies above 1 kHz. Below 400 Hz, the sound-pressure level was mostly invariant to sound-source position.

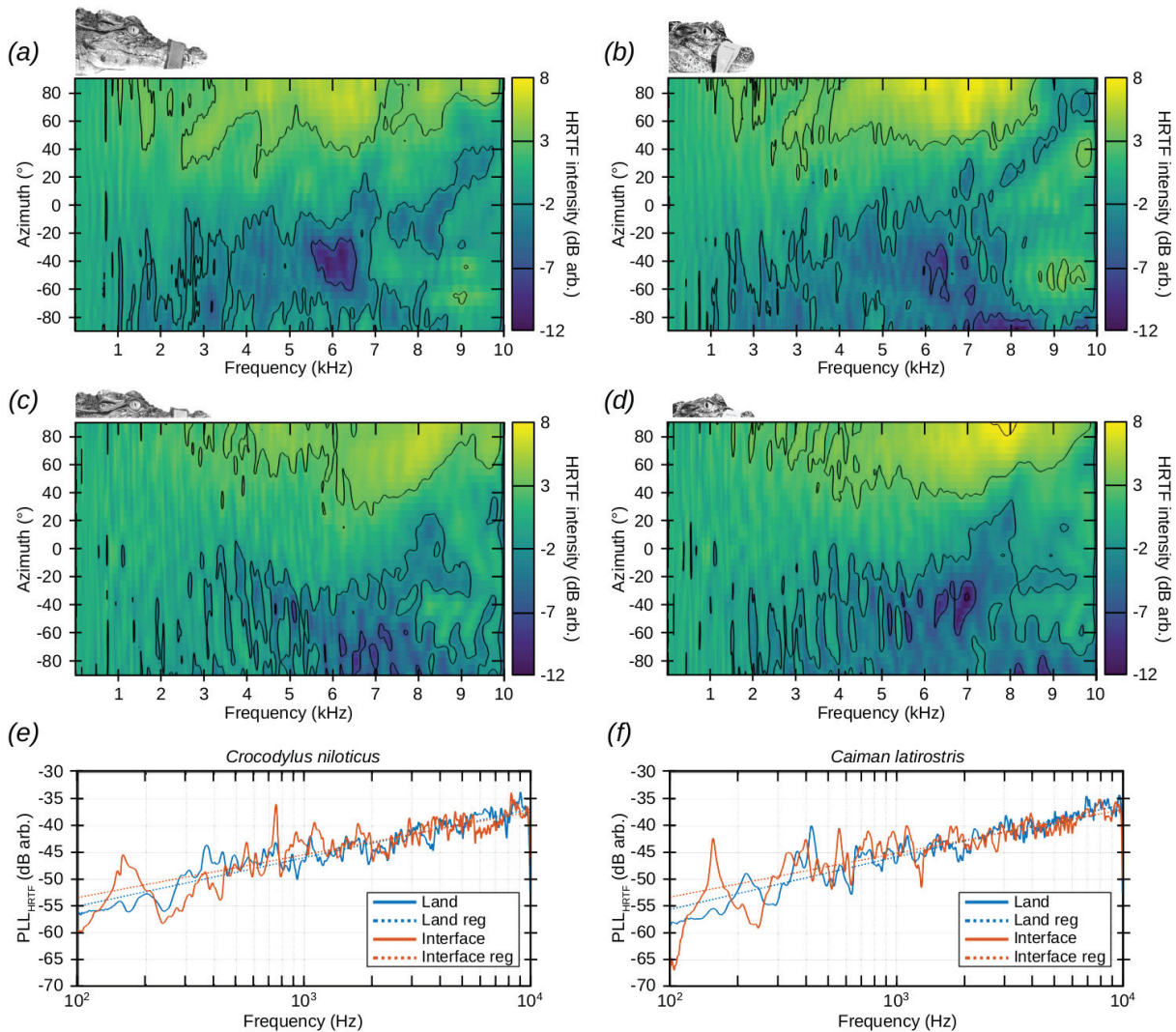


Figure 4.2 – Head-Related Transfer Functions measured on awake animals in two natural positions. (a) HRTF measured on *Crocodylus niloticus* in the land condition. (b) HRTF measured on *Caiman latirostris* in the land condition. (c) HRTF measured on *Crocodylus niloticus* in the interface condition. (d) HRTF measured on *Caiman latirostris* in the interface condition. The considered animal and configuration are represented above each panel at scale 1 / 12. (e) Potential localisation Level measured on *Crocodylus niloticus* in land (blue) and interface (red) conditions. (f) Potential localisation Level measured on *Caiman latirostris* in land (blue) and interface (red) conditions. (e), (f) Solid lines correspond to raw data and dashed lines are linear regressions.

Besides this general picture, HRTFs were characterised by 'bumps' and 'notches' which may increase the locatability of the sound source. Globally, the complexity of the HRTF patterns increases with frequencies (figure 4.2). As the emitted sound signal showed equal levels across the whole frequency spectrum, the variations of this level are due to the filtering effect of the head. These complex shapes may underlie the complexity of the acoustic field surrounding the animals' head. For instance, when the Nile crocodile was in the land condition (figure 4.2a), the sound-pressure level near 6 kHz was strongly influenced by the source angle (variations from -11 dB up to 6 dB), with a marked area of low levels when the source was positioned at -40° .

Overall, these results suggest that HRTF localisation cues are already present near 1 kHz in both land and interface conditions, and become more important when sound frequency increases. This is further illustrated by the Potential localisation Levels (PLLs) displayed on figure 4.2e and f. PLLs represent the amount of external acoustic localisation cues measured at the tympanic membrane level (see Methods). In accordance with HRTF results, PLLs increase exponentially with sound frequency (i.e. linearly with the logarithm of the frequency). They look very similar in both species and conditions (land condition: 2.7 dB/octave for the crocodile and 2.9 dB/octave for the caiman; air-water interface condition: 2.4 and 2.5 dB/octave, respectively).

Impact of skull size and acoustic coupling through the interaural canal

The HRTFs measured on the three skulls of *Crocodylus niloticus* are displayed on figure 4.3a-c. Compared to those obtained in alive animals, HRTFs show mainly the same pattern with more complex cues in high frequencies and a higher intensity level in the ipsilateral side. In the low frequency range ($f < 1\text{kHz}$), it can be noticed that HRTF patterns appear more homogeneous in contrast to those measured on alive animals. Nevertheless, the main difference is the presence of a 'crescent shaped' area of low sound-pressure level (underlined by the white continuous line on the HRTF colour maps in figure 4.3a-c). This pattern, consistently found in the three skulls, is included in a frequency band which is directly dependent on the skull size (3.5 - 6.5 kHz, 2.5 - 6.5 kHz and 1.7 - 5.5 kHz for the small, medium and large skulls, respectively), and may be due to destructive interferences caused by the interaural canal. Considering one ear, the difference of pathway between the direct wave and the wave arriving from the other ear through the interaural canal induces a phase difference Φ :

$$\Phi = 2\pi f \frac{\delta}{c}, \quad (4.6)$$

where δ is the difference of pathway in meters, c the sound velocity and f the frequency. From relation 4.6, if $\Phi = \pi [2\pi]$, we can compute the frequencies corresponding to destructive interferences inside the interaural canal f_{ic} :

$$f_{ic} = \frac{c}{2\delta}. \quad (4.7)$$

This simple geometrical model plotted on figure 4.3a-c indeed suggests that this pattern is due to the interaural canal.

In line with what we found in alive animals, the effect of sound-source position on HRTFs varied as a function of skull size. For instance, a 2 kHz sound produces complex level variation that depended on the sound-source position in the larger skull (between -4 and $+4$ dB), while the sound-pressure level remained constant for all azimuths (0 dB) for the small and medium skulls. Moreover, the maximum sound-pressure level areas measured on the ipsilateral side extended to a lower frequency range when skull size increased. For an incidence of 90° , the 3 dB contour line starts at 4040 Hz, 3050 Hz and 2120 Hz for the small, medium and large skulls, respectively.

In skulls measurements, the Potential localisation Levels (PLLs) did not increase linearly with the logarithm of the frequency (figure 4.3d) and it is not relevant to model its evolution using linear regression. In the low frequency range ($f < 1\text{kHz}$), the PLLs remained almost steady around -60 dB. For frequencies larger than 1 kHz, the PLLs increased with frequency in line with the complexity of HRTF patterns. In skulls, HRTFs depended on the global shape of the head but were also modified by the interaural canal, causing a non linear evolution of the PLLs.

Binaural cues

Based on formula 4.1, PLLs were computed from ILDs and calculated using the relation 4.5 (figure 4.4a and b). As displayed in figure 4.4a-c, the PLLs calculated for alive animals increased monotonically with the logarithm of frequency, with no noticeable impact of species or condition. The effect of head size is emphasised by PLLs calculated from skulls. Thus for a 1 kHz sound, PLL is equal to -52 , -49 and -38 dB for the small, medium and large skulls, respectively (figure 4.4c). ILDs are stronger for frequencies higher than 1 kHz, with a sudden increase of the slope near 1 kHz of PLLs measured on skulls.

We assessed ITDs on the medium size skull in only two conditions: the interaural canal was either obstructed with an adhesive or opened (figure 4.4d). The ITDs results are very close to those obtained by Carr et al. on *Alligator mississippiensis* (Carr et al., 2009): ITDs are symmetrical to the normal incidence and vary monotonically with the position of the sound source. When open (figure 4.4 right side of panel d), the interaural canal led to a decrease in ITDs, offering a shorter pathway to acoustic waves. As a result, the maximum of ITD (at 90°) is decreased by about $50 \mu\text{s}$ when the canal is let

free, independently from the frequency.

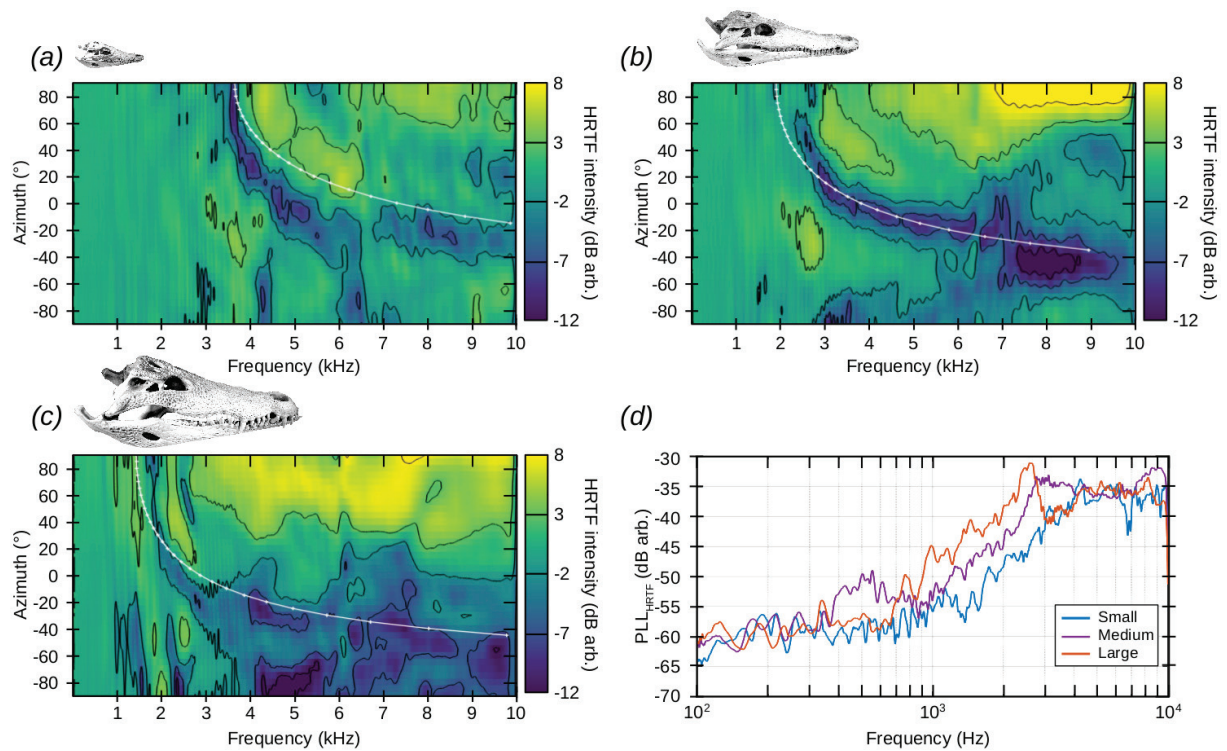


Figure 4.3 – Head-Related Transfer Functions measured on three skulls of different sizes. (a), (b) and (c): HRTFs measured on three *Crocodylus niloticus* skulls of different lengths: 6.9cm, 16.5 cm, and 22.7cm, respectively. The solid white line represents the destructive interferences based on a simple geometrical model of the path difference. The considered skull is represented above each panel at scale 1 / 12. (d) Potential localisation Level computed for the three skulls: 6.9 cm (blue), 16.5 cm (purple), and 22.7 cm (red).

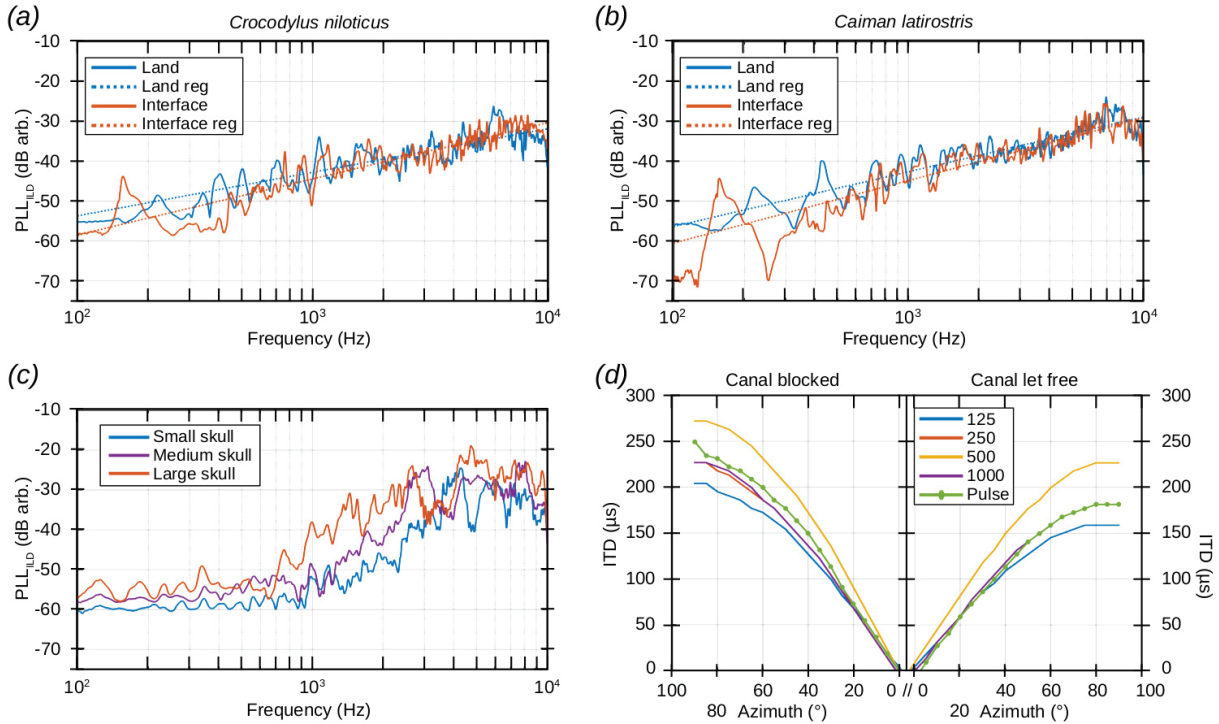


Figure 4.4 – Binaural cues measured on awake animals and skulls of different sizes. Potential localisation Level computed on ILD for *Crocodylus niloticus* (a) and *Caiman latirostris* (b) measured in the land (blue) and interface (red) situations. Dashed lines in (a) and (b) corresponds to linear regressions. (c) Potential localisation Level computed for ILD for three different sized Nile crocodile skulls: 6.9 cm (blue), 16.5 cm (purple), and 22.7 cm (red). (d) ITD measured for 4 pure tones (125, 250, 500 and 1000 Hz) and for a pulse with the interaural canal blocked (left) and open (right).

4.4 Discussion

Our study presents evidence that the morphology of the head of crocodylians induces monaural and binaural acoustic cues available to the animal and potentially useful to obtain information on the position of a sound source. These cues are still present when most of the animal body is underwater, suggesting that the well-developed external ear formed by the horny and prominent bone is efficient to provide external localisation cues both on the land and at the interface. This could represent an evolutionary adaptation to the peculiar amphibious behaviour of crocodylians.

Spectral monaural cues (HRTF) are present mainly for frequencies higher than 1 kHz. Their saliency increases with sound frequency, and they are strongly influenced by head size, with a shift to a lower frequency range in larger heads. Interestingly, we found that HRTFs cues are very similar in both 'land-' and 'air-water interface' conditions. This suggests that the ability to use monaural cues for sound source localisation may be alike in both conditions, despite only part of the crocodile's head being exposed in the interface condition. Our investigations on skulls underline the importance of the interaural

canal, which creates destructive interferences that may further facilitate sound-source localisation. In addition to highlighting HRTF cues, we confirm the presence of ILD cues (mainly for frequencies above 1 kHz) as well as ITD cues (mainly in the low frequency range, below 1 kHz). Altogether, monaural and binaural cues may allow crocodylians to accurately localise the position of a broadband sound source in their environment.

Overall, our results are consistent with Bierman et al. (Bierman et al., 2014). These authors concluded from their measurements of external cues that the *"acoustic space cues generated by the external morphology of the animal are not sufficient to generate location cues that match physiological sensitivity"* (Bierman et al., 2014). Indeed, they demonstrated that the level of physiological sensitivity is due to the contributions of the sound localisation cues, the internal coupling of middle ears and the directionality of the eardrum. However, Bierman et al. worked on very young alligators, with an interaural distance of 2.25 ± 0.2 cm, whereas our animals showed interaural distances of 3.9 cm and 4.7 cm, respectively, for the broad-snouted caiman and the Nile crocodile. The juvenile skull of *Crocodylus niloticus* had interaural distances comparable to those of the alligators studied by Bierman et al. (2.4 cm). Besides, they conducted their experiments for frequencies lower than 4 kHz and they obtained a maximum variation of 8 dB (for a frequency of 2 kHz). In the same frequency range, we measured a slightly higher dynamics of 9 dB maximum (cf. figures 4.2 and 4.3). In the present study, the frequency span is increased up to 10 kHz because for high intensity sounds, the high frequencies may be of interest for crocodylians. Indeed we cannot exclude the potential use of frequencies higher than 2 kHz, and as we have strong dynamics (up to 20 dB), this frequency region may be relevant for sound localisation. Assuming the small size of the animals and that the external cues are shifted to low frequency when size increases (figure 4.3), our results extend Bierman's work and is coherent with their results.

Given that the crocodylians' audiogram is centred on the lower part of the frequency spectrum (1-2 kHz; Wever, 1971; Higgs et al., 2002; Manley, 1970) and that the external localisation cues increase with frequency, the biological relevance of the HRTFs has to be discussed. The frequency span used in our study was chosen to widely cover the audition curve of crocodylians, and to illustrate the low-frequency shift phenomena induced by size. If we consider the maximum of sensitivity of audition in crocodylians (i.e. 1.5 kHz), the dynamics measured on external cues is more than 5 dB (figure 4.2), which is potentially sufficient for sound localisation. In blackbirds, pigeons and in sea lions the minimum detectable binaural level difference is around 3dB (Hienz et al., 1980; Moore et al., 1977) whereas it is 1 dB in humans (Mills, 1960).

Our study focused on two awake juvenile animals belonging to two different species. However, the results could be extended to larger animals. Although we found a comparable amount of potential localisation cues in both experimental animals, slight differences in HRTFs between species were visible in the upper part of the frequency spectrum.

Studies in humans have shown that individual morphology (i.e. rather small morphological differences) may significantly influence HRTFs (Moller et al., 1996). As both our animals had comparable body sizes, these differences may have been induced by their respective head morphology (e.g. the Nile crocodile has a much more slender snout than the caiman). In larger animals, these slight differences should be enhanced and shifted towards lower frequencies. As a consequence, they may significantly influence HRTFs within their hearing range.

Besides HRTFs, the internal acoustic coupling may increase sound localisation because two waves arrive at the same eardrum: one from the outside and one from the inside through the interaural canal. The influences of this coupling were shown using a method of geometrical acoustics on skulls (figure 4.3). The interaural canal also influences the ITD by decreasing its value from 50 μ s. While this result looks opposite to previous published data (Carr et al., 2016; Christensen-Dalsgaard et al., 2011), it is explained by the fact that we consider the interaural canal on skulls but without any soft tissue (such as eardrums). The canal acts as a wave-guide without any obstacle to the propagation of the acoustic wave. Bierman et al. demonstrated the implication of the directionality of the eardrums on physiological relevance of ITD computation thanks to a laser vibrometry method (Bierman et al., 2014).

ITDs are large in the low-frequency region (from 100 to 1000 Hz), whereas ILDs predominate in the high frequencies region ($f > 1500$ Hz). In his duplex theory developed for humans (Rayleigh, 1909), Lord Rayleigh asserted that ITDs and ILDs ensure strong localisation abilities across the full auditory spectrum thanks to an overlap of both binaural cues between 1 and 1.5 kHz (Feddersen et al., 1957). This theory cannot be applied to all vertebrates: as an example, the barn owl combines ITD and ILD information in the same frequency range (between 3 and 10 kHz) to localise respectively the azimuth and the elevation (Coles et al., 1988; Knudsen et al., 1979). In another way, crocodilians might also qualify this theory. Carr et al. (Carr et al., 2009) demonstrated that ITD is not neurally processed for frequencies higher than 1 kHz because of a lack of phase locking. As a consequence, ITDs and ILDs are weak in the band between 1 and 1.5 kHz, creating a lack of localisation cues in this frequency region, at least for juvenile and medium-sized crocodilians. The maximum of vibration of the eardrum was measured in this precise bandwidth (Bierman et al., 2014), which could be used to compensate this 'gap' of localisation.

As a conclusion, our results establish a strong background regarding the acoustic cues available to crocodilians when they localise a sound source in their environment -a frequent situation in several behavioural contexts, from predation to caring for the young. Our study focused on aerial hearing. However, crocodilians are amphibious animals and previous studies suggested a fairly good underwater hearing sensitivity. It would thus be interesting to investigate sound localisation cues in an underwater context.

Finally, sound localisation abilities remain also poorly investigated and, even if a few behavioural observations in crocodylians were published (Beach, 1944; Chabert et al., 2015), the behavioural relevance of sound localisation cues needs to be tested in following research.

Supplementary material

Table 4.1 – Biometry and dimensions of the animals and skulls used in the present study.

Material	Species	Total length (cm)	Rostral snout length (cm)	Rostral snout width (cm)	Interaural distance (cm)	Weight (kg)
Juvenile crocodile	<i>Crocodylus niloticus</i>	91.5	6.9	5.1	4.7	2.7
Juvenile caiman	<i>Caiman latirostris</i>	68.5	4.4	5.0	3.9	1.5
Adult skull	<i>Crocodylus niloticus</i>	×	22.7	10.4	6.0	×
Young skull	<i>Crocodylus niloticus</i>	×	16.5	6.5	4.5	×
Juvenile skull	<i>Crocodylus niloticus</i>	×	6.9	3.8	2.4	×

Sound localisation accuracy in the Nile crocodile *Crocodylus niloticus*

Article in preparation for the **Journal of the Acoustical Society of America Express Letters** (JASA-EL, asa.scitation.org/journal/jel).

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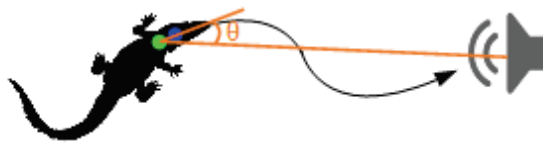
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Graphical abstract

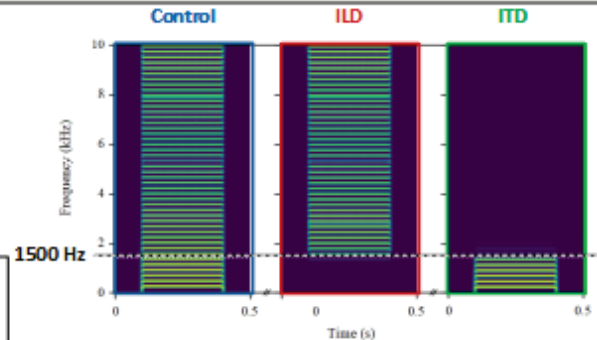
What are the performances of sound localisation in crocodilians?
Do crocodilians use both binaural cues in sound localisation tasks?

The Interaural Time Differences (**ITD**) are not coded for frequencies higher than 1000 Hz (Carr et al., 2009). The Interaural Level Differences (**ILD**) appear potentially relevant for frequencies higher than 1500 Hz (Papet et al., 2019). To test the crocodiles' sound localisation abilities, the signals of interest are high- and low-passed to respectively encourage the use of the **ILD** and **ITD**. The **control** condition is considered as the no filtered signal (i.e. supposed to stimulate both **ILD** and **ITD**).

Methods

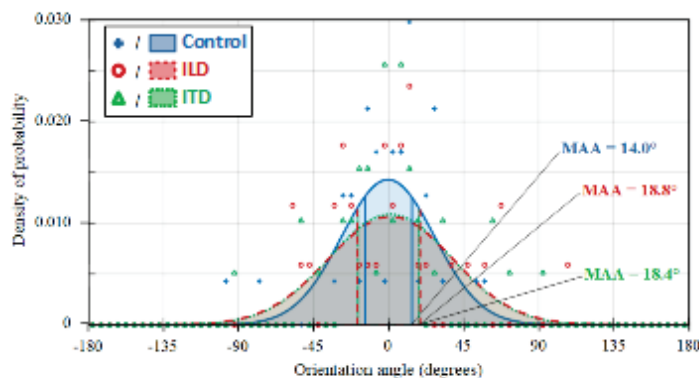


Conditioning
The animal were conditioned to go to the origin of the sound source when playing the signal.

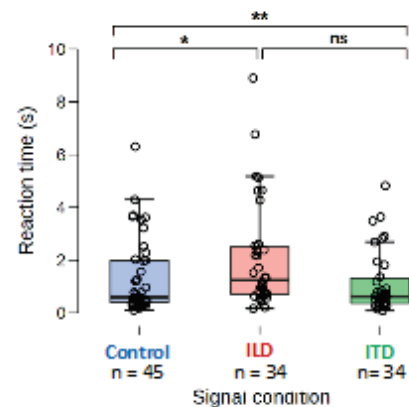


Spectrographic representations of the three considered signals: **control**, **ILD** and **ITD**.

Results



Densities of probability of the final orientation angles (θ) in the three stimulus conditions. The Minimum Audible Angles (MAA) are considered as the half standard deviation of the distributions.



Reaction times measured in the three stimulus conditions. Average values: **Control**: 1.29s; **ILD**: 2.10s; **ITD**: 1.12s.

The distribution of final orientation angles are centred around 0° in the three stimulus condition. The MAA measured in control condition is lower than when only **ILD** or **ITD** is stimulated.

ILD stimuli induced significantly slower reactions than when playing **control** and **ITD** signals.

Comment: The MAA was computed considering the loudspeaker as a punctual source. This may induce an overestimation of the MAA. New analyses considering the loudspeaker as a distributed sound source should substantially reduce the estimated MAA.

Conclusions

The tested crocodiles showed good sound localisation performances and we measured a Minimum Audible Angle (MAA) of 14° . Sound localisation relies on both **ILD** and **ITD**. When using only the binaural cues, the MAA is lower than when playing back control stimuli. When **ITD** is lacking, crocodiles need more time to find the position of the sound source. **ITD** seems predominant in sound localisation compared to **ILD**.

Abstract

Crocodylians have a developed sense of hearing. Here we use behavioural experiments to explore their sound localisation abilities. We trained two Nile crocodiles *Crocodylus niloticus* to come to a sound source (artificial harmonic complex tones) while cruising in water. We gave a first estimation of the Minimum Audible Angle (smallest angle allowing the discrimination between two sound sources with a probability of 50 %) inferior to 14° . We further assessed the respective role of Interaural Time Differences (ITD) and Interaural Level Differences (ILD) by testing the two subjects with filtered versions of the artificial sound stimuli. We found that crocodiles can rely either on ITD or ILD to localise a sound source. However, the MAA is larger when one of these cues is lacking and the absence of ITD increases the time crocodiles need to find the sound source.

Keywords: Nile crocodile, Sound localisation, Bioacoustics, Interaural Level Differences, Interaural Time Differences, Crocodylians.

5.1 Introduction

Sound perception is of paramount importance for many animals to communicate with conspecifics and to detect predators and preys. One important aspect of sound perception is sound localisation. Sound localisation refers to the ability to determine the spatial origin of a sound and is a widely shared ability across species. The nature and the relevance of acoustical cues for sound localisation have been extensively described for both humans and animals (Popper et al., 2005; Klump, 2000). Both monaural and binaural acoustic cues can provide information about the spatial origin of sounds. Monaurally, due to sound reflection and sound absorption by the head ("acoustic shadow"), the frequency content of a sound reaching one ear depends on the direction the sound is coming from (Middlebrooks et al., 1990; De Mey et al., 2008). Binaurally, differences between the propagation times from the sound source to the right and left ears lead to Interaural Time Differences (ITD), a cue which is reputed helpful for sound localisation (Middlebrooks et al., 1990; Carr et al., 2015). Moreover, head acoustic shadow also leads to intensity between both ears named Interaural Level Differences (ILD). ITD and ILD are frequency-dependent. The perception of ITD requires neuronal temporal coding which is reputed to be more accurate for low frequency sounds. Conversely, high frequency sounds are more likely to be filtered by the animal head and body, and the perception of ILD is then enhanced for high frequency sounds (Feddersen et al., 1957). Many species use both ITD and ILD to localise sound sources, e.g. humans (Rayleigh, 1909), Japanese macaques *Macaca fuscata* (Brown et al., 1978), and common vampire bats *Desmodus rotundus* (R. Heffner et al., 2015). However, some animals (e.g. cattle, horse) rely only on ITD for sound localisation (R. Heffner et al., 1992b; H. Heffner et al., 1984), whereas others rely only on ILD (e.g. big brown bat *Eptesicus fuscus*, Norway rat *Rattus norvegicus*; R. Heffner et al., 2016; Koay et al., 1998; Wesolek et al., 2010).

The hearing system of crocodylians is well developed, a trait correlated with their predator and social lives (Vergne et al., 2009). They use sounds in synergy with other senses to find their prey and to communicate (Chabrolles et al., 2017; Vergne et al., 2009). Several studies revealed that the crocodylian hearing range goes from about 100 Hz up to 3000 Hz in the air (Wever et al., 1957; Higgs et al., 2002; Manley, 1970), with a peak of sensitivity around 1000 Hz (Bierman et al., 2014). Regarding sound localisation, both monaural and binaural acoustic cues are available to a crocodile when cruising at the air-water interface with only a small part of the head emerged (Bierman et al., 2014; Papet et al., 2019). In the American alligator *Alligator mississippiensis*, Carr et al. demonstrated that the neural processing of ITD is efficient for sounds up to a maximum frequency of 1000 Hz (Carr et al., 2009). Besides, Papet et al. suggested that ILD cues are available above 2000 Hz (Papet et al., 2019). These results are in line with the duplex theory (Rayleigh, 1909) which emphasises the "frequency of ambiguity" (f_a) that separates the

frequency domain where only ITD are relevant from the frequency domain where only ILD are relevant. Given the published data (Carr et al., 2009; Papet et al., 2019), we thus assume that f_a should be around 1500 Hz in crocodiles.

In the present study, we used behavioural experiments in the laboratory to investigate the sound localisation abilities of Nile crocodiles *Crocodylus niloticus*. We quantified their Minimum Audible Angle (MAA) and tested if they rely preferentially on ITD or ILD to localise a sound source.

5.2 Methods

Animals

The animals included in this study were two 2-year-old Nile crocodiles. They belonged to the zoo "La Ferme aux crocodiles" (Pierrelatte, France), and had been accommodated in the ENES lab in dedicated areas since they were 6 months old. At the time of the experiment, the individuals were 60.0 and 55.5 cm long and their interaural distances were 3.3 and 3.2 cm. Both individuals had never been included in any experimental protocol. The animals were exposed to an artificial 12/12 day/night alternation. This study was conducted under the ethical agreement of the ENES lab (D 42-218-0901).

Apparatus

We conducted the experiments in a square pool of 1.75 m side inside a $1.8 \times 2.3 \times 2.2$ m acoustic booth with panels on the walls to enhance acoustic absorption (Figure 5.1). The experiments were conducted in the dark and in a quiet acoustic environment (background noise below 40 dB SPL). All experiments were filmed with an infrared camera (ABUS TVCC34010). Two loudspeakers (Audiopro Bravo Allroom Sat) were placed on the edge of the pool, just above the water surface. Their position changed randomly between each experimental session (with a minimum distance of separation of 1 m). Both loudspeakers were driven by the experimenter from outside the acoustic booth. The audio-video synchronisation was ensured by a LED triggered by the stimulus emission and flashing in the camera vision field. The LED was oriented such as the crocodile was not able to see it and a control experiment with no sound evidenced that the flash did not influence the crocodile's behaviour. A water level of 15 cm allowed the animal to swim in a natural position with the full body underwater except its nostrils, eyes and ears.

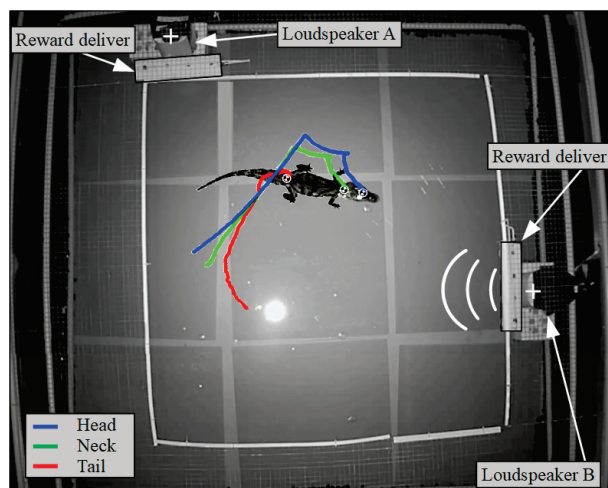


Figure 5.1 – Experimental pool. The subject’s behavioural response to stimuli was tracked using three points: the head (blue), the neck (green) and the base of the tail (red).

Experimental stimuli

As illustrated on Figure 5.2, the signals were 500 ms harmonic complex tones ("buzz") at three different fundamental frequencies ($f_0 = 207, 220$ and 233 Hz). These harmonic complex tones were generated at 44100 Hz sampling frequency by adding all the harmonics from f_0 to 10 kHz. To avoid clicks, they were faded in and out using 50 samples-long half Hann windows and filtered with a 3rd order band-pass filter (cut-off frequencies equals to 70 Hz and 10 kHz). Signals were normalised in RMS levels to be displayed at 60 dB SPL.

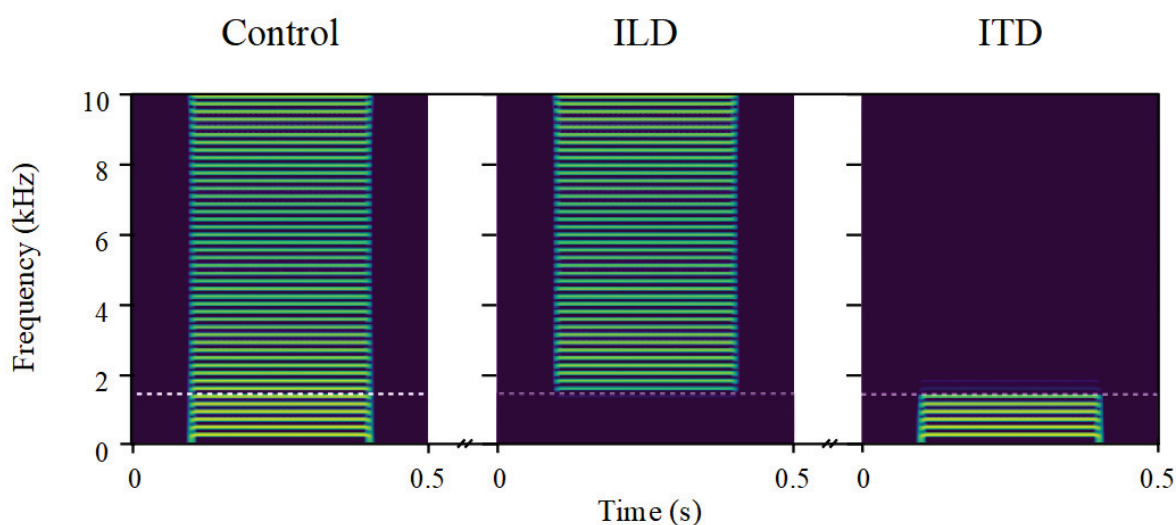


Figure 5.2 – Spectrographic representations of the experimental signals in the three stimulus conditions.

To assess the respective effect of ITD and ILD, we built three families of experimental stimuli from the original buzzes, assuming a "frequency of ambiguity" f_a of 1500 Hz: 1) control buzzes: original signals (bandwidth = [70, 10000] Hz); 2) ILD buzzes: high-pass filtered original signals (bandwidth = [1500, 10000] Hz); 3) ITD buzzes: low-pass filtered original signals (bandwidth = [70, 1500] Hz). We assume that the ITD stimuli should favour the use of ITD while the ILD stimuli should favour ILD cues. Besides and according to Papet et al., 2019, ILD and control buzzes should preserve monaural spectral cues.

The playback sequences were a succession of 4 renditions of identical buzzes, with a pseudo-random rhythm (2 ± 0.2 s of silence between each buzz). The total duration of each sequence was 11 s.

At the end of the study, one subject (crocodile 1) had been challenged with 23 control, 12 ILD and 14 ITD stimuli, while the other subject (crocodile 2) had been challenged with 22 control, 22 ILD and 20 ITD stimuli.

Testing procedure

Prior to any experiment, both crocodiles were trained to come to a sound source to get a food reward ("conditioning experiment", Gomez et al., 2007; Holt et al., 2004; Kastak et al., 2005). A behavioural response was considered as successful when the crocodile approached closer than 15 cm from the loudspeaker playing the target signal (control buzzes).

Once trained, the crocodile was placed in the pool at least 30 minutes before the experiment, and let alone without any stimulation (Figure 5.3). We monitored its behaviour and never started an experiment before it stopped exploring the pool. The stimuli were then played back in a random order, from a randomly selected loudspeaker. Signals were separated by silences randomly selected in the [4, 6] minutes interval (see Figure 5.3 for an illustration of the timeline of the experiment).

The crocodile's behaviour was assessed during the two minutes following the onset of a sound stimulus. If the subject approached the loudspeaker emitting the sound, it was rewarded with food ([5, 10] g of meat) nearby the loudspeaker. We played back a maximum of 8 stimuli during a given testing session (Figure 5.3). After the last stimulus, the animal was let in the pool for at least 30 minutes before returning to its enclosure. The crocodiles were only fed during these experimental trials. The quantity of their food intake was continuously monitored to ensure that they get a sufficient amount of food ([50, 100] g per week).

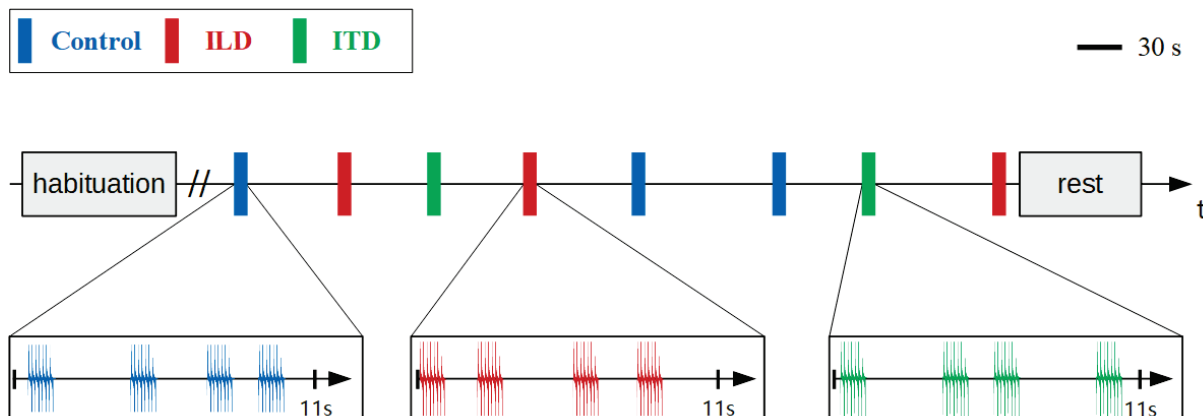


Figure 5.3 – Timeline of the experiment. The light grey areas correspond to the habituation and rest periods. Each thick vertical bar represents a signal emission. The bottom plots represent the detailed temporal organisation of three signals.

Data processing

We assessed the behaviour of the tested animals through video analysis using Kinovea software (www.kinovea.org). We analysed the trajectories using the coordinates of three points on the body of the crocodile: the base of the tail, the neck and between the ears (Figure 5.4). Using these coordinates and the position of the active loudspeaker, we defined the following four parameters: 1) the body flexion angle ϕ : the angle between the head, the neck and the tail (Figure 5.4); 2) the orientation angle θ : the angle between the pointing direction of the animal and the direction between the neck and the loudspeaker position (Figure 5.4) - when the animal was facing the loudspeaker, the orientation angle was 0° ; 3) the instant speed of the animal: the derivative of the movement of the neck of the animal; 4) the reaction time the time delay between the onset of the first signal and the first noticeable movement of the animal.



Figure 5.4 – Illustration of the flexion ϕ angle (left) and orientation θ angle (right). The black cross represents the loudspeaker.

A classical indicator to quantify sound localisation ability is the Minimum Audible Angle (MAA; Mills, 1958a; Feinstein, 1973; Holt et al., 2004). It is computed as the smallest angle of separation allowing the discrimination between two sound sources with a probability of 50 % (or 75 % in some studies). Here we assumed that MAA corresponds to 50 % of the standard deviation of the distribution of final angles of orientation θ centred around 0° .

We normalised trials duration across trials. We defined the beginning of a trial ($\tilde{t} = 0$) as the onset of the first buzz, and the end of a trial as the moment when the animal stopped moving after the last buzz ($\tilde{t} = 1$). For each trial, variations in the orientation angle θ according to the normalised time \tilde{t} were fitted to a simple exponential model as follows:

$$\theta = a \times e^{b\tilde{t}} \quad (5.1)$$

with a and b being the parameters of the model. The horizontal asymptote is a , and $a \times b$ corresponds to the slope the exponential model at $\tilde{t} = 0$. From this model, the temporal constant τ was computed as: $\tau = \frac{1}{b}$. The data set was fitted to the exponential using a least-mean square procedure.

5.3 Results

A typical behavioural pattern observed during an experimental session is plotted on Figure 5.5. The parameters related to the animal's trajectory are displayed according to time: orientation and flexion angles (ϕ and θ) and displacement speed (Figure 5.5). This example illustrates how a played back stimulus can trigger the crocodile's behaviour.

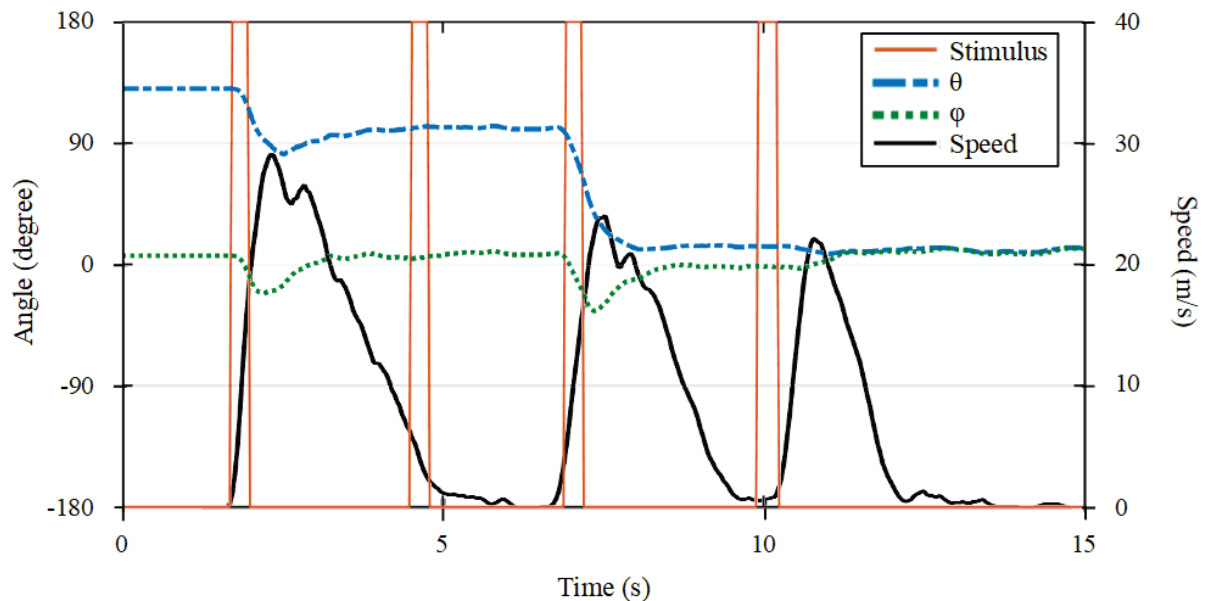


Figure 5.5 – Temporal analysis of a crocodile's behavioural response during a playback trial. Solid orange line: time line of the sound stimulus emission; Blue dashed line: variation of the crocodile's orientation angle θ ; green dotted line: variation of the crocodile's flexion angle ϕ ; black solid line: variation of the crocodile's displacement speed ($\text{m}\cdot\text{s}^{-1}$). In this example, the tested crocodile changed its orientation and moved after the first, third and fourth rendition of the sound stimulus; the second rendition did not drive any specific response.

Figure 5.6 reports the reaction times for the three experimental conditions. The reaction times measured in the control and the ITD conditions ($RT_C = 1.29 \text{ s}$ and $RT_{ITD} = 1.12 \text{ s}$ respectively) were not statistically different ($p = 0.838$). On the contrary, ILD stimuli induced a significantly slower reaction time ($RT_{ILD} = 2.10 \text{ s}$) than the control ($p = 0.014$) and the ITD stimuli ($p = 0.005$). The total duration of trials was between 2.3 and 19.1 s (average values for each conditions: control : 11.2 s; ILD: 13.0 s; ITD: 12.6 s) and show no significant differences between conditions (control-ILD: $p = 0.234$; control-ITD: $p = 0.568$; ILD-ITD: $p = 0.822$).

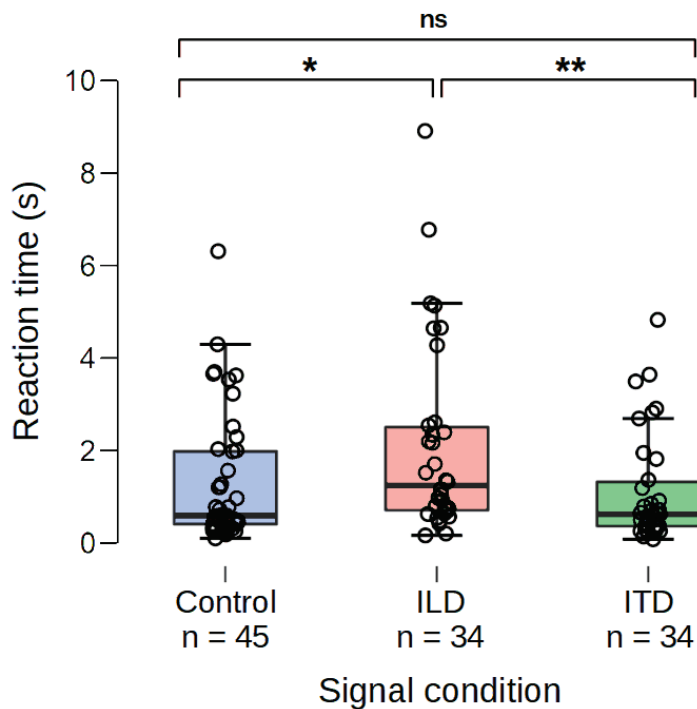


Figure 5.6 – Reaction times of the crocodiles according to the condition. A post-hoc test was computed between each pair of condition: control-ILD: $p = 0.014$; control-ITD: $p = 0.567$; ILD-ITD: $p = 0.005$. Each circle represents a trial and the large line in the box plots are the median values.

The variation of the orientation angles θ during all trials is reported in Figure 5.7 for the three experimental conditions. The “jumps” of the orientation angles which are visible on Figure 5.7 were associated to crocodile’s movements right after the playback of a stimulus. The final orientation angles (black points at $t=0$ on Figure 5.7) were centred around 0° for the three experimental conditions (Figure 5.8). This result suggests that the subjects succeeded in localising the sound source whatever the stimulus condition (average final angles: $-0.3 \pm 27.9^\circ$, $1.2 \pm 37.5^\circ$, and $1.0 \pm 36.7^\circ$ for the control, ILD and ITD conditions respectively). These differences were not significant (control-ILD: $p = 0.966$; control-ITD: $p = 0.995$; ILD-ITD: $p = 0.945$).

Because the mean final orientation angle θ measured in the control condition was very close to 0° and based on the definition of the Minimum Audible Angle presented in the Methods, the measured MAA for a broadband signal was equal to 14.0° (Figure 5.8). The MAA was larger when playing back ILD and ITD stimuli (resp. 18.8° and 18.4° , Figure 5.8).

Finally, the temporal dynamics of the orientation angles were modelled according to the normalised time for each trial. The average temporal constant of all exponential models showed a higher value for the ILD condition ($\tau_{ILD} = 0.717$) than for the control ($\tau_C = 0.476$) and ITD ones ($\tau_{ITD} = 0.563$). This difference was significant between the control and ILD conditions ($p = 0.004$) while no significant difference was noted between

the ILD and ITD conditions ($p = 0.116$) nor between control and ITD stimuli ($p = 0.463$). This result suggests a more rapid localisation in the ITD and control conditions than when playing back ILD stimuli.

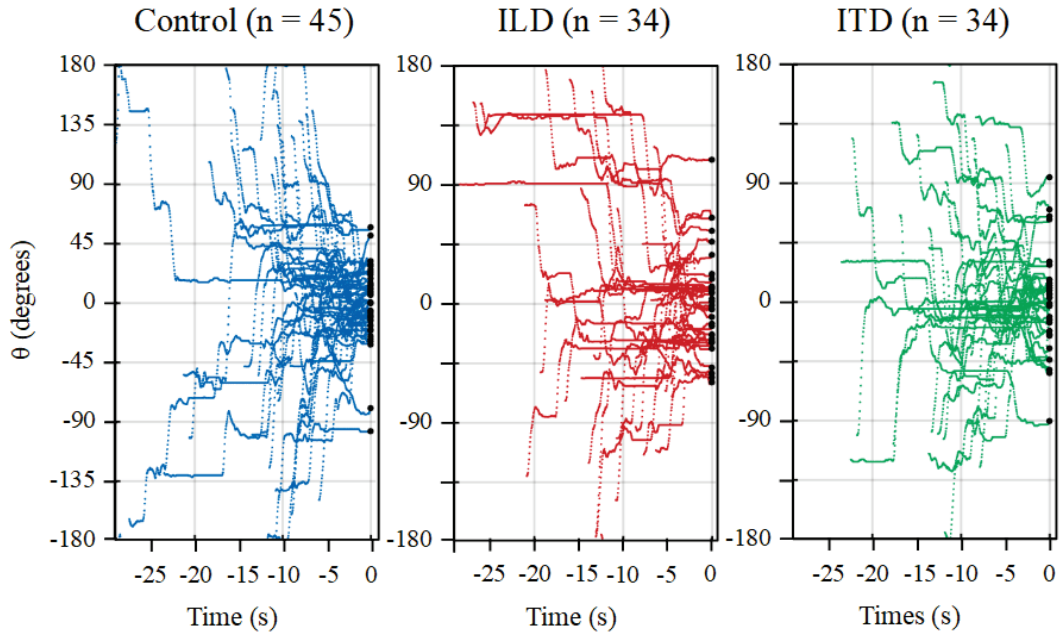


Figure 5.7 – Variation of the crocodiles' orientation angles θ during the playback experiment (all trials are represented; time is scaled across trials). Black points at $t = 0$ s correspond to the final orientation angles.

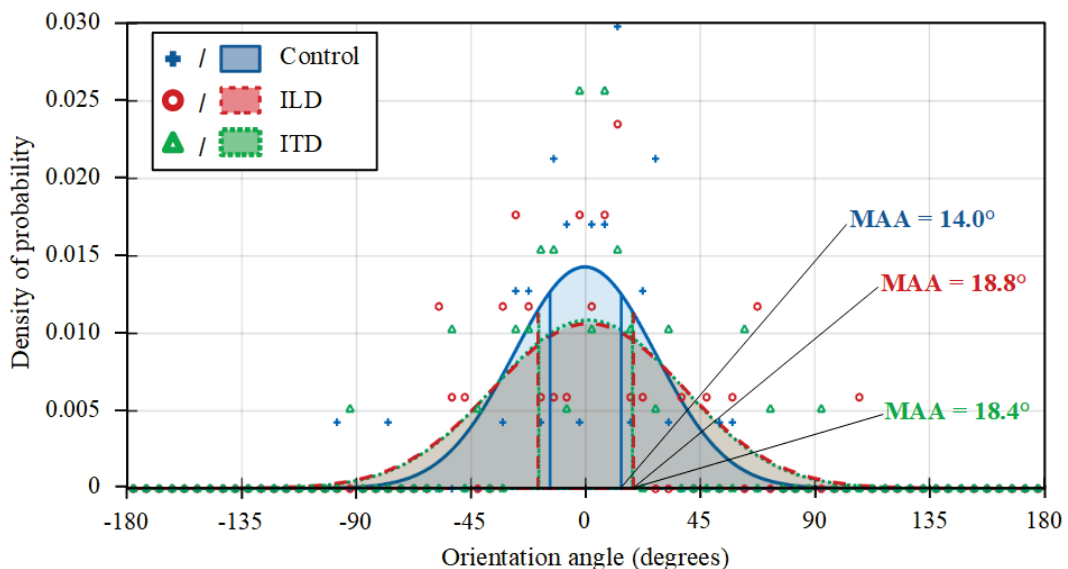


Figure 5.8 – Density of probability of the final orientation angles θ . The points correspond to the raw densities in the control (blue crosses), ILD (red circles) and ITD (green squares) condition. The filled lines are the gaussian fitting to the raw densities of probability (control condition: solid blue line; ILD condition: dashed green line; ITD condition: dotted red line). The vertical lines are plotted for $\theta = \pm$ MAA in each condition.

5.4 Discussion

Our study demonstrates that crocodiles have good localisation abilities, and that they use both ITD and ILD cues to localise a sound source. Interestingly, the Minimum Audible Angle (MAA) was larger when the tested crocodile could rely on only one of the two cues only. Specifically, the absence of ITD cues seems to make harder the task since the crocodiles needed more time to localise the sound source.

Indeed, and although both ILD and ITD stimuli were successfully localised, we measured a larger reaction time and a lower constant time value τ in the ILD condition. It is thus likely that ITD are predominant cues for sound source localisation in crocodiles. However, even though all experimental signals were equalised in dB SPL, the crocodilian auditory curve (centred around 1000 Hz, Higgs et al., 2002; Wever, 1971) may induce differences in loudness. The ILD stimuli may have been perceived by the animal at a lower intensity than the ITD ones.

The control and ILD stimuli produce monaural localisation cues (Papet et al., 2019; Bierman et al., 2014). The animals may thus have used a combination of both monaural and binaural cues to localise the position of the sound sources. The role of monaural cues might be tested by conducting localisation experiments where one of the two ears of the subject would be plugged. However a pilot experiment showed that the animal was bothered by the ear plug and that it is difficult to obtain normal behavioural responses to sound stimuli.

The MAA provided in the result section was computed considering the loudspeaker as a punctual acoustic source. This hypothesis may induce an overestimation of the MAA. New analyses, considering the loudspeaker as a distributed sound source, will be done before the manuscript to be submitted, and should reduce substantially the estimated MAA.

Crocodiles rely on a combination of sensory channels to localise preys and interact with conspecifics. For instance, they may rely on both audition and vision when hunting. This multisensory perception of the environment is a general feature of many animals, and it is interesting to consider sound localisation abilities under this perspective. Heffner and Heffner compiled data about visual and sound localisation accuracy in mammals (R. Heffner et al., 1992c) and found that the sound-localisation acuity of a given species is correlated with the size of its "best" visual field. These authors defend the idea that sound localisation is fitted to help the individual in focusing its visual attention. They report that animals with narrow visual fields as humans and cats require highly reliable sound localisation abilities. Conversely, animals with broad vision such as cows would not need accurate sound localisation abilities since the sound source has good chance to be already within their visual field. Interestingly, a recent study showed that crocodilians have an horizontal, elongated, visual fovea: their field of best vision

is widely expanded in the azimuthal plane (Nagloo et al., 2016). This is in accordance with their life at the interface between air and water: most of their interesting visual targets are located in a two-dimensional space. According to the hypothesis of Heffner and Heffner, crocodilians should display a bad ability of localising a sound source. With a crocodile's MAA of 14.0° , our results give support to this theory. Indeed, we would have expected these top predators which are used to target preys to show sharper sound localisation abilities. Their large visual field might have slightly relaxed the evolutionary constraints leading on their sound localisation abilities.

In conclusion, our study reports the first quantitative investigation on sound localisation behaviour in crocodilians. Using conditioning experiments, we managed to describe and quantify the movements of Nile crocodiles when approaching a sound source. The use of artificial signals allowed us to explore the respective importance of ILD and ITD during a sound localisation task. Our methodology and results thus suggest that the auditory world of crocodilians can be experimentally explored thoroughly, even if setting laboratory experiments on these fierce animals will always remain a challenge.

Acknowledgements

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Spatial Release from Masking in crocodilians



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Graphical abstract

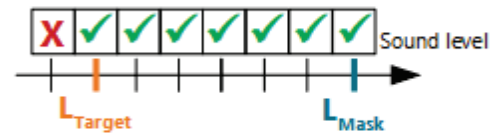
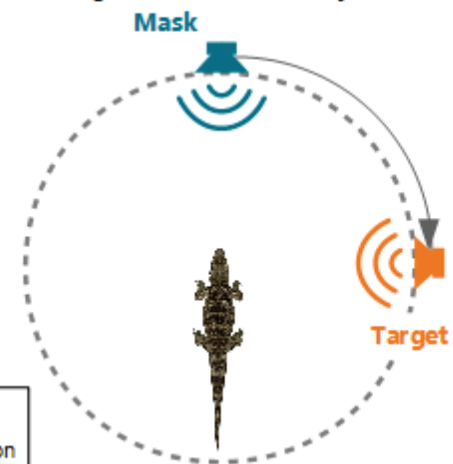
Do crocodilians use Spatial Release from Masking in noisy environments?

Spatial Release from Masking (**SRM**): Increase of the detection performances when spatially separating the target from the mask (compared to the co-located condition).

Target and mask are **co-localized**



Target and mask are **separated**



Methods

Wildlife

Distress calls
Mother-young interaction
Yacare caiman (*Caiman yacare*)



Open-air captivity

Juvenile calls
Young-young interaction
Nile crocodile (*Crocodylus niloticus*)

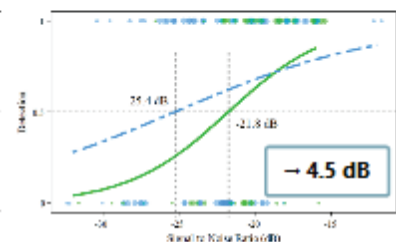
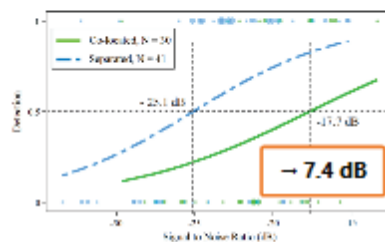
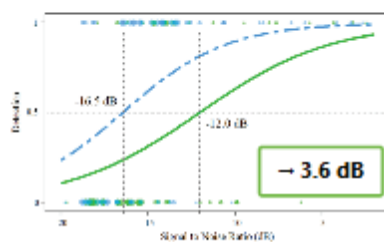


Go / No-Go

Synthetic signals
High motivation
Nile crocodile (*Crocodylus niloticus*)



Results



Conclusions

This study is the first evidence of the use of Spatial Release from Masking in crocodilians. The detection of the target was facilitated by an increase of the SNR and when the target was spatially separated from the mask. If the motivation of the subjects in the Go/No-Go experiment is high, the juveniles tested in open-air captivity and the females included in the wildlife experiment experienced important trade-offs impacting their use of SRM.

Abstract

Signal masking induced by environmental noise is an important constraint impairing acoustic communication. One strategy to overcome this issue is Spatial Release from Masking (SRM), i.e. the ability to discriminate a target signal from a masking noise when the target and the noise sources are spatially separated. In spite of its potential widespread importance, SRM has only been investigated in a limited number of species with a limited number of experimental approaches. Here we investigate SRM in crocodilians, where acoustic communication supports both parent-offspring and between-offspring interactions. We performed playback experiments in three different experimental situations. First, we tested female Yacare caiman *Caiman yacare* in the field, mimicking a situation where an isolated nestling was emitting distress calls in a noisy environment. Second, we tested SRM in semi-captive juvenile Nile crocodiles *Crocodylus niloticus* using juvenile contact calls. Finally, we conducted Go/No-Go experiments where trained Nile crocodiles had to discriminate synthetic sounds against a background noise. We found that detection performances increase when the target source was spatially separated from the noise source. We measured SRM values of 4.5 dB, 7.4 dB, and 3.6 dB in the field, the semi-captivity and the Go/No-Go contexts respectively. This is the first study demonstrating that crocodilians use SRM to discriminate signals of interest in a noisy environment. Our investigations, from naturalistic conditions to laboratory Go/No-Go set up, suggest that these amphibious animals take advantage of SRM in their daily life.

Keywords: Crocodilians, Spatial release from masking, Sound localisation, Bioacoustics.

6.1 Introduction

Acoustic communication is widely used in the animal world: sound signals propagate quickly over great distances even in obstructed environments, and they can support the coding of many information (Busnel, 1964; Bradbury et al., 1998). However, natural soundscapes are full of masking sounds emitted by various sources (Iglesias Merchan et al., 2014; Barber et al., 2011), and transferring information using sound signals in noisy environments can be extremely challenging (Lohr et al., 2003). In response to this constraint, strategies have evolved to improve the efficiency of acoustic communication. For instance, emitters may respond to ambient noise by increasing the signal intensity (Lombard effect; Manabe et al., 1998), by shifting the frequency content to avoid frequency overlapping with the noise (e.g. in great tits *Parus major*; Slabbekoorn et al., 2003; Villain et al., 2016), by increasing signal redundancy (Foote et al., 2004; Lengagne et al., 1999; Aubin et al., 2002), or by choosing specific positions that optimise signal transmission through the environment (e.g. songposts in songbirds, Mathevon et al., 2005; Mathevon et al., 2008; Dabelsteen et al., 1998). Receivers may also choose strategic positions to improve signal reception and limit the influence of noise sources (Mathevon et al., 1997; Nemeth et al., 2006). This behavioural strategy facilitates the Spatial Release from Masking (SRM), a process where the auditory system uses spatial cues to segregate a signal of interest (target) from noise sources (maskers). According to SRM, signal detection is better when the signal source is spatially separated from the noise source than when both signal and noise sources are co-located in the environment (Sabeti et al., 1991; Litovsky, 2012).

SRM has been investigated in several groups of animals, including humans. The seminal study by Sabeti et al. on human subjects demonstrated that SRM can be used in both the horizontal and vertical planes in a free-field situation, and considerably enhances the ability to detect a sound against a background noise (Sabeti et al., 1991). SRM has also been found in a few other mammal species: in ferrets *Mustela putorius* (Hine et al., 1994), cats (Wakeford et al., 1974), big brown bats *Eptesicus fuscus* (Sümer et al., 2009) harbour seal *Phoca vitulina*, and sea lion *Zalophus californianus* (Holt et al., 2007) outside water. In birds, SRM enhances the detection of pure tones masked by a broadband noise by budgerigars *Melopsittacus undulatus* (Dent, 1997), and the detection of bird songs in a song chorus by zebra finches *Taeniopygia guttata* and budgerigars (Dent et al., 2009). In amphibians, SRM has been investigated in a single species (the Cope's gray treefrog *Hyla chrysoscelis*; Caldwell et al., 2016), which shows better detection and discrimination of conspecific calls masked by a chorus-shaped noise when both sources are spatially separated (Bee et al., 2008; Nityananda et al., 2012). Finally, in insects, SRM has been found in two cricket species (*Paroecanthus podagrosus* and *Diatrypa sp.*), where it improves the detection of natural conspecifics calling song against the ambient

noise of the rainforest (Schmidt et al., 2011). Notably, the fly *Ormia ochracea* is the only known species which is not able to benefit from SRM (N. Lee et al., 2017).

Although SRM could appear as a widespread strategy to increase the detection of sound signal sources against noise, it has only been investigated in a limited number of species with a limited number of experimental approaches. To the best of our knowledge, all previous studies investigating SRM in animals have been performed in the laboratory or semi-natural environments (Wakeford et al., 1974; Hine et al., 1994; Dent, 1997; Holt et al., 2007; Bee, 2007; Dent et al., 2009; Sümer et al., 2009; Nityananda et al., 2012; Caldwell et al., 2016). There has been no investigation in completely natural field conditions. Moreover, all studies performed in vertebrates but one (Nityananda et al., 2012) have been conditioning experiments (Go/No-Go; Wakeford et al., 1974; Hine et al., 1994; Dent, 1997; Holt et al., 2007; Bee, 2007; Dent et al., 2009; Sümer et al., 2009; Caldwell et al., 2016). While Go/No-Go experiments exclude variation due to subjects' motivation, an intensive training combined to laboratory conditions may increase their ability to perform SRM compared to natural conditions. Strikingly there has been no study on SRM combining different experimental approaches. In spite of its tremendous utility for the sound scene analysis by animals, SRM remains a poorly investigated phenomenon.

One group of animals where SRM has never been investigated is the crocodilians. As crocodilians, together with birds, dinosaurs and pterosaurs, belong to the Archosaurs, they constitute interesting models to understand the evolution of this clade. Although crocodilians use acoustic communication less intensively than most birds, it is an essential trait characterising their social interactions (Grigg et al., 2015; Vergne et al., 2009). Mature embryos emit calls to synchronise hatching and promote maternal care (Vergne et al., 2008). Juveniles emit contact calls ensuring group cohesion (Vergne et al., 2012), and distress calls inducing maternal protection (Vergne et al., 2012). Adult males of most species attract females and repel competitors by producing a repertoire of vocalisations (bellows, grunts) as well as very low frequency sounds through the vibration of their whole body (Todd et al., 2007), while females emit grunts to attract their young (Vergne et al., 2009).

The natural environments of crocodilians present various sources of noise, either abiotic (e.g. running water) or biotic (e.g. chorusing frogs), including anthropogenic noise (e.g. boats). These noises may mask crocodilians' vocalisations and thus impair their acoustic communication. The receiver individual has to discriminate the signal of interest against these non relevant, masking distractors, and SRM could represent a potential efficient strategy for crocodiles. Besides, the crocodilian amphibious way of life may influence their acoustic environment since water acts as a reflective surface. In a recent study (Papet et al., 2019), we demonstrated that crocodilian head morphology is adapted to acquire reliable localization cues from sound sources when only a small part of their head is above the air-water interface. Here we hypothesise that crocodilians cruising in

water should use SRM to detect target sounds against a noisy background.

In the present study, we investigate SRM in crocodilians by testing their ability to detect a target signal against a background noise in three different, complementary, experimental situations. Firstly, we conducted field experiments with wild Jacare caimans *Caiman yacare* in the Pantanal, Brazil. We challenged females at the end of the hatching period, when they are taking care of their youngs. We mimicked situations where an isolated nestling was emitting distress calls to attract its mother (Vergne et al., 2006b). In a second situation, we set up a naturalistic situation in a large pool where an isolated juvenile Nile crocodile *Crocodylus niloticus* could hear played back calls (juvenile crocodiles are attracted by their siblings calls; Vergne et al., 2012). Finally, we performed Go/No-Go experiments in the laboratory where Nile crocodiles had to discriminate synthetic sound signals against a background noise.

6.2 Experiment 1: Spatial release during mother-young communication in the wild

6.2.1 Methods

Field location and animals.

We conducted the field work at "Nhumirim ranch" (Embrapa research station, Mato Grosso do Sul, Brazil; 18°59'16.1"S 56°37'08.8"W, Figure 6.1), which covers 4310 ha with around 100 lakes (Campos et al., 1995; Campos et al., 2015). We surveyed the area to find nests and females in February - March 2019, and performed the playback experiments at the end of the hatching season (April 30th - May 11th 2019). We tested 16 adult females (*Yacare caiman* *Caiman yacare*) that had been previously identified as having built a nest and laid eggs. We took great care to test naive females: most of the tested females were on separated lakes (10 individuals out of 16, Figure 6.1). When two females living in the same lake were successively tested (3 lakes \times 2 individuals = 6 individuals, Figure 6.1) we always chose individuals separated by at least 100 meters, and carefully checked that the second female to be tested had been unable to hear the sound stimuli broadcast to the first tested female. To avoid habituation, each female was involved in a single experimental session. We conducted all experiments during the day.



Figure 6.1 – **Field area in Brazilian Pantanal (Experiment 1)**. Cartography of the field work area (the white rectangle represents the limit of the reserve; the Nhumirim Ranch is indicated by a black cross, 18°59'16.1"S 56°37'08.8"W). We conducted the experiments in the lakes surrounded by red circles; the number of red hyphens indicates the number of females tested on the same lake (1 or 2 individuals).

Experimental signals.

We challenged the tested females with juvenile distress calls (Figure 6.2a) which are well-known signals eliciting protective behaviour from the mother (Vergne et al., 2009). On the day preceding the first experimental session, we recorded a bank of distress calls from 3 Yacare juveniles (aged around 3 weeks). These individuals belonged to the same clutch, and their mother was not included in the tested females. Distress calls were elicited by handling each individual successively. The handling time did not exceed 2-3 minutes and the juveniles were immediately put again with their mother after having been recorded.

During the playback experiments, we broadcast a "masking noise" and a "target signal". The masking noise was a white noise (frequency range [20, 20000] Hz; 80 dB(A) measured at 1 m). It was played back continuously during the whole duration of each experimental session. The target signals were designed as sequences of ten successive distress calls (randomly chosen among our recording data bank). Each call was low-pass and high-pass filtered (cut-off frequencies: 20 Hz and 10 kHz respectively, 3rd order filters) and normalised by their RMS value (i.e. every call contained the same amount of energy). Within each target signal, the silence duration between two calls varied randomly between 1.25 ± 0.25 s (total duration of the target signal = 17 s). We created a playback data set of 11 target signals differing by their signal-to-noise ratio. Precisely, we adjusted the intensity of each target signal related to the intensity of the masking noise in the range [-20, 0] dB with a 2 dB step.

Playback protocol.

We placed three remotely controlled loudspeakers (FoxPro Fusion) just above the water surface, at around 20 meters from the tested female (minimal distance = 12 m; maximal distance = 50 m; Figure 6.2b). Two of the loudspeakers were positioned side by side: one broadcast the masking noise (noise loudspeaker) and the other was used to play back the target signal (co-located loudspeaker). The third loudspeaker (separated loudspeaker) was positioned in order to form an isosceles triangle with the noise loudspeaker and the female initial position (Figure 6.2b). The "separation angle", θ , was the angle formed by the female, the noise loudspeaker and the separated loudspeaker (Figure 6.2b). The separated loudspeaker was also used to broadcast the target signal -alternatively with the co-located loudspeaker (see description of the playback procedure below). At the start of the experiment, the female was at the same distance from the co-located loudspeaker and the separated loudspeaker (Figure 6.2b). The mask was played continuously during the whole experimental session, starting with a quick fade-in until it raised the intensity level of 80 dB(A). We never noticed any change in the females' behaviour following the onset of the mask. Specifically, we noticed no retreat nor any kind of avoidance of the loudspeaker emitting the mask from the females.

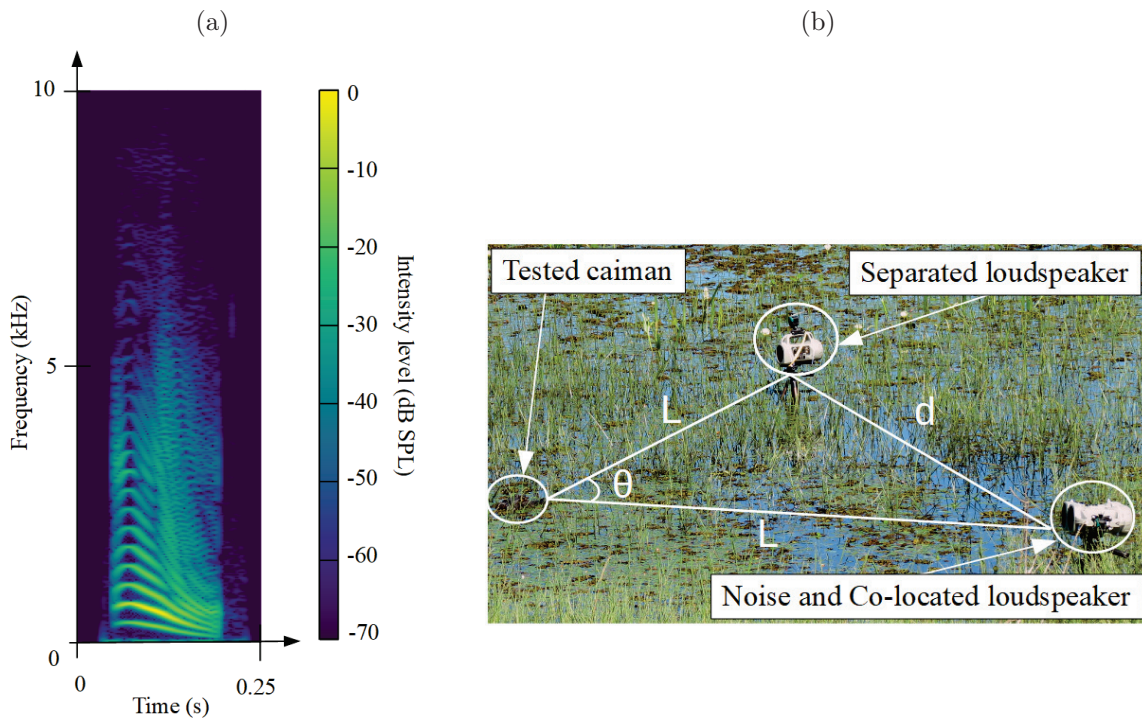


Figure 6.2 – **Field experiments on female Jacare caimans (Experiment 1)**. (a) Spectrographic representation of a distress call from a young Yacare caiman. (b) Illustration of the field experimental design. The distance between the loudspeakers ($d \in [6.5, 19]m$) was always lower than the distance between the female and the loudspeakers ($L \in [12, 50]m$).

Before playing back the first target signal we observed the behaviour of the female during at least 5 minutes (Figure 6.3). If the female moved during this observation period, we waited 5 minutes more. If the female's distance towards the co-located and separated loudspeakers were no more equal, we changed the position of the loudspeakers to create again the isosceles triangle between both loudspeakers (Figure 6.2b), and started a new 5 minutes pre-experiment observation period.

At the end of the observation period we broadcast the first target signal from the co-located speaker ("co-located condition") at a low intensity level (signal-to-noise ratio varying between -18 and -4 dB). The target signal was emitted 3 times, once every minute (Figure 6.3). We increased the delay between these renditions if the female moved or plunged underwater until she stopped or reappeared. After the third rendition of the target signal we waited at least 3 minutes and then repeated the same procedure from the separated loudspeaker (Figure 6.3). After a post-playback delay of minimum 3 minutes, we emitted a new target signal with a +2 dB signal-to-noise ratio from the co-located loudspeaker. We repeated this procedure, alternating between the co-located and the separated loudspeakers, and increasing by +2 dB the signal-to-noise ratio every two playbacks, until the female showed a directional response and approached towards the

emitting loudspeaker (Figure 6.3). The experiments ended when the female modified her initial position from more than one body length. On average, each female was challenged with between 1 pair of target signals (co-located and separated) if she located and moved towards the first separated stimulus, to 9 different pairs of target signals.

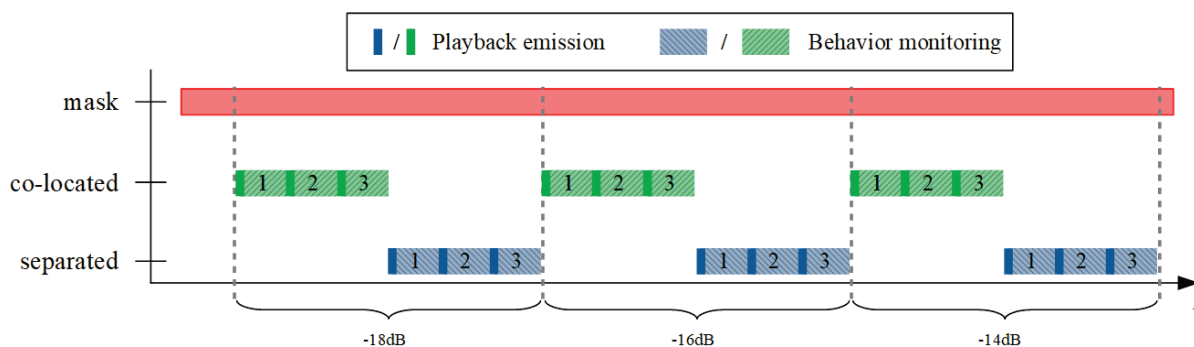


Figure 6.3 – **General timeline of the field experiment. (Experiment 1).** The mask is emitted continuously. The target signal is emitted alternatively from the co-located and separated loudspeaker (see main text for details).

Analysis of behavioural reaction to playback.

We observed and filmed the females' behaviour during the whole duration of the experiments. We then scored the behaviour from the videos according to two different scales aimed at characterising 1) *the female's signal detection ability* and 2) *her motivation to go to the sound source*, as a function of the signal-to-noise ratio and the separation angle θ .

To assess the female's ability to detect the target sound against the background noise, we used a binary scale ("detection scale"), giving the score "1" if the female showed any head or body movement during the playback of the target signal and "0" if she had still not responded after the third rendition of the target signal. For comparison purpose, we used the same kind of binary score in the two other experiments reported in the present paper (Experiments 2 and 3, performed in captivity; see below). We also measured the latency time (in seconds) between the offset of the target signal and the female's response.

As the field experiments were performed on wild animals having the opportunity to express their full range of behaviours, we further assessed the females' motivation by scoring their movement behaviour in more details as follows ("motivation scale"): score "0" = no behavioural response (no movement); score "1" = the female moved the head or the body, but not in the direction of the emitting loudspeaker (misdirected response); score "2" = the female moved her head and looked towards the active loudspeaker without body displacement; score "3" = the female moved less than 1 body length towards

the active loudspeaker; score "4" = the female moved more than 1 body length towards the active loudspeaker. For each tested female, we then fitted two sigmoid functions (one function for the co-located condition and one function for the separated condition), according to the formula:

$$f(L) = \frac{M}{1 + e^{-\lambda(L-L_{50})}} \quad (6.1)$$

where L is the signal-to-noise ratio (SNR) of the target signals; M is the maximum score of the behavioural scale ($M = 4$); L_{50} is the SNR corresponding to a behavioural score of $M/2$; λ is the slope of the function for $L = L_{50}$. The experimental model was fitted to the experimental data based on the least mean square method. If a female had been tested with a single SNR level (which means that she was tested only twice: a first test in the co-located condition and a second test in the separated condition, to which she behaviourally responded), the fitting curves were arbitrarily fixed as $f(L) = \rho$ where ρ is the motivation score measured in each condition. For each female, the average of both exponential curves (in the co-located and separated conditions) gives an estimation of the impact of the SNR on her motivation score.

For each female, we then calculated an index corresponding to the difference of area under the separated and co-located detection curves ΔA_{SC} (for details see supplementary Figure 6.13). This index highlights the difference of motivation between the co-located and the separated conditions. It was computed for each female as follows:

$$\Delta A_{SC} = \int_{L_{min}}^{L_{max}} f_S(L) - f_C(L) dL \quad (6.2)$$

where L_{max} and L_{min} are respectively the maximum and minimum values of SNR used in one session for one female, and $f_C(L)$ and $f_S(L)$ are the scores attributed to the behavioural reaction of the female in respectively the co-located and separated conditions. The area under the curves is homogeneous to the SNR level (in dB) and the behavioural score (arb. unit). The sign of ΔA_{SC} reveals the most favourable source condition in regards to the behavioural score of a full session (i.e. if $\Delta A_{SC} > 0$, the separated condition is the most favourable).

Statistical analysis.

To test the effect of the signal-to-noise ratio and of the position of the target source (co-located versus separated) on signal detection by female caimans, we used a Generalised Linear Mixed Model (GLMM, binomial distribution, logistic regression, R lme4 package) with signal-to-noise ratio, source condition position (co-located versus separated), and initial angle θ as fixed factors. The identity of the tested female was set as a random factor. In a second step, we focused on the data obtained in the separated condition and further tested the effect of the separation angle on the females' detection ability (GLMM,

binomial distribution, with the identity of the tested female as random factor).

To get the signal detection thresholds (corresponding to a success of 50% target detection; Bee et al., 2009), we performed logistic regressions separately for each source position (co-located and separated). The signal detection thresholds were computed as follows:

$$SNR_{50} = \frac{(\log\left(\frac{p}{1-p}\right) - \beta_0)}{\beta_1} \quad (6.3)$$

(algebraic transformation of the log odds equation: $p(x)/(1 - p(x)) = \exp(\beta_0 + \beta_1 \times x_1)$) with $p=0.5$, β_0 as the intercept from the equation, and β_1 as the regression coefficient of the SNR predictor.

Besides, we further tested the effect of the signal-to-noise ratio and of the position of the target source (co-located versus separated) on the females' motivation to move towards the target source (behaviour rated according to the motivation scale). We computed a Linear Mixed Model (LMM, R lme4 package) with signal-to-noise ratio and source position as fixed factors, and the identity of the tested female as a random factor.

We performed all statistical analysis with R Studio 3.6.0 (rejection threshold $\alpha = 0.05$).

6.2.2 Results

Each tested female was challenged with 1-9 pairs of target signals, for a total of 104 target signals equally balanced between co-located and separated conditions (see Supplementary Table 6.8 for details on the signals played back to each female). As a result, both the signal-to-noise ratio of the target stimuli and the source position (co-located versus separated) impact the females' ability to detect the target signal against the background noise (Figure 6.4a, Table 6.1).

Table 6.1 – **Results of GLMM testing the effect of signal-to-noise ratio and source position (co-located versus separated) on the females' ability to detect the target signal against the background noise (Experiment 1).**

Term	Estimate	se	z	p
Intercept	10.626	3.102	3.426	0.000614 ***
SNR	0.759	0.207	3.671	0.000242 ***
Source position	2.283	0.735	3.106	0.001899 **

When considering only the separated condition, we found no significant effect of the separation angle (Table 6.2), which suggests that an increase in the angle (in the range $[4, 44]^\circ$) did not strongly improve the ability of tested females to detect the target signal. However, field constraints limited the number of experiments and it is reasonable to assume that large angles improve detection. This is supported by the raw data reported in

Figure 6.4a: all females tested with separation angles above 30° showed 100 % detection success.

Table 6.2 – Results of GLMM testing the effect of the separation angle on the females’ ability to detect the target signal against the background noise (Experiment 1).

Term	Estimate	se	z	p
Intercept	-0.705	0.818	-0.862	0.389
Angle	0.0073	0.047	1.576	0.115

The modelling of detection probabilities in the co-located and separated conditions respectively (Figure 6.4b) further emphasises that the detection thresholds (i.e. SNR levels inducing a 50 % probability of signal detection) were shifted to lower SNR levels when the target loudspeaker is separated from the noise loudspeaker. In the co-located condition, the detection threshold was around -12.0 dB while it decreased to -16.5 dB in the separated condition (all angles confounded; Figure 6.4b). Roughly speaking, the results of this experiment suggest an amount of spatial release from masking of 4.5 dB.

Both the signal-to-noise ratio of the target stimuli and the source position (co-located versus separated) significantly impact the females’ motivation to move towards the target source (Figure 6.4a, Table 6.3).

Table 6.3 – Results of LMM testing the effect of signal-to-noise ratio and source position (co-located versus separated) on the females’ motivation to move towards the target source.

Term	Estimate	se	df	t	p
Intercept	4.213	0.569	84.73	7.401	<0.0001
SNR	0.204	0.032	97.15	6.245	<0.0001
Source position	0.923	0.222	86.21	4.153	<0.0001

Figure 6.5a illustrates the effect of signal-to-noise ratio on the females’ motivation to move towards the target loudspeaker whatever the separation angle was. In line with the detection ability, females’ motivation to move is highly influenced by the SNR. It appears that the influence of the SNR varies greatly between females: some individuals moved promptly in response to target signals with low SNR levels, while others require higher SNR levels to respond. Figure 6.5b shows that all females except two individuals (females 13 and 4) exhibited stronger responses to playback (more displacement towards the target loudspeaker) when the angle between noise and target was superior to 4° (separated condition). The tested females showed higher motivation scores for higher SNR values and when the target was spatially separated from the mask.

Considering the latency times, we found no significant differences between the co-located and separated conditions. The mean latency time (independently from the source condition) was 8.3 ± 9.5 s.

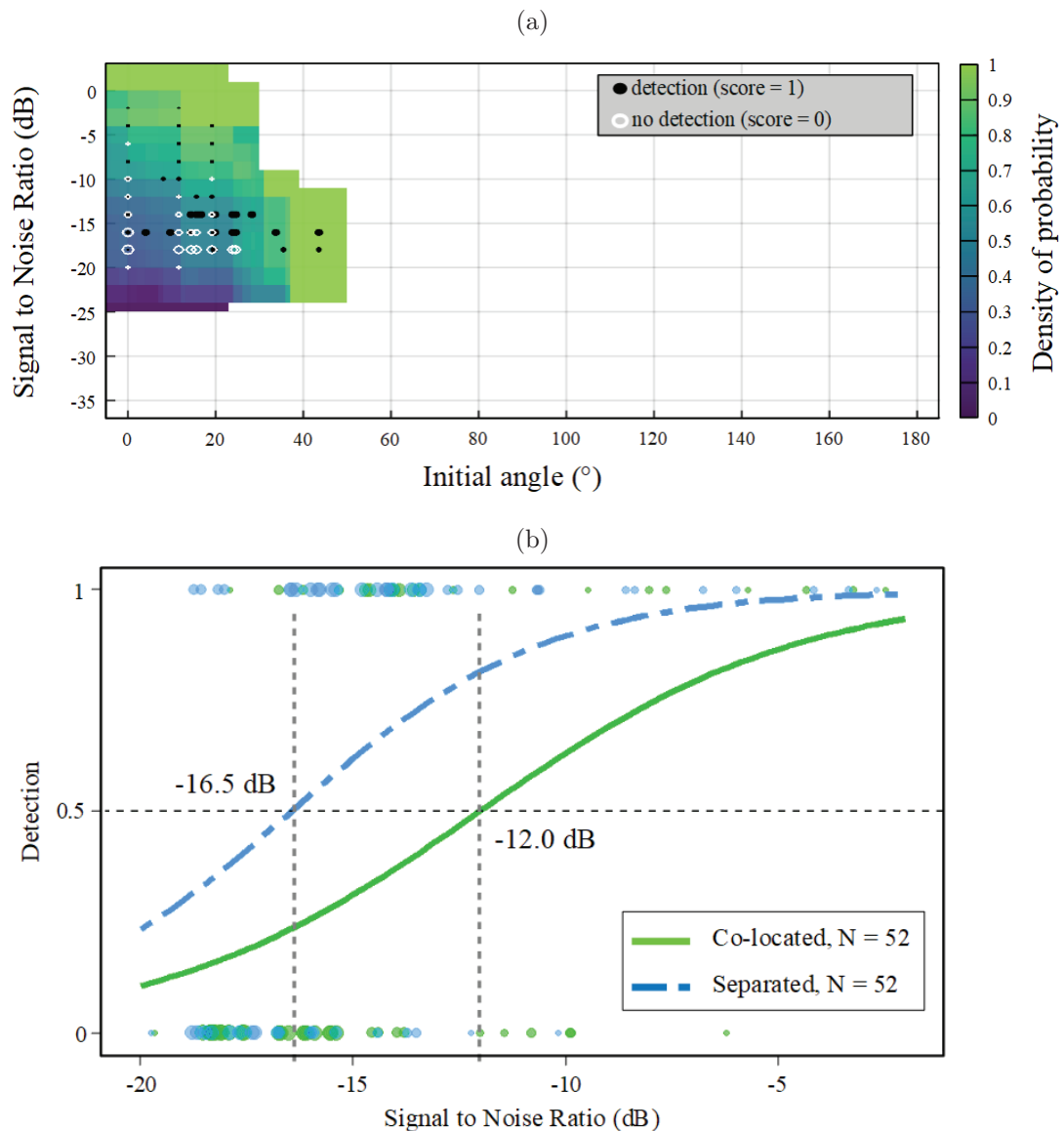


Figure 6.4 – **Results of the field experiments on female *Jacare caimans* (Experiment 1, detection)**. (a) Detection of the target signals (young distress calls) against background noise by tested females ($n = 16$) as a function of the signal-to-noise ratio and the separation angle between the noise loudspeaker and the target loudspeaker. Circles and dots represent experimental trials (one female per trial; white circles: no detection of the target signal, i.e. no behavioural reaction to playback; black dots: effective detection of the target signal). Circles and dots' sizes are proportional to the number of females tested (from 1 to 11). The green-blue colour scale illustrates the probability of detection, ranging from 0 (deep blue, no detection) to 1 (light green, effective detection; probabilities calculated using a sliding squared window $24^\circ \times 12$ dB). (b) Modelling of signal detection probabilities in the co-located and separated conditions. Dots represent experimental trials and dot size is proportional to the number of trials (number of tested females). Green: co-located condition (separation angle = 0). Blue: separated condition (angles between 4 and 44°). The amount of spatial release (difference between both detection thresholds) is 4.5 dB.

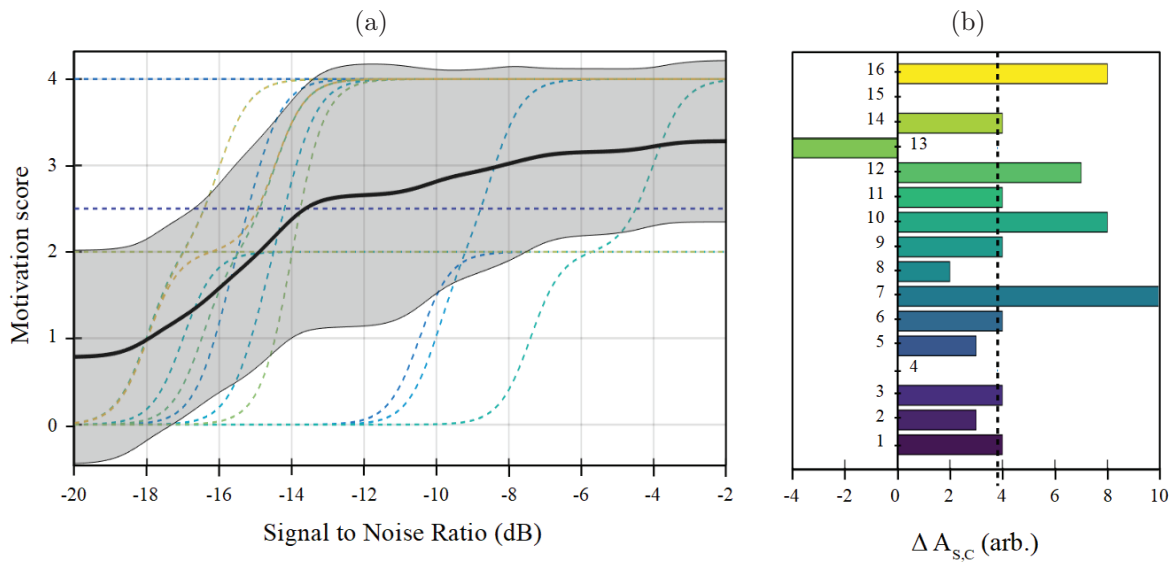


Figure 6.5 – **Results of the field experiments on female Jacare caimans (Experiment 1, motivation).** (a) Relationship between SNR and behavioural motivation to move towards the target loudspeaker. Coloured curves represent the mean behavioural response of each female (fitted for all angles confounded). The black solid line is the average of all individual fitted curves. (b) Individual size effect of the difference between behavioural motivation in the separated and the co-located conditions. Each bar corresponds to a tested female. The vertical dashed line is the mean value $\Delta A_{S,C}$: 3.8 arb. unit.

6.3 Experiment 2: Spatial release during between-juveniles interaction in semi-captivity

6.3.1 Methods

Location and animals.

We performed these experiments in October 2019 at "Crocoparc" zoo (Agadir, Morocco). We worked with juvenile Nile crocodiles (*Crocodylus niloticus*) hatched in captivity (n = 8 individuals; three months old; 36 ± 2 cm length). These animals were housed together in an exterior enclosure not visible by the public. They had never been included in any experiments before. Each crocodile subject was tested only once during only one experimental session.

Experimental signals.

As in the experiment 1, we broadcast a masking noise and target signals. The masking noise (white noise) was played back continuously, starting before we put the crocodile in the pond and during the whole duration of each experimental session (frequency range [20, 20000] Hz; 80 dB(A) at 1 meter). As target signals, we used sequences of three identical Nile crocodile calls from our recording data bank (twelve different calls from wild Nile crocodile hatchlings previously recorded in the Okavango Delta, Botswana by T. Aubin and N. Mathevon; see spectrogram on Figure 6.6b). Each call was previously band-passed filtered between 20 Hz and 10 kHz (filter order of 3) and normalised by its RMS value. In each target signal, the silence durations between the calls were randomly fixed between 5 ± 1.5 s, resulting on a total signal duration of 11 seconds. The intensity level of the target signals was adjusted to get signal-to-noise ratios in the range [-32, -16] dB with a 2 dB step.

Playback protocol.

The experiments were performed outside, during the night, in an artificial pond of around 40 m² (maximal dimensions: 6 × 7 meters; Figure 6.6a). Prior to the experiments we placed four remotely controlled loudspeakers (FoxPro Fusion) on the pond bank (Figure 6.6a). As in the experiment 1, two loudspeakers were positioned side by side: one broadcast the masking noise (noise loudspeaker) and the other emitted the target signal co-located with the mask (co-located loudspeaker). The two other loudspeakers (separated loudspeakers) were placed at distance from the mask (Figure 6.6a). The spatial location of the mask and target loudspeakers around the pond was changed between each tested subject, in order to avoid any side effect and to cover a wide range of possible angles between the target, the mask, and the crocodile positions. Given the size of the

pond, the distance between the tested animal and the loudspeaker which playbacks the target signal was biologically relevant: in the wild, groups of young individuals are often scattered from one to a few meters.

The tested juvenile was placed alone in the pond in the afternoon preceding the experimental trials (at least 3 hours before dusk) to get habituated to its new environment (Figure 6.7). The masking noise was continuously played back, starting before the arrival of the crocodile until the end of the experimental session. The first target signal was played by one of the three dedicated loudspeakers (co-located or separated) and at one specific signal-to-noise ratio. If the crocodile had not moved 90 seconds after the end of the played back target signal, the same signal was played again on the same loudspeaker (Figure 6.7). We waited ten minutes after the emission of the last signal before playing back another random target signal through one of the dedicated loudspeakers. On average, we conducted 8.8 ± 1.4 trials per tested crocodile (Figure 6.7).

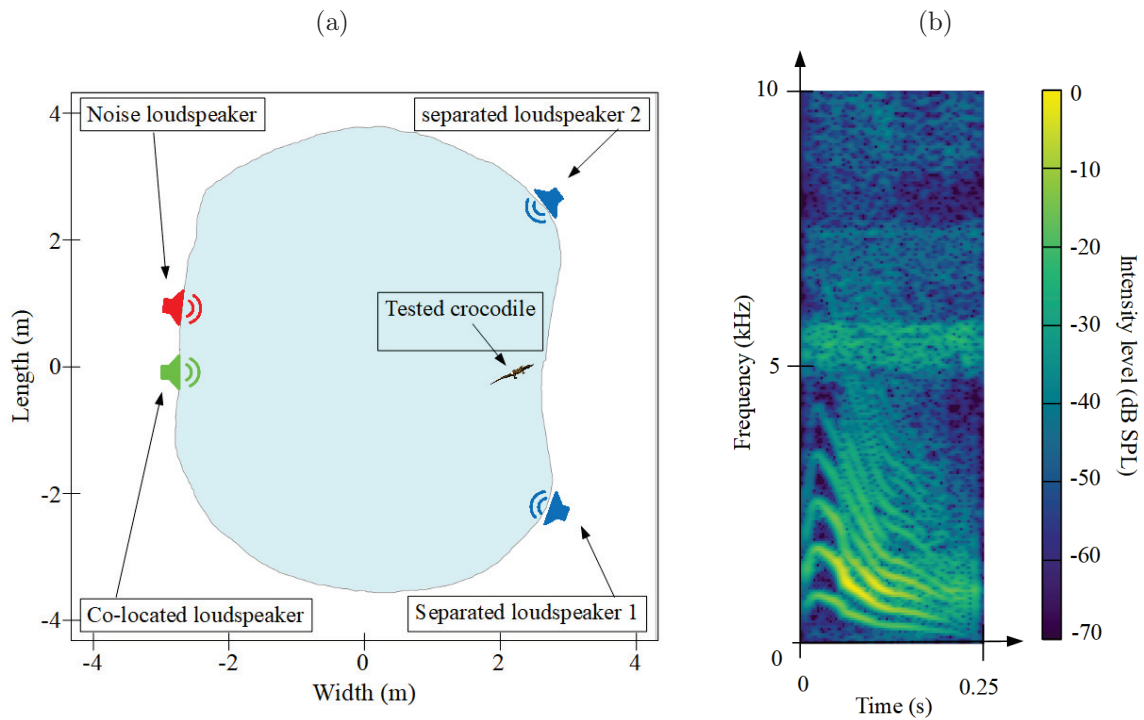


Figure 6.6 – **Experiments on semi-captive young Nile crocodiles (Experiment 2)**. (a) Experimental set-up. (b) Spectrogram representation of a juvenile call used as target.

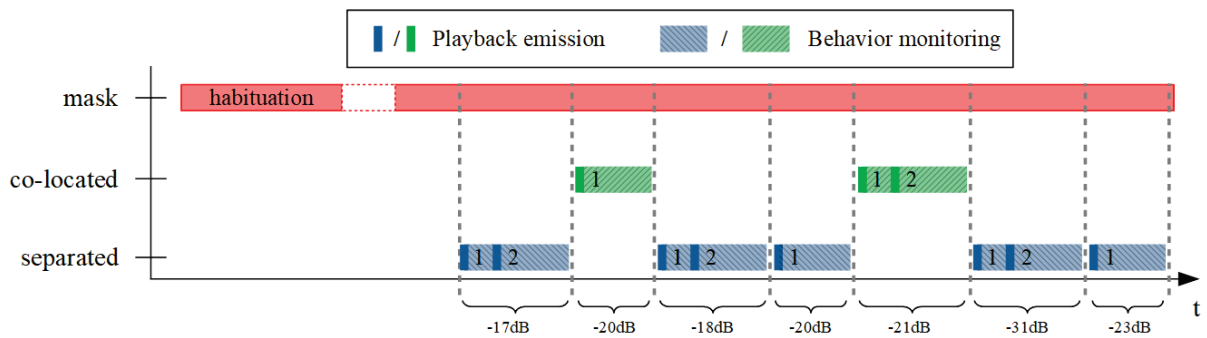


Figure 6.7 – **General timeline of the experiment 2**. The mask was played continuously and before testing the subject. The target signal was randomly emitted alternatively from the co-located and separated loudspeakers (see main text for details).

The initial position of the crocodile in the basin varied across experiments. Thus, the signal-to-noise ratio heard by the crocodiles at the onset of the playback varied accordingly. To get a realistic measure of the initial SNR for each subject, we mapped the variations of the SNR on the surface of the pond by performing an acoustic propagation experiment. We played back distress calls and noise, measured their intensity at a sample of locations, and modelled an acoustic map of the basin revealing a strong variation of the sound level depending on the position in the pond (Figure 6.8). Therefore, the SNR at the position of the crocodile was based on the calculation of the intensity levels of the target and of the mask at the animal position, based on the propagation measures. For each experiment, the initial perceived SNR (SNR_p) was defined as follows:

$$SNR_p(dB) = L_{Tp} - L_{Mp}, \quad (6.4)$$

with L_{Tp} as the target sound level at the crocodile position in dB and L_{Mp} as the sound level of the mask at the crocodile position in dB. Besides assessing the initial SNR perceived by the tested subject, we also measured the separation angle (i.e. the angle formed by the crocodile, the noise loudspeaker and the target loudspeaker). This angle was constrained by both the experimental set-up configuration (Figure 6.6a) and the initial positions of the tested juvenile, and varied between 44 and 156°.

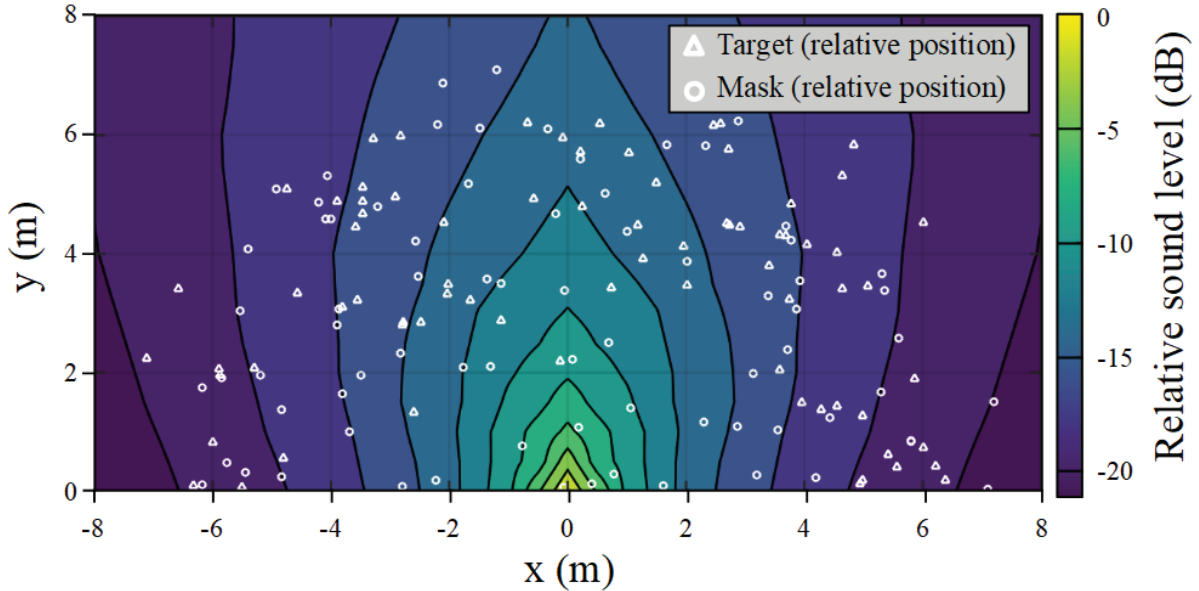


Figure 6.8 – **Acoustic propagation of a juvenile call on the pond (Experiment 2)**. The position of the sound source is normalised at (0, 0). The white triangles and circles represent respectively the positions of the crocodile relative to the target (triangles) and noise (circles) loudspeakers at the beginning of each experimental trial. The sound intensity level is coded by the colour scale.

Analysis of behavioural reaction to playback.

We observed and filmed the juveniles' behaviour during the whole duration of the experiments (infrared cameras ABUS TVCC34010). Prior to the analysis of the videos, we corrected the lens distortion of the cameras and the error in geometrical perspective using Kinovea software. We extracted the position coordinates of the loudspeakers and those of the crocodile (one point between the eyes) at the start of every playback of a target signal. Based on these coordinates, we calculated the separation angle between the crocodile, the noise loudspeaker and the target loudspeaker.

To assess the juvenile's ability to detect the target sound against the background noise, we used the same binary scale as the one used in Experiment 1 ("detection scale"), giving the score "1" if the juvenile showed any head or body movement during the playback of the target signal and "0" if it had still not responded at the end of the playback of the target signal. We also measured the latency time (in seconds) between the first behavioural response and the preceding stimulus (i.e. if the target signal was played a second time, the considered stimulus was the second signal).

To test the effect of the signal-to-noise ratio and of the position of the target source (co-located versus separated) on signal detection by juvenile Nile crocodiles, we computed a GLMM (binomial distribution, logistic regression, R lme4 package) with signal-to-noise ratio and source position as fixed factors, and the identity of the tested subjects as a random factor. In a second step, we focused on the data obtained in the separated condition and further tested the effect of the separation angle on the crocodiles' detection ability (GLMM, binomial distribution, with the identity of the tested juvenile as random factor).

To get the signal detection thresholds (corresponding to a success of 50% target detection (Bee et al., 2009), we performed logistic regressions separately for each source position (co-located and separated) and made the same computation as for Experiment 1 (see Methods of Experiment 1).

6.3.2 Results

Each juvenile Nile crocodile was challenged with 7-11 target signals, for a total of 30 co-located and 41 separated trials (see Supplementary Table 6.10 for details on the signals played back to each juvenile crocodile, Figure 6.9a).

As a result, both the signal-to-noise ratio of the target stimuli and the source position (co-located versus separated) impact the juveniles' ability to detect the target signal against the background noise (Figure 6.9a, Table 6.4). When both the noise and target sound sources were co-located (initial angle equal to 0 in Figure 6.9a), detection scores grow from 0 to 1 for SNR values between -30 dB and -10 dB.

When considering only the separated condition, we found no significant effect of the

separation angle (Table 6.5), which suggests that an increase in the angle (in the range [44, 156]°) did not strongly improve the ability of the tested subjects to detect the target signal.

Table 6.4 – Results of GLMM testing the effect of signal-to-noise ratio and source position (co-located versus separated) on the juvenile Nile crocodiles’ ability to detect the target signal against the background noise (Experiment 2).

Term	Estimate	se	z	p
Intercept	3.539	1.454	2.434	0.0150
SNR	0.197	0.068	2.872	0.00408 **
Source position	1.393	0.590	2.362	0.0182 *

Table 6.5 – Results of GLMM testing the effect of the separation angle on the juvenile Nile crocodiles’ ability to detect the target signal against the background noise (Experiment 2).

Term	Estimate	se	z	p
Intercept	1.641	1.010	1.625	0.104
Angle	-0.0187	0.013	-1.452	0.146

In line with the results of Experiment 1, modelling of detection probabilities in the co-located and separated conditions respectively (Figure 6.4b) emphasises that the detection thresholds (i.e. SNR levels inducing a 50 % probability of signal detection) are shifted to lower SNR levels when the target loudspeaker is separated from the noise loudspeaker. In the co-located condition, the detection threshold was around -17.7 dB while it decreased to -25.1 dB in the separated condition (all angles confounded; Figure 6.4b). As a main result, the amount of spatial release from masking in this experiment is equal to 7.4 dB.

The latency times measured in this experiment were not significantly influenced by the source condition (latency time in the co-located condition = 46.5 ± 50.3 s; latency time in the separated condition = 29.7 ± 26.6 s; $p = 0.225$).

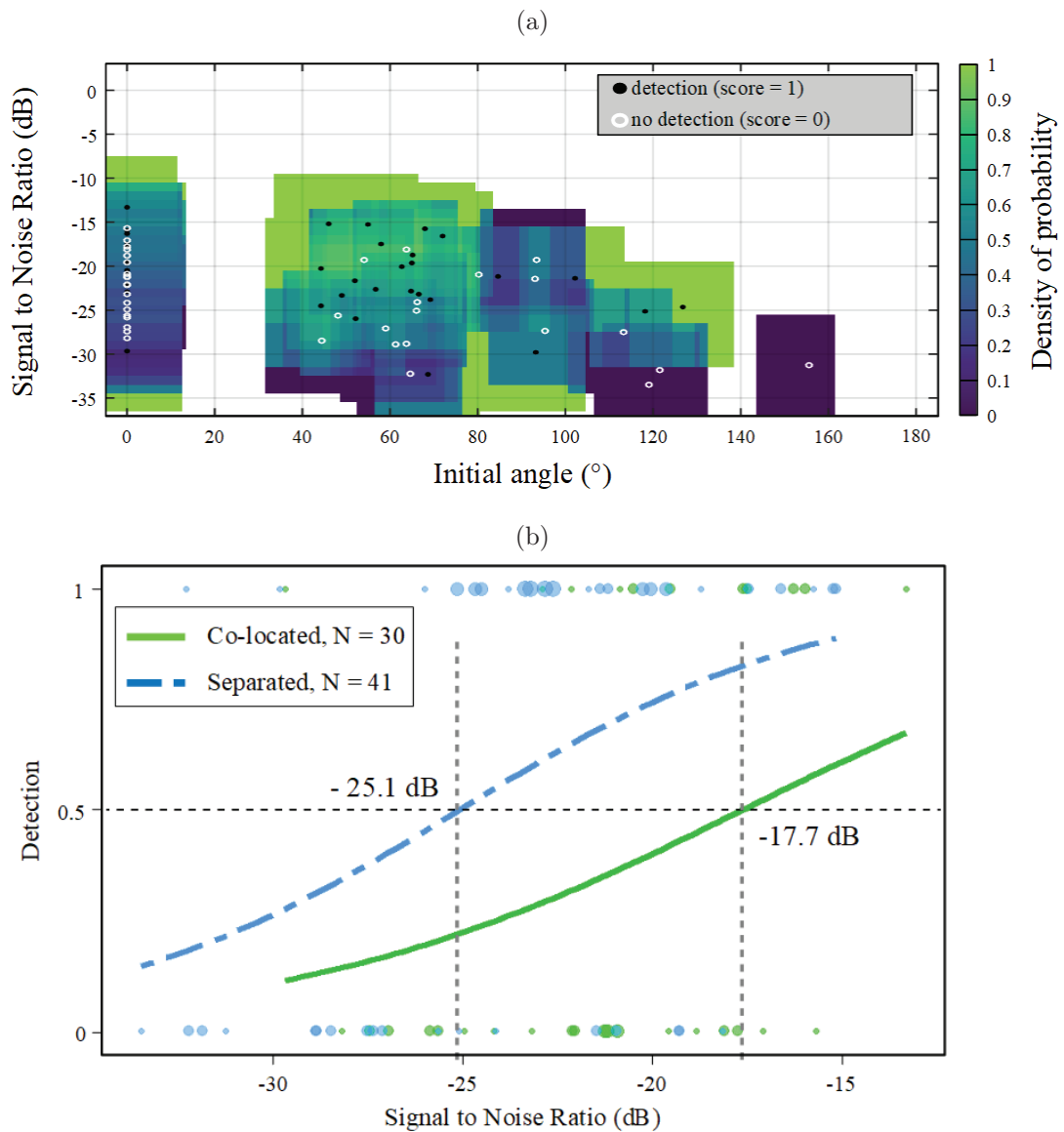


Figure 6.9 – **Results of the semi-captivity experiments on juvenile Nile crocodiles (Experiment 2)**. (a) Detection of the target signal (juvenile calls) against background noise by the tested crocodiles ($n = 8$) as a function of the signal-to-noise ratio and the separation angle between the noise loudspeaker and the target loudspeaker. Circles and dots represent experimental trials (one subject per trial; white circles: no detection of the target signal, i.e. no behavioural reaction to playback; black dots: effective detection of the target signal). The colour scale illustrates the probability of detection, ranging from 0 (deep blue, no detection) to 1 (light green, effective detection; probabilities calculated using a sliding squared window ($24^\circ \times 12$ dB)). (b) Modelling of signal detection probabilities in the co-located and separated conditions. Dots represent experimental trials and dot size is proportional to the number of trials. Green: co-located condition (separation angle = 0). Blue: separated condition (angles between 44 and 156°). The amount of spatial release (difference between both detection thresholds) is 7.4 dB.

6.4 Experiment 3: Spatial release during Go/No-Go tests in the laboratory

6.4.1 Methods

Location and animals.

We conducted these experiments between March and June 2019 at the ENES laboratory. We worked with two Nile crocodiles born in captivity at the zoo "La Ferme aux Crocodiles" (Pierrelatte, France). These animals were three years old (biometrics data are available in the Supplementary Table 6.9). They were housed at the ENES animal facilities. Each subject was tested once a week, during 14 weeks.

Experimental signals.

As in Experiments 1 and 2, we broadcast a masking noise and target signals. The masking noise (white noise) was played back continuously starting before we put the tested subject in the experimental room and during the whole duration of each experimental session (frequency range [20, 20000] Hz; 60 dB SPL at 50 cm). As target signals, we used sequences of three different synthetic buzz (harmonic complex tones; fundamental frequency (f_0) = 208, 220 and 233 Hz, respectively; duration = 500 ms each; signals synthesised with Python 3.7, SciPy; Figure 6.10b). Each target signal was designed as a repetition of three identical buzz, separated by a random interval of 2 seconds \pm 500 ms (total duration of the target signal = 9 seconds). The intensity level of the target signals was adjusted to get a resulting signal-to-noise ratio in the range [-32, -16] dB with a 2 dB step.

Behavioural conditioning.

Prior the experiment, both Nile Crocodiles were trained twice a week to come to a sound source. The training follows a classical Go/No-Go procedure. Two speakers were placed in the subject's enclosure, with only one speaker emitting repetitions of the target signals. The crocodile was rewarded with a piece of meat as soon as it touched the active speaker with its snout. Before and after the testing period, both individuals raised 100 % success during conditioning sessions conducted in their enclosures. The success rate measured among the testing sessions was 56 ± 22 %.

Playback protocol.

We performed the experiments in darkness, in a dedicated sound-attenuation chamber (TipTopWood ©, dimensions = $1.8 \times 2.3 \times 2.2$ meters; Figure 6.10a), where a squared pool (surface = 3 m^2) had been mounted for the purpose of this experiment. The pool

was filled with water at a level enabling individuals to swim (water depth = 10 cm; Papet et al., 2019). Four loudspeakers (AudioPro, Bravo Allroom Sat) were set up just beyond the water surface on the edges of the pool (Figure 6.10a). One loudspeaker was playing continuously the mask (noise loudspeaker). When needed, it also played the target signal mixed with the noise (co-located loudspeaker). Two other loudspeakers could play the target signal (separated loudspeakers). The last loudspeaker was silent (lure loudspeaker). Except for the co-located / noise loudspeaker, the spatial locations of the loudspeakers were changed between each experimental session. A food reward system sat on top of each speaker and can be remotely activated by the experimenter. The sound emission chain was constituted by two computers and two power amplifiers (Yamaha AX-397) connected to the loudspeakers and placed outside the chamber. We recorded the behaviour of the tested subject thanks to an infrared camera (ABUS TVCC34010) connected to a computer.

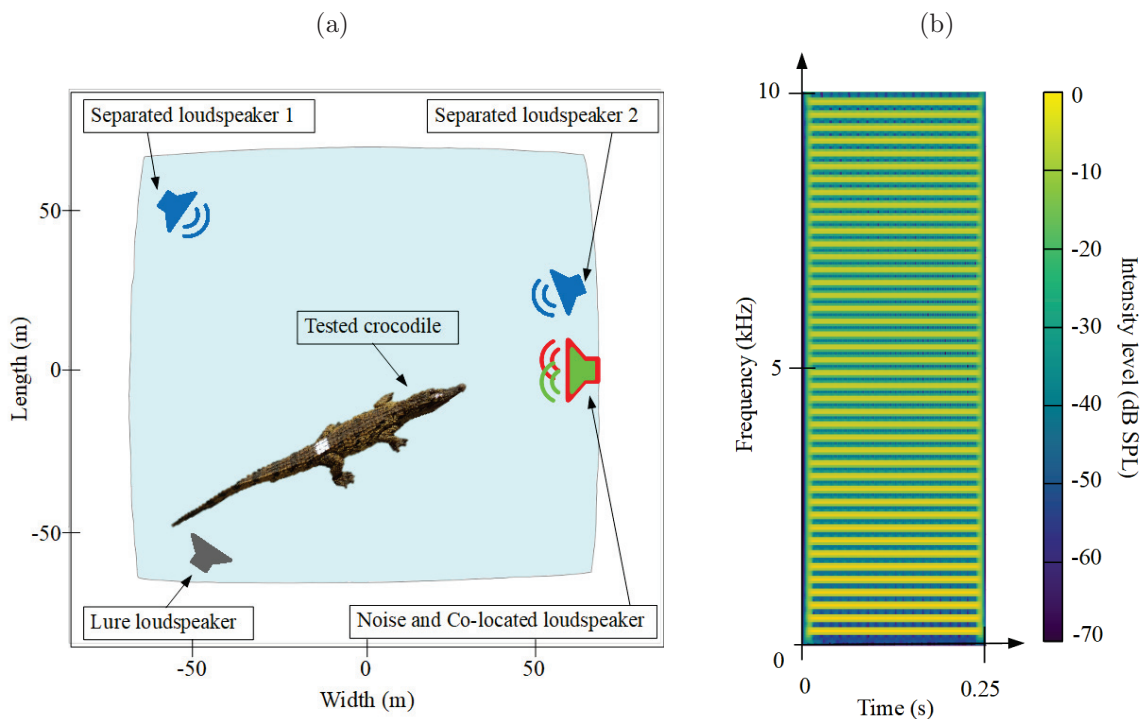


Figure 6.10 – **Go/No-Go experiments on juvenile Nile crocodiles (Experiment 3)**. (a) Experimental set-up (the dimension of the crocodile is scaled to the dimension of the pool). (b) Spectrographic representation of one buzz (synthetic harmonic complex tones) used as a target signal.

The tested crocodile was released in the pool at least 20 minutes before the onset of an experimental session (Figure 6.11). The noise loudspeaker was already running and was stopped only after the crocodile was removed from the pool at the end of the experimental session (Figure 6.11). The first target signal was played either from a separated loudspeaker or from the co-located loudspeaker, at one specific intensity level.

If the crocodile had not moved 45 seconds after the end of the third buzz of the target signal, we repeated the same target signal one time (Figure 6.11). The crocodile was rewarded if it moved near the correct target loudspeaker within the 5 minutes following the last buzz. If the crocodile responded correctly, we waited for another 5 minutes before another random trial began. On average, we conducted 9 ± 2 trials during one experimental session, covering a wide range of SNR. These trials always include some high SNR, to check the crocodile’s motivation to respond. The crocodile was then left 20 minutes in the pool before being recaptured (Figure 6.11), in order to limit an association between the final target signal and a stress-inducing event.

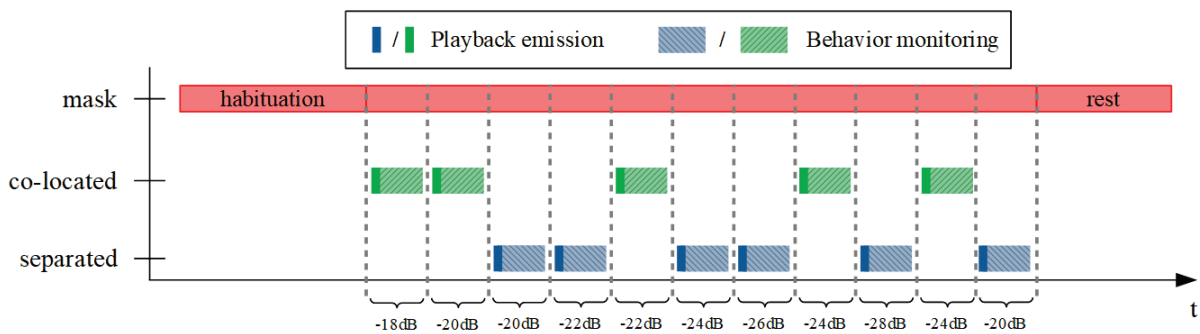


Figure 6.11 – **General timeline of the experiment 3.** The mask was played continuously before and after testing the subject. The target signal was randomly emitted alternatively from the co-located and separated loudspeakers (see main text for details).

Although the position of the crocodile in the pool varied across the experiments, there was no attenuation effect due to sound propagation (conversely to the experimental conditions in Experiment 2): our measures showed that, in the experimental area, the intensity level was constant ± 1 dB all over the pool. We thus considered the SNR at the position of the crocodile as equal to the SNR measured at 50 cm from the loudspeaker.

We measured the separation angle (i.e. the angle formed by the crocodile, the noise loudspeaker and the target loudspeaker) at the onset of the playback. This angle was constrained by both the experimental set-up configuration (Figure 6.10a) and the initial positions of the tested subject, and varied between 16 and 178°.

Analysis of behavioural reaction to playback.

As in Experiments 1 and 2, we observed and filmed the subjects’ behaviour during the whole duration of the experiments. Prior to the analysis of the videos, we corrected the lens distortion of the cameras and the error in geometrical perspective. We measured the position coordinates of the loudspeakers and the initial positions of the crocodile (one point between the eyes) before the playback starts. Based on these coordinates, we calculated the separation angle between the noise loudspeaker, the crocodile and the target loudspeaker.

For each trial, the detection of the target signal was assessed by a binary response as in the Experiment 2. If the crocodile did not respond more than twice to one of the higher SNR (-16 dB or -18 dB) during the same session, the entire session was excluded from the final data set. By checking the subject motivation to respond, this procedure ensured the validity of the negative scores. To assess the subject's ability to detect the target sound against the background noise, we used the same binary scale as the one used in Experiments 1 and 2 ("detection scale"), giving the score "1" if the juvenile showed any head or body movement during the playback of the target signal and "0" if it had still not responded within the 5 minutes observation period following the last buzz of the target signal.

We also measured the latency time of the subject as the time of the first reaction after the preceding stimulus (if the signal was played twice, the considered stimulus was the second one).

To test the effect of the signal-to-noise ratio and of the position of the target source (co-located versus separated) on signal detection by the crocodiles, we computed a GLMM (binomial distribution, logistic regression, R lme4 package) with signal-to-noise ratio and source position as fixed factors, and the identity of the tested subjects as a random factor. In a second step, we focused on the data obtained in the separated condition and further tested the effect of the separation angle on the crocodiles' detection ability. To get the signal detection thresholds (corresponding to a success of 50 % target detection (Bee et al., 2009), we performed logistic regressions separately for each source position (co-located and separated) and made the same computation as for Experiments 1 and 2 (see Methods of Experiment 1).

6.4.2 Results

Each trained Nile crocodile was challenged with 55-65 target signals, for a total of 44 "co-located" and 76 "separated" trials (see Supplementary Table 6.11 for details on the signals played back to each crocodile, Figure 6.12a).

As a result, the signal-to-noise ratio of the target stimuli impacts the juveniles' ability to detect the target signal against the background noise (Figure 6.12a, Table 6.6). On the contrary to Experiments 1 and 2, we found no significant effect of the source position (co-located versus separated; Table 6.6).

Table 6.6 – **Results of GLMM testing the effect of signal-to-noise ratio and source position (co-located versus separated) on the trained juvenile Nile crocodiles’ ability to detect the target signal against the background noise (Experiment 3).**

Term	Estimate	se	z	p
Intercept	4.188	1.145	3.658	0.000255 ***
SNR	0.187	0.0527	3.553	0.00038 ***
Source position	0.4419	0.4226	1.046	0.296

Table 6.7 – **Results of GLMM testing the effect of the separation angle on the trained juvenile Nile crocodiles’ ability to detect the target signal against the background noise (Experiment 3).**

Term	Estimate	se	z	p
Intercept	0.226	0.459	0.492	0.623
Angle	0.000176	0.00476	0.371	0.711

When considering only the separated condition, we found no significant effect of the separation angle (Table 6.7), which suggests that an increase of the angle (in the range [16, 178]°) did not strongly improve the ability of tested subjects to detect the target signal.

As in experiments 2 and 3, modelling of detection probabilities in the co-located and separated conditions (Figure 6.4b) further emphasises that the detection thresholds (i.e. SNR levels inducing a 50 % probability of signal detection) are shifted to lower SNR levels when the target loudspeaker is separated from the noise loudspeaker. In the co-located condition, the detection threshold was around -21.8 dB while it decreased to -25.4dB in the separated condition (Figure 6.4b). This experiment suggests that the amount of spatial release from masking is +3.6 dB.

We found no influence of the source condition on the latency time (average latency time = 15.3 ± 13.8 s).

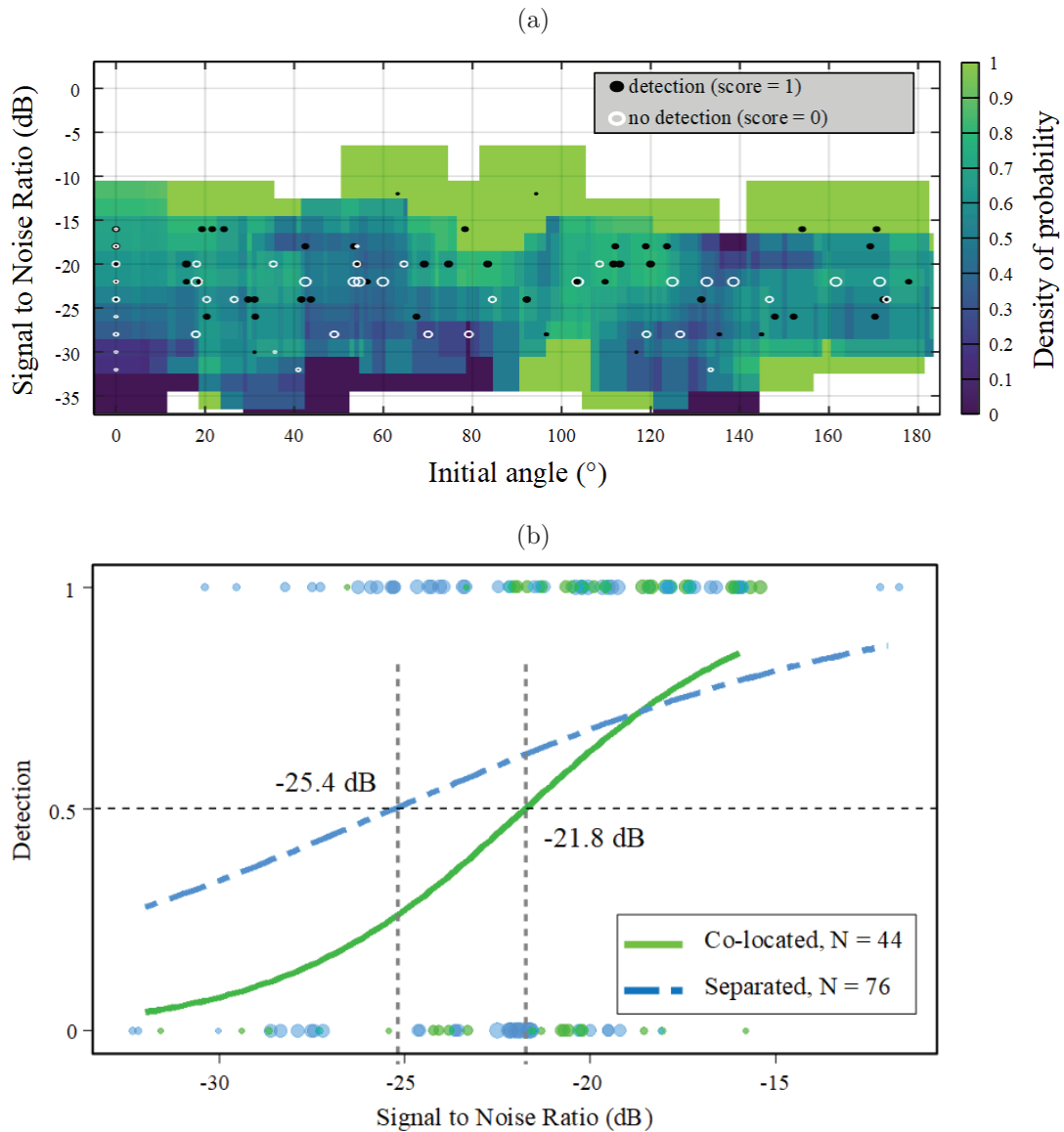


Figure 6.12 – **Results of the Go/No-Go experiments on juvenile Nile crocodiles (Experiment 3).** (a) Detection of the target signals (synthetic buzz) against the background noise as a function of the signal-to-noise ratio and the separation angle between the noise loudspeaker and the target loudspeaker. Circles and dots represent experimental trials (one female per trial; white circles: no detection of the target signal, i.e. no behavioural reaction to playback; black dots: effective detection of the target signal). Circles and dots' sizes are proportional to the number of trials (from 1 to 11). The green-blue colour scale illustrates the probability of detection, ranging from 0 (deep blue, no detection) to 1 (light green, effective detection; probabilities calculated using a sliding squared window $24^\circ \times 12$ dB). (b) Modelling of signal detection probabilities in the co-located and separated conditions. Dots represent experimental trials and dot size is proportional to the number of trials (number of tested females). Green: co-located condition (separation angle = 0°). Blue: separated condition (angles between 16° and 178°). The amount of spatial release (difference between both detection thresholds) is 3.6 dB.

6.5 Discussion

The present study demonstrates that crocodylians are able to perform Spatial Release from Masking: their ability to detect a target sound embedded in a background noise is improved if the target and the noise sources are spatially separated. In our three experimental contexts (maternal response to nestlings' calls in the field, juveniles' response to siblings' calls in semi-natural situation, juveniles' conditioned response to artificial stimuli), the detection thresholds were lower when the target source was separated from the mask.

Detection curves according to the signal-to-noise ratio (SNR) emphasise that spatial separation between the target sound source and the noise source has a major influence on the detectability of target sources. While higher SNRs increase detection abilities in both source positions (co-located and separated), the detection thresholds are always lower in the separated condition, i.e. when the target and the noise sources are spatially separated. It is not possible to compare the absolute values of the detection thresholds across the three experimental conditions because of the different contexts and the differences in the experimental apparatuses. In the experiment 1, Yacare females were tested in the wild in the context of a juvenile calling for rescue; in the experiment 2, the animals were tested in an artificial pond and were isolated from the group; in the experiment 3, the animals were conditioned and tested in a small pool. However, the size effect of SRM remains of close magnitude: 4.5 dB, 7.4 dB, and 3.6 dB, in the field, the semi-natural context, and the Go/No-Go context respectively.

In the Go/No-Go experiment, the subjects' motivation to respond to the stimuli of the individuals can be considered as high and, at least, quite constant across the experimental trials. Indeed, the animals were trained to come to the sound source position in order to obtain a food reward. The detection thresholds measured in the Go/No-Go experiment 3 should thus reflect the physiological feature of the crocodylian audition and their ability to identify the synthetic signals. Trained crocodiles may show higher performances during target-noise segregation even when both sources are co-located, which could explain the smaller amount of SRM observed during this experiment compared to others. In the experiments performed in the field and in the semi-natural setting, we did not train the animals to respond and their behavioural reactions to the stimuli were the results of more intricate processes. In the field, Yacare females were staying close to their own youngs when stimulated. They had to abandon them temporarily to rescue an isolated distressed baby (mimicked by the loudspeaker). This trade-off may lower the females' reaction level and, above all, it probably accounts for the variation in the individual motivation to move towards the sound source. It would have been interesting to get an idea of the number of nestlings attended by the female as well as of their vocal activity since this may impact her decision to move. In the semi-captive condition, ju-

venile Nile crocodiles could have faced another type of behavioural trade-off: moving to join its siblings versus staying immobile to limit predation risk.

The latency times measured in the three experiments were significantly different (Experiments 1-2: $p < 0.001$; Experiments 1-3: $p = 0.002$; Experiments 2-3: $p < 0.001$). This is also probably due to differences in the behavioural context. In the field, reacting mothers showed the shortest latency time (8.3 s): they came rapidly to the target source emitting distress calls in order to protect the young against a danger (predator attack). The longest latencies to respond were observed in the experiment 2, underlying that tested juveniles were quite hesitant to respond to stimuli.

In spite of these limitations and variations across experimental situations, SRM observed here on crocodilians (between +3.6 to +7.4 dB) may be compared to values found in other animals or humans (Bee et al., 2008). Humans show SRM between +15 to +18 dB with "clicks" as target signals, the mask being a broadband noise (Saberri et al., 1991). These high values compared to those obtained with crocodilians may be explained by a higher ability to analyse auditory sound scenes by humans or simply by the fact that human subjects are more likely to understand the task required during the experiment. Indeed, SRM found in other mammal species are closer to those we found in the present study on crocodilians: +10 dB in ferrets (Hine et al., 1994), +12 to +19 dB in pinnipeds (Holt et al., 2007). Gray treefrogs showed SRM from +3 to +12 dB (Nityananda et al., 2012; Bee, 2007). In birds, budgerigars showed a SRM around +9 dB when detecting pure tones in white noise (Dent, 1997) but reached an impressive +20 to +30 dB when facing biological signals (Dent et al., 2009). The amount of SRM that has been reported here (to be from +3 dB to +7 dB) is lower than SRM measured in birds. This may be explained by the fact that birds are, on average, greater users of acoustic communication than crocodiles. While both birds and crocodilians share a common ancestor (monophyletic clade), SRM may have been enhanced in birds -or partially reduced in crocodilians- during evolution.

Performing experiments on crocodiles is challenging. In the field and semi-natural conditions, animals habituate extremely fast to played back signals and it is mandatory to limit the number of experiments performed on a given individual. Go/No-Go experiments require behavioural training of captive crocodilians in the laboratory which is time-consuming and thus limits the number of subjects. As a result, we are aware that our data sets have important gaps, regarding both the range of the tested SNR and angles. This has impacted the statistical power of our analysis and we have to be cautious when interpreting non significant results. Specifically, while spatial separation of the target and noise sources improves signal detectability, none of the three experiments showed a significant effect of variation in the separation angles above a few degrees. Yet, and while our results demonstrate that SRM is already relevant for very small angles in crocodilians (lower than 10°), raw data reported in the Figures 6.4a, 6.9a, 6.12a strongly

suggest that an increase of the angle further improves the detection threshold. An estimation of the Minimum Audible Angles (MAA; Mills, 1958b; Holt et al., 2004; R. Heffner et al., 2015) in crocodylians would be here a valued input.

The present study reports the first experimental investigation of SRM in crocodylians. Our complementary approaches -from investigations in entirely naturalistic conditions to controlled laboratory experiments- underline that these amphibious animals can take advantage of sound sources' spatialisation to analyse sound scenes and improve the detection of signals with relevant information in their daily life. On a general point of view, we assume that naturalistic investigations are needed to fully understand such physiological abilities. Although field experiments can be difficult to perform, they bring the ultimate evidence of the relevance of a biological mechanism.

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Ethics

This research has been conducted under the agreement n° D 42-218-0901. Data collection was noninvasive and in compliance with the requirements and guidelines of the "Association for the Study of Animal Behaviour".

Supplementary material - Experiment 1

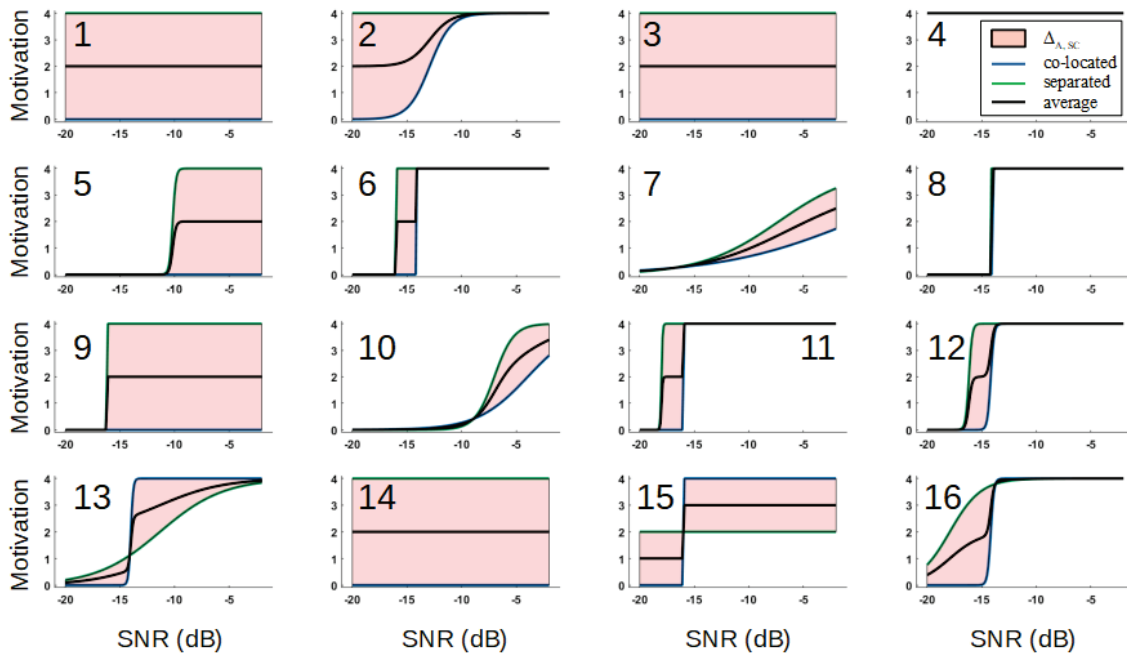


Figure 6.13 – Motivation scores of the 16 tested females included in the experiment 1. The blue and green solid lines corresponds to the sigmoid functions fitted to the motivation data points respectively in the co-located and separated conditions. The black solid lines are the average of both co-located and separated sigmoid functions. The red surfaces illustrate the indicator ΔA_{SC} , i.e. the differences of area under both the co-located and separated curves.

Table 6.8 – **Summary of all testing conditions for each individual considered in the experiment 1 (16 female *Yacare caimans*).** Crosses correspond to the situation in which a female tested in both co-localised and separated conditions. Empty cells correspond to no stimulation.

Subject → SNR (dB) ↓	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
-20					×											
-18					×	×	×	×	×	×	×	×	×	×	×	×
-16			×	×	×	×	×	×	×	×	×	×	×		×	×
-14	×	×			×	×	×	×		×		×	×		×	×
-12					×		×			×			×			
-10					×		×			×			×			
-8							×			×						
-6							×			×						
-4							×			×						
-2							×									

Supplementary material - Experiment 2

Table 6.9 – **Biometric data of the Nile crocodiles (*Crocodylus niloticus*) considered in the Experiments 2 and 3.**

Exp.	Subject	Weight (kg)	Body length (cm)	Interaural distance (cm)
2	1	x	35.0	1.9
2	2	x	33.0	2.0
2	3	x	37.0	2.0
2	4	x	35.0	2.3
2	5	x	35.5	1.9
2	6	x	36.0	1.9
2	7	x	34.5	2.0
2	8	x	38.5	2.0
3	1	2.77	80.0	x
3	2	2.80	83.0	x

Table 6.10 – **Summary of all testing conditions for each individual considered in the experiment 2 (i.e. 8 young Nile crocodiles).** In each cell of the table, the left and right numbers correspond respectively to the number of target signals played in the co-located and in the separated condition.

Subject → SNR (dB) ↓	1	2	3	4	5	6	7	8
-33	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	0 / 0	0 / 0
-32	0 / 0	0 / 0	0 / 0	0 / 1	0 / 1	0 / 1	0 / 0	0 / 0
-31	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1
-30	0 / 0	0 / 0	0 / 0	1 / 0	0 / 1	0 / 0	0 / 0	0 / 0
-29	0 / 0	0 / 0	0 / 1	0 / 1	0 / 0	0 / 0	0 / 0	0 / 0
-28	0 / 0	0 / 0	0 / 2	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0
-27	0 / 0	1 / 0	1 / 0	0 / 0	0 / 0	0 / 1	0 / 1	0 / 0
-26	0 / 0	0 / 0	1 / 0	1 / 1	0 / 1	0 / 0	0 / 0	0 / 0
-25	0 / 1	1 / 0	0 / 0	0 / 1	0 / 0	0 / 1	0 / 1	0 / 0
-24	0 / 2	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0
-23	0 / 2	0 / 0	1 / 1	0 / 0	1 / 0	0 / 0	0 / 0	0 / 1
-22	1 / 0	0 / 0	0 / 0	0 / 0	0 / 1	1 / 0	1 / 0	0 / 0
-21	0 / 0	1 / 1	0 / 1	1 / 0	1 / 1	1 / 0	0 / 1	0 / 0
-20	0 / 0	0 / 1	0 / 0	0 / 0	1 / 1	0 / 0	0 / 0	2 / 1
-19	0 / 0	1 / 1	0 / 0	0 / 0	0 / 0	0 / 1	0 / 1	0 / 0
-18	3 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0	0 / 1
-17	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	1 / 1	0 / 0	0 / 0
-16	1 / 0	1 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0	0 / 1
-15	0 / 0	0 / 0	0 / 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1
-14	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
-13	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0

Supplementary material - Experiment 3

Table 6.11 – Summary of all testing conditions for each individual considered in the experiment 3 (i.e. two conditioned juvenile Nile crocodiles). In each cell of the table, the left and right numbers correspond respectively to the number of target signals played in the co-located and in the separated condition.

Subject → SNR (dB) ↓	1	2
-32	0 / 2	1 / 0
-30	0 / 2	1 / 1
-28	0 / 5	2 / 4
-26	2 / 2	0 / 4
-24	4 / 4	1 / 8
-22	4 / 4	3 / 12
-20	6 / 6	4 / 7
-18	4 / 3	5 / 4
-16	4 / 2	3 / 4
-14	0 / 0	0 / 0
-12	0 / 1	0 / 1

PART IV

Perspectives



The aim of this work was to evidence, describe and quantify sound localisation in crocodilians. We first conducted acoustical measurements to characterise the sound localisation cues available at the eardrum of two juvenile crocodilians. Then, we were able to train two animals to study their localisation abilities and to determine the implication of binaural cues in sound localisation tasks. Finally, we described one strategy used to increase the detection abilities of acoustic signals in a presence of a noise source.

First, we characterised the external sound localisation cues such as the Head-Related Transfer Functions (HRTF), Interaural Level Differences (ILD) and Interaural Time Differences (ITD) in the azimuthal plane (cf. part 4). This work was conducted on two different crocodilians species: one broad-snouted caiman (*Caiman latirostris*) and one Nile crocodile (*Crocodylus niloticus*). The monaural cues (HRTF) measured in both juvenile individuals showed potentially relevant notches for frequencies higher than 2000 Hz. ITD were confirmed relevant up to 1000 Hz and ILD showed detectable variations for frequencies higher than 2000 Hz. Those cues were measured in two natural positions: with the head on the animal on the ground and at the air-water interface, when only the top of the head, eyes, ears and nostrils were emerged from water. The comparison of the cues measured in both conditions evidenced only slight differences. This result suggests a potential adaptation of the external morphology to the air-water interface position producing strong sound localisation cues.

Because the external sound localisation were measured next to the eardrum of the animals, the use of these cues were not demonstrated by our first approach. To test the relevance of the external cues, we conducted conditioning experiments on two Nile crocodiles in laboratory conditions (cf. part 5). The animals were learnt to approach a sound source when emitting a specific signal (buzz). Once the subjects conditioned, we conducted playback experiments by filtering (or not) these buzzes in order to promote the use of ITD (low-pass filter) or ILD (high-pass filter). By analysing the trajectories of the animals approaching the sound source, we were able to estimate their Minimum Audible Angle which was better than 14°. The two subjects included in this study were able to localise sounds precisely based on the use of ILD and ITD (separately and when being combined). Our results suggested the predominance of ITD compared to ILD because sound localisation was more rapid when ITD were promoted.

Because sound localisation may be degraded in a noisy environment, we were interested in testing the use of one strategy widespread in other species to overcome this degradation: the Spatial Release from Masking (SRM, cf. part 6). We conducted three different playback experiments while broadcasting a broadband noise. First, we tested females Yacare caimans (*Caiman yacare*) in the wild with distress calls to elicit a protection behaviour of the female. Then, in open-air captivity, we isolated naive young Nile crocodiles (*Crocodylus niloticus*) from their group and broadcast conspecific calls supposed to attract the young individual. Finally, we conducted Go/No-Go experiments on two con-

ditioned Nile crocodiles in laboratory conditions ensuring a high motivation level. We evidenced that crocodilians do use SRM to increase their ability to detect a sound source in a noisy environment. The amount of SRM was 4.5 dB, 7.4 dB, and 3.6 dB in the field, the semi-captivity and the Go/No-Go contexts respectively.

Previously, the audition of crocodilians was characterised, in three crocodilians species (American alligator, American crocodile and spectacled caiman; cf. part I). The audition thresholds were obtained using the cochlear potential method (Wever et al., 1957; Wever, 1971), the Auditory Brainstem Response (ABR; Klinke et al., 1980; Manley, 1970; Higgs et al., 2002) and characterising the transfer function of the middle ear (Saunders et al., 2000) when playing pure tones. All these electrophysiological methods converged to a U-shaped pattern of audition showing a high sensitivity region between 500 Hz and 2000 Hz. These results suggest that high frequencies signals with energy above 2000 Hz would be difficult to be detected. In the part 5 three different types of signal were played back to the trained Nile crocodiles. They showed energy between 70 and 10000 Hz, between 70 and 1500 Hz and between 1500 Hz and 10000 Hz. In the last condition, the main energy contained in the signal was above 2000 Hz and we demonstrated that the tested individuals succeeded in localising the origin of the sound. Furthermore, we conducted the same types of experiments as in part 5 in the open-air captivity context (April 2018, data not shown). We isolated a young Nile crocodile from the group and played back conspecifics' calls after applying the same types of filters as in part 5 in order to increase the use of ILD or ITD. The results of these experiments are not shown in this manuscript because they were considered too weak to test our hypotheses. However, the young crocodiles were able to localise the signals even when only the high frequency part were broadcast (ILD conditions). This localisation accuracy may be induced by the energy of the band 1500-2000 Hz where the audiograms show high sensitivity of the hearing apparatus. Yet, these behavioural observations may hypothesise that crocodilians potentially use the energy above 1500 and even 2000 Hz when localising a sound source. Indeed, all the audiograms computed on crocodilians were based on electrophysiological measurements such as Auditory Brainstem Response method. If ABR gives a fair estimation of the auditory threshold, it was evidenced several times that ABR thresholds may differ significantly from behavioural thresholds. In humans, ABR overestimated the behavioural auditory thresholds of more than 20 dB (Werner et al., 1993; Goshorn et al., 2017; Gorga et al., 1988). In the túngara frogs *Engystomops pustulosus*, the behavioural thresholds were 10 dB lower than when using ABR (Taylor et al., 2019). In budgerigar *Melopsittacus undulatus* and barn owl *Tyto alba*, ABR thresholds were 30 dB higher than the behavioural ones (Brittan-Powell et al., 2002; Dyson et al., 1998). These huge differences highlight the need to measure behavioural thresholds in crocodilians. We showed through our experiments that it is possible to condition crocodilians on acoustic stimuli. Therefore, it

would be possible to use a Go/No-Go procedure to estimate behaviourally the auditory thresholds.

The experiments described in this manuscript rely on sound localisation abilities of several crocodylian species in air. Indeed, all the tests were led when the ears (at the least ear-opening) were emerged and all stimuli were broadcast in air with classical loudspeakers. Crocodylians evolve in an amphibious environment, most of the time at the interface between air and water but they are able to spend a long time underwater. When diving, the eye is protected by the nictitating membrane which dramatically degrades visual cues (Fleishman et al., 1988). A recent study evidenced that gharials *Gavialis gangeticus*, which are particularly adapted to a water environment, emit sounds underwater (Jailabdeen et al., 2019). These sounds, called "pops" are implied in social interaction and particularly around breeding time. The auditory response measured in water was found close to the audiogram measured in air (Higgs et al., 2002) and sound localisation was observed in American alligators (Dinets, 2013b). Underwater sound localisation abilities remain unknown whereas it seems to be a fundamental question knowing that crocodylians spend half of their time in water.

We evidenced that crocodylians are using spatial release from masking in biological contexts to increase their ability to detect a relevant signal in the presence of a noise source. These results imply that they are able to discriminate two different sound sources and to respectively associate the mask to an irrelevant source of noise and the conspecific call or buzz to a signal of interest. From this statement, crocodylians seem to be able to discriminate two different acoustic signals based on the information they carry. Moreover, naive juvenile and adult crocodiles were attracted to hatchlings calls which were previously filtered above and below 1500 Hz (April 2018, data not shown). This suggests that even an incomplete conspecific call may be associated to a relevant signal arousing interest. Studying this complex cognitive process would considerably increase our knowledge on crocodylians which are often described as instinctive animals acting in direct relation with their sensory skills.

Another interesting feature was observed when conducting sound localisation playback experiments in open-air captivity (April 2018, data not shown). In an isolation context from the group, the tested juvenile Nile crocodiles did approach a loudspeaker playing back conspecific calls. Their reaction were considerably higher than those measured in the conditioning experiment conducted in the laboratory (between 1 and 2s; cf. part 5) and may reach several minutes (average value: 82 s; maximum reaction time: 5 minutes and 26 seconds). These observations let think that the juvenile crocodiles were able to, first, detect the signal, then to identify it as a conspecific call, to localise it in space and to keep in memory the sound source position before going toward it. Even if this hypoth-

esis remains speculative and more precised experiments are needed, crocodilians may be able to keep in memory the position of a sound source for several minutes.

Crocodilians rely on a wide range of well developed sensory skills. Here, we detailed one aspect of their accuracy dealing with acoustics but, crocodilians reached their apex predator status by combining all their senses together. Analysing their ability in each sensory channel is primordial to increase our knowledge about how they use visual, olfactory or mechanical inputs cues in their natural behaviour. Yet, crocodilians are constantly stimulated by a wide diversity of inputs and they must adapt their behaviour based on the combination of these sensory stimuli. In this way, Chabrolles et al. demonstrated the cross-sensory modulations between olfactory and acoustic stimuli in Nile crocodiles (Chabrolles et al., 2017). Based on this work, it would be very interesting to test the interactions between different modalities in several contexts. This multimodal approach would offer new perspectives on crocodilians behaviour and would allow more accurate descriptions of their natural behaviours.

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Abstract

Keywords: Crocodylians, Sound localisation, Bioacoustics, Head-Related Transfer Functions, Interaural Level Differences, Interaural Time Differences, Spatial Release from Masking.

Crocodylians develop very accurate sensory skills to effectively probe their environment before reaching their apex predator status. They demonstrate excellent vision above water, a highly developed sense of smell, an impressive use of mechanoreceptors and a precise sense of hearing. These sensory abilities are essential for hunting and facilitate social interactions between sexual partners or parents and young. Along with birds and dinosaurs, crocodylians form the Archosaur order. There is strong evidence for acoustic communication in a range of Archosaur species, and indeed, crocodylians are actively vocal throughout their lives. Even inside the egg, mature crocodylian embryos use acoustic communication to synchronise the hatch. In their first years of life, juveniles vocalise in response to danger to elicit help from their parents and to ensure the cohesion of the group to limit predation risk. Finally, adult crocodylians regularly use vocalisations during courtship before mating and when hunting prey at the air-water interface. To ensure effective acoustic communication across these varied contexts, crocodylians must precisely localise multiple sound sources within their environment.

The crocodylians' sound localisation abilities appear to be highly accurate however this capacity has only been empirically investigated in a small number of studies. Birds, and particularly vocal birds, have been tested many times to understand sound localisation mechanisms and performance, yet these same features remain poorly understood in their closest relatives: crocodylians. One critical situation in which crocodylians need to precisely locate a sound source is during hunting. Most crocodylian species are opportunistic, and show a common method of hunting in which they submerge themselves under water, with only the eyes, ears and nostrils emerged for prey surveillance. Sound localisation is also necessary during their first years of life when they are most subject to predation. Finally, sound localisation may be used by crocodylians to gauge information about their surrounding environment.

To explore sound localisation in crocodylians, we had the opportunity to work in different contexts in order to: identify which cues are needed to localise a sound in space; quantify their sound localisation abilities; describe how they are able to localise sounds within a noisy environment. Firstly, we measured sound localisation cues by placing microphones inside the ears of juvenile animals: one Nile crocodile (*Crocodylus niloticus*) and one broad-snouted caiman (*Caiman latirostris*). By moving a sound source around the animal, we were able to quantify monaural (Head-Related Transfer Functions, HRTF) and binaural cues (Interaural Level and Time Differences, ILD and ITD) classically involved in sound localisation in other species. In a second step, we trained Nile crocodiles to approach a sound source emitting a specific signal. By filtering these signals before playing them to the animal, we were able to quantify the animal's sound localisation performance when relying on either ILD or ITD. Finally, we conducted playback experiments in an artificially noisy environment. This final step involved three approaches, testing: Yacare caimans (*Caiman yacare*) in the wild with distress calls of hatchlings; Nile crocodile hatchlings while simulating a separation from the group and broadcasting conspecific calls; trained Nile crocodiles in a Go/No-Go experiment, ensuring high motivation.

Our results demonstrated that the external morphology of the crocodylians head induces potentially relevant external acoustic cues depending on the position of the sound source. By measuring the monaural cues in two situations – when the animal was resting on the ground, or in the natural hunt position at the interface between air and water – we demonstrated that those cues are preserved at the interface even when only a small part of the head is emerged. This result may suggest a potential adaptation to this specific hunting position, ensuring strong localisation cues. Binaural cues appeared complementary in a wide frequency span with strong ITD in the low frequency range and powerful ILD for higher frequencies. The trained crocodiles showed very precise abilities in sound localisation behavioural tasks. Our experiments showed that both ITD and ILD are relevant when estimating the position of a sound source, and we computed the Minimum Audible Angle for the first time in the crocodylian order. Finally, in the presence of a source of noise in their environment, crocodylians perform Spatial Release from Masking to increase the detection of relevant acoustic signals. These features work in cohesion to confer the highly developed sound localisation abilities of crocodylians.

Résumé

Mots-clefs: Crocodiliens, Localisation des sons, Bioacoustique, Fonctions de transfert liées à la tête (HRTF), Interaural Level Differences, Interaural Time Differences, Démasquage spatial.

Les crocodiliens ont développé des compétences sensorielles très précises pour sonder leur environnement, leur permettant de s'élever au rang de super prédateur. Ils possèdent une excellente vision dans l'air, un odorat très développé, une utilisation impressionnante de mécanorécepteurs et une ouïe précise. Ces capacités sensorielles sont primordiales en situation de chasse et sont nécessaires pour assurer les interactions sociales entre partenaires sexuels ou entre parents et jeunes. Comme les oiseaux et les dinosaures, avec qui ils forment l'ordre des Archosaures, les crocodiliens vocalisent activement tout au long de leur vie. Dès l'intérieur de l'œuf, les embryons matures utilisent la communication acoustique pour synchroniser l'éclosion. Dans leurs premières années, les jeunes crocodiliens appellent à l'aide en cas de danger et assurent la cohésion du groupe par des cris de contact pour limiter les risques de prédation. Enfin, les signaux acoustiques sont utilisées lors des parades nuptiales avant l'accouplement. Pour assurer la communication acoustique et pour chasser leurs proies depuis l'interface air-eau, les crocodiliens ont la nécessité de localiser avec précision les multiples sources sonores de leur environnement.

Les capacités de localisation sonore des crocodiliens ont été rapportées à plusieurs reprises très précises, mais n'ont été étudiées que quelques fois. Les oiseaux, et en particulier les oiseaux vocaux, ont été testés de nombreuses fois pour comprendre les processus et les performances de localisation des sons, mais ces caractéristiques restent mal connues chez les crocodiliens, la famille la plus proche. Une situation nécessitant une localisation sonore précise demeure la chasse. La plupart des espèces de crocodiliens sont opportunistes mais une caractéristique commune demeure leur méthode de chasse à l'affût avec seulement les yeux, les oreilles et les narines émergées. Une bonne localisation est également nécessaire au cours de leurs premières années lorsqu'ils sont sujets à la prédation. Enfin, la localisation sonore peut être utilisée pour accumuler des informations sur l'environnement.

Afin d'explorer la localisation des sons chez les crocodiliens, nous avons eu l'occasion de travailler dans différents contextes afin d'identifier les indices nécessaires pour localiser un son dans l'espace, de quantifier leurs capacités de localisation sonore, et de décrire leur comportement face à un environnement bruyant. Tout d'abord, nous avons mesuré les indices de localisation sonore en plaçant des microphones à l'intérieur des oreilles d'individus juvéniles : un crocodile du Nil (*Crocodylus niloticus*) et un caïman à museau large (*Caiman latirostris*). En déplaçant une source sonore autour de l'animal, nous avons pu quantifier les indices monauraux (fonctions de transfert liées à la tête, HRTF) et binauraux (différences interaurales de niveaux et de temps, ILD et ITD) qui sont classiquement impliqués dans la localisation acoustique. Dans un deuxième temps, nous avons entraînés deux crocodiles du Nil à approcher une source sonore à l'émission d'un signal spécifique. En filtrant ces signaux avant de les rejouer à l'animal, nous avons pu quantifier leurs performances de localisation sonore lorsqu'ils utilisaient séparément les indices d'ILD et d'ITD. Enfin, nous avons mené des expériences de playbacks dans un environnement artificiellement bruyant. Cette dernière partie a été menée selon une triple approche en testant : des caïmans Yacare (*Caiman yacare*) dans la nature avec des cris de détresse de nouveau-nés ; de très jeunes crocodiles du Nil en simulant une séparation du groupe et en diffusant des cris de congénères; des crocodiles du Nil entraînés dans une expérience Go/No-Go, assurant un niveau de motivation élevé.

Nous avons observé que la morphologie externe de la tête des crocodiliens induit des indices acoustiques externes potentiellement significatifs dépendant de la position de la source sonore. En comparant les indices monauraux obtenus dans deux situations - lorsque l'animal se repose sur le sol et dans la position naturelle de chasse à l'interface entre l'air et l'eau - nous avons démontré que ces indices sont préservés à l'interface même lorsque seulement une petite partie de la tête est émergée. Ce résultat suggère une adaptation potentielle à cette position de chasse spécifique assurant des indices de localisation robustes. Les indices binauraux semblent couvrir une large gamme de fréquences, avec de forts ITD dans les basses fréquences et des ILD importants dans les hautes fréquences. Des expériences comportementales menées sur des individus entraînés ont démontré une grande précision de localisation. L'ITD et l'ILD se sont avérés tous deux efficaces pour estimer la position d'une source sonore et nous avons donné une première estimation de l'angle minimum audible chez les crocodiliens. Enfin, lorsqu'ils sont exposés à une source de bruit, les crocodiliens utilisent le démasquage spatial afin de faciliter la détection de signaux acoustiques pertinents. Toutes ces caractéristiques convergent et confirment de grandes capacités de localisation sonore chez les crocodiliens.

