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Why do dogs head tilt?

Head tilting behaviour in domestic dogs (*Canis familiaris*) and their ancestors the grey wolves (*Canis lupus*).

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1. Abstract

The head tilting behaviour in dogs (*Canis familiaris*) is an extremely appealing and yet scarcely studied behaviour as its frequency, triggers and function are unknown in dogs. In the dog's ancestor, the wolf (*Canis lupus*), not even the presence of this behaviour is known. Regarding the function of head tilting, there are two hypotheses both related to sensory improvements: auditory (better sound localisation on the vertical axis) or visual (removal of the muzzle impediment). The aim of this study was to investigate the possible function of head tilting in dogs and its possible presence in wolves. Dogs (N=36) and wolves' (N=8) response to a squeaky toy sound coming from different positions and under different conditions was tested. Wolves never head tilted, while dogs head tilting significantly decreased with trials. Dogs head tilted more when the sound source was invisible and located on the vertical axis, in particular in the frontal position with a tendency of significance. Female dogs' head tilting and attentiveness lasted more than males but not significantly. Head tilting decreased with age in dogs, as did attentiveness with a trend of significance. The pinnae shape, the muzzle length and the breed group the dog belonged to did not seem to have a significant effect on the behaviour. In conclusion, head tilting is abundant in dogs and more research is needed to understand the function of head tilting and its triggers.

Keywords: Dogs, Wolves, Head tilting, Sound localisation, Ears asymmetry

2. Introduction

Despite humans finding head tilting extremely cute, this behaviour is still scarcely studied. Its presence in wolves is unknown while in dogs it is only known that it is performed in response to known words. However, its triggers and function are still unknown, only unproved hypotheses currently exist.

2.1 Sound perception

Hearing is the ability of an organism to perceive vibration, which are changes in pressure of a mean the organism is immersed into, and translate them into sounds (Plack, 2014). The two ears capture and transduce sound waves to the auditory nerve, which in turn bring the impulses to the brain to be elaborated and converted into what humans call sounds (Poli et al., 2018). In vertebrates, the ear is composed of one to three areas (outer ear, middle ear and inner ear), which collect sounds and allow to gain information about sound intensity and frequency, but also about the location of the sound source.

2.1.1 Outer ear

The outer ear is composed of the auricle (or pinna) and the ear canal (Poli et al., 2018). The auricle is a cartilaginous structure that, depending on the species, can take on different shapes or be mobile (Barber et al., 2020; Cole, 2009; Poli et al., 2018). Its function, relative to hearing, is to collect, funnel and amplify sound waves towards the ear canal (Barber et al., 2020; Poli et al., 2018; Strain, 2011). Once the sound waves reach the ear canal they are further amplified and channelled to the middle ear (Poli et al., 2018).

In wolves and dogs the pinna is mobile and, in dogs, its shape is highly variable depending on the considered breeds (Barber et al., 2020; Strain, 2011). In fact, the dimension and form of the pinnae define which sound wave frequencies are optimally collected. The effects of the shape of the pinna on the amplification of sound waves have not been assessed, but there seems to be a correlation between bigger erect ears and a better performance in localising distant sounds (Nummela, 2008; Strain, 2011), even though this has never been tested in dogs.

2.1.2 Middle ear

The middle ear is separated from the outer ear by the tympanic membrane and consist of the tympanic cavity containing the auditory ossicles (Cole, 2009; Poli et al., 2018). The tympanic membrane of the middle ear vibrates and transmits the sound waves to the auditory ossicles. In mammals there are three ossicles, the malleus, the incus and the stapes, forming the ossicular chain. The tympanic membrane makes the ossicles vibrate in turn, transferring the

sound waves vibrations to the vestibular (or oval) window of the inner ear. The malleus of dogs is quite big (their malleus-incus ratio is 3:1) compared to other animals like humans, allowing for a magnification of the energy transduced and potentially increasing their sound sensitivity (Barber et al., 2020).

2.1.3 Inner ear

The inner ear is responsible for both static and sound perception (Cole, 2009; Poli et al., 2018; Torres & Giráldez, 1998). The sacculus is a ventral chamber from which evaginates the lagena (or cochlea if coiled), containing the basilar membrane on which are distributed sensory outer and inner hair cells (stereocilia) (Cole, 2009; Poli et al., 2018; Robles & Ruggero, 2001). The basilar membrane is thicker, narrower and stiffer at the base of the cochlea compared to its apex. Due to the variation in the basilar membrane stiffness, the stereocilia on different parts of the cochlea are sensitive to different sound frequencies, higher to lower progressing through the cochlea itself, which is especially important to be able to perceive a greater amount of auditory information from the surrounding environment. From the vestibular (or oval) window, the sound vibrations propagate through the endolymph inside the cochlea. The fluid sets in motion the stereocilia, which transduce the vibration into an electric signal that is transferred by the static-auditory nerve to the brain to be elaborated into what is commonly known as sound.

Dogs' basilar membrane is quite stiff at the base and this is the reason for their ability to perceive high frequency sounds (Barber et al., 2020). Indeed, their hearing ranges, thus the ranges of frequencies an animal can perceive, spans from 65 Hz to 45 kHz (Barber et al., 2020). It is slightly wider and shifted towards higher frequencies compared to the human's one, which ranges from 20 Hz to 20 kHz.

2.2 Hearing importance

The auditory system serves the purpose of gaining information on the surrounding environment, in particular regarding the location from which the sound is coming (Heffner & Heffner, 1992). Consequently, it aids in the orientation of vision and other senses, resulting in a more detailed and complete analysis of the surrounding environment. Therefore, it is evident why hearing plays a key role in prey/predator detection for certain species. It seems a particularly important sense especially for mammals, which naturally orientate their pinnae (Preyer reflex), or entire head in case of immobile pinnae, towards the direction of a sound to better evaluate it (McFadden et al., 2022).

As for prey animals, auditory cues can provide information about the presence and location of predators, especially for nocturnal animals (Rosier & Langkilde, 2011). Prey animals that rely more strongly on auditory cues have developed bigger, mobile pinnae to better capture sounds, as in the case of the mule deer (*Odocoileus hemionus*) (Lingle & Wilson, 2001). A similar argument could be made for predators, which use auditory cues to locate their prey and that is especially true for nocturnal species (Carr & Christensen-Dalsgaard, 2015).

For predators, it is particularly important to determine the position of the prey as precisely as possible to maximize the chances of capture. To achieve this, they rely mainly on two types of information of the sound perception: the differential spectral amplitude and the differential arrival time (Carr & Christensen-Dalsgaard, 2015; Klump, 2000; Wightman & Kistler, 1993). A sound coming from a random direction in the space reaches the two ears with different intensity (differential spectral amplitude), if the wavelength of the sound is small compared to the head size. In fact, the ear closer to the sound source capture a higher intensity sound than the other, as the head creates an obstacle that diminish the intensity of the sound captured by the other ear (head shadow). Alternatively, they can use the differential arrival time of the sound to their ears (interaural time difference) for sounds between few hundred and few thousand Hz. In other words, a sound coming from the side arrives to one ear slightly before the other and this difference in the arrival time allows to understand the direction the sound is coming from, which is the one closer to the ear at which the sound arrived first. However, for sounds coming from above or below, it becomes harder to precisely locate the sound's position because the sound arrives at the two ears almost simultaneously.

Thus, some species have developed morphological and behavioural adaptations to localise the prey more precisely, independently of its position, using the aforementioned physical properties. Hereafter, some examples of animals that developed morphological and behavioural adaptations to improve their performance in localising sounds situated on the vertical axis.

2.2.1 Owls ear asymmetry

Owls are mostly crepuscular or nocturnal predators, which means that, given the scarcity or total absence of light, some species have developed adaptations that rely on senses other than vision to individuate preys (König & Weick, 2008). For example, hearing can be used to pinpoint the exact location of a prey. Furthermore, considering they are flying predators, the capability to identify with precision the location of a prey's sound coming from below them,

so a sound located on the vertical axis, can highly increase their chances of success during the hunt. For the aforementioned reasons, many nocturnal or crepuscular owl species have evolved an asymmetry between the two ears compared to the vertical axis (Gutiérrez-Ibáñez et al., 2011; Kelso, 1940; Krings et al., 2019; Norberg, 1978; Norberg, 2002). The asymmetry can involve the morphology of skull structure (e.g. *Aegolius funereus*) (Norberg, 1978; Norberg, 2002) or be more superficial and entail only the position and form of the ear skin opening (e.g. *Tyto alba*) (Norberg, 2002). Owl species with asymmetrical ears have been found to have larger auditory nuclei compared to species with symmetrical ears, which is thought to reflect their finer ability of accurately locate sound sources and wider hearing range (Gutiérrez-Ibáñez et al., 2011). Moreover, the accuracy with which owls localise sounds on the vertical axis is furtherly enhanced by the ruff feathers that frame their facial disc, since it helps in collecting and amplifying sounds (Hausmann et al., 2009; Knudsen & Konishi, 1979; Konishi, 1973; Norberg, 1978). Thus, owl species with the aforementioned morphological features can accurately locate preys in low visibility conditions or if they are hidden under the vegetation or the substrate.

Barn owls (*Tyto alba*) are the species with ears asymmetry on which most studies have been made. They have the highest sound localisation accuracy among all terrestrial animals that have been tested (Knudsen et at., 1979). Their extraordinary sound localisation performance on the vertical axis is due to the asymmetrical position of their ears in respect to the vertical axis (Carr & Christensen-Dalsgaard, 2015; Knudsen, 1980; Knudsen & Konishi, 1979; Knudsen et at., 1979; Konishi, 1973; Konishi, 1973; Payne, 1971). This morphological feature creates interaural level differences and interaural intensity differences, varying with elevation. This means that not only sounds on the horizontal axis, but also sound on the vertical axis arrive at their ears at slightly different times and with slightly different intensity, allowing barn owls to precisely identify a sound location with origin on the vertical axis too. In particular, it seems that the sound elevation is estimated through interaural intensity cues, while the sound azimuth is appraised by the interaural time difference. Thus, with the combination of interaural time difference, interaural intensity difference and interaural level difference, barn owls have a bi-coordinate system for sound localisation to their disposal, granting them the ability to efficiently locate sounds coming from all directions in/of the space. Overall, this system seems especially effective for high frequency sounds (Volman & Konishi, 1990; Volman, 1990). Indeed, these animals can effectively use interaural time difference for sound localisation for sounds up to 8-9 kHz, while most birds and mammals, as

aforementioned, can only use this feature for sounds up to a few thousand Hz (around 2 kHz) (Grothe et al., 2004).

In conclusion, some owl species have developed morphological adaptation, like ruff feathers on the facial disk and asymmetrical ears, to accurately locate prey sounds on the vertical axis without moving their head and increase their hunting success. This prompts the question, can animals with symmetrical ears obtain the same result in a different way?

2.2.3 Foxes head tilting

Canids belonging to the genus Vulpes have colonized almost every continent and habitat on the planet, and they are characterised by a nocturnal or crepuscular life style (Audet et al., 2002; Dempsey et al., 2009; Hersteinsson & MacDonald, 1992; Sillero-Zubiri et al., 2004). Their diet is mainly composed of small preys, like rodents, lizards or insects (Angerbjörn et al., 1999; Brahmi et al., 2012; Elmhagen et al. 2002; Fedriani, et al., 2000). What is common to many foxes' preys (e.g. burrowing rodents like lemmings, voles and gerbils), is their inclination to spend much time underground, hidden in burrows and tunnels they dig in the ground or in the snow (Knaust, 2014; Laundré & Reynolds, 1993; Wiedenmayer, 1997).

Basically, foxes hunt in low to no light conditions and often their preys cannot be located by sight, since they are often hidden below layers of snow, vegetation or underground. Therefore, to locate and capture this kind of preys, foxes cannot count on vision but use a peculiar strategy based on hearing, called "mousing" behaviour (Bahr, 1989; Ĉervený et al., 2011; Henry, 1986). First the prey is located through hearing, as the ears are erect and the animal tilts its head from side to side to perceive where the prey noises are coming from. In fact, since the prey is not visible and hiding underground, foxes have to locate an invisible sound source below them, i.e. on the vertical axis. They tilt their head and, therefore, their ears reach an asymmetrical position in respect to the vertical axis. This behaviour might be performed to create interaural level, time and intensity difference of the sound between the ears and, thus, increase foxes' ability to locate the prey sound on the vertical axis. The mousing behaviour sequence is concluded by the fox leaping through the air and pinning the prey down to the ground with the forepaws, to finally bite it to death (Bahr, 1989; Ĉervený et al., 2011; Henry, 1986). Alternatively, the prey can be dug out. As it can be deduced, this hunting technique and prey localisation strategy are used and particularly useful for red and arctic foxes, whose preys hide beneath the snow, the soil or under thick vegetation. Fennec foxes does not seem to

perform mousing behaviour but they do use their extremely large ears to locate prey hiding underneath the sand, which they then proceed to dig out (Asa et al., 2004; Ewer, 1973).

2.2.4 Do wolves head tilt?

Wolves (*Canis lupus*) are crepuscular pack hunters so they usually collaborate to capture big preys (Ciucci et al., 1997; Earle, 1987; MacNulty et al., 2007; Mech, 1981; Mech & Boitani, 2003; Merrill & Mech, 2003; Theuerkauf et al., 2003). In fact, the main components of their diet are large ungulates like elks, bisons, deers or caribous (Mech & Boitani, 2003; Mech & Peterson, 2003; MacNulty et al., 2007; Zlatanova et al., 2014). They use all their senses to precisely locate the prey, which are big enough to be pretty visible and produce sounds easily localisable by the wolves on the horizontal axis (Mech, 1981; Mech & Boitani, 2003). However, wolves integrate their diet with other components when the big preys run low (Geptner, 1988; Zlatanova et al., 2014). This is especially true for young temporarily solitary individuals that are looking for a new pack and, thus, cannot hunt large preys alone. In fact, wolves can be seen eating wild berries and small preys, such as rodents like lemmings and voles. The latter, as in the case of the preys of foxes, tend to hide underneath the vegetation or in tunnels dug beneath the snow or the soil (Knaust, 2014; Laundré & Reynolds, 1993). Therefore, wolves could actually benefit from the head-tilting behaviour to localise with precision sounds on the vertical axis coming from hidden preys. However, there seems to be limited research concerning the topic.

2.2.4 Why do dogs head tilt?

Dogs (*Canis familiaris*) are the direct descendants of wolves but, contrary to them, they are domesticated (Freedman & Wayne, 2017; Lindblad-Toh et al., 2005). In fact, during the Pleistocene, some wolves-like canids began to live in human families instead of groups of conspecifics (Bergström et al., 2020; Frantz et at., 2020; Freedman et al., 2014). Indeed, the domestication process not only changed the physical appearance of these animals but also some of their behaviours (Coppinger & Coppinger, 2001). For example, since dogs have been fed by humans for a long time, the evolutive pressure to hunt has undergone a relaxation (Christiansen et al., 2001; Coppinger et al., 1987; Udell et al., 2014; Mehrkam & Wynne, 2014). This phenomenon is further accentuated on certain dog breeds by the human artificial selection process.

Therefore, the presence of head tilting behaviour for a function similar to the foxes' one might not seem so useful, but that might not be true for all breeds. In fact, breeds with a strong

predatory drive, like those selected for hunting purposes, could have maintained the behaviour since the ability to perceive hidden preys (like the one hiding in bushes and burrows) would make them better hunters, possibly selected by humans too (Christiansen, Bakken, Braastad 2001b; Mehrkam and Wynne 2014).

Dogs spend a great deal of their time with humans as their companions and, thus, they are extensively exposed to human language throughout their entire life (Cuaya et al., 2022; Pongrácz et al., 2001). Consequently, what originated from this, is what Pongrácz et al. (2001) defined as social understanding, meaning dogs have learnt to interpret and integrate different human cues, like a verbal command, in specific contests and modify their behaviour accordingly. Indeed, dogs seem to be sensitive to vocal stimuli since their brain has voice-sensitive areas dedicated to compute vocal cues with patterns similar to humans' brain voice-sensitive areas (superior temporal cortex) (Andics et al., 2014). Also, they seem to be sensitive to voice manifesting emotional valence. Furthermore, dogs present lateralization for speech analysis, with meaning being processed by the left hemisphere and intonation by the right one (Andics et al., 2016). Then both components are integrated and used to establish the reward value/intentions (higher if they are concordant) of what they heard/speaker. Dogs can also recognise speech naturalness and discern known languages from unknown ones, by extracting auditory regularities (Cuaya et al., 2022). Moreover, this ability seems correlated with the amount of time a dog has been exposed to human language and to the breed. In addition, dogs have the ability to memorise more than 1000 human words (e.g. objects names) and their meaning and distinguish them from novel words (Kaminski et al., 2004; Pilley & Reid, 2011; Prichard et al., 2018). Finally, dogs, similarly to humans, can also recognise a voice identity (speaker identity) through secondary auditory regions in the brain (Boros et al., 2020). Thus, dogs head-tilting behaviour could be a way to better locate the source of an interesting or valuable sound, like a known word coming from their owner or another human.

Currently, head tilting in dogs is still a scarcely studied behaviour. Despite multiple speculations about the reasons for the aforementioned behaviour, the scientific literature counts very few articles about it, whereof only one investigates the behaviour itself (Sommese et al., 2022). Fritts (2018) provides a perspective on the state of knowledge about head tilting in dogs. They illustrate how there are multiple disparate speculations about the function of this behaviour. For example, Amry et al. (2018)'s study discovered that people seem to find this behaviour cute and so, they hypothesised that dogs (in particular shelter dogs) do it to appear more likeable to humans (Amry et al., 2018; Fritts, 2018). Other hypotheses relate the

head tilting to sensory improvement. The other sensory improvement theory hypotheses a visual improvement since the tilting of the head to one side would reduce the muzzle impediment (Fritts, 2018). This would allow the dog to see better, for example, the human face and expressions, therefore aiding in the interpretation of the human itself. Nevertheless, for this hypothesis to be true, short muzzle dogs should not be performing the head tilting behaviour. The only study present in literature that tried to investigate the cause/function of head tilting is Sommese et al. (2022). Their results showed that some dogs performed head tilting upon hearing a known word, like the name of an object they are required to fetch, as during the experiment. The researchers also found that the head tilting direction is individual-specific and consistent. However, there is no mention of the direction or position from which the sound was originating nor they tried using different kind of sounds. Furthermore, the study subjects were mainly border collies, so no consideration regarding head tilting in different breeds can be elaborated. Finally, it must be taken into account that this study is placed in the context of other studies that were already taking place. In fact, Sommese et al. (2022) used the dogs employed for Fugazza et al. (2021) and Dror et al. (2021) studies about dogs learning abilities and long-term memory.

2.3 Aim of the study

This study's aim is to investigate the head tilting behaviour in the dog (*Canis familiaris*) and in its closest relative species the wolf (*Canis lupus*). In particular, the experiment is designed to examine if the reason for this behaviour is present in wolves and if, in both species, it can be a sensory improvement as it is in foxes. Starting from the current hypothesis regarding the reason for the head tilting behaviour in dogs, which are an auditory or a visual enhancement, the objective of this study is to investigate if this behaviour has any correlation with the visibility of the sound source. In order to test this, the head tilting behaviour of dogs will be assessed when presented with both visible and invisible sound sources. Such a finding would suggest if dogs head tilting is more related to vision or hearing. Furthermore, this study plans to investigate the relation between head tilting in dogs and wolves and the position of the sound source, to comprehend if this behaviour is performed for a similar reason as foxes or owls' ear asymmetry (i.e. higher precision in sound localisation on the vertical axis). Therefore, the behaviour of dogs and wolves will be evaluated when presented with sounds originating from different positions. Finally, this study analyses if the head tilting behaviour in dogs has any correlation with the age of the subject, due to higher degree of experience or learning, its sex or breed group.

3. Materials and Methods

3.1 Research subjects

The animal species included in the project are the domestic dog (*Canis familiaris*) and the grey wolf (*Canis lupus*).

Thirty-six privately owned dogs of different breed and age participated in the main experiment, while twelve dogs participated to the pilot studies. Among the participating subjects there were 23 females and 13 males and their mean age was 4.91 years ± 0.41. All the dogs have previously shown the head tilting behaviour during their everyday life, as stated by their owners. The dogs presented various pinnae shape that were classified as follows: "erect" (E) (the dog presented straight erect pinnae that leave the ear canal uncovered), "semi-erect" (S) (the dog presented straight erect pinnae that leave the ear canal uncovered, but the upper point in dropped) and "dropped" (D) (the dog presented floppy pinnae that cover the ear canal) (Barber et al., 2020; Cole, 2009) (figure 1). The muzzle length of the dogs was classified as follows: "brachycephalic" (B) (short muzzle dogs), "mesocephalic" (M) (intermediate length muzzle dogs) "dolichocephalic" (D) (long muzzle dogs) (figure 2). The pinnae shape and the muzzle length of dogs assessed visually. The breed group the dogs belonged to was assigned following the Fédération Cynologique Internationale (FCI) breeds nomenclature (Fédération Cynologique Internationale (FCI), n.d.)). More information about the individual dogs can be found in Table 1, while their pictures can be visioned in Appendix A.

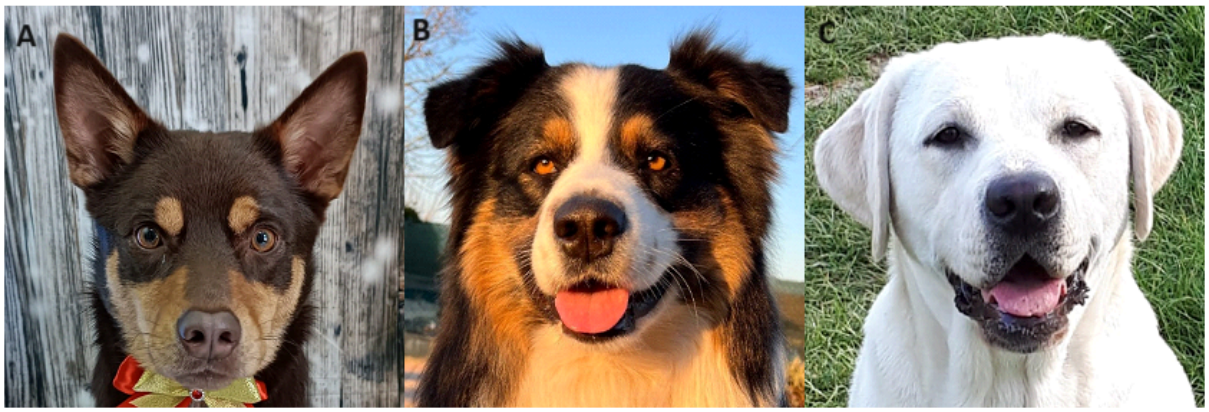

***Figure 1**. Dogs' pinnae shapes: **A)** erected, **B)** semi-erected and **C)** dropped.*

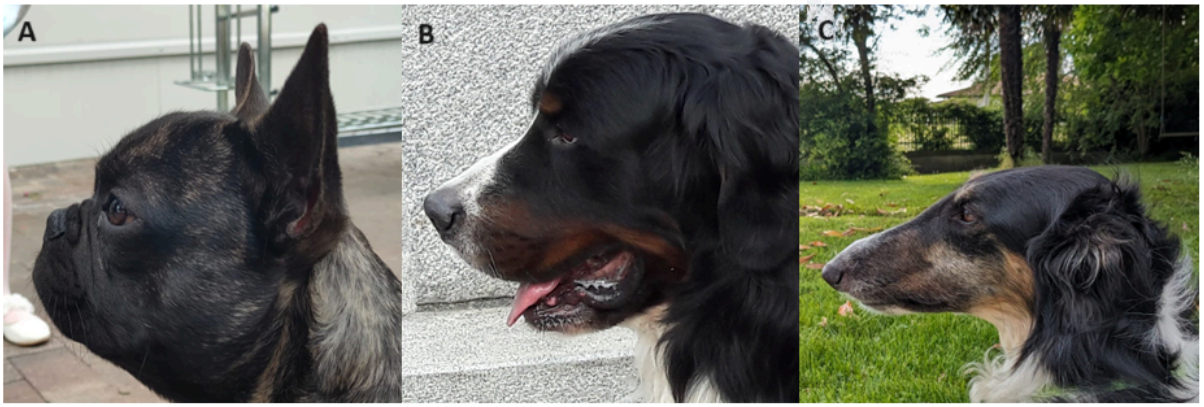

Figure 2. *Dogs' muzzle length:* ***A)*** *brachycephalic,* ***B)*** *mesocephalic and* ***C)*** *dolichocephalic.*

Table 1. *Information about participating dogs (Name, sex (female(F)/male(M), age, breed, FCI breed group, pinnae shape and muzzle length).*

Name	Sex	Age (in years)	Breed	FCI breed group	Pinnae shape	Muzzle length
Aili	F	2	Eurasier	5	E	M
Apollo	M	2	Australian Kelpie	1	E	M
Ares	M	3	Australian Shepherd	1	S	M
Arya	F	5	Mongrel		D	M
Ayla	F	1	Shepherd of Lessinia and Lagorai	1	E	M
Bambu	F	5	Mongrel	/	D	M
BB	F	9	Boxer	2	S	B
Birra	M	6	Bulldog	2	D	B

Blake	M	3	Australian Shepherd	1	S	M
Caren	F	7	Belgian Malinois	1	E	M
Daisy	F	4	Golden Retriever	8	D	M
Dolly	F	6	American Staffordshire Terrier	3	S	M
Drago	M	8	Labrador Retriever	8	D	M
Guenda	F	2	Whippet	10	S	D
Hope	F	2	Golden Retriever	8	D	M
Iris	F	2	Labrador Retriever	8	D	M
Isotta	F	3	Lagotto Romagnolo	8	D	M
Kicco	M	11	Mongrel	/	S	M
Kyra	F	5	Greater Swiss Mountain Dog	2	D	M
Lea	F	2	Shiba Inu	5	E	M
Lola	F	5	Mongrel	/	S	M
Lucky	M	10	Mongrel	/	S	M
Luna	F	7	Mongrel	/	S	M
Mila	F	6	Mongrel	/	E	D
Mimma	F	4	French Bulldog	9	E	B

Mustikas	F	5	Mongrel	/	E	M
Napoleone	M	7	Mongrel	/		
Neve	F	4	Mongrel	/	D	M
Pupy	F	3	Mongrel	/	E	M
Roxy	F	5	German Shepherd	1	E	M
Rufus	M	7	Poodle	9	D	M
Stewe	M	9	Mongrel	/	D	M
Sunny	F	4	Czechoslovakian Wolfdog	1	E	M
Tobby	M	4	Border Collie	1	S	M
Vic	M	3	Mongrel	/	D	M
Vik	M	6	Eurasier	5	E	M

A pack of eight grey wolves (C*anis lupus*) living in the faunal park "Belpark" of Spormaggiore (TN, Italy) were included in the study. The pack was composed by the breeding pair (Balto and Sissi, coming respectively from the faunal park "La Torbiera" of Agrate Conturbia (NO, Italy) and from the zoological park "Natura Viva" of Bussolengo (VR, Italy)) and their offspring, born at the park in 2015. Sissi, the breeding female, unfortunately passed away in 2022. The current members of the pack were the breeding male, one cub (now adult) from the first litter and six cubs (now adults) from the second litter. In the wolves' pack there were 3 females and 5 males and their mean age was 9.5 years ± 0.38. More information about the individual wolves can be found in Table 2, while their pictures can be visioned in appendix.

Table 2 *Information about tested wolves (name, sex, age).*

Name	Sex	Age (in years)
Balto	male	12
Semiluna (Maya)	female	10
Sentinella	male	9
Abisso	male	9
Sorriso (Guance bianche)	male	9
Mononoke	male	9
Nebbia (Grigiolina)	female	9
Lentiggine (Due punti)	female	9

3.2 Pilot studies

Before designing the main experiment, a pilot study was conducted with 6 dog subjects, in which I experimented with different sounds, their source position and the experimental conditions. Furthermore, a second pilot study was performed with a small group of dogs to reveal possible problems and issues with the experimental procedure.

In the first pilot study, different sounds were played with the speaker hidden behind the screen or visible and from different directions on the vertical axis (superior, inferior, frontal) in front of various dogs. The dogs were tested with various sounds as squeaky toy (one squeak), training whistle, rustling leaves, unknown word “università” (plain voice tone), unknown word “università” (motherese voice tone), known word (experimenter plain voice tone), known word (experimenter motherese voice tone), known word (owner plain voice tone), known word (owner motherese voice tone).

The aim of this first pilot study was to understand which sound would have been more interesting for dogs and, therefore, would seemingly have been the most suitable to induce head tilting. Moreover, the pilot study was also performed to assess under which conditions the dogs would head tilt and to highlight problems with the experimental setup and procedure and consequential adjustments to make.

The second pilot study was used to test the effectiveness of the experiment that had been devised, which involved only sounds on the vertical axis, one played from the top of the screen and one in front of the dog's head. However, it was quickly noticed that dogs would react and tilt their head in both conditions. Therefore, the lateral position of the sound source was added as a control.

3.3 Experimental setup

The experimental field was composed of an outdoor fenced area and the surrounding area. Directly outside the fence a dark screen (185 x 150 cm) was placed, consisting of a dark blanket (200 x 150 cm) mounted on a framework made by wooden trestle (75 x 70 cm) and a U-shaped iron support (120 x 60 cm). The screen presented 15 cm vertical slits at different heights (30 cm, 55 cm, 85 cm and 170 cm from the ground) in the central part. The dog-owner dyad stayed inside the fence at a distance of 2.5 m from the screen and centred in relation to the screen. For the wolves' experiment the owner-dog dyad was substituted by wolves. One to two wolves would stand in front of the setup, since they could not be separated into single units, at a distance between 2-5 m. The camera and its stand were positioned behind the dark screen with the lens in front of one of the slits, so that the camera itself was hidden but it could still film the animal through the slit. The height of the camera was adjusted depending on the height of the subject. The experimenter was positioned behind the screen holding the mobile phone (model Redmi Note 11) and the Bluetooth speaker JBL-GO. The Bluetooth speaker was taped with a bright yellow coloured tape to increase the contrast between the dark screen and the sound source. The sound used was the double squeak sound from a squeaky toy. It had a duration of 2 s, a frequency range of 1-10 kHz and a sound intensity of 100 dB. The complete experimental set-up for dogs and wolves can be visioned in figure 3A and 3B respectively.

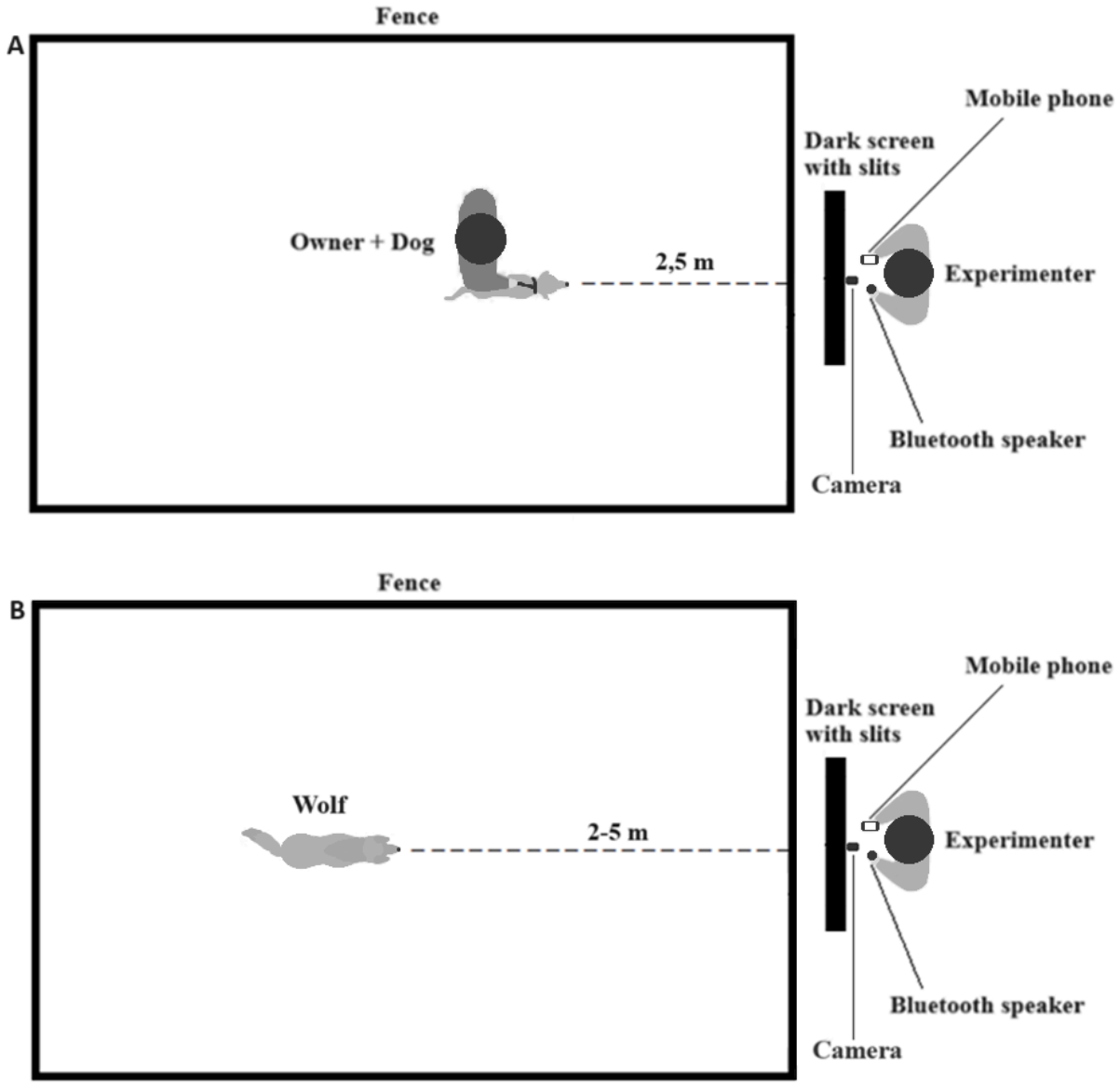

Figure 3. *Scheme of the experimental set-up for* ***A)*** *the dogs and* ***B)*** *the wolves*

3.4 Experimental procedure

Each experiment involved one animal that underwent 6 trials, in each trial a squeaky toy sound was played twice under one of the two source visibility conditions (Invisible or Visible) and from one of the three positions (Superior, Frontal or Lateral). The squeaky toy sound was played twice to allow the animal to focus its attention on the sound and its position even if it was momentarily distracted when the sound started playing. In the first 3 trials the sound was played from the three different positions but under the same source visibility condition, while in the other 3 trials the sound was played from the three different positions but under the other source visibility condition. The wolves were tested only with the invisible condition due to

their shy nature, as the movements of the blanket caused by the change of position of the Bluetooth speaker would scare them away.

The positions of the sound source were pseudo-randomized and balanced so that half the dogs would start with the invisible condition and the other half with the visible one. Furthermore 1/3 of each half started with the upper position of the sound, 1/3 with the frontal one and 1/3 with the lateral one, Finally, half the dogs had the lateral sound to the left and half to the right.

Concerning the source visibility conditions, they were defined as Invisible sound source (I), when the sound source (Bluetooth speaker) was hidden behind the dark screen and as Visible sound source (V), when the sound source (Bluetooth speaker) was held in front of the dark screen through one of the slits.

Regarding the positions on the vertical axis, they were outlined as “Superior (S)”, when the sound was played from the top of the screen (170 cm from the ground), “Frontal (F)”, when the sound was played in front of the animal at head’s height and “Lateral (L)”, when the sound was played at head’s hight but 75 cm to the left (l) or to the right I) of the screen (in relation to the animal position). The distance was decided using Guérineau et al. (2022) study on sound localisation in dogs. The study showed that dogs were, on average, able to discern the position of a sound (left or right) when the sound sources formed a minimum audible angle of 7.6°, at a distance of 3 m. Therefore, being the dogs distant 2.5 m from the dark screen, a 75 cm distance for the lateral sound was deemed enough for the dogs to easily distinguish the sound position (left or right) (16 cm was the minimum distance considering the 7.6° angle and the 2.5 m dog distance from the screen).

A scheme of the sound positions can be visioned in figure 4A and 4B. Note that when the sound was presented in the side position it was either played from the left or from the right, never from both.

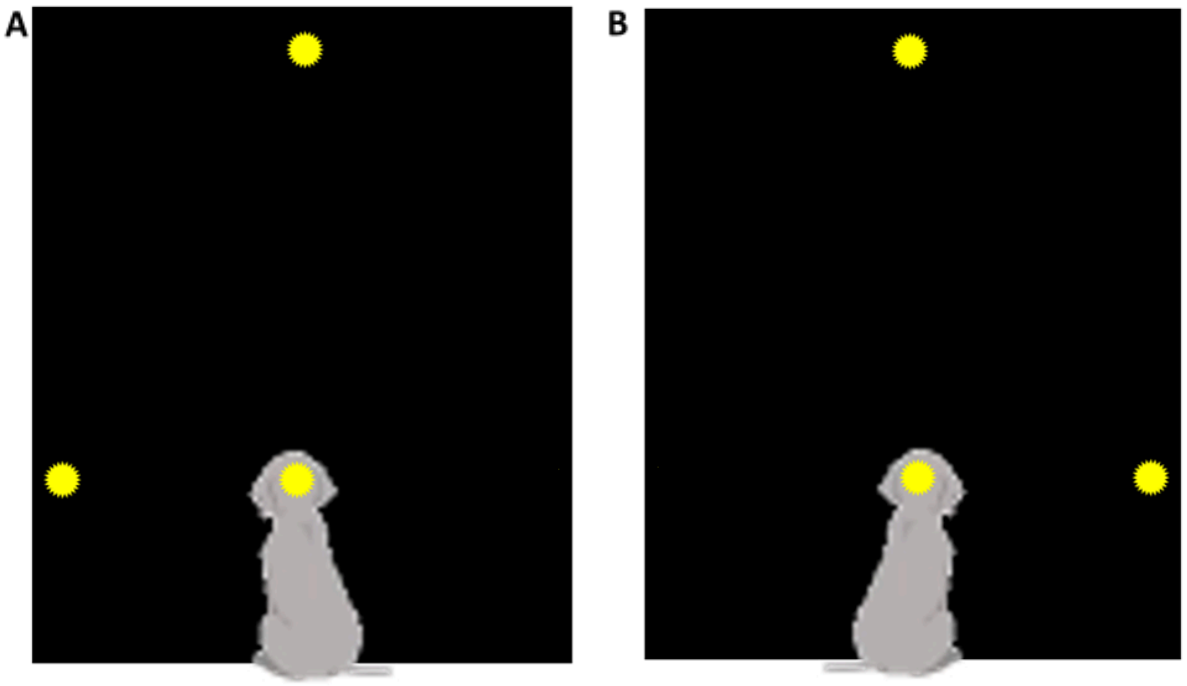

Figure 4. *Scheme of the sound positions* ***A)*** *Superior-Frontal-Lateral-left (SFLl) and* ***B)*** *Superior-Frontal-Lateral-right (SFLr).*

3.4.1 Experimental procedure for dogs

The dog's owner was asked to enter the fenced area with the dog and unleash it to allow it to explore and familiarize with the area for 2-3 min. In the meantime, the experimenter instructed the owner about the experiment. The owners were asked to wear sunglasses (supplied by the experimenter) to avoid giving any cues to the dog about the behaviour it should keep/perform. Furthermore, they were told they would hear sounds and that they should not interact with the dog unless requested by the experimenter (e.g. to reposition the dog if it went outside the camera frame). Moreover, the owner was asked in which situations its dog would usually perform head-tilting. Finally, they were told that, when signalled by the experimenter, they should recall the dog, put it on leash and position themselves at a distance of 2-3 m in front of the screen (centred) to start the experiment. While the owner and dog moved into the starting position, the experimenter hid behind the screen and checked if the dog could be clearly seen in the camera frame.

When the dog was in the correct position (visible inside the camera frame and centred compared to the dark screen) and was looking at the dark screen, the experimenter proceeded to play the sounds. The sounds were played in the predetermined pseudorandomised order of visibility condition (visible/invisible sound source) and positions (superior/frontal/lateral) indicated in the list, following the order designated for the dog under consideration. Each dog was presented the squeaky toy sound twice from all three positions, as aforementioned, and under both source visibility conditions (visible/invisible sound source), with a brief pause before the change of source visibility condition. The sounds were reproduced with a 2 s interval between each position and with a 10 s interval between the two source visibility conditions. All tests were videorecorded for later analysis.

3.4.2 Experimental procedure for wolves

The experimenter waited hidden behind the dark screen until one or two wolves were positioned in front of the screen, at a suitable distance (2 to 5 m).

When at least one wolf was in the correct position (visible inside the camera frame and centred compared to the dark screen) and was looking at the dark screen, the experimenter proceeded to play the sounds. Similarly to the dogs, the sounds were presented in the predetermined pseudorandomised order of positions (superior/frontal/lateral), following the order designated for the wolf under consideration. The wolves were only tested with the invisible sound source condition. Each wolf was presented the squeaky toy sound twice in each position, with a 2 s interval between the sounds reproduced in each position. The only exception was the male wolf Abisso, which sat still 2 m from the dark screen, unbothered by the blanket movements. Therefore, he was tested under both the visible and the invisible sound source conditions. All tests were videorecorded for later analysis.

3.5 Data analysis

The head tilting behaviour was recorded as a 0/1 outcome (0 if the behaviour was not performed, 1 if the behaviour was performed) for each trial. The head tilting behaviour is defined by Sommese et al (2022) as the “lateral, horizontal movement of the head out of the vertical plane”. Some examples of head tilting can be visioned in figure 5. In the current experiment this was the reference definition and the degree of head inclination was not taken into account. Therefore, the head tilting behaviour was considered performed even if the head of the animal was only slightly tilted.

Figure 5. *Some examples of head tilting with different degrees of inclination.*

The videos were watched and coded also by a second observer which double checked them to increase the reliability of the data. The results were then compared and analysed to calculate the Cohen's kappa coefficient and estimate the interobserver reliability. The obtained Cohen's kappa coefficient was 0.77, so the observers were in substantial agreement.

Furthermore, the behavioural analysis software BORIS (Friard & Gamba, 2016) was used to obtain data about the attentiveness of the dogs, namely the time they spent paying attention to the sound source after the sound was played the first time in each trial. The dog was considered attentive when its muzzle was oriented towards the dark screen and its eyes were fixed on it. The attention of the dog was considered interrupted when it would look away from the dark screen for more than one second.

All data have been analysed using the statistical software R (R Core Team, 2021) and RStudio (Posit team, 2023). The same software was also used to realise the plots.

3.5.1 Descriptive statistics

The owners reported frequency of the head tilting behaviour was obtained by comparing the answers of all the owners contacted for the experiment (included the ones that were not available to participate in the experiment), establishing the ratio between the positive ones

(the dog has performed head tilting behaviour) compared to the total. The total numbers of dogs whose head tilting outcome was obtained with this method was 85 and they were aged from two months old to 12 years old.

During the experiment, half the dogs had the lateral sound reproduced from the left and the other half of the dogs had it from the right side of the dark screen. Afterwards, a Welch Two Sample t-test was conducted to investigate a possible bias in the head tilting frequency. There was no significant difference in the head tilting behaviour frequency of the dogs that heard the lateral sound coming from their left and the ones that heard the lateral sound coming from their right ($p = 0.80$). Therefore, the head tilting outcome from the lateral sound sources were pooled.

A general analysis of the attentiveness of the dogs towards the sound source after the first sound repetition in each trial was performed through the calculation of the mean time spent paying attention to the sound source throughout the entire experiment and for each trial. Furthermore, the percentages of time spent paying and not paying attention to the sound source were estimated, again throughout the entire experiment and for each trial.

As the wolves never head tilted, no generalized linear mixed model (GLMM) or plots were created to analyse their data. However, a descriptive qualitative statistic of their behaviour during the experiment was created.

3.5.2 Generalized linear mixed models (GLMM)

First, a R code was used to reorganise the database into a more suitable data frame for the data analysis.

For the dogs, an all-encompassing generalized linear mixed model (GLMM) was created using the R package “lme4” (Bates et al., 2015). The GLMM was used in order to study the association between the head tilting behaviour and the different variables that could have affected the aforementioned behaviour.

The response variable considered was the binary behavioural outcome after the sound was played (“outcome”), specifically whether the dog performed the head tilting behaviour (1) or not (0).

The fixed effects, or predictor variables, and their respective levels, included in the model were both variables related to the sound, like the sound source visibility condition (“condition

(I/V)"), the sound source position ("position (S,L,F)"), the starting experimental sound source visibility condition ("start" (I/V)") and order of trials ("order (1/2/3/4/5/6)"), and variables related to the dogs, as the sex of the dog ("sex (M/F)"), the pinnae shape ("ears (erect/semi-erect/dropped)") and the dog's age ("age (juvenile/adult/senior)"). The "age" variable represents the dog's age by age class and it had three levels: "juvenile" (the dog was younger than three years old), "adult" (the dog's age ranged from three to seven years old) and "senior" (the dog was older than seven years old) (Harvey, 2021).

The fixed variables representing the dog breed group ("group" (group 1/group 2/group 3/group 5/group 8/group 9/ group 10/mongrels)") and the dogs muzzle length ("muzzle" (brachycephalic (short muzzle)/mesocephalic (intermediate length muzzle)/dolichocephalic (long muzzle)) were excluded from the study as the number of dogs in certain categories was too low.

The random effect of the model was the dog's identity and it was added to take into account the individual variability of the different individuals.

The chosen distribution family for the model was "binomial" as the response variable had a binary outcome. The link function that best approximated the data distribution was "logit", as it can be observed in the QQ plots.

Afterwards, given the results obtained with the GLMM (a considerably higher percentage of head tilting in the first three trials compared to le last three), a second GLMM was created, with the same structure and characteristics of the aforementioned one but comprehensive only of the first three trials of the experiment. Hence, either visible or invisible condition for each dog. In the end, this model was used to assess the correlations between the response variable (head tilting behaviour) and the different fixed effects.

Additional models that were created were a GLMM identical to the first aforementioned one but with "probit" instead of "logit" as the link function. Another model that was realised is a GLMM identical to the first GLMM as above but with the addition of the interactions between variables, for example between the order of trials and the position of the sound source or the order of the trials and the visibility of the sound source. Other GLMMs were created using just the dogs that started the experiment with the invisible condition and the ones that started the experiment with the visible condition, both comprehensive of all the variables (except the breed groups and the muzzle shape). In another GLMM that was created,

all the variables were included, also the ones with a very bad proportion of individuals regarding the levels, which are the breed groups and the muzzle shape.

To conduct the dog attentiveness analysis a GLMM was realised using the time the dog spent paying attention to the sound source as the response variable. However, the data were first filtered. The trials when the dogs were not paying attention (attention span = 0) were excluded. Furthermore, only the attention spans relative to the 1st, the 2nd, the 4th and the 5th trials were used. In fact, the attention spans from the 3rd trial were overestimated due to the longer pause occurring in the sound source visibility condition change. On the other hand, the attention spans relative to the 6th trial were underestimated due to the videos being interrupted after the experiment was concluded. After an analysis of the data distribution, which was not normal (Shapiro-Wilk normality test $p = 0.024$), "poisson" was chosen as the distribution family which would better fit the data distribution for the model. Due to the chosen distribution, the data were considered as integers. The fixed and random effects considered are the same used for the previous aforementioned models.

3.5.3 Post-hoc analysis

To further analyse the difference existing between the paired levels, the pairwise comparison through Tukey's range test was used as a post-hoc analysis for all the variables that resulted significant in the GLMM. This test was used to compare the means of the different levels of the variable "order" and assess between which trial there was a significant difference in the percentage of the head tilting behaviour in dogs.

3.5.4 Data distribution

The normality of the experimental data distribution was analysed through the creation of quantile-quantile plots (QQ plots), realised from the GLMMs described above using the package "ggplot2" of the statistical software R. The aim of these plots was to assess whether the residuals from the logistic regression model behave according to the assumptions of normality, by comparing the distribution of the residuals from the logistic regression model and the expected distribution of residuals under the assumption of normality. Furthermore, the QQ plots were used to evaluate how well the GLMM explained above would fit the data and which link function would be the most suited for the model of this study. More information on the topic can be found in Appendix B.

3.5.5 Plots

Grouped bar plots were realised using the package "ggplot2" (Wickham, 2016) of the statistical software R to visually represent the percentage of head tilting behaviour in dogs in respect to various variables, both sound related and dogs related. The bar plots do not represent the absolute number of head tilting events but the percentual performance of the head tilting behaviour. In fact, for the realisation of the bar plots relative to the head tilting behaviour, the data were first normalised through a conversion of the absolute frequency in percentages (relative frequency). Furthermore, the same R package was used to create the quantile-quantile plots (QQ plots) and histogram to analyse the data distribution. Finally, boxplots were realised to visually represent the attentiveness of dogs towards the sound source after the first sound reproduction in each trial.

4. Results

4.1 Dogs

The grouped bar plots depict the percentage of head tilting behaviour as a binary outcome, with green representing the behaviour being performed and violet representing the behaviour not being performed.

4.1.1 Head tilting frequency

Out of the 85 dogs whose owners were contacted to participate in the experiment, 85% exhibited the head tilting behaviour during their everyday life. These data were obtained through owners' statements of having observed their dog performing the behaviour. Dogs were of various breeds, sex and ages (2 months old and above).

4.1.2 Influence of sound-related variables on the head tilting behaviour

Overall, the first three trials had a higher incidence of head tilting behaviour compared to the last three trials. The first trial had the highest head tilting percentage compared to all the other trials, while the sixth trial had the lowest head tilting frequency compared to all the other trials.

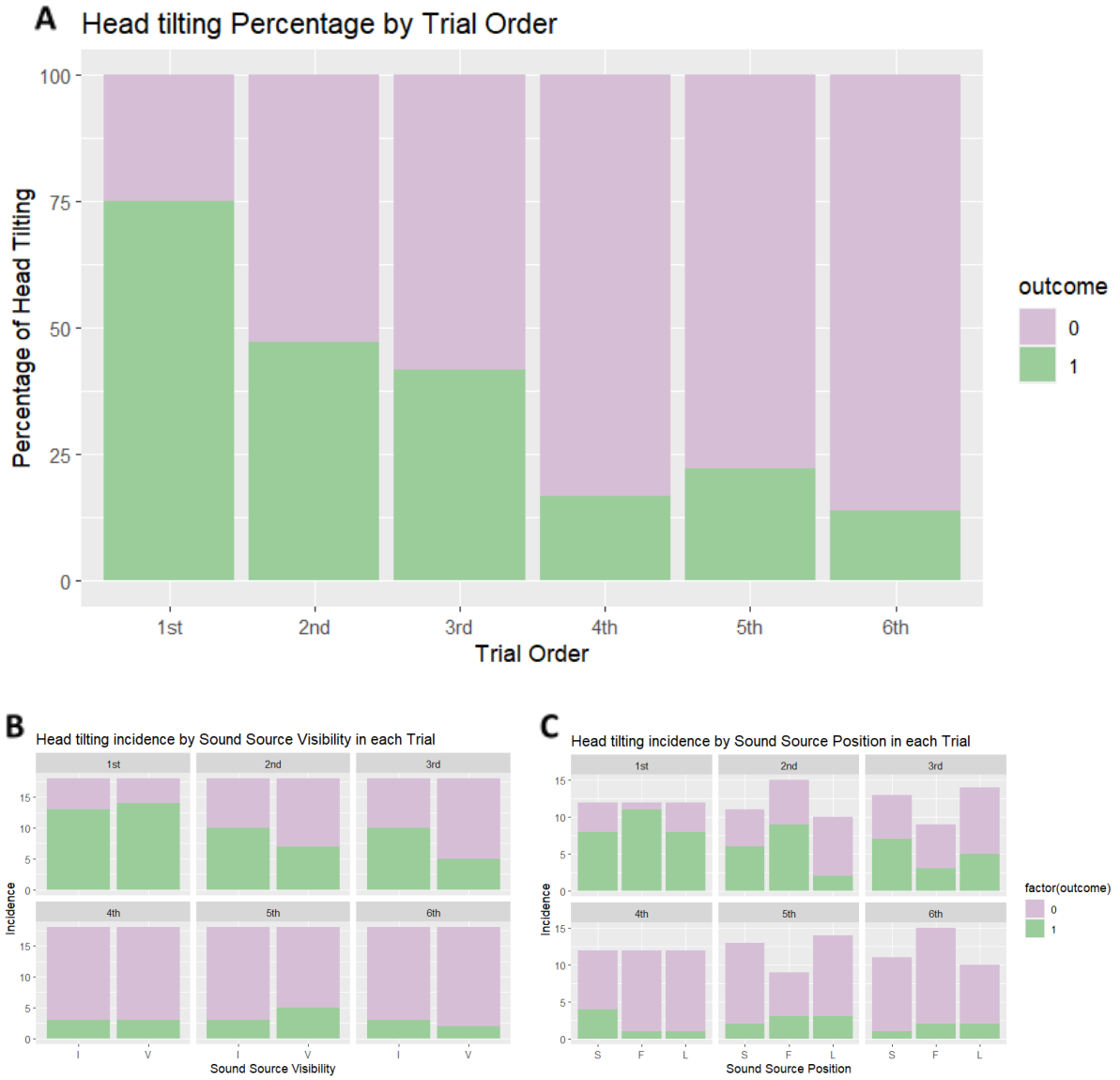

Figure 6. *Percentage of head tilting in dogs* ***A)*** *for all six trials.* ***B)*** *for all six trials in relation to the sound source visibility (invisible (I) and Visible (V)) and* ***C)*** *for all six trials in relation to the position of the sound source (Superior (S), Frontal (F) and Lateral (L))*

Trial order (1-6) had a significant effect on the head tilting behaviour ($p < 0.001$, figure 6A). The post-hoc test revealed that the first had a significantly higher percentage of head tilting behaviour than the third trial ($p = 0.029$), the fourth trial ($p < 0.001$), the fifth trial ($p = 0.001$) and the sixth trial ($p < 0.001$). Also, the head tilting percentage was significantly higher in the second trial compared to the fourth trial ($p = 0.037$) and the sixth trial ($p = 0.013$). Additionally, the head tilting percentage was significantly higher in the third trial than in the sixth trial ($p = 0.036$).

No significant effect was found in the interaction between the order of trial and the sound source visibility (p = 0.29, figure 6B), nor between the order of trial and the position of the sound source (p = 0.47, figure 6C). However, in figure 6B it might be noticed that the head tilting percentage decreased faster, in the first three trials, if the sound source was visible compared to when the sound source was invisible. Then, in the last three trials, it sets and the percentage of head tilting in the visible condition matches the one in the invisible condition.

Due to the rapid decrease in head tilting behaviours, most of the following analyses were performed with the first three trials only. The GLMM comprehensive only of the first three trials, showed a significant decrease in the head tilting incidence in the first three trials (p = 0.006, figure 5). Post-hoc tests revealed that the first trial had a significantly higher percentage of head tilting compared to the second trial (p = 0.014) and the third trial (p = 0.007). Due to this decrease the analysis was performed on the first three trials only.

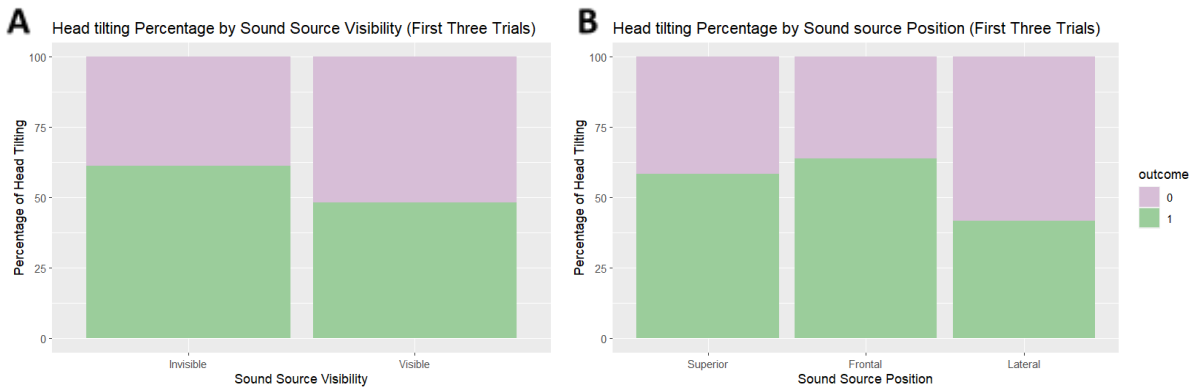

Figure 7. *Head tilting percentage of dogs in the first three trials in relation to* ***A)*** *the sound source visibility and* ***B)*** *the sound source position*

The sound source visibility condition (visible or invisible) had no significant influence on the head tilting percentage (p = 0.44, Figure 7A). However, as it might be observed in figure 7A, the dogs performed the head tilting behaviour slightly more when the sound source was invisible.

A trend of significance was found regarding the effect of the position of the sound source (S, F, L) on the head tilting incidence (p = 0.078, Figure 7B). In fact, as it might be observed in figure 7B, dogs performed the head tilting behaviour more when the sound origin in the superior position (S) and in the frontal position (F), so on the vertical axis, compared to when the sound was coming from the lateral position (L). The post-hoc test revealed a tendency of

significance between the head tilting percentage when the sound was in the frontal position compared to when it was in the lateral (p = 0.075).

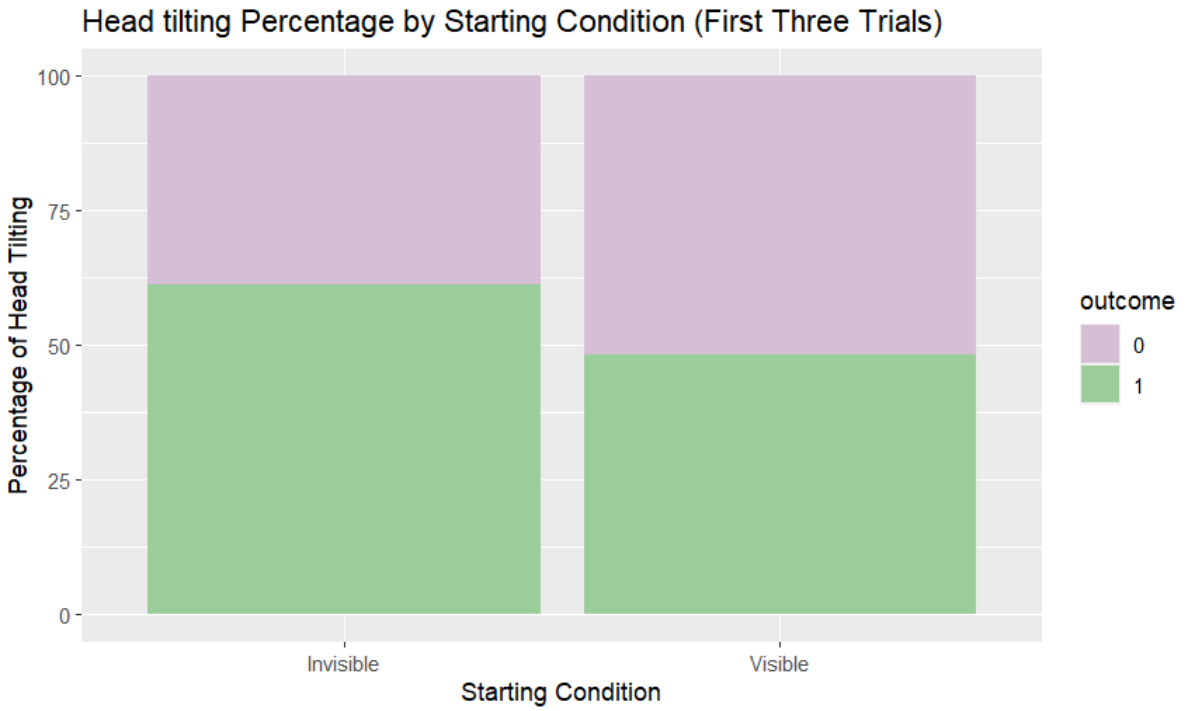

Figure 8. *Head tilting percentage of dogs in the first three trials in relation to the starting condition*

There was no significant difference between the percentage of the head tilting behaviour if the dog started with the invisible condition and or with the visible condition (p = 0.44, figure 8). However, as it might be observed in figure 8, dogs performed the head tilting behaviour slightly more when they started the experiment not being able to see the sound source.

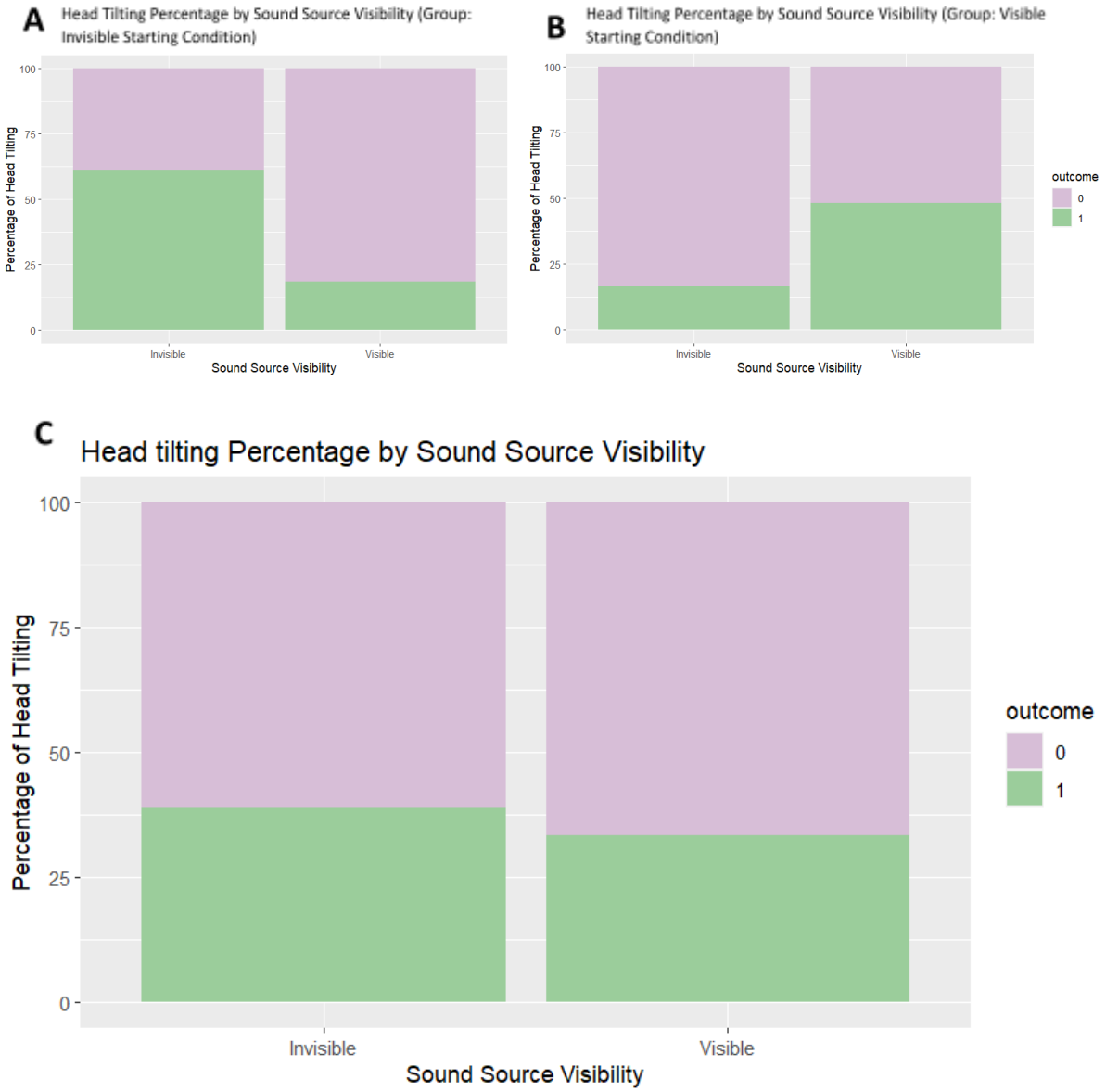

Figure 9. *Head tilting percentage for all trials of the dogs that* ***A)*** *started the experiment with the invisible condition and* ***B)*** *started the experiment with the visible condition, both in relation to the condition under which the sound was played.* ***C)*** *Head tilting percentage for all trials in relation to the visibility of the sound source.*

Considering all trials and analysing the dogs with different starting conditions separately revealed a significant difference in the head tilting percentage depending on the starting condition (Starting condition invisible sound source: $p < 0.001$, figure 9A; Starting condition visible sound source: $p < 0.001$, figure 9B). Hence, they tilted more in the condition they started with. However, since the two opposite trends balance each other, if the head tilting percentage of all dogs during all the six trials is taken into account, no significant difference is present regarding the head tilting percentage in relation to the sound source visibility ($p = 0.39$, figure 9C).

4.1.3 Influence of dog-related variables on the head tilting behaviour

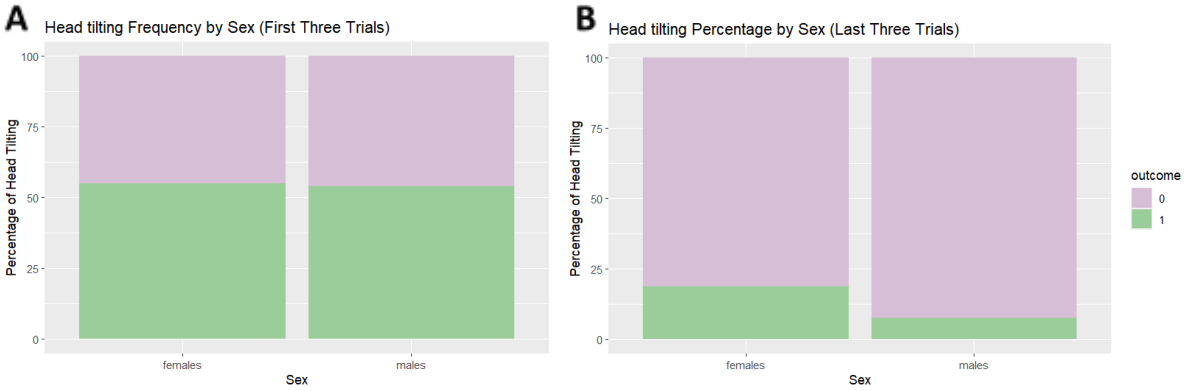

Figure 10. *Head tilting percentage of dogs in relation to the sex of the dog* ***A)*** *in the first three trials and* ***B)*** *in the last three trials.*

During the first three trials, there was no significant difference in the percentage of head tilting behaviour of female and male dogs (p = 0.89, figure 10A). However, in the last three trials females head tilted more than males, despite not significantly (p = 0.18, figure 10B).

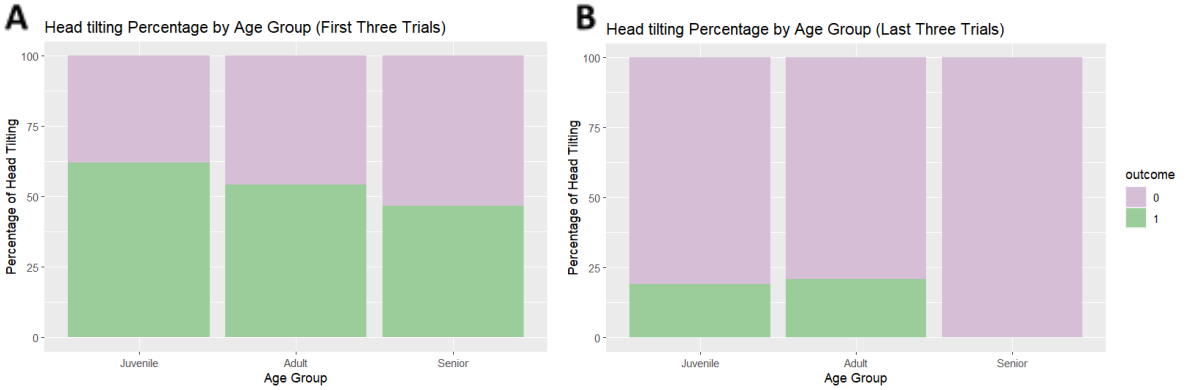

Figure 11. *Head tilting percentage of dogs in relation to the age groups juvenile, adult, and senior* ***A)*** *in the first three trials and* ***B)*** *in the last three trials.*

There was no significant difference in the percentage of the head tilting behaviour between dogs belonging to different age groups (p = 0.71, figure 11A). However, a gradual decrease of the head tilting behaviour incidence can be noticed with the ageing of the dogs, until the total absence of head tilting of senior dogs in the last three trials, but no significant effect was found (p = 0.98, figure 11B)

Note that there were more females (N=23) than males (N=13) and most females belonged to the juvenile (6) and adult group (16) while most males were senior dogs (4) (Appendix B, figure 3).

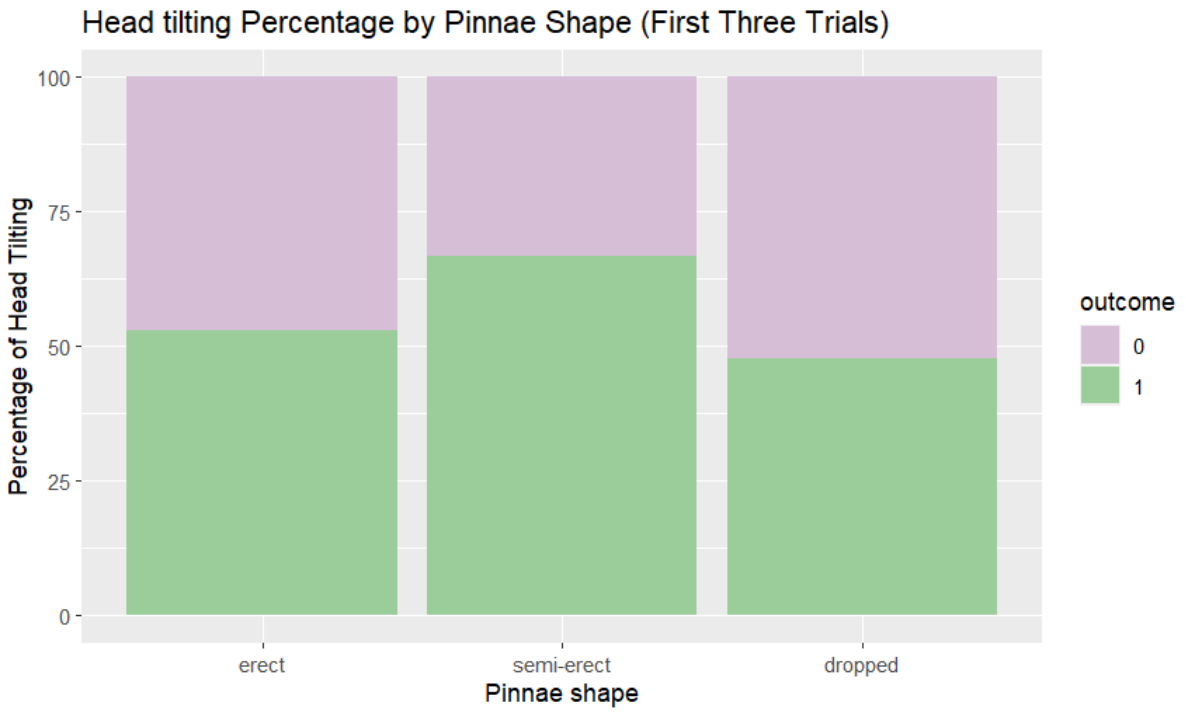

Figure 12. *Head tilting frequency of dogs in the first three trials in relation to the dog's pinnae shape.*

There was no significant difference between the percentage of the head tilting behaviour of dogs with erected ears compared to dogs with semi-erected or dropped ears (p = 0.38, figure 12). However, dogs with semi-erected pinnae head tilted slightly more compared to the dogs with erected or dropped pinnae.

4.1.4 Attentiveness analysis

The mean attentiveness of dogs (attention towards the sound source after the first repetition of the sound) in each trial was 8.26 s. Dogs were not paying attention to the sound source (0 s attentiveness) in 16.20 % of trials, mostly the fifth and the sixth ones (25% of trials). On the contrary, in the first and second trials they were attentive for the 8.33% of trials, with a mean attention of, respectively, 9.30 s and 8.03 s. In the fourth and fifth trials dogs had a mean attentiveness of, respectively, 8.00 s and 8.07 s.

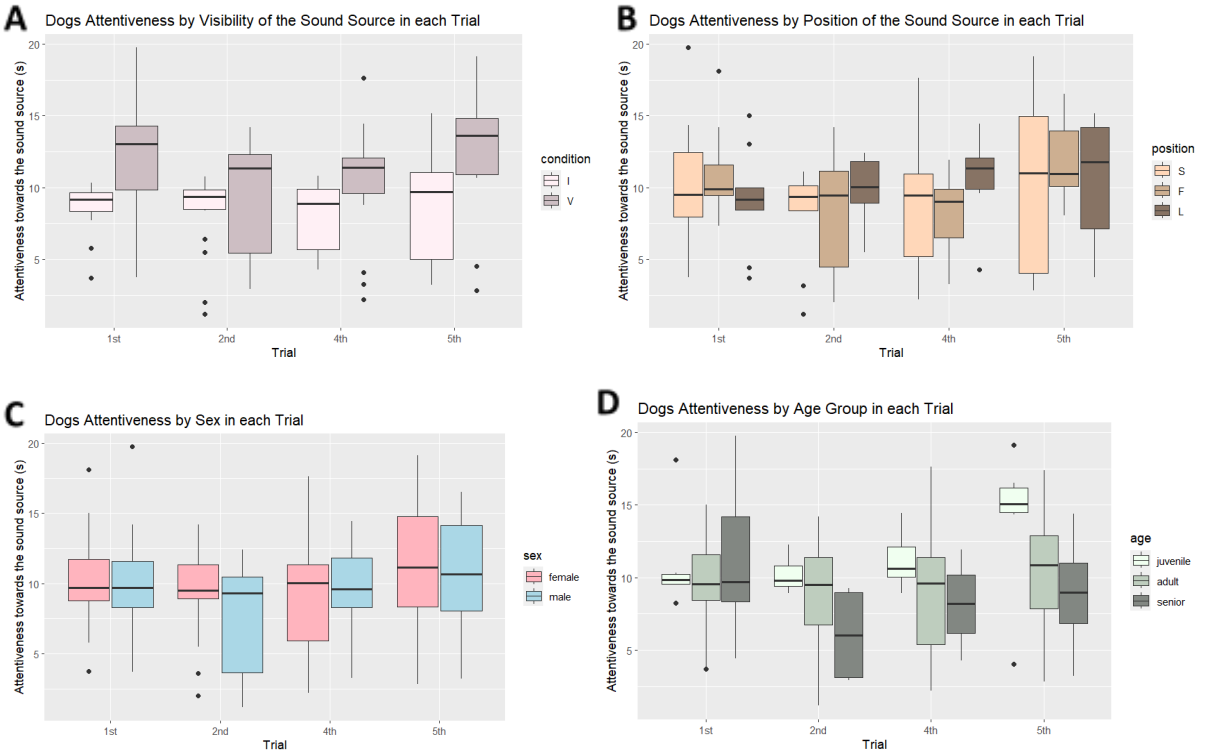

Figure 13. *Attentiveness of dogs in the 1st, 2nd, 4th and 5th trial in relation to* ***A)*** *the visibility of the sound source,* ***B)*** *the position of the sound source,* ***C)*** *the sex of the dog and* ***D)*** *the age group the dog belonged to.*

The visibility of the sound source had a significant effect on the attentiveness of dogs ($p < 0.001$, figure 13A), as dogs paid more visual attention when the sound source was visible. The position of the sound source (S, F, L) did not have a significant effect on attentiveness of dogs ($p = 0.89$, Figure 13B).

There was a tendency of a significant difference between the attentiveness dogs belonging to different age groups ($p = 0.073$, figure 13D), with juvenile and adult being more attentive than senior dogs. There was no significant difference in the attentiveness of female and male dogs ($p = 0.80$, figure 13C). However, as it might be observed in figure 13C, females paid slightly more attention to the sound source than males in the last trials.

The other variables had no significant effect on the dogs' attentiveness (trials order $p = 0.12$, starting condition $p = 0.79$, pinnae shape $p = 0.20$, muzzle length $p = 0.81$, breed group $p = 0.38$).

4.2. Wolves

The wolves never head tilted and most of the time they were laying on the ground, sitting or standing while looking around. Six wolves were standing for the whole duration of the experiment, their ears erected and the tail dropped but not tucked between the legs. Two wolves, on the contrary, stayed seated through the experiment. Two wolves looked at the dark screen the first time they heard the sound but then proceeded to look elsewhere.

5. Discussion

The aim of the study was to investigate the head tilting behaviour in dogs and in their closest relative species, wolves. In particular, the experiment was designed to assess if the behaviour was present (in wolves) and if it had any correlation regarding the sound source position and visibility.

5.1 Dogs

5.1.1 Head tilting frequency

The frequency of dogs that perform the head tilting behaviour in their ordinary life was quite high (85%), according to owners. It can be argued that the sample was small, so future studies could increase the precision of the frequency of head tilting behaviour in the dog population. However, 85% of dogs exhibiting head tilting seems promising for future studies regarding the head tilting behaviour, as it would be easy to find dogs suitable to participate in possible experiments. Certain dogs, despite their owner stating that they head tilted in their everyday life, never performed the behaviour during the experiment but, as in the case of one female dog, were seen head tilting it in another context by the experimenter too. This occurrence, together with the fact that the wolves never head tilted and the observations from the pilot study on various sounds, might suggest that the sound triggering this behaviour must be interesting and biologically relevant for the animal (Sommese et al., 2022). Since, if the aim of the head tilting behaviour is to collect information on the sound and its position, the animal would not perform it if it was not interested in the sound that it is hearing. For example, in the first pilot study, the squeaky toy sound seemed to elicit more the head tilting response compared to other sounds (which was the reason why it was then chosen as the sound for the experiment). This might be because the squeaky toy sound is associated by many dogs to play and a toy, so something fun they like and want to reach (Sommese et al., 2022). Therefore, they would head tilt to collect more information on the position of the squeaky toy to locate and get it. For these reasons, it would be interesting to perform an extensive study with

different sounds to verify this hypothesis and deepen the knowledge about the sounds triggering the head tilting behaviour in dogs and, perhaps, also in other animals.

5.1.2 Influence of sound-related variables on the head tilting behaviour

The head tilting behaviour in dogs seemed to significantly decrease with the trial order but it was not significantly linked to other sound-related variables like the position or the visibility of the sound source, despite some trends.

The trial order effect is probably due to a progressive reduction of the dogs' interest towards the sound, also incremented, in case of certain individuals, by the understanding that they would not be able to reach the sound source because of the fence and the leash. This result does not refute the hypothesis of head tilting as a way to better locate the sound yet, as it should mean that the majority of dogs would locate the sound source within the first three attempts and then, consequently, would stop head tilting. The attentiveness analysis revealed no significant difference in the attentiveness between the considered trials (first, second, fourth and fifth). However, while the mean attentiveness stayed quite constant, the percentage of trials in which dogs paid no attention at all to the sound source at all increased with the passing of trials. This result is in concordance with the low and decreasing percentage of head tilting in the last three trials.

Visual inspection of the figures permits cautious speculations. It is possible that certain differences might have achieved significance with larger sample size. Regarding the visibility of the sound source, the dogs seemed to head tilt more often when the sound source was not visible. Also, the head tilting frequency seemed to decrease faster when the sound source was visible compared to when it was invisible. However, in the last three trials, the frequency of head tilting becomes very low, regardless of the sound source visibility. This could indicate that dogs head tilt to obtain more information through hearing, in particular when they cannot see the source of the sound. It would be in line with the strategy adopted by other animals like owls and foxes, which use their hearing to locate a prey hidden or in low to no visibility condition (Bahr, 1989; Carr & Christensen-Dalsgaard, 2015; Ĉervený et al., 2011; Gutiérrez-Ibáñez et al., 2011; Henry, 1986; Knudsen, 1980; Knudsen & Konishi, 1979; Knudsen et at., 1979; Konishi, 1973; Konishi, 1973; Payne, 1971). Even though dogs head tilted more when they could not see the sound source, the attentiveness analysis revealed that they were significantly more attentive towards the experimental layout when the sound source was visible, staring at the sound source longer. This result is reasonable as, when the sound

source was visible, dogs would focus their attention on it because they had a target origin for the sound. Thus, they could also add their sight as a mean to collect more information about their current situation. Instead, when the sound source was invisible, dogs tended to look away faster either because they would get distracted more easily or because they were trying to locate the sound source also with sight, looking around.

The results regarding the sound source position reveal a tendency of significance that in the first three trials dogs head tilted more when the sound was coming from the frontal position compared to the lateral one (i.e. the sound presented to the side). Furthermore, as it can be seen in figure 6B, dogs head tilted more when the sound was in the superior position compared to when it was in the lateral one, despite not significantly. These results provide a weak support to the auditory hypothesis as the function of head tilting behaviour, as dogs head tilted more when the sound was on the vertical axis compared to when it was to their side. In fact, since the lateral sound position would already result in time and intensity differences between the ears without tilting the head, the head tilting behaviour should be useless in this condition. Nevertheless, dogs head tilted when the sound was coming from the lateral position too. This result could be due to the layout of the experiment, as the superior sound was not placed exactly above or to the side of the dog's head. Indeed, in foxes the head tilting behaviour is used to locate hidden preys when the prey is hidden in the ground spot located, approximately, under the head of the fox itself (Bahr, 1989; Ĉervený et al., 2011; Henry, 1986). The same is true for the human voice triggering the behaviour in dogs, as in Sommese et al. (2022) the humans pronouncing the words were close to the dog itself, placing the sound source almost exactly above the dog's head. In this study, the sounds were further away from the dogs as, otherwise, it would have not been possible to realise a comparative experiment for the wolves, being impossible to place the sound source exactly superior or lateral to them. For future studies, it would be interesting to present the sound exactly above and directly underneath the dogs' head and from its side, to reproduce a condition similar to when the foxes localise preys (Bahr, 1989; Ĉervený et al., 2011; Henry, 1986).

Dogs head tilted more when they started the experiment with the invisible sound source condition and those dogs also head tilted significantly more in the invisible condition. On the contrary, dogs that started with the visible sound source condition head tilted significantly more in the visible condition. Reunited together, the two opposite trends balance each other into the plot in figure 5A. This result suggests that habituation and attention seem to play a

big role for this behaviour supporting the hypothesis that it could be performed to gain a higher amount of information on a sound. Obviously, the behaviour would not be performed anymore once it has fulfilled its function.

To summarise, regarding the initial hypotheses of the current research, it cannot be confirmed that the head tilting behaviour is performed by dogs to obtain more information about the position of the sound, especially on the vertical axis. However, the fact that sound reproduced from the vertical axis triggered a higher head tilting response compared to sound from the side, with a tendency of significance for the frontally positioned sound, seems to support it. Also, the visibility improvement hypothesis was not confirmed either, since the head tilting frequency did not differ significantly in relation to the visibility of the sound source, despite it being higher when the sound source was invisible. Again, the only significant result concerned the order of trials, suggesting that the dogs lost interest for the sound or became habituated to the experiment quite fast. Therefore, if the head tilting behaviour has actually a function, it might be fulfilled quite fast, after only three trials. Hence, future studies should try to minimise the number of repetition of sounds for each animal.

5.1.3 Influence of dog-related variables on the head tilting behaviour

The head tilting behaviour was not linked to any dog-related variable like the sex of the dog, its age or pinnae shape but some tendencies could be noticed.

No significant difference was found between males and females in their head tilting frequency during the first three trials. However, during the last three trials females persisted in the head tilting, contrary to the males, which might indicate a greater interest of females towards the sound itself or a higher attention to collect more information about it. The test sound in this study was produced by a squeaky toy sound, which generated a high-pitched sound. It could be hypothesised that females associated it to the high-pitched sound of whining puppies (frequency up to 5000 Hz; Lehoczki et al., 2019), thus explaining their higher and lasting interest and attention for the sound. This result would also be in line with Scandurra et al. (2018), which suggests that male dogs tend to shift their attention to different stimuli, in particular the visual ones, more often than females. This seems to be due to higher vigilance in males, which leads to greater distractibility. Hence, male dogs in this study might have been more easily distracted by surrounding environmental stimuli like smells, sounds or visual cues. The attentiveness analysis is in line with the result regarding the head tilting

incidence in the two sexes, with females' mean attention being higher than the males' one, despite not significantly, especially in the last trials.

The age of the dog was not correlated to the head tilting frequency. Still, a decreasing trend of the head tilting frequency progressing with the dog's ageing might be noticed through visual inspection of the results. This might be due to the play-related sound of the squeaky toy and the fact that with ageing dogs becomes less playful and, consequently, less interested in a playful sound (Chapagain et al., 2020; Salvin et al., 2011). In fact, juvenile dogs head tilted more in response to the sound compared to adult or senior dogs. An alternative explanation could be presbycusis, the progressive hearing loss that happens in senior dogs due to ageing (Shimada et al., 1998; Ter Haar et al., 2008). Age-related hearing loss seems to be associated especially to high-frequency sounds as a result of considerable modification at the base of the cochlea. Therefore, senior dogs could have head tilted less and lost interest more rapidly because they had difficulties in hearing the high-frequency squeaky toy sound. However, this result could have been accentuated by the ratio of females and males in the different age groups. Females were almost double in number compared to the males and the majority of juvenile dogs were females while, on the contrary, the majority of senior dogs were males. Hence, it might be hypothesised that the head tilting frequency of senior dogs would have been even lower if the age groups were balanced for sex. Nevertheless, dogs from all age groups head tilted in response to the sound, thus head tilting does not seem a behaviour that is learned. Result furtherly supported by the fact that puppies as young as two months old spontaneously head tilt in response to certain sounds, as reported by the owners contacted to participate in the experiment. The attentiveness analysis furtherly supports the results regarding the head tilting incidence in relation to the age of the dogs, which seemed to almost significantly influence dogs' attentiveness. In fact, although in the first trial dogs of all age groups were equally attracted/interested by the sound given the same mean attention, senior dogs attentiveness drastically dropped in the following trials. On the contrary, juvenile mean attention increased, corroborating the idea that the play-related nature of the sound might have been more interesting for juvenile than senior dogs.

The head tilting frequency between dogs with different pinnae shape was not significantly different in the first three trials. This result was unexpected as the dogs with one of the two extreme pinnae shape conditions (erect and dropped) might have been presumed to head tilt more. In fact, dogs with erect ears present a pinnae shape more similar to the foxes 'ones. On the contrary, dropped ears might have represented an impediment and lead to a higher head

tilting frequency. Overall, it does not seem that the pinnae shape influences the head tilting and, thus, the dog's pinnae shape is probably not correlated with a possible function of head tilting.

There was no significant difference between the frequency of the head tilting behaviour of dogs belonging to different breed groups but dogs belonging to group 1 (herding dogs, e.g. Border Collie) and group 3 (terriers, e.g. Jack Russell Terrier) seem to have head tilted the most, while dogs belonging to group 5 (spitz and primitive dogs) seem to have head tilted the least. The higher head tilting frequency of dogs from group 1 could be due to their role as working dogs, where they have to maintain their attention on a cue for an extended period of time. As for dogs from group 3, they could have been particularly attracted by the sound as they were historically used for hunting small squeaking creatures like rats, rabbits or even foxes (Cummins, 2019; Lee, 1896). However, the scarce number of individuals in the breed groups prevents to draw any conclusion. Hence, the data about the head tilting frequency in relation to breed group should be interpreted very cautiously. In the future it would be interesting to test the evolutionary value of the cutesy hypothesis, maybe with a further analysis of head tilting in different breeds or with the evaluation of the head tilting frequency in response to the human presence.

Concerning the muzzle length, no significant difference was found in the head tilting frequencies of dogs with different muzzle length. However, mesocephalic dogs seem to have head tilted slightly more than brachycephalic and dolichocephalic dogs. Again, this data must be interpreted with caution, since, in this study, the number of brachycephalic and dolichocephalic dogs was extremely small (3). Still, brachycephalic dogs did head tilt in this study, weakening the muzzle impediment hypothesis. Indeed, if the muzzle represented an impediment for the dog sight, leading it to incline its head for a better view, only dogs with a long or intermediate muzzle should show the head tilting behaviour.

Despite the head tilt inclination was not measured nor taken into account, the observed variation between subjects was important, with some dogs performing very prominent head tilts, while others barely noticeable ones. It would be interesting for future studies to measure the degree of head tilting to examine possible correlations with other variables. For example, if the head tilting is connected to an evolutionary adaptation to increase the dog cuteness, certain dog breeds could be performing it more extremely to increase their cuteness (Amry at al., 2018). A possible hypothesis could hint to the breeds belonging to group 9 (companion

and toy dogs such as Pug or Chihuahua) whose only function is being with the humans, therefore being cuter could be a selected trait.

To summarise, the head tilting behaviour in dogs does not appear to be influenced by the sex or the age of the dog. However, with age there is a decline in the head tilting frequency and attentiveness, probably due to the nature of the sound, which is probably associated with play that, for an old dog, might be less interesting. Furthermore, females' attention/interest for the sound was more long-lasting, despite not significantly, compared to the one of the males. It could be because males tend to become distracted more easily due to their higher vigilance. In alternative, females might have associated the squeaky toy sound with the one of whining puppies. At the same time, it must be taken into consideration that the majority of young dogs were females while the majority of male dogs were males, a ratio that could have influenced the results. The pinnae shape does not seem to have any influence in the frequency of the behaviour either. Regarding any possible link between the head tilting frequency and the breed group or the muzzle length of the dogs, the number of dogs present in certain categories was too small to allow for a reliable statistical analysis. Still, brachycephalic dogs did head tilt, weakening the probability of the muzzle impediment hypothesis.

5.2 Wolves

The wolves of this study never head tilted but that does not demonstrate that they do not perform the behaviour at all. Overall, they did not seem interested in the sound at all, since only few individuals looked at the dark screen and did it just once after hearing the sound, proceeding then to look elsewhere around and focus on the surroundings. They showed a relaxed body stance, inferable by their body language (Goodmann et al., 2002), and one of the wolves was so unbothered that it started sleeping. Thus, they were not scared by the sound.

If the aim of the behaviour is actually to better understand the position of the sound or collect a greater amount of information about it, it is only logical to assume that to trigger the behaviour the sound has to be interesting or biologically relevant for the animal, so to interest the animal enough to motivate it to perform the behaviour (Sommese et al., 2022). The initial hypothesis was that the squeaky toy sound could resemble a screaking prey for the wolves but, since they did not seem interested in the sound at all, it could be that the sound was too different from the one of a real prey. Another reason for their disinterest could be due to their nature of captive wolves that never hunted and, therefore, there is a possibility that they are not driven by the sound of a screaking prey. An alternative explanation could be a previous

habituation to this sound or a similar one caused by the visitors which stroll around the park during summer. At the same time, it could be that the behaviour is completely absent in wolves and it was a result of domestication, consequently present only in dogs. This hypothesis could be supported by the fact that the head tilting behaviour is triggered, in dogs, by known words (Sommese et al., 2022). Furthermore, the fact that humans find the behaviour cute (Amry at al., 2018) would make it advantageous for dogs, or their wolf-like canid ancestor, as it would have increased their chances to be chosen and kept by humans. Alternatively, the sound source not being exactly above or to the side of the wolves' head creates a different condition compared to the foxes' hunting one, where they head tilt to locate hidden preys exactly beneath them (Bahr, 1989; Ĉervený et al., 2011; Henry, 1986). Unfortunately, it was impossible to place the sound exactly above the wolves' head or to its side, as they would have been scared by it and, if not, the possibility of them placing themselves exactly underneath or to the side of the sound source would have been extremely low.

It must be kept in mind that known words are not the only trigger for head tilting, as the current study shows with the squeaky toy sound. The strange behaviour of the wolves looking up was clarified by the keeper which explained that the previous enclosure of the breeding male (in another park) had an elevated point from which the visitors could look at the wolves from a higher ground. Consequently, the wolves residing there developed the habit of looking up to check on the visitors. After the breeding male was moved to his current home, he transferred the aforementioned habit to his offspring.

5.3 Conclusions

In conclusion, head tilting is a scarcely studied behaviour, whose motives and triggers are still unknown in dogs, as it is its presence in their ancestor species the wolves. This study shows how the head tilting behaviour seems to be quite widespread in dogs, on the contrary, the wolves never head tilted under the experimental condition nor were seen doing it in other situations. A significant difference was found in the head tilting frequency of dogs regarding the trial order suggesting a correlation with habituation and interest in the sound itself. No significant effect of the sound source visibility on the head tilting behaviour was found, despite a higher head tilting frequency when the sound source was not visible and on the vertical axis. In fact, a tendency of significance was found between the head tilting percentage when the sound was in the frontal position compared to when it was in the lateral one, weakly supporting the auditory hypothesis. The head tilting frequency of dogs of different age was

not significantly different but it declined with age, as did attentiveness with a trend of significance. Also, the females' head tilting behaviour and attentiveness results suggest that their interest for the sound lasted longer than the one of males. As aforementioned, further studies are needed to obtain more conclusive results with regard to the head tilting behaviour, its function and what triggers it, both in dogs and in other species.

6. Societal and ethical considerations

All animals participated voluntarily at the experiment and they were never forced to perform certain actions or behaviours in any part of it. The experiment itself was not harmful in any way to the animals, since they just listened to a squeaky toy sound, a stimulus which they could be easily exposed to in their everyday life, and their reaction and behaviour were recorded. Before the experiment all the animals were given time to explore and familiarise with the arena, so to minimise any possible stress due to the novel environment they were staying in. Before and after the experiment all the animals were rewarded for their collaboration with suitable treats or toys, depending on the individual preference. The aim of the reward was to lead the animals to preserve a good memory of the experience, motivating them to collaborate again for similar or other experiments in the future.

Overall, the results of this experiment can shed new light on dogs' behaviour and especially on the curious behaviour of head tilting, that humans seem to find particularly cute (Amry et al., 2018). Therefore, there is a higher probability that the owners in particular, but also other people, will be captivated and extremely interested in unveiling the reasons behind the head tilting behaviour. In fact, I can testify how eager end enthusiastic the owners were when answering the question regarding their dogs performing the head tilting behaviour during their everyday life, often adding details about the situation triggering the behaviour and excitingly asking me the reasons behind the aforementioned behaviour. Consequently, more dog owners will gladly offer to participate in experiments with their dogs and, hopefully, more people will take an interest and support researches about this and others dog behaviours.

In fact, discovering and learning more about the behaviour of dogs, which live next to us and help humans in multiple ways is fundamental for a better welfare of both dogs and humans. Indeed, as we have such different behaviours and ways of communication, being such different species, can highly improve to solve possible conflicts and, therefore, highly improve the life quality of both humans and dogs. All aforementioned can be summarised and demonstrated by the concept of One Welfare (Garcìa Pinillos et al., 2016). In fact, we humans

are connected to the animals and the environment, therefore, improving their wellbeing will benefit us/ours too. Thus, it is paramount to increase our knowledge about animals and their behaviour to increase their welfare and, at the same time ours and the environmental one.

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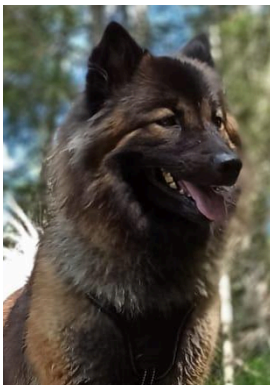
List of appendices

Appendix A - Research Subjects

Dogs



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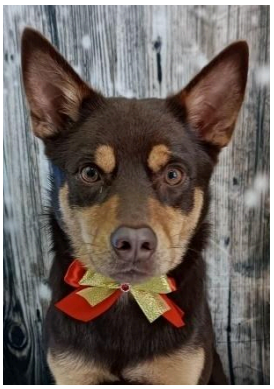
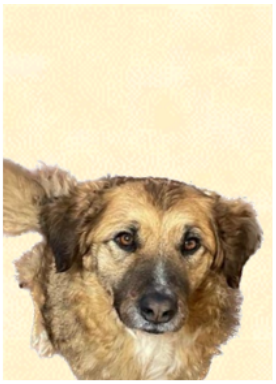


Apollo

Ares

Arya

Ayla



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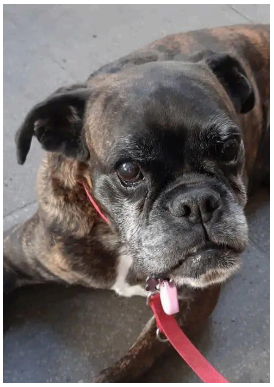

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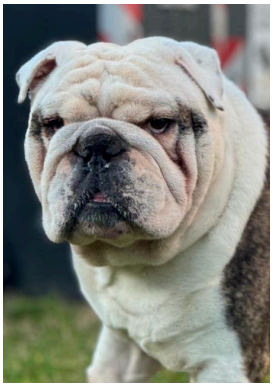
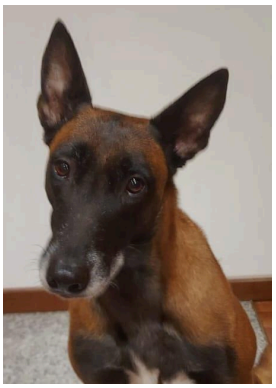


Birra

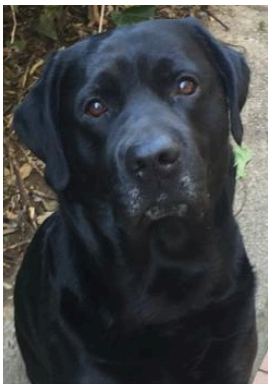
Blake



Caren

Daisy

Dolly



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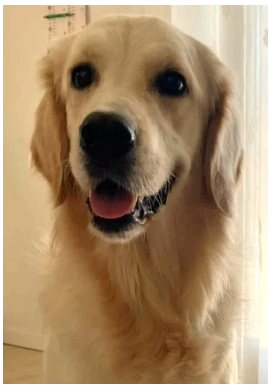
Guenda



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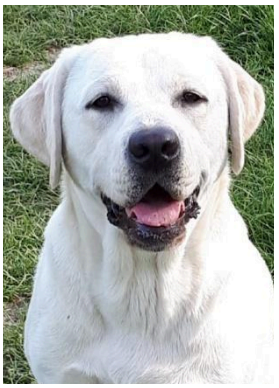

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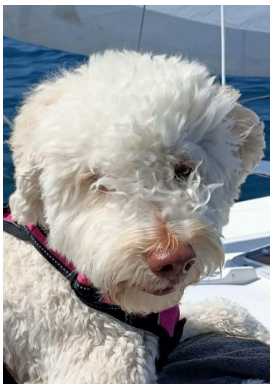

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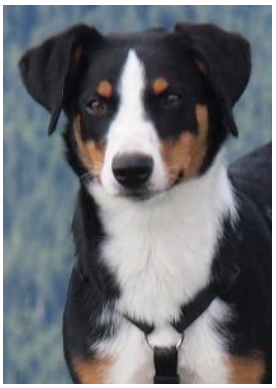

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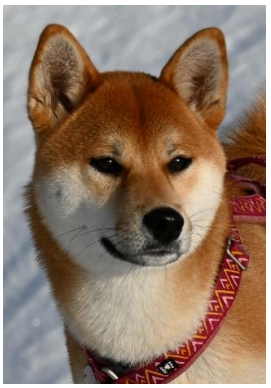

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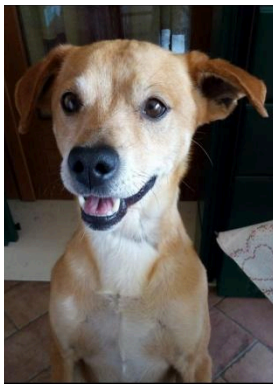
Lola



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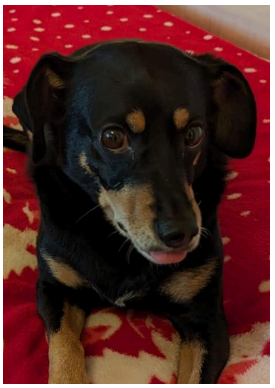

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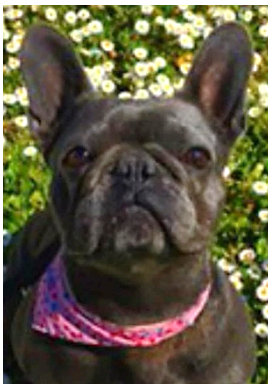
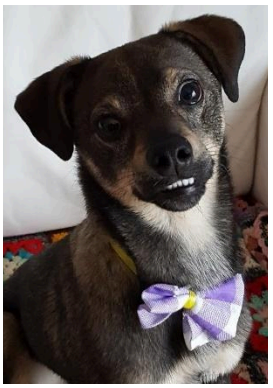


Mimma

Mustikas



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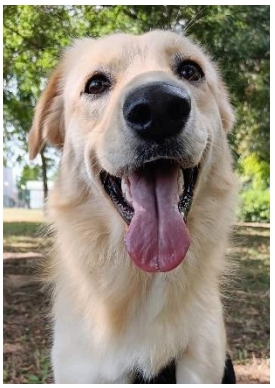

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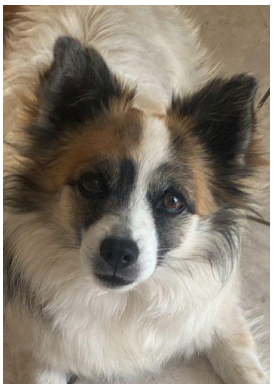

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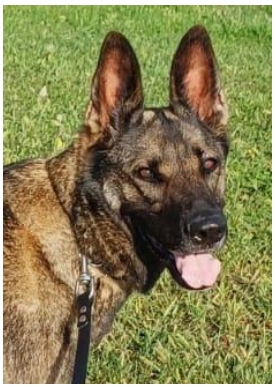

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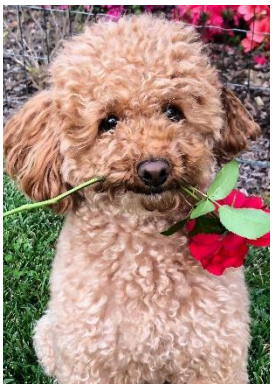

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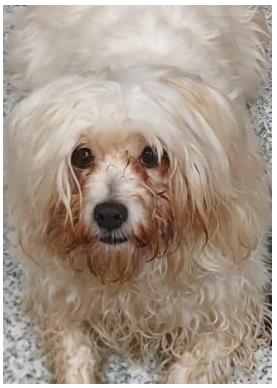

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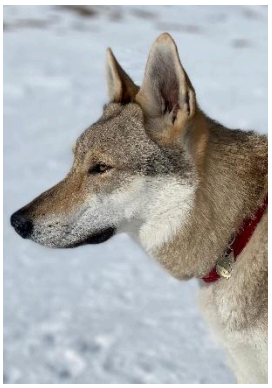
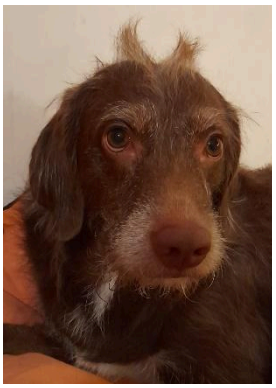


Sunny

Tobby



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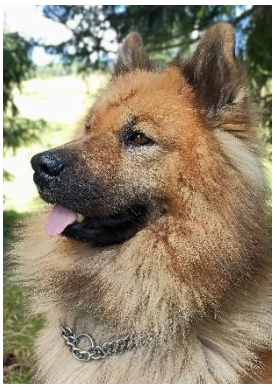


Vik

Pictures by dogs' owners

Wolves

Balto

(Picture by Alice Galotti)

Semiluna (Maia)

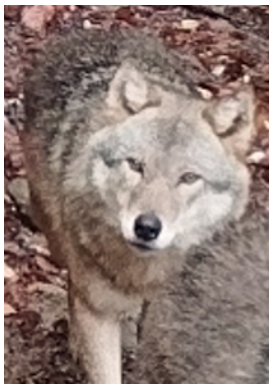
(Picture by Alice Galotti)

Sentinella

(Picture by Veronica Maglieri)

Abisso

(Picture by Martha Hirber)



Nebbia (Grigiolina)

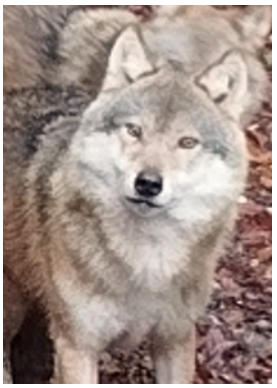
(Picture by Lisa Calearo)

Lentiggine (Due punti)

(Picture by Alice Galotti)

Mononoke

(Picture by Lisa Calearo)



Sorriso (Guance bianche)

(Picture by Lisa Calearo)

Appendix B - Data distribution analysis

Analysis of the GLMMs' residuals distribution

The quantile-quantile plot (Q-Q plot) in figure 1 represents the distribution of the residuals from the logistic regression model (GLMM) comprehensive of all six trials, compared to the expected distribution of residuals under the assumption of normality. The model from which it was realised had "logit" as the link function. The head of the residuals seem to have a linear tendency but with a less steep slope compared to the predicted distribution for normality, from which it deviates. In particular, there are more negative residuals than expected (points above the diagonal line) in the left side, while, on the right side, there are more positive residuals than anticipated (points below the diagonal line). The tail of the residuals tends to follow the line of tendency but do not strictly adhere to it, curving slightly.

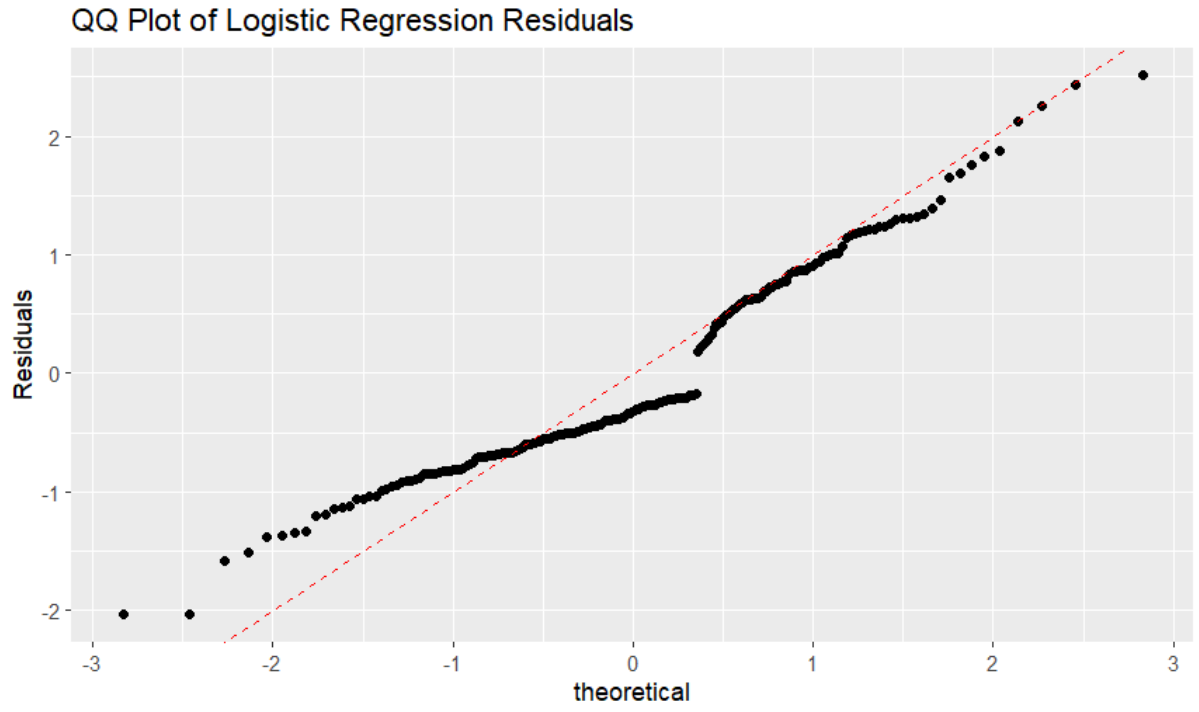


Figure 1. *Distribution of the residuals from the logistic regression of the all-encompassing GLMM (black points) compared to the expected distribution of residuals under the assumption of normality (red dotted line), when the link function used in the model was "logit".*

The quantile-quantile plot (Q-Q plot) in figure 2 represents the distribution of the residuals from the logistic regression model (GLMM) comprehensive only of the first three trials, compared to the expected distribution of residuals under the assumption of normality. The

residuals seem to have a linear tendency but with a less steep slope compared to the predicted distribution for normality, from which it deviates. In particular, there are more negative residuals than expected (points above the diagonal line) in the left side, while, on the right side, there are more positive residuals than anticipated (points below the diagonal line). In the middle part the residuals distribution is extremely close to the predicted one.

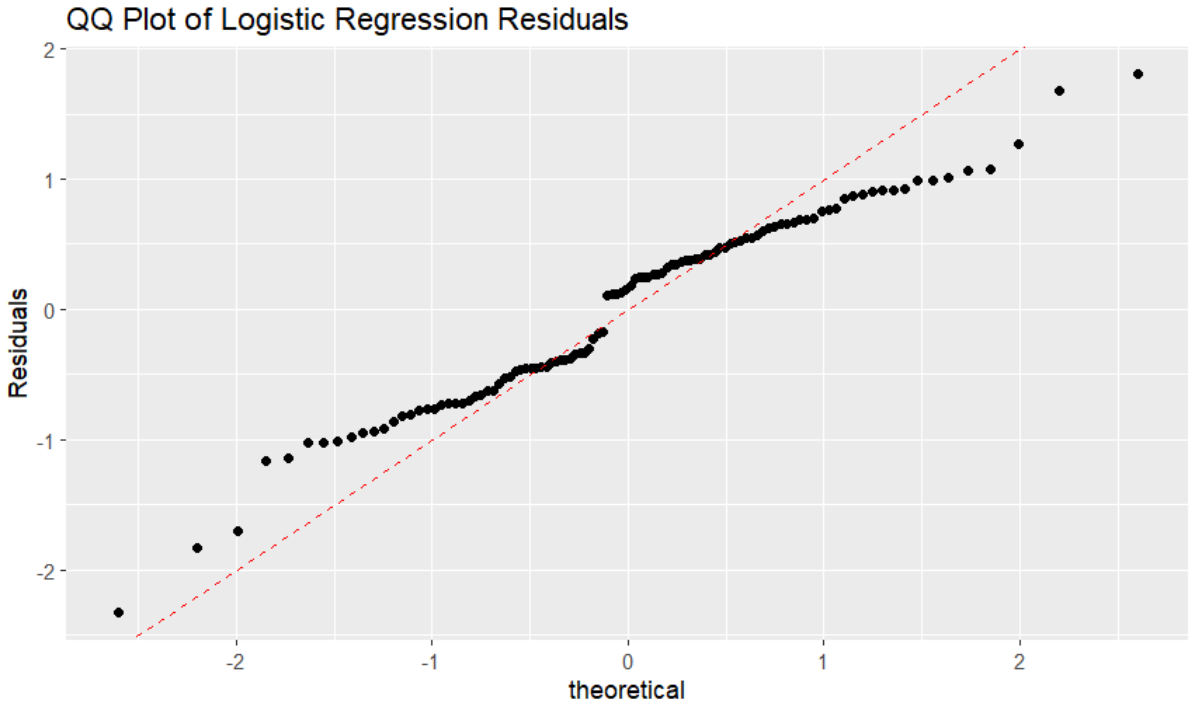


Figure 2. *Distribution of the residuals from the logistic regression of the second GLMM (comprehensive only of the first three trials) (black points) compared to the expected distribution of residuals under the assumption of normality (red dotted line).*

The residuals' distribution of the QQ plot in figure 1 is quite close to the theoretical distribution under the assumption of normality (red dotted line). Nevertheless, it does not represent perfectly normally distributed data as the residuals distribution slightly deviates from the theoretical distribution under the assumption of normality. The head of the residuals seems to have a linear tendency but with a lower angle of inclination, with more negative residuals than expected on the left side and more positive residuals than expected on the right side. Instead, the tail of the distribution seems to follow more closely the theoretical distribution under the assumption of normality. The residuals' distribution of the QQ plot in figure 2 is not too far from the diagonal line representing the theoretical normal distribution, so the departure from normality may not be too severe. However, the head and the tail of the distribution deviate slightly from the theoretical distribution under the assumption of

normality, as there are more negative residuals than expected (points above the diagonal line) in the left side, while, on the right side, there are more positive residuals than anticipated.

Dogs' distribution by sex and age group

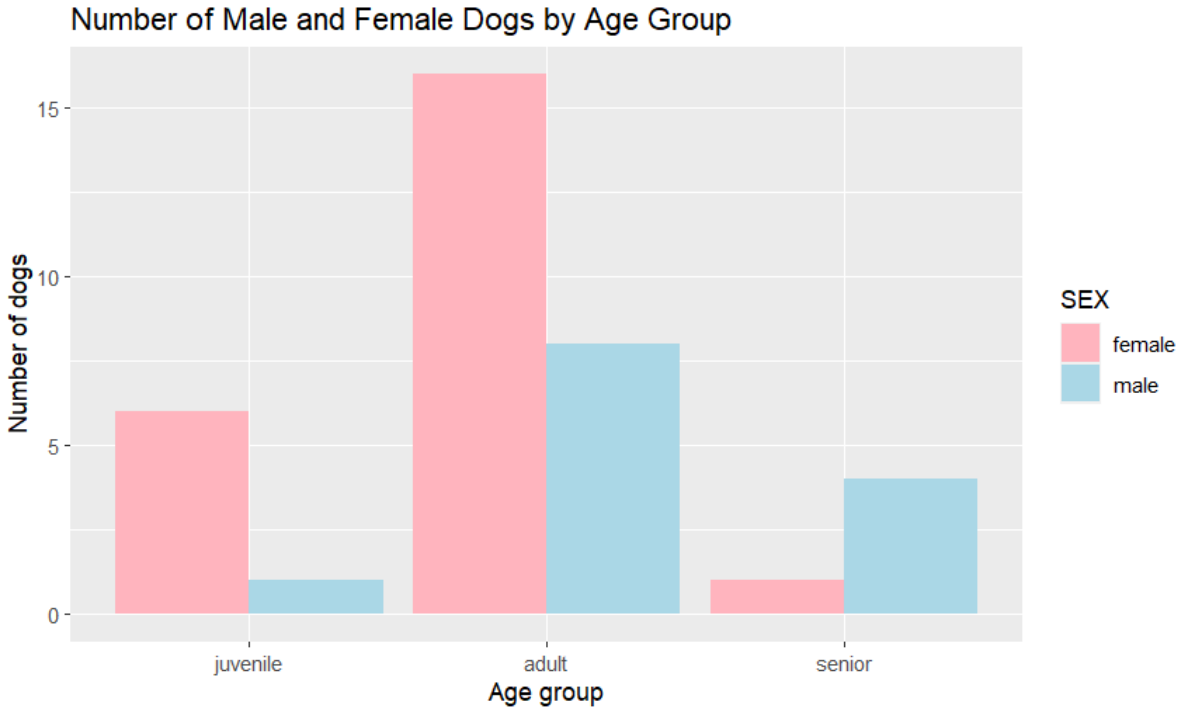


Figure 3. *Number of dogs of each sex in each age group.*

There was an imbalance in the number of dogs belonging to different age groups, as in the ratio between the two sexes, overall and in the different age groups.

Dogs' attentiveness distribution and analysis of the GLMM's residuals distribution

The data distribution shows two peaks, one at 0 s attentiveness and one at 10 s attentiveness (figure 15A). If the trials with 0 s attentiveness are removed, the attentiveness data, considered as integers and normalised, fit quite well a Poisson distribution.

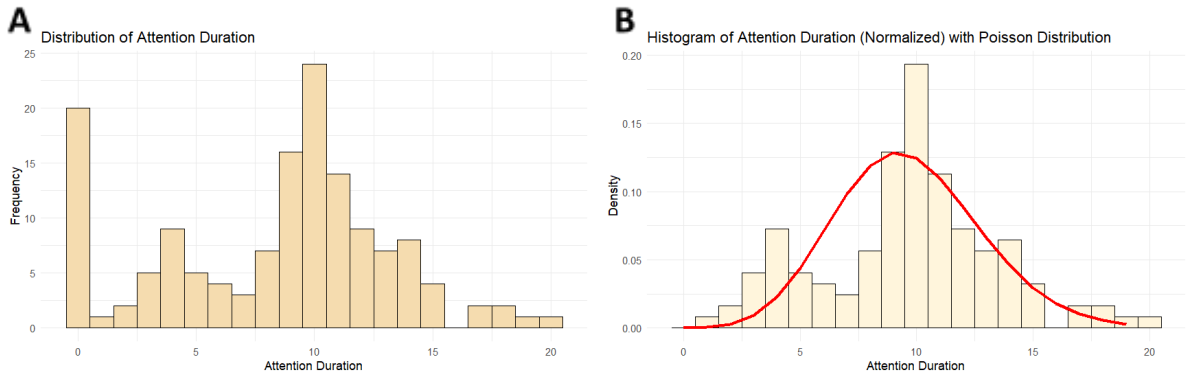


Figure 4. *Distribution of dogs' attentiveness to the sound source after the sound was played the first time in each trial (data from the first, second, fourth and fifth trials)* ***A)*** *comprehensive of the trials with 0 s attentiveness and* ***B)*** *not comprehensive of the trials with 0 s attentiveness, normalised and with the additional representation of a Poisson distribution fitting the data (red line).*

The quantile-quantile plot (Q-Q plot) in figure 16 represents the distribution of the residuals from the logistic regression model (GLMM) relative to the dog's attentiveness in the first, second, fourth and fifth trials, compared to the expected distribution of residuals under the assumption of normality. The residuals seem to have a linear tendency, as they fall approximately along the red line representing the predicted distribution for normality. However, there are more positive residuals than anticipated (points below the diagonal line).

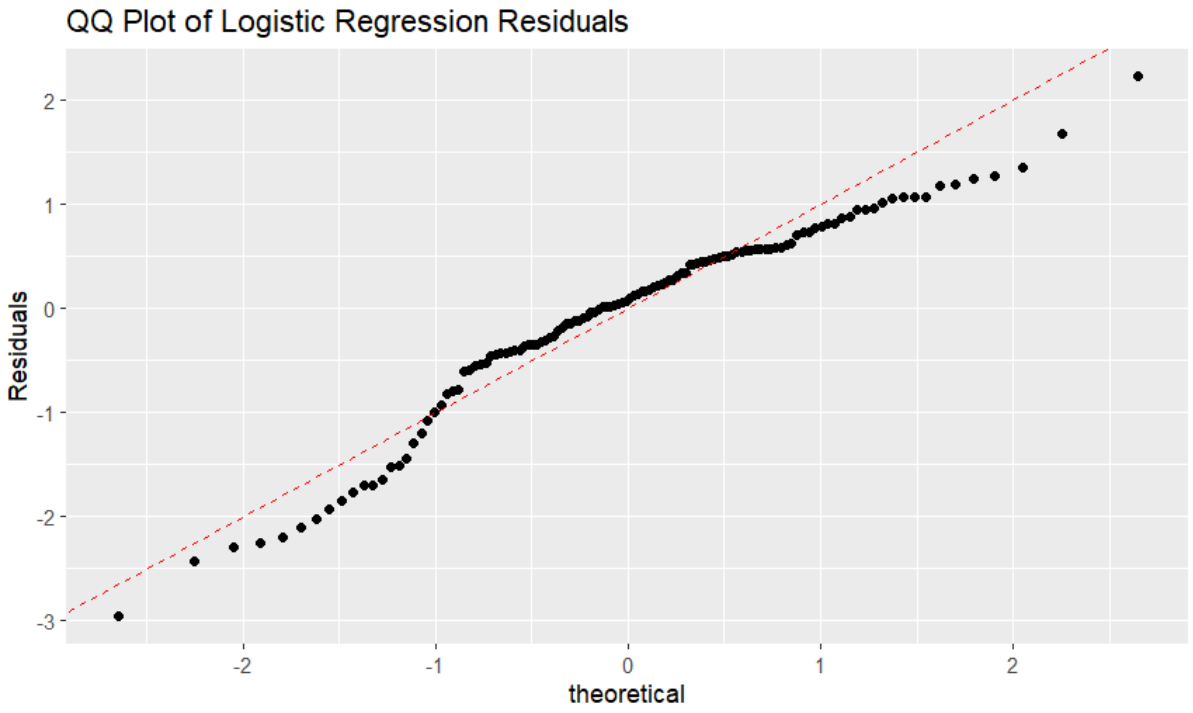


Figure 5. *Distribution of the residuals from the logistic regression of the GLMM modeling attentiveness (comprehensive of the 1st, 2nd, 4th and 5th trials) (black points) compared to the expected distribution of residuals under the assumption of normality (red dotted line).*

The residuals distribution of the QQ plot in figure 16 is quite close to the theoretical distribution under the assumption of normality, with the residuals falling approximately along the red dotted line. Just a few negative residuals in the head and the tail of the distribution deviates from those of a normal distribution. Considering both the plot in figure 15B and the one in figure 16 it can be concluded that a Poisson distribution could approximate quite well the attentiveness data and therefore "poisson" could be chosen as the family to model the data with a GLMM.

Appendix C - Results of dogs' breed group and muzzle length influence on head tilting

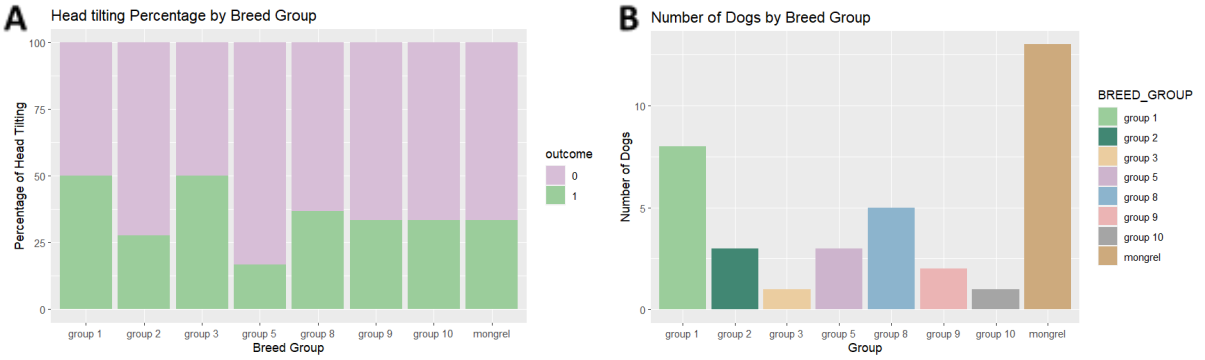


Figure 1. A) *Head tilting percentage of dogs in relation to the breed group the dog belongs to.* ***B)*** *Number of dogs belonging to each breed group that participated in the experiment.*

There was no significant difference between the percentage of the head tilting behaviour of dogs belonging to different breed groups (p = 0.66, figure 17A). However, it can be noticed that dogs belonging to group 1 and group 3 head tilted the most, while dogs belonging to group 5 head tilted the least. Note that the majority of dogs were mongrels, most dogs belonged to group 1 and for certain breed groups like group 3 and group 10 only one individual was present in the experiment (figure 17B).

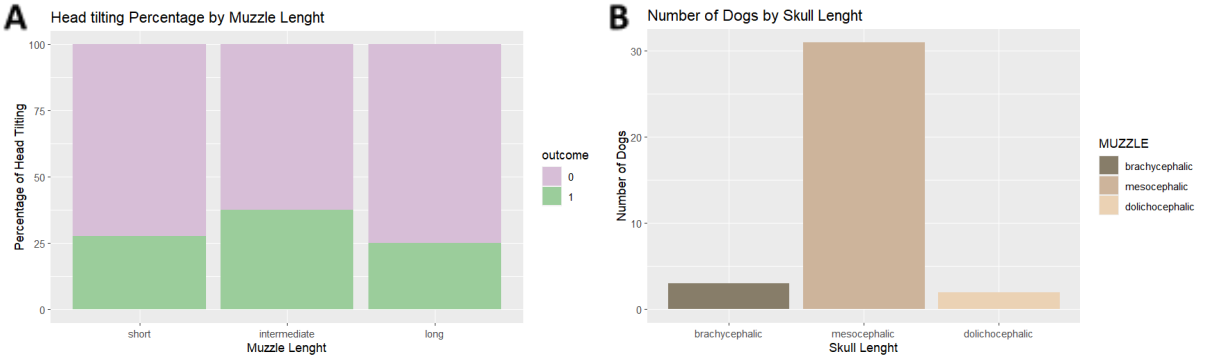


Figure 2. A) *Head tilting percentage of dogs in relation to their muzzle length.* ***B)*** *Number of dogs in relation to their muzzle length.*

There was no significant difference between the percentage of the head tilting behaviour of dogs with different muzzle length (p = 0.90, figure 18A). However, dogs with intermediate muzzle length (mesocephalic) head tilted slightly more than dogs with short (brachycephalic) and long (dolichocephalic) muzzles. Note that the majority of dogs were mesocephalic (intermediate length muzzle), while only two to three dogs were brachycephalic (short muzzle) or dolichocephalic (long muzzle) (figure 18B).