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# SENSING LIFE IN A NOISY WORLD: HOW CAN ANIMALS DETECT ANIMATE ORGANISMS THROUGH SOUND?

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*To my parents, without whom none of this would have been possible.*

*To Marino, to whom I owe so much.*

*To Luca, Martino and Matteo, for being patient and loyal friends.*

*To my animals, eternal source of joy and contemplation.*

*To the glorious Ukrainian people, because the search for truth cannot exist without the defence of freedom and justice.*

*To anyone struggling with mental illness, navigating dark times, or feeling utterly alone, because I know what it feels like.*

# Abstract

Acoustic communication has evolved to play a critical role in the survival of animals. From the great apes to insects, a great variety of living organisms rely on auditory communication. Specifically, taxa that live in groups are particularly committed to using sound to navigate complex social interactions such as individual recognition, kin discrimination, and conflict resolution. Nevertheless, despite the recent advancements in bioacoustics research and its increasing significance in elucidating animal behaviour, there exists a paucity of studies investigating how animals perceive auditory cues that can tell them whether they are dealing with another animal or a non-living thing. Consequently, this thesis aims at broadening our knowledge concerning the biological roots underlying the ability to produce and perceive auditory signals and cues that facilitate an animal's ability to detect animate objects and differentiate them from inanimate ones.

In particular, Chapter 1 aims to provide a complete overview of the state of scientific research on auditory animacy cues, describing our knowledge of the main cues, i.e. vocalisations, acoustic motion sounds - sounds produced involuntarily by the locomotory movement of an organism - and consonance - the stability of a sound, linked to the presence of an animate being - and then briefly suggesting some lines of future research. The chapter then introduces our study species, the domestic chick (*Gallus gallus domesticus*), highlighting the characteristics that make it an excellent model species for our purposes and what it is known about its hearing and vocal abilities.

The next issue discussed is how 'animated' sounds differ from those that are not. More precisely, Chapter 2 aims to answer this question by presenting the results of a study that, using the domestic chick as experimental model, asks whether or not

the voluntary acoustic emissions of animals may contain regularities characterised by power laws or 1/f^β spectral distributions from the first day of life, i.e. long-range correlations - already identified in the vocalisations of adult animals of numerous species - that reflect fractal structures of the physical world and can thus be characterised as an acoustic building block.

Chapter 3, on the other hand, is devoted to the analysis, from a biomusicological perspective, of those features of vocalisations that are at the intersection of different musical abilities and that may be at the same time auditory animacy cues. Two studies are described in this chapter: the first experiment deals with the innateness of vocal plasticity – that is, the ability to modify certain features of vocalisations, such as intensity or frequency, in response to environmental changes - proving that newborn domestic chicks are able to adjust both the intensity and the fundamental frequency of their distress calls to the loudness of the background noise, an ability possessed only by animate beings; the second experiment described here, instead, shift the attention to the innateness and evolutionary significance of non-linear vocal phenomena – irregular and unpredictable acoustic features in vocalizations often produced under conditions of high arousal or stress – a phenomenon closely associated with music expression and that is highly exploited in animal communication to convey a set of different information in the receivers.

Finally, in Chapter 4, we investigated for the first time timbrical perception innateness by presenting both natural and musical acoustic stimuli to 3-day-old domestic chicks in an attention-grabbing paradigm, discovering that this species relies on different auditory cues when listening to vocalisations belonging to their own vocal repertoire than when processing unknown musical sounds.

Taken together, the findings described in the present thesis support the existence of innate auditory and vocal predispositions that are closely linked to auditory animacy.

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# Chapter 1

## General Introduction

Chapter 1.1 was published as the following paper:

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### 1.1 When Sounds Come Alive: Animacy in the Auditory Sense

#### *1.1.1 Introduction*

Why are some sounds perceived as coming from living things and others not? Is there a sense of auditory animacy in different animal species? It is well known that animacy perception plays a crucial role in the survival of animals from an early age, enabling individuals to automatically and effortlessly locate biological cues of animate beings and then react according to the nature of the perceived entity, predator, prey, conspecific, etc. However, most research in this area has focused on the visual domain, particularly exploring the role of biological motion (Lorenzi et al, 2024), face perception (Kobylkov and Vallortigara, 2024; Kobylkov et al., 2024), and changes in speed and direction of moving objects (Di Giorgio et al, 2016; Lorenzi et al. 2017; review in Lorenzi and Vallortigara, 2021), while few researchers have addressed the possibility of an auditory counterpart to animacy perception (but see Tremoulet and Feldman, 2000).

This relative paucity of studies should not be surprising, however, given that auditory perception is characterised by a completely different psychophysical nature compared to the

visual modality. As a result, the features that might constitute an animacy cue in the auditory sense are not necessarily the same as those that have been identified in visual research. When we think about how animals, relying solely on their sense of hearing, are able to discriminate between living and non-living entities, the first feature that comes to mind is something unique to the auditory sense: the voice. Indeed, authors such as Patterson (2014) identify in the pulse-resonance structure of animal voices one of the key features at the basis of living organisms' recognition through sound.

It follows that all those sounds that are sufficiently similar in their acoustical structure to that of the voice - the so-called *voicelikeness* - should be able to elicit neurophysiological and behavioural responses similar to those of the voice (Broze, 2013). This was used by occultists at the turn of the 19th and 20th centuries, who argued for an ability allegedly demonstrated by certain people to perceive human voices in the noise produced by mechanical-electronic devices such as the radio, a phenomenon that became known as Electronic Voice Phenomena (Leary and Butler, 2015). They were actually documenting the auditory equivalent of pareidolia (a well-known phenomenon in vision), i.e. misperceiving or misinterpreting random noise or ambiguous acoustic stimuli as meaningful sounds, such as words or even sentences (Blom, 2015). This perceptual illusion suggests that the human species has a hypersensitivity to searching for and identifying voices within the auditory scene in which one is immersed, similar to what happens in the visual modality when faces are perceived in inanimate objects (Liu et al., 2014) also by non-human primates (Taubert et al., 2017). From a neuroanatomical perspective, the processing of voices of both conspecific and heterospecific individuals is supported by a dedicated extensive network of cortical areas (Broze, 2013).

In addition, another acoustic feature at the basis of the recognition of animate entities is consonance, i.e., sound frequencies that, when combined, produce the perception of a single

sound and are therefore considered pleasant (Trulla et al., 2018). Because this feature is prominent in all acoustic events characterised by a well-defined and clear harmonic structure - such as the vocalisations of many species of songbirds and human speech - it is considered a hallmark of sounds produced by animate beings, which would explain the attraction that consonance exerts from an early age in distantly related taxa such as humans, domestic chicks and chimpanzees (Chiandetti and Vallortigara, 2011).

Finally, the perception of animacy in the auditory sense also occurs because of another acoustic feature that is closely related to one of the most important visual cues to animacy, i.e. locomotory movement. When animals move through space, they frequently simultaneously produce characteristic sounds - just think of the buzzing of a flying insect - defined as motion-induced sounds (Clark, 2016). These are involuntary acoustic events generated by the movement of anatomical parts of the body that are not specialised in producing communicative sounds, so that their conveyed information - i.e. the presence of a moving animal - is exploited by listeners rather than being transmitted directly and voluntarily (Clark, 2016). Neuroscientific studies have also demonstrated the existence of brain areas dedicated to the detection of acoustic motion, similar to those devoted to motion perception in other sensory modalities, such as vision (Wagner et al., 1997).

This work offers one of the first reviews in the field of auditory animacy perception and aims to fill this gap by systematising the existing knowledge into a coherent description, identifying the main lines of research and proposing a global interpretation of the results obtained.

### *1.1.2 Voicelikeness*

In vertebrates, voice production and perception are phenomena with a long evolutionary history. Voice generation mechanisms are the output of a system, the vocal tract, whose functional and neural control components are highly conserved across species

(Newman, 2010; Fitch and Hauser, 2003). Furthermore, the ability to perceive conspecifics' voice is encoded in species-specific auditory nuclei in the auditory forebrain of birds (Louder et al., 2019) and, in the mammalian brain, regions such as the superior temporal plane and auditory neurons in the ventrolateral prefrontal cortex are involved in all studied primate species (Petkov et al., 2008; Romanski and Averbeck, 2009), with the anterior superior temporal sulcus specialised in humans (Belin et al., 2000; Fecteau et al., 2004). Moreover, the ability to recognise and approach the voice of a conspecific, especially if it is the mother's, is an ability shown early in life in many avian species, such as domestic chicks (Gottlieb, 1965; Fält, 1981; Van Kampen and Bolhuis, 1991), pekin ducklings (Gottlieb, 1965), wood ducklings (Gottlieb, 1965), willow grouses (Allen, 1977), Japanese quails (Park and Balaban, 1991) and bobwhite quails (Heaton et al., 1978), which prefer the voice of their own species to that of another taxon or noise. As shown by Long et al. (2001), species-specific neural development underlies auditory preferences in taxa such as the domestic chicken and the Japanese quail: specifically, the authors transplanted developing neural tubes from embryonic quails to embryonic chickens and then tested the auditory preferences of the chimeric domestic chicks, finding that they began to prefer quail vocalisations.

However, voice-sensitive brain areas also recognise specific characteristics of the voice - such as fundamental frequency, call length and harmonic and phase-coupling content - regardless of the species. These neural correlates include the middle portions of the left and right superior temporal gyri, the right posterior superior temporal gyrus, the left Heschl's gyrus and left planum temporale in humans (Lewis et al., 2005; Bálint et al., 2023) and the mid and caudal ectosylvian gyri in dogs (Bálint et al., 2023). It can thus be posited that there exists an ancient neural predisposition to perceive sounds that exhibit characteristics that are analogous to those observed in acoustic events produced by vocal folds vibrations, a feature called *voicelikeness* (Schubert and Wolfe, 2016; Bálint et al., 2023). Consequently, auditory stimuli

characterised by vocal similarity to certain innately encoded acoustic features will elicit a preference/approaching response. For example, one- and three-day-old domestic chicks run faster towards pure tones or tapping sounds when their frequency (Fischer, 1972), duration (Fischer, 1972), intensity (Fischer and Gilman, 1969), and rate (Fischer, 1972) are similar to those of the ideal maternal attraction call (Collias and Joos, 1953; Collias, 1987; Kent, 1993). In addition, sounds that emphasise a particular fundamental feature may be perceived as a superstimulus, and then be preferred over the original natural vocalisation, as is the case with three-day-old chicks that run faster toward stimuli with a higher rate than natural mother's clucks (De Tommaso et al., 2018).

Most importantly, as demonstrated by Gilbert Gottlieb and colleagues in different auditory vs. visual choice experiments studying imprinting in domestic chicks (Gottlieb and Simner, 1969), pekin (Gottlieb and Klopfer, 1962; Klopfer and Gottlieb, 1962), mallard (Gottlieb, 1968) and wood ducklings (Gottlieb, 1968), the magnitude of attractiveness of vocal stimuli as animacy cues exceeds that of visual stimuli, showing that - at least in the first days of life - the auditory recognition prevails, as ducklings prefer to follow a concealed moving loudspeaker broadcasting the species-specific maternal call instead of a silent moving visual replica of the hen, while domestic chicks are more attracted to an even simpler stimulus as an auditory flickering than to its visual version. Similarly, in the early stages of development, bobwhite quail chicks primarily rely on auditory cues for species identification and filial behaviour, but as they mature, visual cues are integrated, with auditory stimuli remaining dominant (Lickliter and Virkar, 1989). Overall, these results support the cue hierarchy hypothesis proposed by Johnston and Gottlieb (1985), according to which sensory systems are organised hierarchically in early development, with the brain giving greater priority to auditory information as the auditory system matures faster than the visual system (Lickliter and Virkar, 1989).

### *1.1.3 Consonance*

Analyses of the human voice have shown that when frequency and intensity values intersect, peaks corresponding to consonant melodic intervals emerge, suggesting that consonant intervals may represent the default state of human intonation (Schwartz et al., 2003). This phenomenon aligns with a distinctive characteristic of biological vocalisations: the presence of a well-defined harmonic structure, consisting of a fundamental frequency and harmonic overtones - a feature also shared by the sounds produced by musical instruments. This aspect was first noted in the 18th century by the French music theorist and composer Jean-Philippe Rameau, who observed that there was a connection between tonal sounds - often produced by living beings - and harmonic structure, particularly consonance (Christensen, 2004). Consonance is defined as the combination of two or more sound frequencies played simultaneously or consecutively that the brain perceives as stable, predictable and qualitatively pleasing. Conversely, dissonance results from the interaction of frequencies that when combined result as unstable, thus creating a perception of roughness or harshness in the auditory system.

This intuition has been confirmed by a number of studies of the vocalisations of different oscine species, such as the musician wren and the great tit, whose songs are characterised by a heavy use of consonant notes (Doolittle and Brumm, 2012; Richner, 2016), or, like the hermit thrush, which arranges its songs according to an overtone structure (Doolittle et al., 2014). Furthermore, in great tits, there is also a relationship between male fitness and the accuracy with which they produce consonant notes in their songs, showing that females prefer sounds characterised by stability and predictability (Richner, 2016). However, it is not even necessary for an animal to sing in order to “speak” consonant, since domestic chicks, for instance, emit perfect consonances across all types of calls, highlighting that consonant sounds are inherently present in animal communication (Maldarelli et al., 2024).

Not only that, but the tone of our species' voice in dyadic interactions was shown preliminarily to be consonant when there is agreement between the speakers, and dissonant when disagreement arises (Okada et al., 2012).

Taken together, these results suggest a fundamental similarity between the harmonic structure of periodic sounds, whether the sound of the voice or that of musical instruments, thus making consonance a prominent aspect of vocalisations emitted by animate beings (Bowling and Purves, 2015; Wagner and Hoeschele, 2022). This conclusion is further supported by the evidence that, in studies employing a spontaneous preference paradigm, consonant sounds are favoured over dissonant ones in newborns of distantly related species, including domestic chickens (Chiandetti and Vallortigara, 2011), chimpanzees (Sugimoto et al., 2010) and humans (Masataka, 2006; Perani et al., 2010). This finding corroborates the idea that consonance is employed as a distinctive auditory cue for the presence of an animate object (Chiandetti and Vallortigara, 2011; Chiandetti, 2016; Vallortigara, 2021), as opposed to an inanimate one. Moreover, it suggests that this discriminative capacity may be a shared trait among species and may constitute an acoustic unlearned predisposition before experience, culture and training shape our preferences (Lahdelma and Eerola, 2020; Prete et al., 2020; Lahdelma et al., 2022).

### *1.1.4 Acoustic Motion*

The world is full of things that move and produce sound as a by-product. Some of them are alive - and the acoustic events produced are then called motion-induced sounds - and some of them are not, like leaves rustling, rocks tumbling or ocean waves. So, how does the auditory system discriminate between sounds produced by moving biological entities and those produced by moving objects? The first study to attempt to answer this question is that of Bidet-Caulet and colleagues (2005), in which the authors used fMRI technique to investigate in humans the neural correlates of auditory biological motion, more precisely the

perception of footsteps. The results showed that the superior temporal sulcus was mainly involved in the processing of human motion sounds, irrespective of the sensory modality. A few years later, Cottrell and Campbell (2014) investigated auditory sensitivity to footsteps compared to non-biological impact sounds, such as a bouncing ball or drumbeats. Contrary to expectations, they found no increased sensitivity to biological motion compared to non-biological sounds, a finding that seems to indicate a difference between sensory modalities, with the visual domain being more fine-tuned when compared to the auditory domain. However, despite this discrepancy, both studies seem to converge on one aspect, namely the importance of temporal cues in the detection of human motion, especially if related to footsteps, a sound with high biological value (Bidet-Caulet et al., 2005; Cottrell and Campbell, 2014; Larsson, 2014).

The role of timing in the perception of auditory animacy was later taken up in the field of musical cognition, where there is a debate about the characteristics impacting the "aliveness" of a musical piece performance, an issue that, as some authors have noted (Blust et al., 2015), overlaps with that of auditory animacy. In particular, the bridge linking music to animacy is *rubato*, a performance technique used to convey greater expressiveness consisting of slight changes in the timing of a musical piece by slowing it down or speeding it up, giving also an acoustic motion sensation. In their 2015 paper, Blust and colleagues investigated the role of rubato in making music sound animated, asking participants to rate on a Likert scale the perceived animacy of computerized and human performances, both varying in rubato level. Results showed that both fixed and excessive timing variations led to a decrease in perceived animacy, while minimal levels of rubato resulted in significantly higher ratings of animacy (Blust et al., 2015).

The work of Nielsen and colleagues (2015), instead, made a significant contribution to the advancement of the field by investigating the effects of cues such as changes in the

speed and direction of acoustic motion on the perception of animacy in humans. To this end, they designed a study that represents the auditory analogue of the previously conducted research in the visual domain by Tremoulet and Feldman (2000). This was done by using binaural spatialisation to generate acoustic stimuli that mimicked the motion in three-dimensional space of a synthesised mosquito sound, varying in speed and direction - thus creating the impression of a living entity - or keeping the values constant in both dimensions. Participants were then asked to rate on a Likert scale their confidence that the perceived sound was lifelike or not, showing a significant difference between changes in speed and no changes, but unexpectedly also between changes in speed and changes in direction, suggesting the existence of a hierarchical organisation of animacy cues with respect to acoustic motion. No study has yet addressed whether it is possible, in the acoustic domain, to distinguish causal interactions between inanimate and animate objects, as has been observed in the visual domain early in ontogenesis (Kominsky et al., 2022).

Finally, how do animals perceive acoustic motion? Even if animacy-related data are still absent, it is known that brain structures like the inferior colliculus are at the basis of the detection of acoustic motion direction, a process that is then refined in sensitivity through GABAergic inhibition, while motion information is then further processed by higher regions such as the auditory cortex (Wagner et al., 1997). Some animal taxa specialised in hunting using auditory cues even possess auditory space maps that integrate and help localise motion information (Wagner et al., 1997). (For a comprehensive review on this topic, see Carlile and Leung, 2016).

### *1.1.5 Discussion*

This review has provided a full description of the area of auditory animacy, stressing the multifaceted nature of the acoustic mechanisms at the basis of animate beings' perception, going from voice features to sounds emitted involuntarily during biological motion. As

outlined here, parallels between auditory and visual animacy cues are striking, with the voice being the acoustic analogue of the face, and voicelikeness - resulting from the abstraction of vocal fundamental features - leading to a sensitivity comparable to that for face-like stimuli, causing the occurrence of phenomena such as auditory pareidolia, similar to face pareidolia. While the link between biological and acoustic movement is evident and very close, consonance as a feature of vocal prosody may instead fulfill a role akin to that of eyes and gaze, which are key characteristics in face and social perception.

Future research should consider whether face perception offers further analogies, such as in upside-down processing and backward speech, a domain where potential influences of rhythm, stress, and intonation can be examined (Toro et al., 2005). Studies should also address the potential effects of high-level cognition in modulating animacy perception - as done by Kim and Schachner (2021) who linked causal reasoning to animacy perception in music - and explore new potential cues, such as affective prosody (Zimmermann et al., 2013), or auditory regularities like fractal structure in vocal emissions (Jermyn et al., 2023). Finally, more research should investigate the cross modality of perceptual animacy, which may be part of a larger integrated system of social perception that includes different sensory modalities such as vision and hearing, and maybe even other unexplored domains, such as touch or olfaction.

## 1.2 From Instinct to Harmony: Auditory Perception in Galloanserae

### *1.2.1 Introduction*

The interaction between sensory systems and innate behavioural responses has long been understood through the study of different avian species. In particular, fowls, also known as *Galloanserae* - an ancient and diverse group of birds including species like domestic chickens, ducks, geese, or pheasant - have rapidly become in the last century an interesting model for examining the influence of innate predispositions on visual perception and

behaviour. What is less known about this group of animals, however, is the complex of those predispositions that are directly connected to the auditory sense. Indeed, while songbirds have been used extensively in auditory research, the study of non-passerine species such as *Galloanserae* has remained largely limited, focusing in particular on characterising the vocal repertoire of the taxon of interest.

Despite their underrepresentation in auditory research, *Galloanserae* present a unique opportunity for understanding the evolutionary origins of acoustic communication and auditory perception beyond the specialized realm of songbirds. The vocal and non-vocal sound interactions of these species, many of which date back millions of years, suggest a deeper and potentially more widespread role of sound in shaping behaviours and sensory systems across avian taxa. By examining these ancient lineages, we not only shed light on the sensory ecology of fowl but also provide new insights into the evolutionary pressures that may have driven the development of auditory-related behaviours in birds more broadly.

This work has been divided into three parts. The first one provides a detailed overview of the innate acoustic predispositions in fowls, identifying the main spectral and temporal features that are used in animal communication – some of which are also shared with music, such as pitch, rhythm, or consonance – and examining the results provided by those studies that have tested the responses of newborn chicks of different *Galloanserae* species to these acoustic characteristics, distinguishing those that are present from an early age – which probably imply an essential role in the sensory ecology of the taxon studied, often related to mother-offspring communication - from those that require a longer time span to fully mature.

The second part deals with acoustic communication in fowls, describing the main vocalisations constituting their vocal repertoire, also describing the emotional valence and the context of emission of the calls. As a group, *Galloanserae* taxa exhibit a relatively complex set of vocalisations from early ontogenetic stages, building on the many innate predispositions

they possess, but it is also interesting that the adult communicative system is not simply a set of stereotypical calls produced in a particular social or emotional context, but is modulated by cognitive features such as referential function and perspective taking, demonstrating how genetically determined traits can be accompanied by flexible and cognitively sophisticated modes of information transmission.

Finally, the last section of this review is concerned with music perception and appreciation in fowls, distinguishing the effect on chicken embryos from those experienced by young and adult individuals of the same species. The study of music and animal responses is indeed an increasingly important area of bioacoustics and biomusicology, but the role played by non-singing species, particularly in the avian group, is often overlooked. In the present work, we aim to provide a comprehensive description of the main studies carried out on poultry, presenting what is known about the perception of specific musical parameters, as well as the effects of musical compositions as a whole, in an attempt to reconstruct the evolution of music-related traits.

Overall, this work represents one of the first examinations of the abilities exhibited by *Galloanserae* species in the realm of sound perception and vocal production, with a particular focus on their acoustic innate predispositions and the skills associated with musical cognition.

### *1.2.2 Innate Acoustical Predispositions*

An innate acoustic predisposition consists of an inborn, non-learned tendency or ability to respond to, produce or interpret certain sounds in the surrounding environment. Notably, as these abilities are present from the earliest stages of life, they are the product of a genetic encoding resulting from evolutionary pressures arising from the animal's ecological niche, where recognizing and responding to certain sounds or sound patterns is essential for a range of activities, such as locating parents, avoiding predators or finding mates. As it will be explored, this set of survival skills includes different acoustic properties - such as pitch,

amplitude, rhythm and others - all of which characterise the sounds emitted by other animals, whether conspecifics or not.

*(a) Pitch perception*

A first property that characterises the sounds produced by a phonatory apparatus such as that of tetrapods is pitch, or fundamental frequency, which is the lowest frequency of a sound wave and is particularly important in animal communication, since it helps to identify species or individual animals on the basis of their voice (Hoeschele, 2017). Although very few studies have investigated the preference of *Galloanserae* infants for sounds with different pitch values, the results that have emerged clearly support the existence of an innate auditory predisposition to prefer acoustic stimuli with a fundamental frequency within a precise range. More specifically, Fischer (1972) demonstrated that one-day-old domestic chicks follow those sounds that are similar in frequency to their mother's clucking, both when the acoustic stimulus consists of a pure tone and when it consists of tapping sounds. This preference would allow newborns to follow only those sounds that are likely to have been emitted by the mother, ignoring those with pitch differences that could be dangerous because they are emitted by a predator.

*(b) Amplitude perception*

Another fundamental property of acoustic signals is the amplitude, which can be defined as a measure of the energy level of a given sound, often interpreted by listeners as the perceived intensity of an acoustic emission. Amplitude variations are used in acoustic communication systems to convey information and emotions to the listeners. An example is when someone shouts our name, another is when we listen to soft music: in the first case, our reaction will consist of an increase in arousal and attention, while in the second, the acoustic stimulation will have a calming effect. This influence of amplitude on the physio-emotional system is also typical of animals, whose vocalisations incorporate similar amplitude variations

depending on the meaning - positive or negative - that they convey, thus eliciting congruent responses from the listeners (Snowdon, 2021). Whether or not these reactions may be an innate adaptation to the perception of amplitude variations has not been extensively investigated by researchers, although there seem to exist innate responses and preferences for certain features that distinguish the intensity of sounds.

More specifically, experiments conducted on newborn domestic chicks as part of the study of imprinting showed that from the first hours of life, these animals exhibited significantly greater approach responses when presented with acoustic stimuli-whether maternal clucking or tapping sounds-whose intensity was within a specific range of 55 to 75 dB (Fischer and Gilman, 1969; Robinson-Guy and Schulman, 1980). Furthermore, the intensity of maternal clucking could also modulate the emission of distress calls by domestic chicks, with the frequency of distress calls decreasing as the intensity of clucking increased (Evans, 1974). Although these findings are limited to a single species, they highlight that there may be an innate predisposition to prefer those sounds characterised by a particular amplitude value that can capture the attention of the listener by inducing a state of activation and arousal associated with a biological meaning of urgency and need to be reunited with the parent.

*(c) Rhythm perception and production*

Most of the acoustic signals produced by animals, whether vertebrates or invertebrates, are characterised by being timely arranged, that is, the acoustic units in a sequence are temporally spaced according to a structured, non-random pattern. This temporal structure, commonly known as rhythm, is not a monolithic phenomenon, but consists of a multifaceted, complex acoustic feature that can be divided into at least four components: the first one is certainly the rhythmic pattern, or the way in which acoustic events are grouped into detectable units; the second component, instead, is meter, which consists of regularly recurring patterns of accents (that is, intensity) of acoustic units; then, there's tempo, which

refers to the perceived speed of a given rhythmic pattern; finally, the perceived pace is denoted as timing (Honing, 2013). It is interesting to note that these aspects contributing to the definition of rhythm are used not only in the musical field, but also in the communication strategy of some animal species for the purpose of conveying different types of information, and this thanks to the fact that the acoustic temporal structure is able to influence the emotional state of the listener (Snowdon, 2021). A clear example of this is the variation in tempo: by decreasing the distance between the acoustic elements, the tones or vocalisations will result accelerated, more pressing, so as to induce an arousing effect in the receiver; conversely, by increasing the duration of the intervals of silence between the acoustic events, time slows down, producing a calming effect in the listener (Snowdon, 2018). However, a pressing question naturally arises at this point, that is: which of the previously described aspects are biologically innate - thus constituting acoustical innate predispositions - and which, instead, are acquired through learning?

Fowls appear once again to be an excellent behavioural model for responding to such a question. Turning their attention to 3-day-old domestic chicks, De Tommaso and colleagues (2018) performed an experiment aimed at investigating whether this species' perception of rhythmic features such as meter and tempo, as well as their interaction with pitch, could constitute an acoustical innate predisposition or not. In particular, exploiting the running wheel paradigm - in which the chick is free to run forward or backward within a wheel in response to the presented stimuli - the authors measured the behavioural tendency to approach or avoid regular versus irregular patterns of hen's clucks with strong and weak beats. Taken together, the findings of this study reveal a pattern where chicks' motor activity was minimal when the acoustic stimuli consisted of continuous tones; on the contrary, when the presented sounds were discrete pulses, the approaching response then increased as the perceived tempo augmented in speed and the rhythmic events became more complex. Interestingly, this last

result was observed both when acoustic stimuli were arranged in regular rhythmic patterns and when these pulses' rhythm was non-regular (De Tommaso et al., 2018).

These findings clearly suggest that tempo plays a fundamental role in eliciting the approaching responses of animals belonging to this initial developmental stage. In contrast, the more complex, strictly rhythmic aspect seems to be ineffective, suggesting that its perception may not constitute an acoustic innate predisposition. This also accords with earlier studies, which showed that newborn domestic chicks and mallard ducklings innately distinguish between tempos, with a strong preference for those aligning to that typical of maternal call rate, which makes sense since it is a vocalisation precisely evolved to induce an arousing effect in the listening infants so that they can reach her for food or protection (Miller, 1980; Kent, 1993). However, as stated previously, tempo variations are exploited not only to convey a sense of urgency, but also to calm or even behaviourally inhibit the listener: that is the case of both domestic chicks and mallard ducklings again, who diminish their vocal and/or locomotor activity when the repetition rate of the acoustic event - being it a pure tone or the maternal call - is slowed down or is naturally slow - as in mallard alarm call (Fischer, 1972; Miller, 1980; Miller and Blaich, 1986; Kent, 1993). Taken together, these results suggest that tempo perception and discrimination originated very early in the avian evolutionary lineage, also implying that more complex rhythmic- and music-related behaviours observed in certain bird species - such as duetting, synchrony and dancing - have an ancient, innate precursor in the *Galloanserae* clade.

However, the discussion of rhythm perception is far from over. Although the perception of rhythmic patterns in the context of imprinting does not seem to be encoded by an innate acoustical predisposition, it does have an effect on cognitive tasks, especially those involving memory. Indeed, the brief exposure of day-old domestic chicks to complex rhythmic sequences of synthesised auditory stimuli for 1 minute strongly enhances long-term

memory formation during a passive avoidance learning task (Toukhsati & Rickard, 2001). These cognitive facilitating effects of rhythmic stimulation are mediated by increases in physiological arousal levels - a phenomenon well-known to be responsible for memory formation enhancing - due to activation of noradrenergic pathways in the brain (Toukhsati et al., 2005). But why does the rhythmic pattern have an innate effect on a cognitive task while being ineffective in the mother-offspring communicative dyad? The reason seems to be that the hen's natural calls that increase arousal - such as the food call or the follow me call - are all characterised by a complex rhythm, unlike other vocalisations that lack it. This association between arousal and rhythm thus seems to be the key leading to the conclusion that there is an innate predisposition to noradrenergic activation in response to acoustic stimuli that induce attention (Field et al., 2007).

*(d) Consonance perception and production*

Can a general attunement to consonance be a universal predisposition in animals? One way to find out is to test newborn animals that have not been exposed to musical stimuli in a preference test where they have to choose between two stimuli, one consonant and the other dissonant. This is exactly what Chiandetti and Vallortigara (2011) did, testing newborn chicks (*Gallus domesticus*) hatched from eggs incubated in an acoustically isolated environment: placed in the centre of a rectangular arena, at the extremes of which were two identical imprinting objects associated with a dissonant and a consonant piano melody respectively, the animals showed a preference for the latter. This experiment is important for two reasons: firstly, it demonstrated an innate preference for consonance, and secondly, in a context in which animals search for a conspecific voice, consonant sounds seem to be a reliable cue to the presence of another organism. This biological association between consonance and living things makes sense in terms of imprinting, since domestic chicks are attracted to the hen's follow me call, a harmonic vocalisation similar to consonant intervals.

Recently, a number of studies have consistently shown that consonance production is a feature of the songs of many bird species, such as the musician wren, hermit thrush and great tit (Doolittle and Brumm 2012; Doolittle et al. 2014; Richner 2016). But is this trait also present in animals that do not have learned song forms in their acoustic repertoire? And if so, is it an innate phenomenon or one that has to be acquired? Like the preference for consonant sounds, their production is also an innate acoustic predisposition, as the vocal repertoire of 3–5-day old domestic chicks (*Gallus domesticus*) - consisting of isolation, food and brood calls - consistently contains harmonic intervals, suggesting that this acoustic organisation may be a social component of biological sounds (Maldarelli et al., 2024).

*(e) Vocal plasticity*

Vocal plasticity consists of the ability to modify the characteristics of one's voice in response to environmental abiotic factors, such as background noise, or biotic ones, like the presence of other conspecifics' vocalisations (Genzel et al., 2019). This acoustic change can be instantiated in several ways, for example by increasing the call intensity (a phenomenon also known as Lombard effect), the peak frequency, the call rate and duration, and the number of call elements. Although the presence of this behavioural trait is well renowned in numerous vertebrate species, the evidence in its favour in the *Galloanserae* group is limited to domestic chickens (*Gallus gallus domesticus*), Japanese quails (*Coturnix japonica*) and mallards (*Anas platyrhynchos*) only (Brumm et al., 2009; Potash 1972; Dorado-Correa et al., 2017). However, the study involving the latter species is of particular interest here, because by recording the animals' vocal responses at different levels of background noise, the authors demonstrated that vocal plasticity is already present - at least in the form of increased call intensity - in individuals of just two days of life, thus suggesting for the first time that a specific form of vocal plasticity - that is, the Lombard effect - can constitute an acoustical innate

predisposition. Such a hypothesis seems to be further supported by a study conducted on newborn domestic chicks using the same methodology (see chapter 3.1).

### *1.2.3 Vocal Communication*

The vocal repertoire of *Galloanserae* consists of a set of mostly innate vocalisations used to express a range of emotional and physiological states, both positive and negative. Although some of these calls are emitted from the first day of life and are an essential part of early social interactions within this group, as individuals grow there is an expansion and diversification of the vocal repertoire as well as a modification of some of the acoustic characteristics of these signals (Collias 1952; Collias & Joos 1953).

#### *(a) Perinatal Vocal Communication*

Even before hatching, fowl embryos – particularly those of the domestic duck (*Anas platyrhynchos*), Muscovy duck (*Cairina moschata L. f. domestica*), and domestic chicken - produce a series of vocalisations with a rather simple frequency modulation structure, consisting of ascending sounds or sounds with a chevron modulation, i.e. an ascent followed by a descent - interpreted by the scholars as expressions of pleasure or contentment states - and descending sounds - interpreted as expressions of discomfort, and therefore named distress calls (Gottlieb and Vandenbergh, 1968; Rumpf and Nichelmann, 1993; Tuculescu and Griswold, 1983; Rumpf and Tzschentke, 2010); as noted by Gottlieb and Vandenbergh (1968), such vocalisations are similar in structure and presumably in meaning to those constituting the vocal repertoire of post-hatching chicks and ducklings. These calls, which are often irregular in their emission rate, increase in number as the day of hatching approaches (Gottlieb and Vandenbergh, 1968; Rumpf and Tzschentke, 2010); similarly, in more advanced ontogenetic stages of prehatching Muscovy duck embryos, vocalisation activity is gradually organised into sequences that are emitted with increasing frequency (Rumpf and Tzschentke, 2010).

However, vocal activity alone does not guarantee the presence of an information exchange system between conspecifics. So, the question is: are these calls part of a prenatal acoustic communication system between siblings and mother and between siblings, or do they have no communicative function? The answer to this question is more complex than it seems at first sight: on the one hand, in the domestic chicken it has been observed that the acoustic distress signals emitted by the embryos are able to influence the behaviour of the mother, who moves around the nest in response to the vocalisations or produces response calls, thus attenuating the frequency with which the embryos emit distress calls (Tuculescu & Griswold, 1983); on the other hand, in another fowl species, more precisely the Muscovy duck, perinatal acoustic interaction through vocalisations appears to develop only after the first individual in the brood emerges from the egg, and therefore may not represent a pre-established means of communication between embryos or with the mother, but only an embryos-chicks acoustic interaction (Rumpf and Nichelmann, 1993; Rumpf and Tzschentke, 2010).

*(b) Young Vocal Communication*

After hatching, the vocal repertoire of *Galloanserae* infants can be divided into two broad categories on the basis of their emotional meaning: the positively valenced calls, emitted in affiliative contexts in which the animal is in a state of contentment elicited by a safe environment, and the negatively valenced vocalisations, mostly corresponding to the expression of an internal state of discomfort, pain, or fear due to the infant's isolation from the mother (Guyomarc'h, 1964; Scoville and Gottlieb, 1980). The first category includes vocalisations characterised by a short duration, a high repetition rate (notes/s) and a relatively variable frequency modulation pattern, which may be ascending or chevron-shaped, similar to the positive calls of the embryonic vocal repertoire (Collias and Joos 1953; Collias 1987; Scoville and Gottlieb, 1980; ten Thoren and Bergmann, 1987a; ten Thoren and Bergmann, 1987b). These calls, that can be more precisely differentiated in pleasure calls, contentment

calls or brood calls, are generally produced by *Galloanserae* infants in reassuring situations such as during feeding, when the animal is safe under the care of the mother or when it is in the presence of other siblings, respectively (Collias and Joos 1953; Collias 1987). In contrast, negatively valenced calls are characterised by a relatively long duration, a lower repetition rate if compared to emotionally positive notes, and their pattern of frequency modulation may be descending, chevron or consisting of rapid inflections (Collias and Joos 1953; Collias 1987; Scoville and Gottlieb, 1980; ten Thoren and Bergmann, 1987a; ten Thoren and Bergmann, 1987b). This category includes vocalisations such as the distress or isolation call – often produced when infants are in a condition of social isolation from the mother or other siblings – or like the trill – consisting of a sound with rapid frequency modulation often emitted when the infant is experiencing strong fear (Collias and Joos 1953; Collias 1987; Scoville and Gottlieb, 1980; ten Thoren and Bergmann, 1987a; ten Thoren and Bergmann, 1987b).

However, the vocal repertoire of *Galloanserae* infants and juveniles is not limited to calls expressing basic needs or emotions, but also includes intermediate signals, often used to express surprise or triggered by the presence of darkness or the perception of ambiguous visual stimuli, such as moving shadows (Guyomarc'h, 1964). It should also be noted that the vocal repertoire in this ontogenetical stage is in constant modification, as it diversifies to include vocalisations with more complex frequency modulations, capable of conveying finer information. More precisely, it can be seen a rapid expansion of the vocal repertoire, a phenomenon that in certain species, such as the Greylag goose, can be appreciated within the first three weeks of life (Würdinger, 1970). Once adulthood is reached, some types of vocal emissions may be lost, as in the case of the contact calls in the mallard (Caswell, 1972) or of the trill in the Barnacle goose (ten Thoren and Bergmann, 1987a), while other vocalisations

undergo a process of modification and diversification, such as the crying sound produced by the Greylag goose (ten Thoren and Bergmann, 1987a).

A general trend that characterises the ontogenetic vocal development of many *Galloanserae* species in the young and juvenile stages is a gradual decrease in the frequency parameters of the vocalisations produced, an effect resulting from the increased weight of the animal, which has the anatomical and physiological consequence of an enlargement of the phonatory apparatus, with longer resonant cavities and larger structures that vibrate more slowly, resulting in the emission of a lower fundamental frequency. This trend has been documented in all the taxa studied, namely Bar-headed Goose (*Anser indicus*) (Würdinger, 1970), Barnacle Goose (*Branta leucopsis*) (ten Thoren and Bergmann, 1987a), Black Grouse (*Tetrao tetrix*) (Meinert and Bergmann, 1983), Canada Goose (*Branta canadensis*) (Würdinger, 1970), Greylag Goose (*Anser anser*) (ten Thoren and Bergmann, 1987b), Japanese Quail (*Coturnix japonica*) (Garskaia and Chernyi, 1979), Shelduck (*Tadorna tadorna*) (Engländer and Bergmann, 1990), Snow Goose (*Anser caerulescens*) (Würdinger, 1970), and White-fronted Goose (*Anser albifrons*) (Würdinger, 1970).

However, vocal communication in these ontogenetic stages is not limited to the mere emission of vocalisations in response to environmental or internal physiological stimuli but can also exhibit prosodic aspects that constitute musical evolutionary precursors of language (Filippi, 2016). An example of this is call alternation or antiphonal calling, a form of interactional prosody that consists of coordinating vocal production with another individual, avoiding acoustic overlap and generating a turn taking dynamic (Filippi, 2016). This phenomenon has been observed in domestic and mallard ducklings (Gaioni, 1982; Gaioni and Platte, 1982), as well as in bar-headed goslings (Lamprecht, 1985): specifically, isolated pairs of infants of the tested species were able to significantly avoid acoustic overlap by emitting distress calls when the other member of the pair was silent. However, the interpretations

proposed by the authors are contradictory: On the one hand, the behaviour studied could be the result of cooperation between siblings aimed at reducing the energy expended on vocalisations and at the same time facilitating the localisation of the young by the mother, cooperation that may also represent a precursor of vocal turn-taking in human infants and other animal species (Gaioni, 1982; Gaioni and Platte, 1982). On the other hand, the antiphonal calls of young *Galloanserae* may simply be the result of fear reactions experienced by one member of the pair during the acoustic emission of the other, generating a call alternation that is nothing more than a mere artefact (Lamprecht, 1985).

*(c) Adult Vocal Communication*

As adults, members of the *Galloanserae* display a complex range of vocalisations to express different needs and emotional states to conspecifics. Although the vocal repertoire varies considerably from species to species, some call types remain common to the different groups, such as contact calls to maintain social cohesion, alarm calls to signal the presence of a threat, courtship calls to attract a mate, parental calls to recall offspring, and threat calls to be uttered in aggressive contexts.

Among the species belonging to the *Galloanserae* clade, the best-studied and best-described adult vocal repertoire is probably that of the domestic chicken and its wild ancestor, the red junglefowl. Specifically, in this taxon the vocal repertoire diversifies further to include up to 24 different vocalisations, reflecting a wide range of social and behavioural functions (Collias 1987; Collias and Joos 1953). These acoustic emissions can be grouped into a few macro-categories. One of these includes attraction calls, such as the female's clucking to attract chicks or the male's food call to attract a female to a food source, which are characterised by short, repetitive notes, generally at low frequency, that convey a sense of calm and security. In contrast, another category of vocalisations are the alarm calls, which are intended to convey urgency and danger and are characterised by higher intensity and

frequency. These calls are also often accompanied by defensive behaviour, such as rapid flight to cover in response to an approaching predator. The adult vocal repertoire also includes dominance and territorial signals, such as the characteristic male crowing, which is used not only to demarcate territory but also to signal its presence and status to other group members. These vocalisations reflect a complex interaction between acoustic signals and behaviour that is crucial for social cohesion and survival in the Red Junglefowl's natural environment.

However, the vocalisations that make up the *Galloanserae* vocal repertoire are not simply the involuntary product of internal emotional states but are supported by a sophisticated cognitive system that allows the birds to control the emission of different calls according to the social context, demonstrating their ability to use a complex communication system made up of many signals with a referential function, i.e. conveying information about elements in the environment. This aspect of communicative cognition has been particularly studied in domestic chickens. Specifically, it has been shown that adult males have the ability to discriminate between aerial and terrestrial predators and, consequently, when they emit the alarm call to signal their presence, they use specific and distinct vocalisations depending on the type of predator, just as has been found in mammals such as vervet monkeys (Evans et al., 1993a; Seyfarth et al., 1980). In addition, the intensity of alarm calls varies with the level of predation threat, peaking at the sight of large, rapidly approaching hawks (Evans et al., 1993b). Adult males also modulate the emission of alarm calls based on the social context, a phenomenon known as the audience effect: when alone or in the presence of individuals of another species, the animal will emit proportionally fewer alarm calls than when in the company of a conspecific, all the more so if it is familiar (Karakashian et al., 1988), just as it is more likely to produce alarm calls in the presence of a female to ensure the survival of a reproductive partner and potential offspring (Wilson and Evans, 2008). Examples of referential communication can also be found in communicative contexts other than alarm

communication: a case in point is foraging behaviour, during which males perform the so-called tidbitting display, which consists of a multisensory signal directed at females in the herd, characterised by rhythmic head movements in which food is repeatedly grasped and then dropped to the ground, while at the same time food calls are emitted; this display is modulated in intensity both on the basis of the quality of the food and the likelihood of a female approaching (Marler et al., 1986). Finally, studies such as that conducted by Kokolakis et al. (2010) suggest the existence of a perspective-taking ability that influences communication strategies: indeed, males that are in a location that is not visible to an aerial predator emit longer duration alarm calls - which are easier for listeners, including predators, to locate compared to shorter ones - in order to increase the likelihood of being heard by group members without risking being detected by the predator. However, further studies on other *Galloanserae* species are needed to understand whether these cognitive abilities underlying acoustic communication are exclusive to domestic chickens or whether they are shared within this group of birds.

A final feature of interest that distinguishes the adult vocal repertoire of *Galloanserae* is vocal individuality, i.e. the presence of values of a set of acoustic characteristics, such as fundamental frequency, peak frequency, mean frequency or spectral entropy, that are unique to each individual and allow it to be distinguished from other conspecifics. In a recent study conducted on greylag geese by Guggenberger et al. (2022) it was showed that distance calls - an affiliative vocalisation used to keep the individuals constituting a social group in contact over long distances in poor visibility (Fischer, 1964; Lorenz, 1988) - encode acoustic variations that allow the receiver to recognise who is the emitting individual, as well as information about the sex of the vocalising animal. It has previously been shown that another goose species, the barnacle goose (*Branta leucopsis*), can also produce vocalisations - loud calls to be precise - with a high degree of individuality encoded in the frequency spectrum

and fundamental frequency modulation (Hausberger et al., 1994). Similar results were obtained in three studies conducted on quails: the first focused on the analysis of the separation call of the bobwhite quail (*Colinus virginianus*), establishing that the fundamental frequency contour can be used as a quantitative cue to vocally distinguish each individual from the others (Bailey, 1978); the second discovered that the long-distance call of the European quail (*Coturnix coturnix*), used in pair-bonding, also contains individual vocal cues (Guyomarc'h et al., 1998); finally, the third study showed that the temporal structure of crowing - a call used to attract mates and signal territory - in both European and Japanese male quails can be used to discriminate between individuals (Collins and Goldsmith, 1998). The discovery of such a trait in different basal bird species demonstrates that vocal individuality, often described in animal taxa capable of vocal learning (Carlson et al., 2020), may instead be an acoustic feature that appeared early in the evolutionary history of *Aves* and may therefore be much more widespread than is currently thought.

### *1.2.4 Effects of Music on Galliformes*

So far, we have concentrated on the innate acoustic predispositions that we can find in the *Galloanserae* clade, predispositions that, as we have seen, underlie the complex vocal communication of the species that make up this group of birds. A particular form of acoustic communication, however, is music, which, as Charles Darwin wrote, can be considered a kind of proto language (Darwin, 1872). Indeed, musical sounds can influence the emotional state of listeners, including animals of different classes, such as mammals, birds and fish (Snowdon 2021). But what about *Galloanserae*? What are the effects of music on this group? Attempts to study this issue on fowls can be divided into two lines of research, one aimed at understanding how the musical sounds perceived by animals during the pre-hatching stage may influence subsequent cognitive development, while the second line has focused on the

interaction in breeding contexts between musical perception and welfare in individuals that have now reached sexual maturity.

Prenatal music stimulation seems to provide positive effects on the development of auditory-related brain areas as well as of other regions. A first example of this is a study conducted by Sanyal et al. (2013a) on domestic chick embryos, that were divided into three groups, each of them exposed from embryonic day 10 until hatching to arrhythmic noise, rhythmic sitar music or silence. After hatching, chicks were tested in both T-maze and open field tests, with those previously exposed to music that demonstrated higher levels of spatial orientation, spatial learning and memory. Subsequently, the Authors analysed the chicks' forebrain, discovering that music exposure increased synaptic hippocampal binding proteins, that play a key role in regulating synaptic function, plasticity, and memory processes within the hippocampus. Similarly, Panicker et al. (2002) demonstrated that prenatal music stimulation has a facilitating effect in neuronal development of the domestic chicks' medio-rostral neostriatum/hyperstriatum ventral region (MNH), a higher auditory associative area located in the chick forebrain and involved in auditory imprinting. More precisely, domestic chick embryos were firstly divided into two groups, one exposed to natural species-specific vocalisations from embryonic day 10 and the other one to sitar music from embryonic day 15, stimulation that ended on the hatching day for both groups. Subsequent brain tissue analysis suggested that both conditions enhanced both the neuronal size and the proportion of neurons expressing calcium binding proteins - such as parvalbumin (PV) and calbindin D28K (CaBP) - which are essential in long-term potentiation, a key physiological process in learning and memory formation. Increased neuronal density was further confirmed by Sanyal et al. (2013b), who exposed two groups of domestic chick embryos from embryonic day 10 until hatching to loud (110 decibel) sitar music and loud noise, respectively. The subsequent tissue analyses revealed that prenatal music stimulation led to a significant increase in the number

of neurons, neuronal nuclear area and brain volume of all chick brain areas studied, namely brainstem, auditory nuclei, field L - analogous to the auditory cortex - and the hippocampus. On the contrary, chicks exposed to loud noise, besides presenting decreased neural density and volume in the same brain areas, were characterised by an increase in the glial cell number, suggesting that these cells enhance their presence as a consequence of damage or of an increase in metabolic cost due to noise exposure. Finally, a study conducted by Kumar et al. (2014) demonstrated that prenatal high decibel music exposure enhanced the expression of synaptic stability proteins in the auditory cortex analog (AuL) of domestic chick brain, consequently enhancing the auditory function, while high level noise produced the opposite outcome.

While studies conducted on embryos paint a rather clear picture that makes musical stimulation an important auditory enrichment strategy, research conducted on young and adult individuals paints a less unambiguous picture. For instance, laying hens of various Spanish breeds exposed to Mozart's String Quartets at 75 dB were negatively affected by the presented music in a tonic immobility duration test, in which the animals stayed still for longer time than those that were exposed to background noise, suggesting that music increased fearfulness (Campo et al., 2005); however, there was no effect on blood measurements of heterophil-to-lymphocyte ratio, indicating that music did not increase distress levels (Campo et al., 2005). In another research, instead, music produced no effect on domestic chickens, while noise was responsible for inducing an aversive effect (McArdie et al., 1993). However, in a more recent study conducted by Dávila at al. (2011), in domestic chicks exposed to Mozart’s music it was registered a lowering in heterophil to lymphocyte (H/L) ratios resulting in a reduction in stress physiology.

But what is the common thread that links the results of the studies described so far? Looking at the research carried out on adult fowl we can conclude that the positive effects of

music on the welfare of these animals are mostly related to intensity modulation, in line with what has already been outlined by Charles T. Snowdon (2018), according to whom sounds - whether music or signals - characterised by low amplitude have a calming effect, different from those with a loud amplitude, which are responsible for reactions that increase arousal and/or fear. These emotional responses are present not only in *Galloanserae*, but also in other vertebrates (Snowdon, 2021) - such as monkeys - proving that these reactions are abilities shared between species whose evolutionary origin is ancient and therefore probably to be identified in an ancestor common to them all. Therefore, it can be concluded that the use of music in a breeding environment - and particularly in those high-density poultry housing structures that are often associated with relatively high levels of distress - can be an effective form of environmental enrichment that can improve animal welfare, but only and exclusively if the role played by the intensity of the sound is duly taken into account.

However, a major limitation of all the reviewed studies - conducted in both embryos and adults - is that the authors focused only on behavioural effects induced by a global perception of musical stimuli, and thus did not consider the effects of those specific acoustic features that typically characterise musical compositions and are responsible for conveying emotions in listeners, such as the role of tempo, pitch modulation, amplitude variation, and many others (for a review, see Snowdon 2021).

### *1.2.5 To wrap it up: sound, animal welfare, and farming*

How can the knowledge we have presented so far be used to improve the welfare of *Galloanserae* species used in anthropic contexts such as farming? So far, the application of what we know about the bioacoustics of taxa belonging to this clade has mainly focused on the development of artificial intelligence algorithms to analyse the sounds - be they vocalisations or involuntary noises - emitted by fowl species used in large breeding farms

(mainly domestic chickens and turkeys) in order to assess their welfare based on acoustic parameters contained in distress vocalisations (Herborn et al., 2020), the detection of the spatial position of breeding chickens emitting abnormal vocalisations at night (Du et al., 2018), the automatic recognition of vocalisation types in adult chickens (Du et al., 2021), the automatic sexing of chicks by analysing distress calls (Li et al., 2022), the detection of incubation stage (Exadaktylos et al., 2010) and the prediction of growth trend in young chickens (Fontana et al., 2015), the monitoring of feeding behaviour and feed intake in fowl adults (Aydin et al., 2015; Huang et al, 2021), the detection of aggressive behaviour that may anticipate cannibalism phenomena such as pecking (Gonzalez et al., 2020) and, finally, the detection of diseases, especially those of a respiratory nature such as Newcastle disease, bronchitis virus and avian influenza (Banakar et al., 2016; Huang et al., 2019; Cuan et al., 2022). The emerging picture outlines the use of artificial intelligence methods to improve the automated monitoring of fowls, enabling better management of large-scale farms. However, it is clear that the application of knowledge on acoustic perception and communication in *Galloanserae*, as well as the exploitation of specific musical characteristics that have an impact on their welfare, is still at an embryonic stage.

### *1.2.6 Concluding remarks*

This review has provided a comprehensive depiction of the complex perceptual and communicative system in the auditory sense employed by species belonging to the *Galloanserae* group, with a particular focus on a taxon such as the domestic chicken, often used as a model species to investigate phenomena like auditory imprinting, musical cognition, and acoustic communication. An important consideration that emerges from this discussion is that the presence of innatisms that guide acoustic perception and vocal production does not exclude the existence of a complex communication system that is not only based on

predispositions, but also includes the influence of cognition, leading to the existence of a complex interplay between innate tendencies and learned behaviours.

Moreover, the results presented in this work are significant in at least two major respects: the first one, is that they demonstrate that audio-vocal traits which are strictly connected to music computation such as rhythm and consonance perception and production are present since an early age in animals that do not have the ability to emit learned, complex songs, hence suggesting that these abilities evolved for reasons that are not specifically linked to musical behaviour, but may constitute instead adaptations to sensory ecology problems that were subsequently co-opted in other domains; the second one, is that music is able to influence emotion, physiology and even development of non-singing animals, meaning that it exists a strong link between constituent parameters of music and natural communication signals, making music a sort of universal, more fundamental system of communication whose comprehension constitutes a shared trait among distantly related species.

However, our work has highlighted the lack of studies on the occurrence of the abilities described here in a sufficiently large number of species belonging to the *Galloanserae* group, with the vast majority of studies discussed in the review focusing on domestic chickens. Therefore, to develop a full picture of auditory perception and vocal production in fowls, additional studies will be needed that replicate those already conducted on chickens, with a particular focus on water species belonging to the *Anatidae* family, with the aim to assess if ecological differences have an impact on the set of innate auditory predispositions and communication systems or if these behaviours can be considered universal traits among fowls. Not only that: more research is also needed to better understand, in the broader context of the nature vs. nurture debate, which factors are responsible for the emergence of the described innate behavioural biases i.e. genetics, ecological constraints, hardwired neural circuitries, etc. (Sosa, 2024).

# Chapter 2

## The acoustic features of animated sounds

### 2.1 What does animacy sound like? 1/f laws and domestic chicks' vocalisations

#### *2.1.1 Introduction*

It is well known that the physical world is full of structural regularities, such as the laws of kinematic motion, of causal physical interaction, and of gravity, or like the patterns of sounds emitted by living creatures, in particular tetrapod species. Therefore, it is not surprising that the brains of various animal taxa possess perceptual-cognitive universals (Shepard, 1994; Shepard, 2001) that reflect these regularities, some of which are perceived by the visual domain (Carlton and Shepard, 1990; Dayan et al., 2007) while others are detected by the auditory sense (Jermyn et al., 2023), thus constituting an adaptive solution allowing animals to navigate the world and survive.

However, despite the great diversity of physical regularities, there is one of such patterns that is more widespread than others: the fractal structure (Richardson, 1961), which can be found in a vast array of different entities, such as neuronal spike patterns (Yu et al., 2005; Qu et al., 2019), noise in physical systems (Van der Ziel, 1988), phase transitions in thermodynamics (Goldenfeld, 2018), human classical music (Hsü and Hsü, 1991; Levitin et al., 2012), speech (Voss and Clark, 1975), animal vocalisations (Jermyn et al., 2023), and even coastline topography (Mandelbrot, 1967). The key element that distinguishes the fractal structure from other physical regularities is that it is generally characterised by power-law correlations or $1/f^{\beta}$ spectral distributions, where $\beta$ is the slope that measures the amount of autocorrelation of a signal - in other words, how much the signal is similar to itself over time - with larger values of $\beta$ indicating a signal with more long-timescale correlations and

therefore more predictable (Voss and Clark, 1975; Levitin et al., 2012). For instance, if □ is 0, the signal has no temporal correlations and is random, as in white noise; conversely, if □ tends to an infinite value, the signal is fully correlated over time and highly predictable, as in pure tones.

What about animal vocalisations and other sounds produced by animate beings, such as music? Recent studies (Levitin et al., 2012; Jermyn et al., 2023) have highlighted that these sounds tend to stabilise around □ values in a range between 0.5 and 1.5, suggesting that both acoustic emissions produced by animals endowed with a phonatory apparatus and musical compositions - two types of acoustic signals sharing many structural similarities (Snowdon, 2021) - tend towards a balance between predictability and variation. The fact that this tendency has been found by Jermyn et al. (2023) in no less than 17 animal species belonging to the classes *Mammalia*, *Aves*, *Amphibia* and *Insecta* suggests that it may be an acoustic universal and thus a fundamental property of vocalisations that may constitute an auditory animacy cue. However, one aspect that has not been investigated is whether this feature is innate or only appears in a fully developed vocal repertoire typical of adult individuals. Moreover, another aspect that has not been considered in previous studies is whether fractal structure is only present in emotionally positive acoustic signals, such as non-human musical calls, or whether it is a universal feature that also characterises negatively emotionally valenced calls. In this study, we aim to answer these questions by using one-day-old domestic chicks as an experimental model, recording and analysing their vocal repertoire of both positive and negative calls.

### *2.1.2 Materials and methods*

#### *(a) Animals and rearing conditions*

In this study, we analysed the vocalisations of 23 domestic chicks (females = 11) (*Gallus gallus*) belonging to the Ross 308 broiler line (Aviagen). The animals hatched from

eggs supplied to the Laboratory of Animal Cognition (Trieste, Italy) by a local commercial hatchery (Agricola Berica S.C.R.L., Montegalda, Italy). The eggs were then placed in an automatically turning incubator capable of maintaining them in an environment where variables such as darkness, temperature and humidity were kept under control. After hatching, the chicks were sexed, weighed and placed in pairs in rectangular cages (width, height, depth: 22, 30, 40 cm respectively) located in a room with controlled temperature (31°C). Then, on the first day of life, the chicks' vocalisations were recorded.

*(b) Experimental apparatus and recording procedure*

Domestic chicks' vocalisations were recorded inside a cylindrical apparatus (diameter: 60 cm, height: 80 cm), the walls of which were completely covered with sound-absorbing material in order to reduce external acoustic interference. In the centre of the apparatus, at a height of approximately 40 cm above the floor, an AKG C1000S microphone (Vienna, Austria) was placed to record the vocalisations of the animals tested and connected to a computer via a Focusrite Scarlett 2i4 sound card (High Wycombe, UK), which converted the sound into a digital format (sampling frequency: 44.1 kHz; amplitude resolution: 16 bit). Each chick was placed in the arena and three types of vocalisations were recorded for each one of them, one with negative emotional valence and two with positive emotional valence.

In fact, as mentioned above, the vocal repertoire of domestic chicks seems to be defined from the first day of life and consists of vocalisations expressing different emotional states associated with different social contexts and communicating their needs to conspecifics, especially the hen (Collias and Joos, 1953; Collias, 1987). More specifically, the negative call, that is emitted by domestic chicks in the context of separation from the mother and/or siblings, or when the animal feels uncomfortable, consists of the distress call. This vocalisation is characterised by a tonal structure, a descending frequency modulation pattern between 2000 and 6500 Hz and the presence of a number of harmonics ranging from one to

four (Collias and Joos, 1953; Collias, 1987; Marx et al., 2001). In contrast, positive calls consist of (1) the food or pleasure call, a tonal vocalisation produced when the chick is in the presence of a food source and characterised by an ascending frequency modulation pattern between 2500 and 5500 Hz and the presence of no or one harmonic (Collias and Joos, 1953; Collias, 1987; Marx et al., 2001), and (2) the brood call, a tonal call emitted when domestic chicks are in the presence of other siblings and characterised by the peculiarity of being able to occur in two different forms, namely the short peep - descending frequency modulation pattern between 3000 and 5500 Hz and with no harmonics - and the warbler - ascending and descending frequency modulation pattern between 2500 and 5500 Hz and with no or one harmonic (Collias and Joos, 1953; Collias, 1987; Marx et al., 2001). (For a comprehensive review on this topic, see Collias and Joos, 1953, and Collias, 1987; Marx et al., 2001.)

To obtain recordings of the vocalisations described above, it was necessary to stimulate domestic chicks to produce them naturally using the same methodology as Maldarelli et al. (2024). Specifically, each chick was placed inside the experimental apparatus and subjected to three different emotional contexts: first, in social isolation to stimulate the production of distress calls; second, in the presence of an imprinting object suspended in the centre of the apparatus to facilitate the emission of brood calls; and finally, third, in the presence of a food jar placed in the centre of the apparatus to stimulate the production of food calls.

*(c) Acoustic analysis*

Acoustic analysis was performed using Python v 3.10.12 (Van Rossum and Drake, 2009). In particular, following the same approach described in Jermyn et al. (2023), continuous recordings of domestic chicks' vocalisations were firstly preprocessed by squaring the amplitude of the audio signal, thus obtaining the instantaneous power; after that, in order to focus on the relevant frequencies and at the same time reduce the data size, three stages of

eighth-order Chebyshev Type I filters that downsampled the signal from 44.100 Hz to 200 Hz were applied. The final stage of audio preprocessing was the calculation of spectral density - a measure of how power or variance of a signal is distributed across different frequency components - using the Fast Fourier Transform (FFT). The analysis was focused on frequencies between 0.01 Hz and 10 Hz, truncating frequencies outside this range to eliminate tonal effects and irrelevant data. After all these transformations, what is produced for each recording is a time series consisting of a sequence of amplitude values at a given time, sampled at a relatively low rate (~5 milliseconds).

*(d) Data analysis*

Statistical analysis of data obtained throughout the acoustic preprocessing was performed using Python v 3.10.12 (Van Rossum and Drake, 2009), implementing the same algorithms and metrics previously employed by Jermyn et al. (2023). Specifically, to characterise the temporal structure of domestic chicks' vocalisations, the previously computed power spectra were analysed by applying two different mathematical models, the first one represented by a power-law spectrum revealing long-term correlations - the fractal model (Thornton and Gilden, 2005) - and the second one that captures short-term correlations in the data without assuming a fractal structure - the autoregressive moving average (ARMA) model (Box et al., 2015). To fit both mathematical models to the spectral data, we employed Bayesian inference by using the MultiNest nested sampling algorithm for parameter estimation and model comparison, computing the log-evidence (logZ) for each model per recording. To determine which model (fractal or ARMA) was the best fit for each call type (distress call, brood call, food call), we used the difference in log-evidence ($\Delta \log Z = \log Z_{Fractal} - \log Z_{ARMA}$), and finally we assessed if model preference distributions differed significantly among call types by applying a chi-square test of independence.

*2.1.3 Results*

The table below illustrates for each call type the difference in log-evidence (ΔlogZ), as well as the log-evidence (logZ) for both mathematical models. It can be seen from the data that the ARMA model is favoured across the entire vocal repertoire of one-day-old domestic chicks. Moreover, if we consider the best fit for each tested individual and then assess the model preference by treating it as a categorical variable, the chi-square test of independence revealed a non-significant difference for model preference among call types ($\chi^2 = 4.365$, $p = 0.113$).

**Table 1**. List of call types with the corresponding logarithmic evidence for both models and difference in log-evidence.

| **Call type** | **logZ$_{Fractal}$** | **logZ$_{ARMA}$** | **ΔlogZ** |
|---|---|---|---|
| *Distress call* | -3054887.845 | -3039179.73 | 15708.11478 |
| *Brood call* | -3440075.554 | -3428664.952 | 11410.60182 |
| *Food call* | -3597461.261 | -3581107.51 | 16353.75064 |

The strong preference for the ARMA model can be also appreciated from a visual inspection of the spectra of the recordings of each participant in the study. In particular, as shown in Figure 1.1, 1.2 and 1.3, the ARMA spectral model has a better fit when compared to the fractal one, thus reproducing better the data structure.

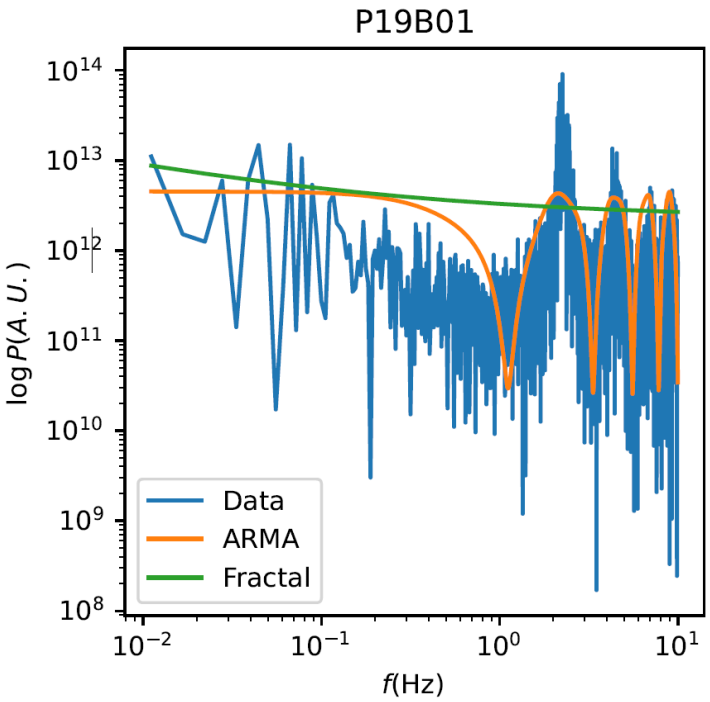


**Figure 1.1** Spectrum of the recording of distress calls emitted by domestic chick named P19B01, showing the best-fit for both ARMA and fractal model.

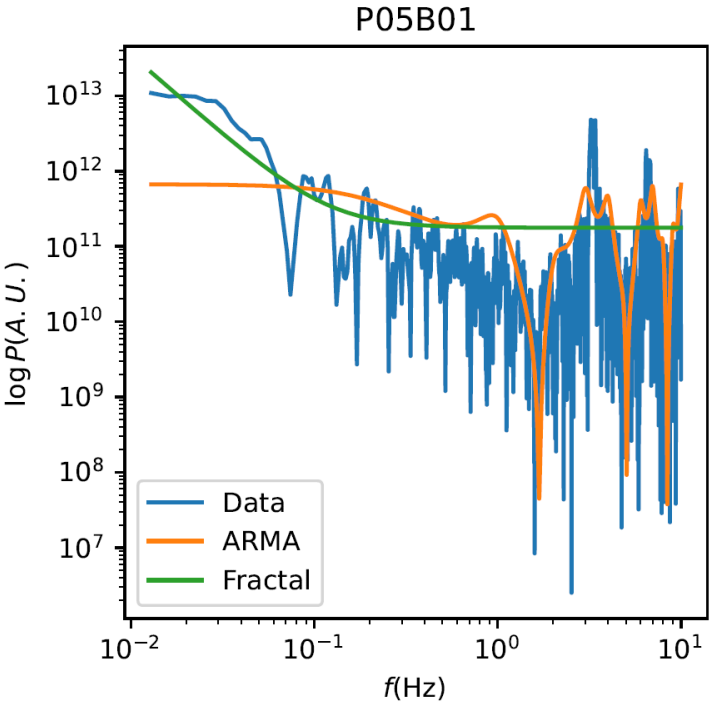


**Figure 1.2** Spectrum of the recording of brood calls emitted by domestic chick named P05B01, showing the best-fit for both ARMA and fractal model.

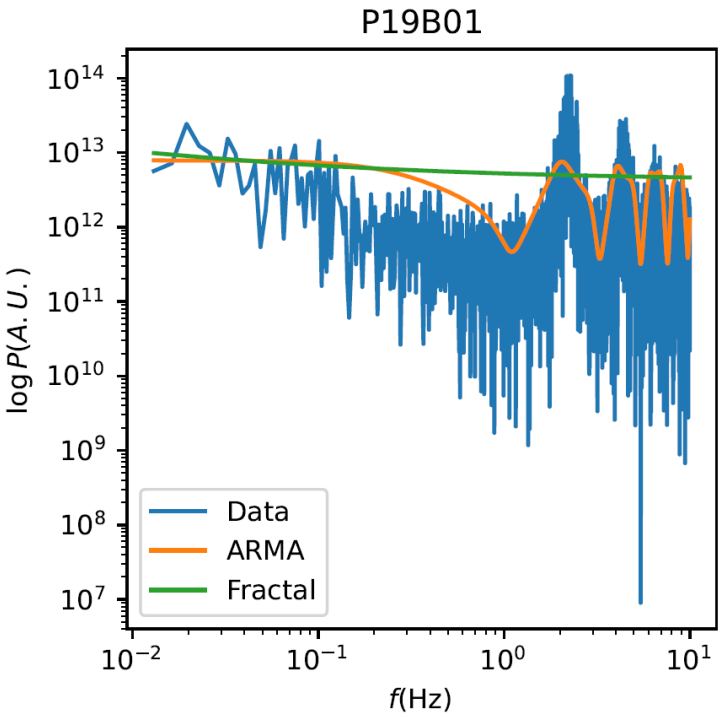


**Figure 1.3** Spectrum of the recording of food calls emitted by domestic chick named P19B01, showing the best-fit for both ARMA and fractal model.

*2.1.4 Discussion*

As mentioned in the introduction, prior studies have noted the pervasiveness of fractal structure in animal vocalisations emitted by adults of different species - both birds and mammals - suggesting that this feature may be an acoustic universal typical of those sounds produced by animate beings, and thus could constitute an auditory animacy cue. In contrast to these earlier findings, however, our study indicates that the vocalisations of one-day-old domestic chicks significantly exhibit short-term correlations instead of long-term ones, therefore suggesting that the vocal repertoire of our model species is not characterised by signals with a fractal structure. More specifically, a non-fractal vocalisation would have a spectral distribution characterised by the presence of specific peaks with amplitude correlations that, instead of extending over long-time scales, fade relatively quickly and are

limited to short intervals. It can therefore be said that, in the context of short-range correlations, there is a specific time scale beyond which knowledge of previous amplitude values cannot provide any predictive capacity for subsequent values.

A possible explanation for this might be that the neural and physiological mechanisms for producing vocalisations with spectral properties that can be better described by the fractal model are not mature from birth, hence indicating that this feature is the product of a developmental trajectory that is ready only at the adult stages. As domestic chicks mature, their vocalisations might develop stronger fractal properties due to brain development, environmental interactions and/or social learning. On the other hand, the initial reliance on short-term correlations could also be evolutionarily adaptive, favouring survival by ensuring that critical signals are easily recognised and acted upon by the listeners, particularly the mother hen. However, the predominance of short-term correlations in the acoustic signals of domestic chicks indicates that fractal properties may not be a strong auditory animacy cue, thus suggesting that other acoustic features may play a more important role in conveying the perception of animacy in the auditory sense.

Additional research is needed to better understand the nature of acoustic signals in relation to their structure, being it fractal or not, comparing different species in different ontogenetic stages to assess if the absence of 1/f laws in the vocal repertoire of domestic chicks is a condition shared by other young animals or a unique trait of domestic chicks.

# Chapter 3

## Auditory Innate Predispositions in Domestic Chicks

Chapter 3.1 has been prepared to be submitted to *Animal Behaviour* journal.

### 3.1 Born to be loud: investigating the innateness of noise-dependent vocal plasticity in domestic chicks

#### *3.1.1 Introduction*

Vocal plasticity is a fundamental property of animal vocal communication, one that has a profound impact on the acoustic interactions of animals that take place in an ever-changing soundscape. This phenomenon, which is central to the field of bioacoustics, refers to the ability of an individual to modify a set of acoustic features that characterise its vocalisations in response to a range of different environmental variables, be it background noise induced by natural phenomena - such as rain, watercourses, thunderstorms, etc. - or the interfering vocalisations of conspecifics or other animal taxa. Extensive research has demonstrated that vocal plasticity is not a monolithic entity but instead unfolds across a spectrum of diverse adaptations. These adaptations encompass a variety of characteristics, including amplitude, spectral, and temporal-related features of the emitted signal (Velilla & Halfwerk, 2019).

One key aspect of vocal plasticity, and perhaps the best-known, is the phenomenon referred to as the Lombard effect, an acoustic modification that involves an increase in the amplitude of vocalisations in response to increasing ambient noise (Lombard 1911). As the Lombard effect is generally recognised as one of the most cost-effective ways of maintaining efficacious vocal communication, it is then not surprising that such an audiovocal

phenomenon is so widespread among vertebrates (ranging from fish and amphibians to birds and mammals) and is also phylogenetically ancient, having probably emerged around 450 million years ago (Zollinger et al. 2011; Luo et al. 2018).

In addition to changes in the amplitude of vocalisations, there are also spectral adjustments involved in the phenomenon of vocal plasticity. One of these, which is less common than the Lombard effect although it often co-occurs with it, is the avoidance of spectral overlap with noise frequencies, i.e. the raising or lowering of the fundamental frequency so that the signal is not masked by the noise. This phenomenon, which is widespread in birds, was first discovered in great tits (*Parus major*) living in urban environments characterised by anthropogenic noise, which were able to emit the notes of their songs at higher frequencies (Slabbekoorn & Peet 2003). Conversely, harbour seal pups (*Phoca vitulina*) can lower the fundamental frequency of maternal attraction calls to avoid spectral overlap with noise (Torres Borda et al. 2021). It should be noted, however, that an upward shift of the fundamental frequency is a very different phenomenon if compared to a downward one, since the former effect usually consists of a mere byproduct of increased amplitude. A second example of how animals use spectral adjustment to improve the perceptibility of their signals in noisy environments is by increasing the length of their calls. This strategy is particularly effective because it enhances temporal summation, i.e. the incremental accumulation of signal energy in the auditory periphery of the receiver. Call lengthening is a well-documented phenomenon in humans (Tartter et al. 1993; Pittman & Wiley 2001; Newman 2003; Patel & Schell 2008), the common marmoset (*Callithrix jacchus*) (Brumm et al. 2004), the cotton-top tamarin (*Sanguinus oedipus*) (Egnor & Hauser 2006), and the tree swallow (*Tachycineta bicolor*) (Leonard & Horn 2005).

A final mechanism for counteracting environmental noise during acoustic exchanges involves temporal adjustments. One strategy is the repetition of emitted vocalisations to

increase the chances of being detected by receivers, a phenomenon known as signal redundancy. Birds such as Japanese quail (*Coturnix c. japonica*), king penguins (*Aptenodytes patagonicus*) and chaffinches (*Fringilla coelebs*), all produce more vocalisations when background noise is absent (Potash 1972; Lengagne et al. 1999; Brumm & Slater 2006). A different strategy concerns the choice to avoid temporal overlap with noise by signalling during periods when disturbing biotic and/or abiotic sounds are not present. It is found in avian species such as the American Robin (*Turdus migratorius*), and especially in those individuals living in urban environments that tend to sing more frequently at night than during the day in areas with high daytime noise (Fuller et al. 2007), but also in invertebrates such as the bushcricket (*Neoconocephalus spiza*), a typically nocturnal taxon that shifts its communication activity to the daytime to avoid overlap with similar nocturnal species in the same habitat (Greenfield, 1988).

Despite the great scientific interest in vocal adaptations to noise, up to now far too little attention has been paid to investigate whether such a set of skills is present at birth or acquired through a learning process. An early origin of the ability to optimise one's communication in variable environmental conditions has been demonstrated on Tree Swallow (*Tachycineta bicolor*) nestlings. By the age of 9 days, these animals increase the intensity of the begging calls, and such increment is directly proportional to the amplitude of the background noise in both natural and laboratory contexts (Leonard & Horn 2005). Alongside the same line, 7–10-day old harbour seals pups (*Phoca vitulina*) alter some vocal features in response to environmental noise conditions by lowering the fundamental frequency, but with no changes in call sound pressure level or SPL (Torres Borda et al. 2021); 5-day old pale spear-nosed bats (*Phyllostomus discolour*) emit more intense calls under noise conditions than during silence (Luo et al. 2017), and mallard ducklings (*Anas platyrhynchos*) of 10 days of

age or younger show a similar response pattern when uttering distress vocalisations (Dorado-Correa et al. 2018).

In all mentioned examples, the first 5 to 10 days of life for both avian and mammal altricial species could have already shaped a response which is initially absent at birth. Indeed, none of these studies has exerted a rigorous control on precocious auditory experiences. Furthermore, Dorado-Correa et al. (2018) showed that there is a clear influence of age at least on the magnitude of the increase in call intensity, with a Lombard strength of less than 5 dB in 2-day old mallard ducklings and of more than 15 dB in 10-day old individuals. This result is likely a sign of how the maturation of the neural circuits may be responsible for noise-dependent vocal plasticity, which undergoes profound changes that can be controlled by factors that are not necessarily genetic.

Vocal plasticity abilities are often described in the scientific literature as involuntary phenomena based both on brain localisation data, identified with a subcortical network, and on the broad phylogenetic distribution that includes animal species without a cerebral cortex (Luo et al. 2018). However, none of the cited studies explicitly addressed the issue neither by testing naïve day-old individuals, nor by controlling environmental influences (such has the presence of parents and siblings and/or the rearing in naturalistic contexts) on the development of the neuro-behavioural abilities of the subjects during the perinatal period. To fill this gap, we capitalized on the domestic chick (*Gallus gallus domesticus*), an ideal model species belonging to altricial taxon whose vocal and auditory systems are sufficiently mature at birth to allow the implementation of studies aimed at understanding innate responses to sound. A previous study on this species has shown that 28-day-old individuals significantly increase the intensity of emitted distress calls when exposed to five different noise levels (43, 60, 67, 75 and 80 dB SPL) but, given the age of the animals, leaving it impossible to establish whether this vocal response was the product of an acoustic predisposition or the result of learning.

### *3.1.2 Materials and methods*

#### *(a) Animals and rearing conditions*

We employed 36 domestic chicks (females = 18) from the Ross 308 strain that were less than 24 hours old. The entire development of these animals took place under controlled conditions. More precisely, the fertilised eggs, supplied by a local commercial hatchery (Società Agricola La Pellegrina s.p.a., San Pietro in Gu, Padua, Italy), were placed in the completely darkened environment of an incubator, where the temperature and humidity values were kept constant - 37.7° C and 80%, respectively - until the day of hatching, when the temperature was lowered to 32° C and the chicks were taken out individually to be tested.

#### *(b) Experimental apparatus, stimuli and procedure*

Each participant in the experiment was in turn placed inside a confining box located in the centre of a square test arena with an area of 50 x 50 cm surrounded by 40 cm high plastic panels covered with sound-absorbing material. The chicks' vocalisations were recorded using a unidirectional microphone (AKG C1000 S) positioned 40 cm above the confining box, which was connected to a USB audio interface (Focusrite Scarlett 2i4) fed through a PC. Every stimulus was broadcasted via four loudspeakers positioned in the centre of each side of the squared arena at the same level of the chick's head (approximately 12 cm above the ground). All the loudspeakers were connected to an amplifier (Philips 5.1 HTD3510/12) connected to a PC.

The experimental stimuli were derived from a white noise band ranging from 1650 to 6000 Hz. This sound was obtained by applying bandpass filtering to white noise in Praat (v. 6.3.03), so that the frequency range overlapped with the fundamental frequency of the distress calls emitted by 1-day-old domestic chicks. During the experimental trials, this filtered noise was played back at two different levels (60- and 70-dB SPL, measured with a Brüel & Kjær 2260 sound-level analyser in the centre of the confining box at the chicks' head height)

together with the no noise condition (~35 dB, measured when no playback was broadcasted). More specifically, each experimental trial consisted of 3 minutes of audio stimulation, composed of three randomised, 1 minute playback sequences, one for each condition. The three experimental treatments - aside from the 'no noise condition' - were continuous, which means that the shift between treatments consisted of adjusting the sound pressure level without pausing sound reproduction.

*(c) Acoustic analysis*

The distress calls emitted by domestic chicks were recorded as single mono audio files (WAV format) with a sampling rate of 44.1 kHz and 16-bit resolution. For every individual, the start and end points of each vocalisation were marked automatically by using the Praat v. 6.0.52 and a custom script; all the resulting annotations were then manually reviewed and saved as Praat TextGrids. Two custom macros were subsequently applied to, respectively, extract data on the number of calls made, the call rate (number of vocalisations per minute) and the inter-onset interval (time between the beginning of one note and the start of the next), and to save every annotated note as an individual mono audio file in .wav format, so that they could then be imported into R v. 3.5.1 (R Core Team, 2021) for successive acoustic analyses. More precisely, after annotation, the *analyze()* function from the Soundgen package (Anikin, 2019) was implemented so that the duration (s) and fundamental frequency of each vocalisation could be extracted, using the autocorrelation and dominant frequency methods as pitch trackers, a time step of 0.01 s, a pitch floor and ceiling of 1600 Hz and 5000 Hz respectively.

Instead, to measure the intensity of each call, the maximum root-mean-squared (RMS) sound pressure level was calculated by applying the *rms()* function from the Seewave package (Sueur et al., 2008) to the element envelope, and then calibrating the value obtained with that of a recording of known sound pressure level acquired at the beginning of each testing session,

consisting of a white noise sound of 1-minute duration and 70-dB SPL, measured with a Brüel & Kjær 2260 sound-level analyser in the centre of the confining box at the chicks' head height. The final intensity value was then obtained by subtracting the energy of the background noise following the mathematical computations described in the previous scientific literature (see Weißing 1984).

*(d) Data analysis*

All statistical analyses were conducted in R v. 3.5.1 using the *lmer()* function from the lmerTest package (Kuznetsova et al., 2017) to fit linear mixed-effects models for each acoustic variable: more precisely, we set as response variable the acoustic trait of interest (intensity, duration, frequency, call elements, call rate and inter-onset interval), while the background noise (dB SPL) was considered as fixed effect and the individual ID as random effect. Sensitivity analysis was conducted using G*Power 3.1 (Faul et al., 2007) on our sample size with an error probability (α) of 0.05, and a power (1 – β error probability) of 0.80 to establish the minimum detectable effect for our design. The sensitivity analysis revealed that the smallest detectable effects fall within the small range. This was observed for the model analysing call intensity, which had a critical F value of 3.13 and a partial eta squared ($\eta^2$p) of 0.23.

*3.1.3 Results*

Our experiment revealed that domestic chicks significantly increased the intensity of their distress calls as the background noise level increased. Specifically, the linear mixed effects model showed that vocal intensity increased significantly in the low noise (estimate = 3.195, SE = 1.235, $t(72) = 2.588$, $p = 0.014$) and high noise (estimate = 6.157, SE = 1.309, $t(72) = 4.705$, $p < 0.0001$) conditions compared to baseline (estimate = 87.437, SE = 1.615, $t(72) = 54.139$, $p < 0.0001$). These results highlight a significant effect of the background noise level on the regulation of vocal intensity in domestic chicks.

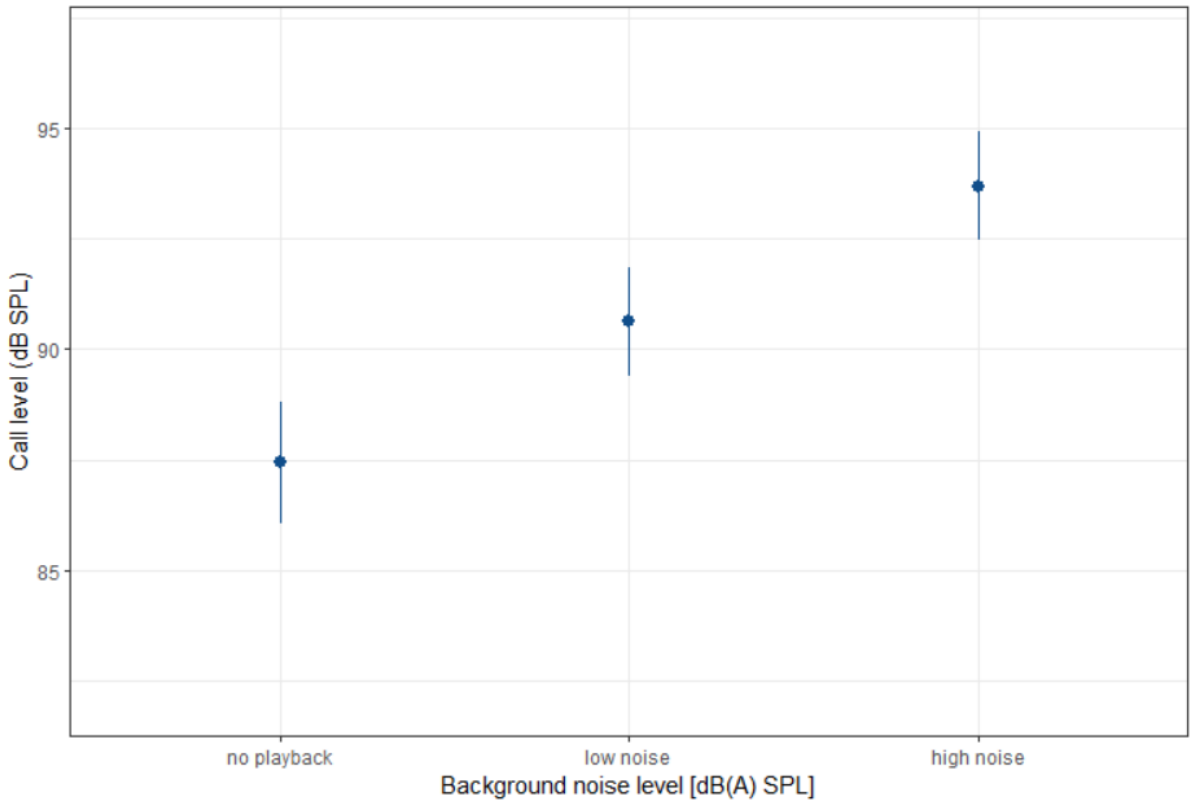


**Figure 3.1** Point-range graph representing the mean intensity value (expressed in dB SPL) of distress calls produced by domestic chicks for each background noise level condition. The error bars show the standard error of the mean for each call type.

On the other hand, the number of calls was not significantly affected by variations in background noise intensity - although a visual inspection (see Fig.3.2) shows some increase with higher noise levels - as the linear mixed model did not detect differences between the different experimental conditions (low noise: estimate = 3.083, SE = 5.027, $t(72) = 0.614$, $p = 0.541$; high noise: estimate = 8.611, SE = 5.027, $t(72) = 1.713$, $p = 0.091$).

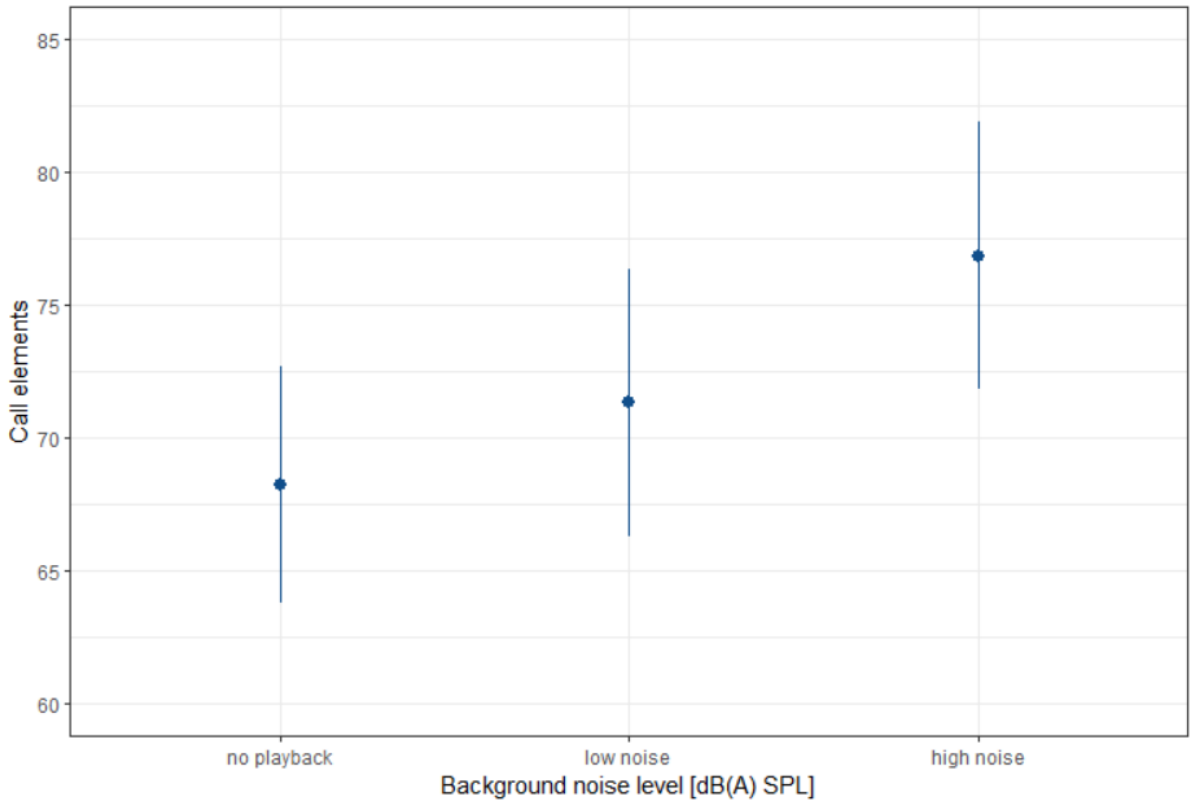


**Figure 3.2** Point-range graph representing the mean call elements of distress call produced by domestic chicks for each background noise level condition. The error bars show the standard error of the mean for each call type

Similarly, the linear mixed effects model revealed that domestic chicks did not significantly increase the duration of emitted calls in relation to the background noise condition (low noise: estimate = 0.0002, SE = 0.0029, $t(72) = 0.064$, $p = 0.949$; high noise: estimate = 0.0033, SE = 0.0029, $t(72) = 1.134$, $p = 0.261$).

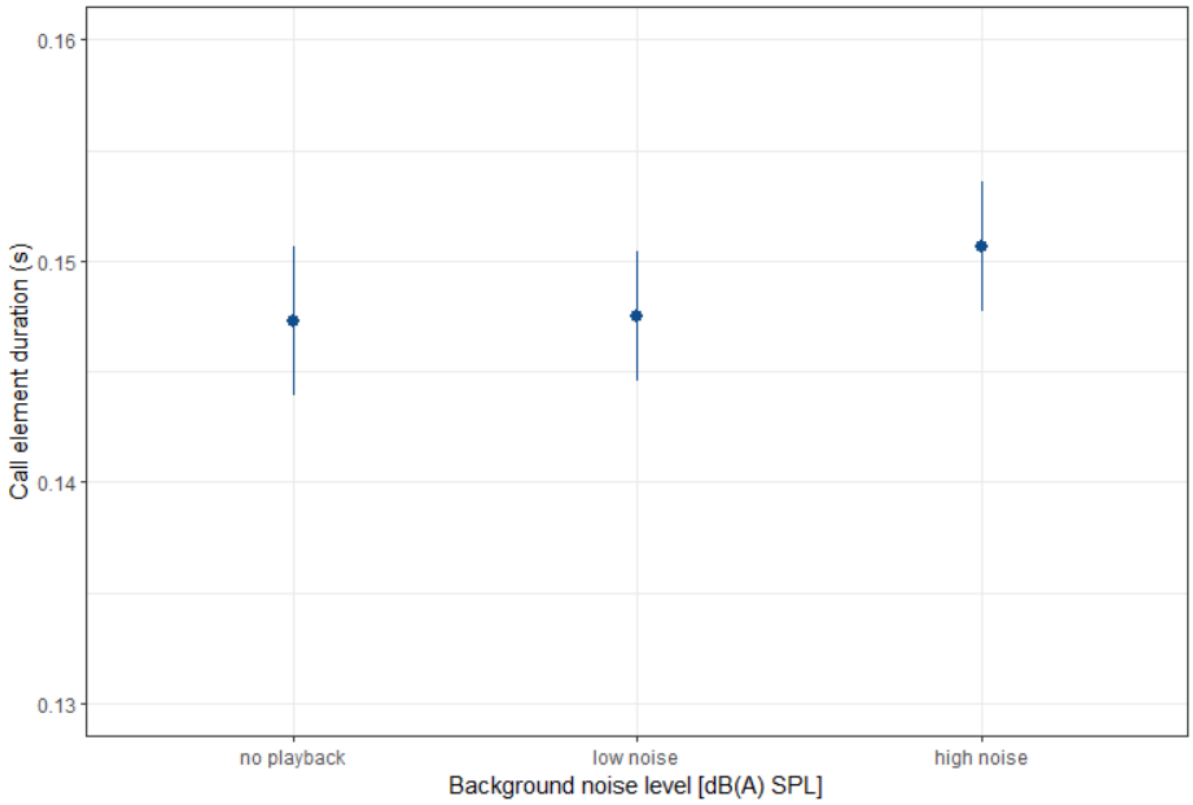


**Figure 3.3** Point-range graph representing the mean call element duration (expressed in seconds) of distress calls produced by domestic chicks for each background noise level condition. The error bars show the standard error of the mean for each call type.

Furthermore, even if there is a slight increase in the call rate in the low and high noise conditions compared to the no playback treatment (as can be seen in Fig.3.4), this visual difference is not statistically significant (low noise: estimate = 0.0374, SE = 0.0838, $t(72) = 0.446$, $p = 0.657$; high noise: estimate = 0.1435, SE = 0.0838, $t(72) = 1.713$, $p = 0.091$).

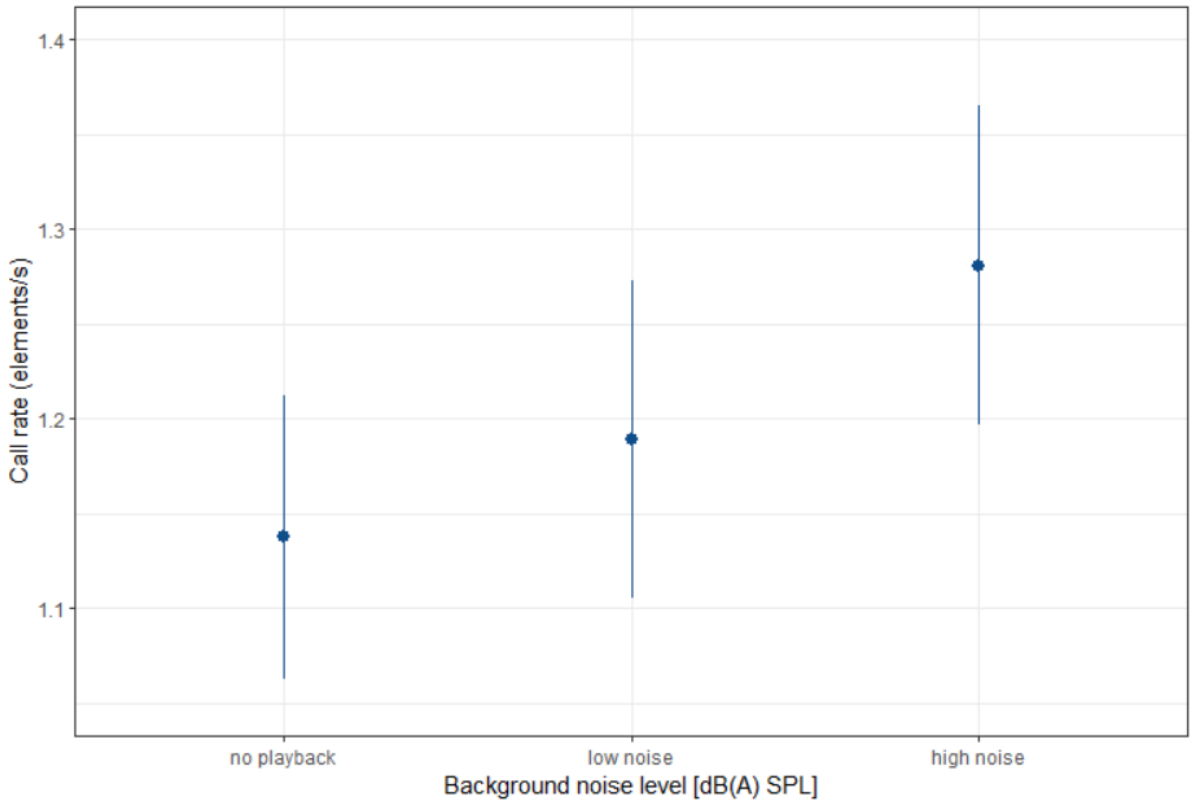


**Figure 3.4** Point-range graph representing the mean call rate (expressed as elements/seconds) of distress calls produced by domestic chicks for each background noise level condition. The error bars show the standard error of the mean for each call type.

### *3.1.4 Discussion*

As summarised in the introductory section, previous studies have shown that vocal plasticity is a highly widespread behaviour among vertebrates, particularly in the form of rising voice intensity level. Furthermore, recent studies in both birds and mammals have shown an early emergence of this audiovocal phenomenon during the ontogenetic development, suggesting that it may be an innate capacity. Therefore, the purpose of the current study was to determine which of the noise-dependent vocal plasticity abilities used by animal species can be considered as an acoustic predisposition.

We found that one-day-old domestic chicks do indeed increase the intensity of their distress calls in response to an increase in the background noise level in absence of any

interaction with conspecifics before the onset of this ability. The fact that this response is present within a few hours of the chick's life is evidence that the Lombard effect is subjected to a strong selection pressure, making it an unlearned acoustical predisposition which plays an essential role in maintaining an effective exchange of information with conspecifics, especially in the early stages of life during which the animal is particularly vulnerable to stressful contexts that can be a source of potential danger to the survival of the individual. The early development of the Lombard effect also provides further evidence of its positive cost-benefit ratio, as it is a simple immediate response to environmental noise and other sources of potential interference with vocal communication.

On the other hand, if we consider noise-dependent temporal adjustments, as the lengthening of the duration of silent intervals between calls and the call rate, we can conclude that they are not present at birth, rather they develop later during ontogeny either with maturation or exposure, being present in adult individuals of *Galloanserae* species such as the Japanese quail (*Coturnix coturnix japonica*) and the domestic chicken (Potash 1972; Brumm et al. 2009). Taken together, these data suggest that temporal adjustments to noise are a set of communication strategies that require a greater degree of audio-vocal integration, the maturation of which is likely to occur at later stages of development and may also involve higher cortical - or homologous - brain areas.

In addition, we also found no evidence for the innateness of noise-dependent spectral adjustments such as call duration. This result is not only consistent with the findings of Brumm et al. (2009) in 28-day-old domestic chickens, but also with data from species phylogenetically close to the domestic chicken, belonging to the *Galloanserae* clade. Indeed, as reported by Dorado-Correa et al. (2018), this type of adaptation appears to be absent even in ducklings as young as two days old, as well as in the same individuals at 8 and 10 days of age.

In order to obtain a complete picture of the innateness of vocal plasticity, further studies on infants of other species are needed to investigate and clarify whether there are interspecific differences in the development of noise-dependent acoustic adjustments: in particular, it will be essential to advance knowledge by integrating animal psychoacoustic studies with neurobiological investigations, so as to be able to identify the neural networks and brain areas responsible for the different types of noise-dependent vocal plasticity. In this way, it will be possible to reconstruct the evolutionary trajectories that led to the emergence of these audiovocal phenomena, distinguishing those that are the most ancient, and therefore most likely to be present in the phylogenetic memory of the majority of vertebrate species, from those that have instead developed in more recent phases of evolutionary time. In this regard, future studies should investigate whether there is a correlation between these abilities and vocal learning, in order to clarify whether forms of noise-dependent vocal plasticity that are absent in basal groups such as the *Galloanserae* are not present because their development is associated with more complex forms of vocal control.

In conclusion, this is the first study which examines associations between noise-dependent vocal plasticity and acoustical predispositions present from birth. Our research has indeed identified the Lombard effect as an acoustic building block, supporting the hypothesis that audiovocal responses to background noise represent a set of independent phenomena, some of which are under strong selective pressure and thus fully developed from the first hours of life, while others require a learning process to be fully mastered.

## 3.2 Harsh Calls in the Poultry Yard: are Nonlinear Vocal Phenomena an Innate Ability to Signal Negative Valence in Domestic Chicks?

### *3.2.1 Introduction*

Are nonlinear vocal phenomena an acoustic feature shown early in life? Do they signal negative valence or high emotional intensity? Finally, are they an ancient evolutionary feature? Nonlinear phenomena (hereafter "NLPs") result from irregular vibrations of the vocal folds and are an integral part of the vocal repertoire of many animal species - such as humans (Herzel and Wendler, 1991), dogs (Marx et al., 2021), the little spotted kiwi (Digby et al., 2013) or the concave-eared torrent frog (Suthers et al., 2006) - and are even used in contemporary vocal music (Neubauer et al., 2004). However, NLPs are not a monolithic trait, but can be divided into several subtypes: one of these is biphonation, which consists of the occurrence of two or more simultaneous and independent fundamental frequencies; other examples include subharmonics - frequencies that are integer fractions of a fundamental frequency and occur below it; sidebands - frequencies that occur above or below a carrier frequency, often as a result of amplitude or frequency modulation; frequency jumps - sudden changes in the fundamental frequency of a signal; and deterministic chaos - broadband energy in the signal.

Despite the widespread distribution of NLPs in animal communication systems, it is still not clear which is the functional significance of this acoustic feature. A first hypothesis suggests that vocal nonlinearities are exploited by animals to convey the expression of high arousal or emotion intensity, as in the context of play or in interactions with neighbours in wolves (Schneider and Anderson, 2011) or in alarm signalling in yellow-bellied marmots (Blumstein and Chi, 2011). A competing hypothesis, instead, states that NLPs signal the emotional valence of the emitted vocalisation, an idea supported by the presence of this acoustic feature in negative calls such as those produced in aggressive interactions (Fitch et

al., 2002; Anikin et al., 2021) or to express distress (Facchini et al., 2005; Lingle et al., 2012; Koutseff et al., 2018). Alternative, but not necessarily mutually exclusive, hypotheses suggest that NLPs may convey individual identity (Volodina et al., 2006), enhance call unpredictability and then reduce the risk of habituation in the listeners (Fitch et al., 2002; Blumstein and Recapet, 2009), or honestly signal mate quality by exaggerating body size (Riede et al., 2007). Moreover, it should be noted that the study of NLPs and their adaptive functions has been focused mostly on mammals, while investigations conducted on avian species are quite rare (Fee et al., 1998; Zollinger et al., 2008; Suthers et al., 2011).

Although some research has been carried out on NLPs, focusing in particular on the adaptive significance of nonlinearities as described above, there is still very little scientific understanding of the ontogenetic nature of this trait - i.e. whether it is the end product of a learning process or an acoustic ability shown early in life - as well as the evolutionary history of NLPs, especially in avian species. Therefore, the aim of this study is to investigate the adaptive, evolutionary and ontogenetic aspects of NLPs by analysing the vocal repertoire of naïve individuals belonging to a basal avian species capable of emitting distinct acoustic signals with positive and negative emotional valence from the first day of life. For this purpose, we chose one-day-old domestic chicks (*Gallus gallus*) as a model species, an ideal taxon that already possesses a relatively complex and emotionally nuanced vocal repertoire from birth (Collias and Joos, 1953; Collias, 1987).

### *3.2.2 Materials and methods*

#### *(a) Animals and rearing conditions*

In this study, we analysed the vocalisations of 23 domestic chicks (females = 11) (*Gallus gallus*) belonging to the Ross 308 broiler line (Aviagen). The animals hatching and rearing conditions were the same as already described in Chapter *2.1.2*.

*(b) Experimental apparatus and recording procedure*

Domestic chicks' vocalisations were recorded using the same apparatus and procedure previously described in Chapter *2.1.2*.

*(c) Acoustic analysis*

Acoustic analysis was performed using Praat 6.3.03 software (Boersma and Weenink, 2022). Specifically, the audio recordings were annotated using a custom script, the accuracy of which was then manually verified. The spectrogram of each annotated call was then examined to confirm the vocalisation type. This step was necessary because, within a given emotional context, there could be calls that did not match it - presumably due to transient changes in the animal's arousal or emotional state - or there could be vocalisations with a frequency modulation pattern that made the classification uncertain. Calls that fell into any of the above conditions were discarded in the following stages of the study.

The selected calls were then visually analysed using a narrow-band spectrogram with a 25 ms Gaussian window and a dynamic range equivalent to 50 dB. Following the criteria previously outlined in the reference literature (Fitch et al., 2002; Zollinger et al., 2008; Suthers et al., 2011), each call was carefully examined for nonlinear phenomena (NLPs), and the presence or absence of nonlinearities was annotated accordingly.

*(d) Data analysis*

Statistical analysis of data obtained from acoustic analysis was performed in R v. 3.5.1 (R Core Team, 2021). More precisely, for each call type, the number of vocal emissions containing NLPs was normalised taking into account the total number of emitted vocalisations for each domestic chick. Transformed data were then entered in a beta generalized linear mixed-effects model (beta GLMM) – which is an optimal statistical technique for delving with proportions – by using the *glmmTMB()* function of the glmmTMB package, and then, if

the beta GLMM indicated a significant difference among the three call types, Tukey's Honest Significant Difference tests were performed.

### *3.2.3 Results*

The beta generalized linear mixed-effects model indicated a significant difference among the three call types ($z$ = -5.82, $p < 0.001$). Post hoc comparisons using Tukey's HSD test showed significant differences between Distress and Brood calls ($z$ = -4.54, $p < 0.001$, log odds ratio = -1.52) and between Distress and Food calls ($z$ = 4.34, $p < 0.001$, log odds ratio = 1.59). However, no significant difference was found between Brood and Food calls ($z$ = 0.22, $p$ = 0.97, log odds ratio = 0.07). These results suggest a significant effect of the emotional context of emission on the occurrence of nonlinearities in domestic chicks' vocalisations.

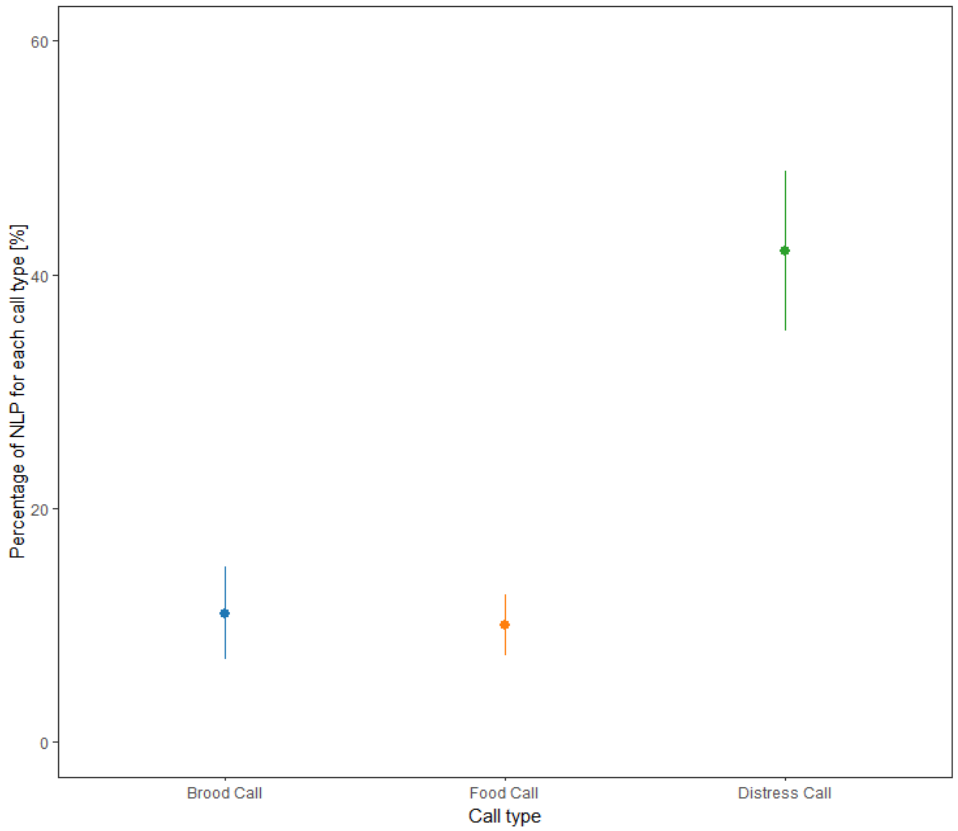

**Figure 3.5** Point-range graph representing the mean percentage of nonlinear vocal phenomena produced by domestic chicks for each call type. The error bars show the standard error of the mean for each call type.

On the other hand, we were not able to find significant differences between sexes within each vocalization type. Specifically, pairwise comparisons within each call type indicated non-significant differences between males and females for Brood calls ($z$ = -0.72, $p$ = 0.47, log odds ratio = -0.36), Distress calls ($z$ = -0.71, $p$ = 0.48, log odds ratio = -0.33), and Food calls ($z$ = -0.87, $p$ = 0.39, log odds ratio = -0.43). This lack of significant differences suggests that sex does not influence the occurrence of nonlinear phenomena within the different call types.

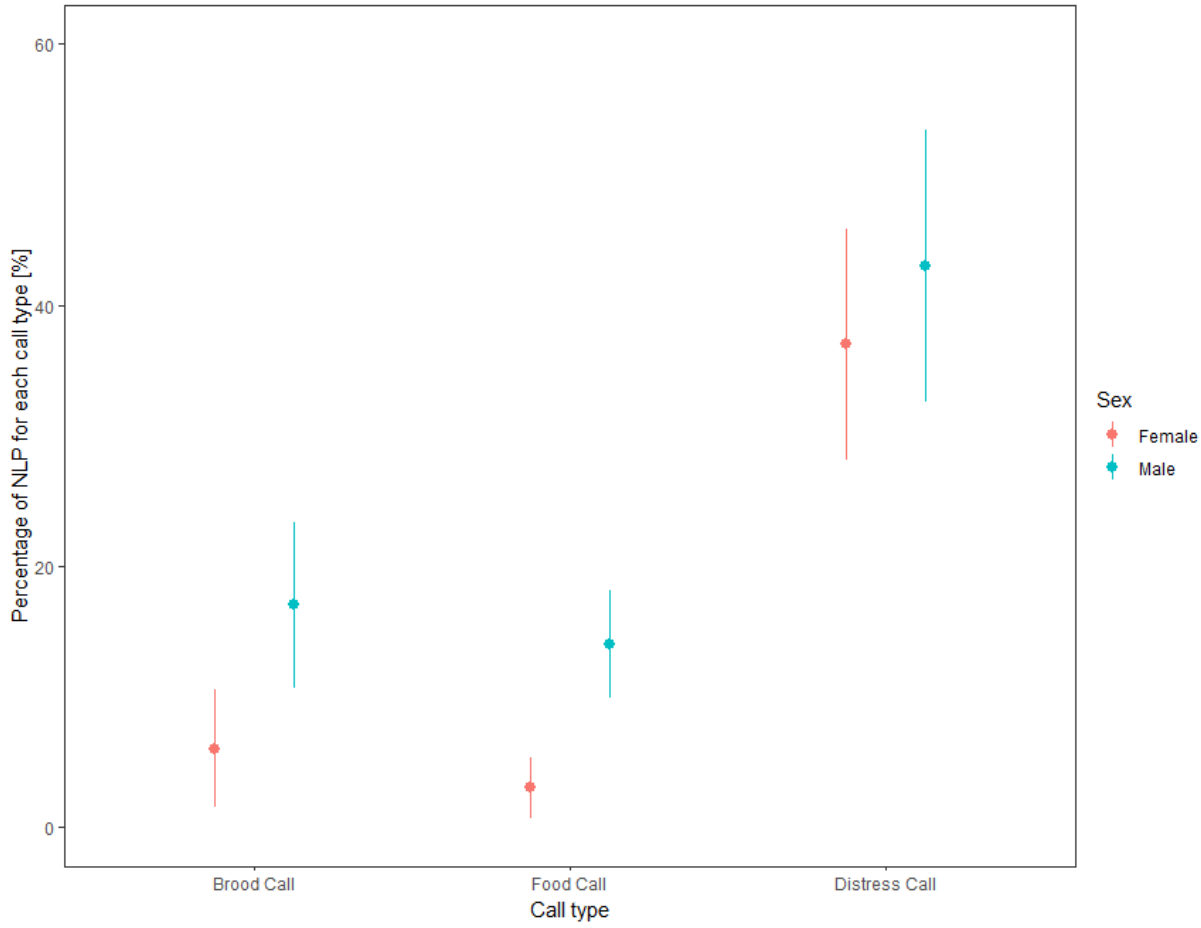

**Figure 3.6** Point-range graph representing the mean percentage of nonlinear vocal phenomena produced by domestic chicks for each call type divided per sex. The error bars show the standard error of the mean for each call type.

### *3.1.4 Discussion*

As mentioned in the introduction, previous studies have shown that NLPs are an important component of the vocal repertoire of many tetrapod species and that their evolutionary adaptive value may encompass different aspects of behaviour, from signalling negative emotions to indicating arousal. However, few studies have investigated this acoustic feature in birds and considered the possibility of an early developmental origin of NLPs. Therefore, the aim of the current study was to determine for the first time whether nonlinearities (1) are present in the vocalisations of a *Galloanserae* taxon, (2) can be considered an acoustic predisposition, (3) are present in all extant birds, and (4) have an adaptive value connected to negative emotions or arousal expression.

The results of our experiment revealed that one-day-old domestic chicks produce a wide range of NLPs, such as sidebands, subharmonics, amplitude modulation and frequency jumps, and that they produce a statistically significant higher proportion of these acoustic features in negatively valenced distress calls. This is the first evidence ever of the presence of nonlinearities in the vocal repertoire of a *Galloanserae* taxon. In addition, since the influence of learning and experience is clearly limited at this early ontogenetic stage, our results suggest that the production of NLPs may represent an innate vocal predisposition, and thus that these acoustic traits are likely stemming from the fact that if the phonatory apparatus is in a state of tension due to the animal's negative emotional state, the biomechanical functioning of the organ loses precision, thus increasing the likelihood of decoupled oscillations that produce NLPs in the signal as an end product. This finding is consistent with what is already known

about the production of NLPs in the human species, as newborns emit cries presenting noise concentration patterns in response to high levels of physical pain after only 24 hours of life (Facchini et al., 2005), thus providing a comparative perspective on the production of NLPs as a non-learned skill.

Furthermore, our results suggest that the production of NLPs may be present in all extant avian species, thus representing a trait that appeared early in the evolutionary history of birds. Since the presence of NLPs was detected in *Galloanserae* in this experiment, whereas in previous studies this phenomenon was documented in three species belonging to the *Neoaves* group (Fee et al., 1998; Zollinger et al., 2008; Suthers et al., 2011), we can conclude that nonlinearities are present in the vocal repertoire of both major lineages of Neognathae (Braun and Kimball, 2021). If NLPs are also documented in the early diverging clade of *Palaeognathae*, for which we only have positive data for *Apteryx* (Digby et al., 2013), then we can conclude that nonlinear phenomena are a synapomorphy of all avian species.

Finally, our findings show that nonlinear phenomena signal negative valence in domestic chicks, supporting the hypothesis that this acoustic feature is associated with negative affect. It should be noted, however, that the perception of this characteristics in humans - particularly with regard to signalling negative valence or high emotional intensity - appears to be influenced by the presence of contextual cues (Anikin et al., 2020): consequently, it cannot be excluded that NLPs may serve multiple functions in different species, depending on the context and information available. It should also be noted that there may even be a link between non-linear phenomena and animacy in the auditory sense, since the variation, unpredictability and emotional content introduced by NLPs in vocalisations may help listeners distinguish them more easily from sounds produced by inanimate objects.

# Chapter 4

## Timbre Perception in Domestic Chicks

### 4.1 Bound for (certain) sounds: innate cognitive and emotional predispositions in domestic chicks

#### *4.1.1 Introduction*

Do animals have innate preferences for specific acoustic properties? It is well known that auditory perception and production play a pivotal role in the lives of almost all tetrapod species, particularly for survival and during early ontogeny (Chen and Wiens, 2020). The importance of this sense is underlined by the fact that many abilities - such as singing, vocalising or responding to different sounds – are based on auditory memories that guide the acoustic and vocal ontogeny in a large group of species (see Chapters 1.1.2 and 1.2.2). One well-known example is that of the domestic chicken (*Gallus gallus*), in which the newborns are endowed with a set of innate auditory predispositions that play a crucial role, for instance, in the recognition of animate entities (Chiandetti and Vallortigara, 2011), following behaviour (Fischer, 1972) and auditory imprinting (Fischer and Gilman, 1969).

However, surprisingly little is known about the innate cognitive and emotional auditory predispositions that characterise animals from birth, especially those related to social communication of emotions. In particular, several studies conducted on newborns belonging to *Galloanserae* taxa – such as domestic chicks - have focused solely on the auditory perception of specific acoustic parameters, such as a certain range of pitch (Fischer, 1972), intensity (Fischer and Gilman, 1969) or timing values (De Tommaso et al., 2019), often derived from those typical of the mother's call and applied on pure tone sounds. As a result, there are currently no data available on the innate responses to natural calls that are part of the vocal repertoire of the species studied, vocalisations that largely represent the acoustic

environment in which these animals are constantly immersed.

In addition, an aspect that has not been considered by many authors so far concerns the perception of timbre – a complex and unique quality of a sound, deriving from a set of acoustic features such as amplitude envelope, frequency spectrum and harmonics, that distinguishes it from other acoustic events with the same pitch, loudness, duration and location (Siedenburg et al., 2019) - in non-human animals, i.e. whether, when the quality of the timbre of a sound varies, the behavioural responses also vary, or whether they remain unchanged because they are based on acoustic characteristics that remain stable when the timbre varies. In other words: do auditory preferences remain consistent across different timbres, or do they change? Answering this question is very important because many animal psychoacoustics studies use artificial stimuli that are not related to the natural timbre of the species, and therefore the results may be limited to the timbre used and not generalisable. Therefore, the study of timbre perception in natural and artificial sounds allows us to understand how this acoustic attribute can modulate attention and emotional responses in animals, which may have an auditory predisposition to respond more to vocalisations with a particular timbre quality, especially in contexts of high emotional intensity (Town and Bizley, 2013).

To fill this knowledge gap, we have directed our attention on a species that represents an optimal model to investigate the existence of innate predispositions: the domestic chick. In order to accomplish this, we used a head orienting paradigm and recording the latency to resume feeding as a behavioural response, we exposed 3-day-old chicks to a series of playback experiments aimed at characterising their response to sound samples ranging from conspecific vocalisations to musical timbres. By focusing on the cognitive and emotional predispositions of domestic chicks in response to both natural and altered sounds, our research aims to extend our understanding of how innate auditory mechanisms function in a non-songbird species. We explore not only the potential biological significance of these preferences but also how the

transition from natural calls to artificial timbres affects attention and response, shedding light on the broader sensory and cognitive systems at play in early animal development.

### *4.1.2 Materials and methods*

#### *(a) Experiment 1*

##### *(i) Animals and rearing conditions*

To conduct our study, we tested a total of 56 domestic chicks (females = 28) (*Gallus gallus*) belonging to the Ross 308 breed (Aviagen). The animals hatching and rearing conditions were the same as already described in Chapter *2.1.2*.

##### *(ii) Experimental apparatus, stimuli and procedure*

Three-day-old domestic chicks were tested inside a rectangular apparatus (length: 75 cm, depth: 40 cm), with the walls entirely covered with sound-absorbing material in order to reduce external acoustic interference. Every participant was inserted inside a confining box - placed in the centre of one of the long sides of the apparatus - with a round frontal opening (diameter: 3 cm) to allow the animal to put its head out. In fact, a rectangular feeder filled with chicken feed was placed in front of the circular window of the confining box. The chicks' behaviour was recorded using a camcorder (Microsoft LifeCam) positioned in front of the confining box, 40 cm above the apparatus floor, connected to a computer. The acoustic stimuli were played back by two loudspeakers, each one positioned in the middle of one of the short sides of the apparatus and connected to an amplifier (Philips 5.1 HTD3510/12) controlled by a computer.

The experimental stimuli consisted of natural calls produced by both newborn and adult domestic chickens in different emotional contexts. Specifically, the following sound stimuli were used: the distress call, the brood call, and the food call, all already described in Chapter 2.1.2; in addition, we also employed the fear trill, a negatively valenced call produced when the animal perceive fear or anguish, marked by a strong frequency modulation pattern

(Collias and Joos, 1953; Collias, 1987), and finally, as control stimulus, we used the adult hen's cluck, a vocalisation emitted to attract chicks (Collias and Joos, 1953; Collias, 1987).

The procedure consisted of placing each domestic chick in the confining box, then removing the panel in front of the circular window to allow the animal to begin feeding. After the participant had pecked at the food in the food tray for at least three seconds, the first acoustic stimulus was played. Subsequent stimuli were played in random order at 10-s intervals, ensuring that the domestic chick was focused on its pecking behaviour for at least three consecutive seconds and had not lifted its head from the food at the time of the sound stimulus onset; if this was not the case, the stimulus was delayed until the condition for delivery of the stimulus was optimal. To ensure that participants' attentional responses were stimulus specific and thus not influenced by the order in which the sounds were presented, each stimulus sequence was randomised across chicks to avoid order effects. The behaviour of interest was the orienting reflex in response to the perceived sound, measured in seconds and considered to begin when the domestic chick lifted its head and to end when it returned to feeding. In all cases, the total duration of each trial did not exceed five minutes. Trials in which the domestic chick was not focused on pecking at the time of stimulus onset were excluded from subsequent analyses. Domestic chicks' behaviour was analysed using the event logging software for video recordings Boris (Friard and Gamba, 2016).

*(b) Experiment 2*

*(i) Animals and rearing conditions*

We tested a total of 65 domestic chicks (females = 32) (*Gallus gallus*) belonging to the Ross 308 breed (Aviagen). The collection and care of the eggs, the hatching procedure and the animals rearing conditions were exactly the same as in Experiment 1.

*(ii) Experimental apparatus, stimuli and procedure*

The experimental apparatus and test procedure were exactly the same as in Experiment 1. On the contrary, the experimental stimuli consisted of the distress call and the fear trill, the timbre of which was modified to that of two wind instruments, the trumpet and the violin, using the Tone Transfer synthesis software (Carney et al., 2021), thus producing a total of four sound stimuli, more precisely: a distress call with the timbre of a flute - named *distress flute* - and another one with that of a trumpet - called *distress trumpet*; a fear trill with the timbre of a flute - named *fear flute* - and another one with that of a trumpet - called *fear trumpet*.

The acoustic stimuli employed in this experiment, instead, differed from those of the previous one. Notably, musical stimuli were generated by means of Tone Transfer (Carney et al., 2021), an interactive machine learning software able to transform the timbre of an audio input into that of a musical instrument. In particular, the distress call and fear trill stimuli that were used in Experiment 1 were then imported into Tone Transfer, then the software automatically measured the fundamental frequency of the stimuli using the SPICE model, and finally transformed their timbre into that of two different wind instruments, the trumpet and the violin, resulting in a total of four sound stimuli. The transformation process altered the timbre, harmonic content, and noise components of the original distress call and fear trill, while preserving their pitch and loudness, ensuring that the melodic and dynamic characteristics of the stimuli remained intact despite the instrumental conversion (Carney et al., 2021).

*(c) Acoustic analysis*

The annotation of the sound stimuli used in both experiments was performed by using a custom script in Praat 6.3.03 software (Boersma and Weenink, 2022). Then, thanks to a second macro, every labelled call or note was saved as a single mono .wav file. The newly created audio files were then imported into R v. 3.5.1 (R Core Team, 2021) and analysed

using the *analyze()* function of the Soundgen package (Anikin, 2019), which measured the following twenty-three spectral descriptives: total length in seconds (*duration*), minimum fundamental frequency (*pitch_min*), mean fundamental frequency (*pitch_mean*), maximum fundamental frequency (*pitch_max*), frequency of amplitude modulation (*amEnvFreq*), depth of amplitude modulation (*amEnvDep*), frequency of amplitude modulation estimated from the modulation power spectrum (*amMsFreq*), purity of amplitude modulation estimated from the modulation power spectrum (*amMsPurity*), root mean square of amplitude (*ampl*), Wiener entropy (*entropy*), Shannon entropy (*entropySh*), rate of change in acoustic features (*flux*), depth of frequency modulation (*fmDep*), frequency of frequency modulation (*fmFreq*), purity of frequency modulation (*fmPurity*), amount of energy in upper harmonics (*harmEnergy*),height of harmonics in the spectrum (*harmHeight*), harmonics-to-noise ratio (*HNR*), spectrum variability (*novelty*), peak frequency (*peakFreq*), auditory roughness (*roughness*), centre of gravity of the spectrum (*pecCentroid*), slope of linear regression fit to the spectrum (*specSlope*).

*(d) Data analysis*

The statistical analyses were initially performed in R v. 3.5.1 (R Core Team, 2021) using the *lmer()* function from the lmerTest package (Kuznetsova et al., 2017). Specifically, a linear mixed-effects model was fitted with domestic chicks' orientation time as the response variable, acoustic stimuli as the fixed effect, and individual ID as the random effect. In addition, to identify the acoustic features that could explain the observed behaviour of the domestic chicks, we performed two partial least squares regressions - one for each experiment - on all twenty-three acoustic descriptives characterising the respective auditory stimuli. Specifically, we used a custom function in Python v 3.10.12 (Van Rossum and Drake, 2009), with domestic chicks' orientation time as the response variable and the acoustic features as predictors.

### *3.2.3 Results*

In Experiment 1, the linear mixed model revealed a significant main effect of condition on the response variable ($F(4, 258.60) = 4.68$, $p < 0.001$)). Post-hoc pairwise comparisons indicated that the fear trill stimulus resulted in significantly higher responses compared to both adult call ($p < .0001$) and brood call ($p = 0.0073$), as well as distress call ($p < .0001$) and food call ($p = 0.0194$). No significant differences were found between other condition pairs. Moreover, the partial least squares regression indicated that the attentional response of domestic chicks is predicted by specific acoustic features of the stimuli. In particular, the response of domestic chicks to natural calls is predicted by high duration [0.14, 0.57], Shannon entropy [0.14, 0.55] and spectrum variation (*novelty*) [0.16, 0.32], and by low change in acoustic features such as pitch, amplitude and harmonicity (*flux*) [-0.34, -0.18], harmonic-to-noise ratio [-0.29, -0.07], harmonic energy [-0.34, -0.18], roughness [-0.34, -0.18], frequency of frequency modulation [-0.34, -0.18], purity of frequency modulation [-0.35, -0.18], depth of amplitude modulation [-0.9, -0.24].

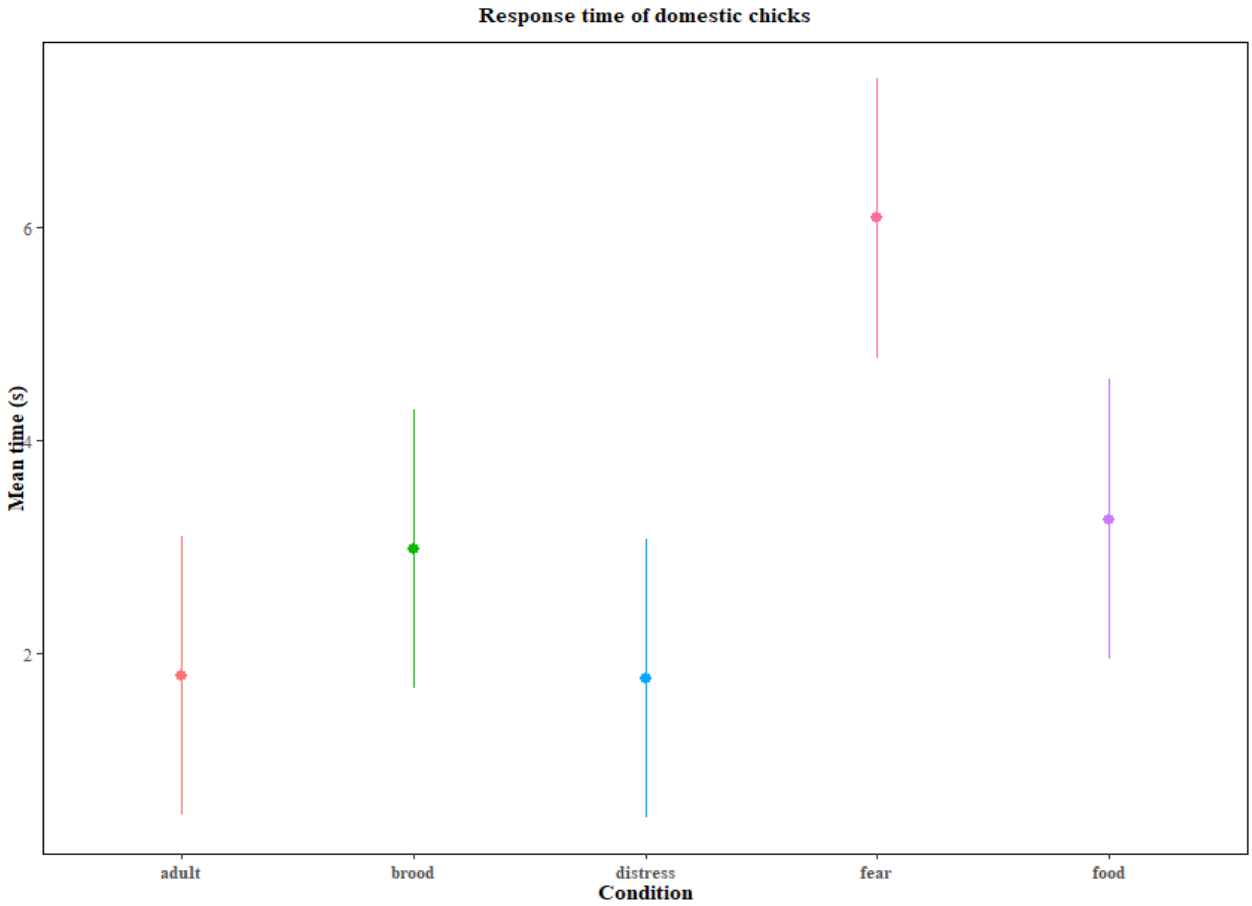


**Figure 4.1** Point-range graph representing the mean response time (in seconds) by domestic chicks under the five natural calls used as acoustic stimuli. The error bars show the standard error of the mean for each condition.

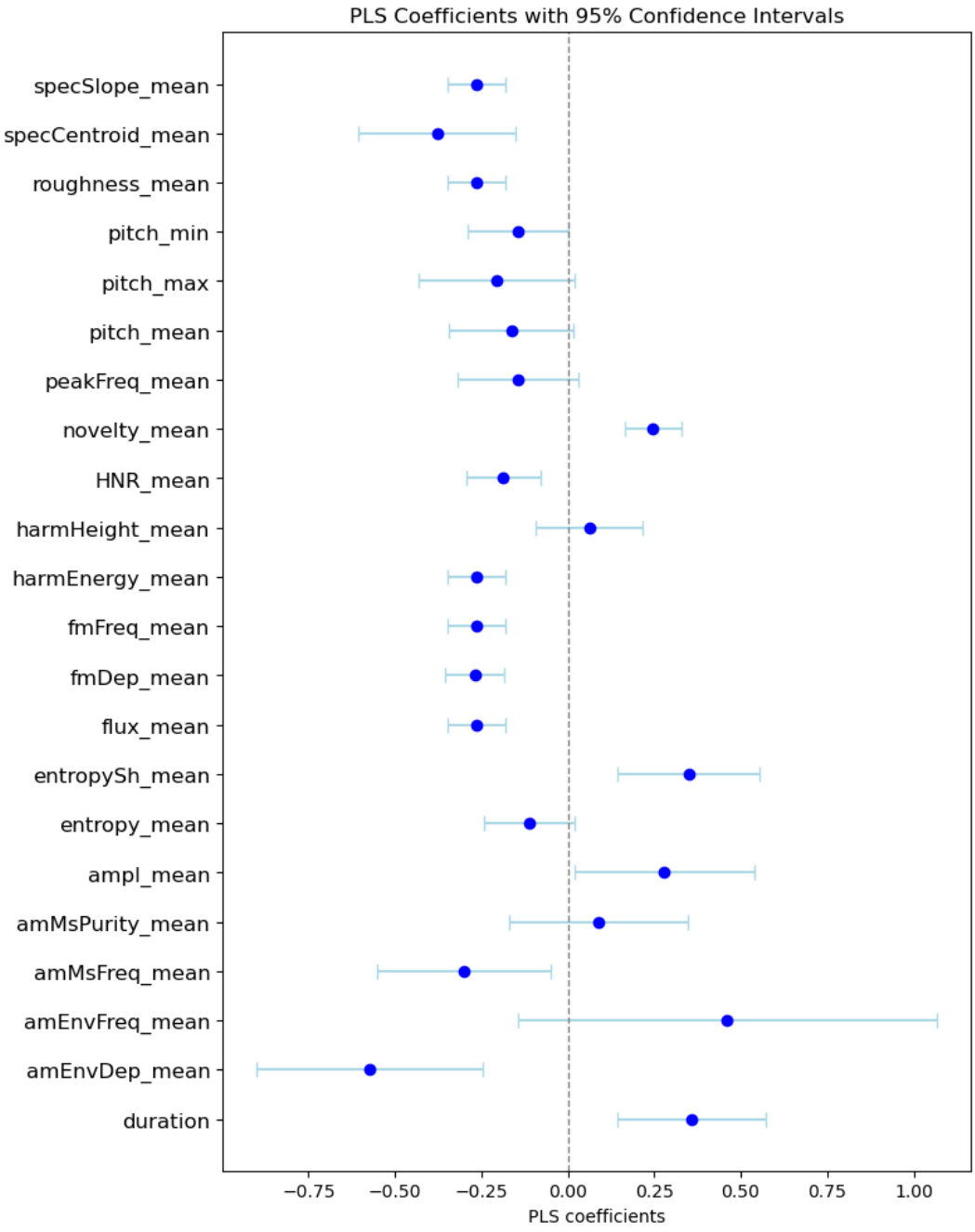


**Figure 4.2** Partial least squares regressions of acoustic predictors of domestic chicks' attentional response to the five natural calls. The statistically significant predictors are those whose bootstrap distribution is above or below zero.

In Experiment 2, instead, the linear mixed model revealed a significant main effect of condition on the response variable ($F(3,253.23) = 5.03$, $p = 0.0021$). Post-hoc pairwise comparisons indicated that the "fear trumpet" stimulus resulted in significantly higher

responses compared to both "distress flute" ($p$ = 0.0102) and "distress trumpet" ($p$ = 0.0220), as well as "fear flute" ($p$ = 0.0025). No significant differences were found between other condition pairs. Moreover, the partial least squares regression indicated that the attentional response of domestic chicks is predicted by specific acoustic features of the stimuli. In particular, the response of domestic chicks to musical timbre vocalisations is predicted by high harmonic-to-noise ratio [0.04, 0.41], harmonic height [0.06, 0.31], harmonic energy [0.002, 0.10], peak frequency [0.03, 0.25], pitch minimum [0.07, 0.44], pitch mean [0.07, 0.44], pitch maximum [0.06, 0.37], and frequency of amplitude modulation [0.04, 0.33], and by low change in acoustic features such as pitch, amplitude and harmonicity (*flux*) [-0.36, -0.02], and spectrum variation (*novelty*) [-0.13, -0.02].

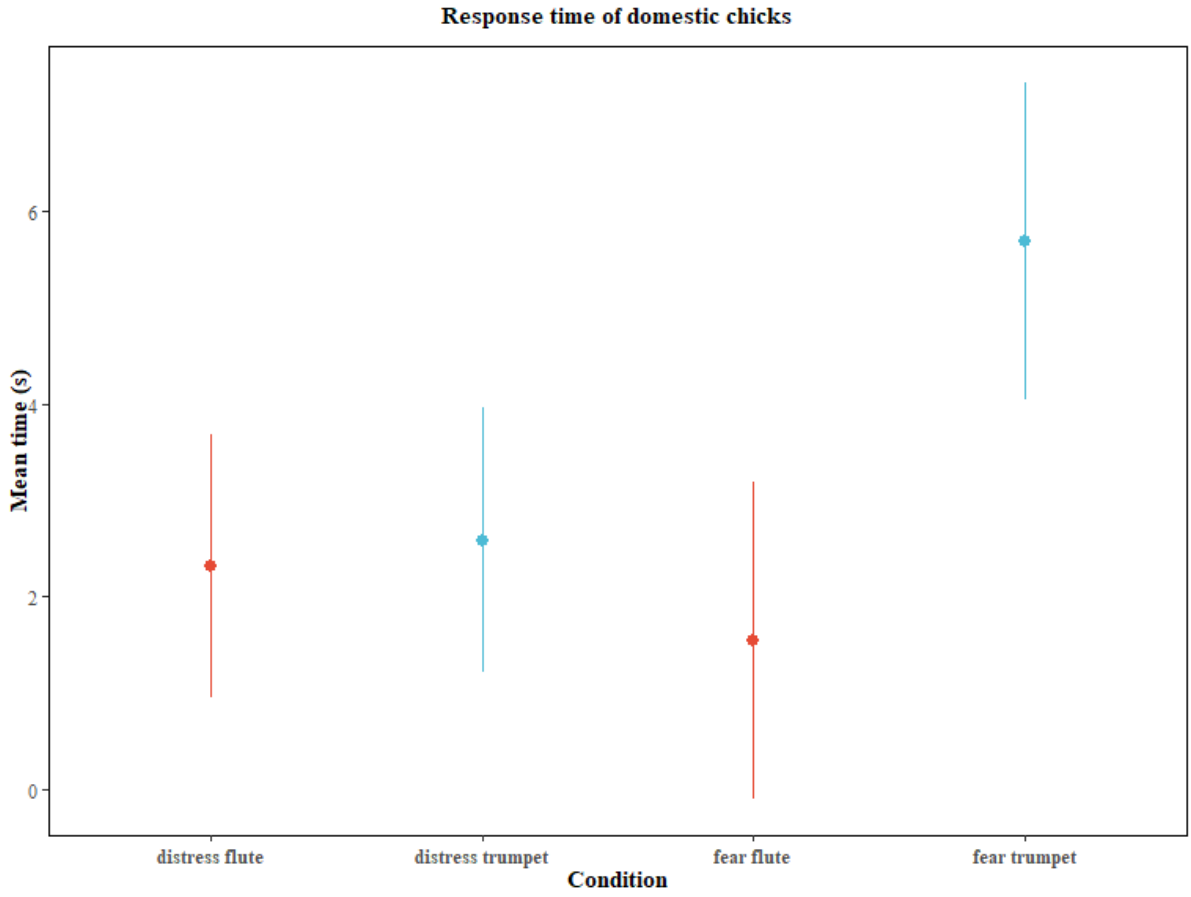

**Figure 4.3** Point-range graph representing the mean response time (in seconds) by domestic chicks under the four musical timbre vocalisations used as acoustic stimuli. The error bars show the standard error of the mean for each condition.

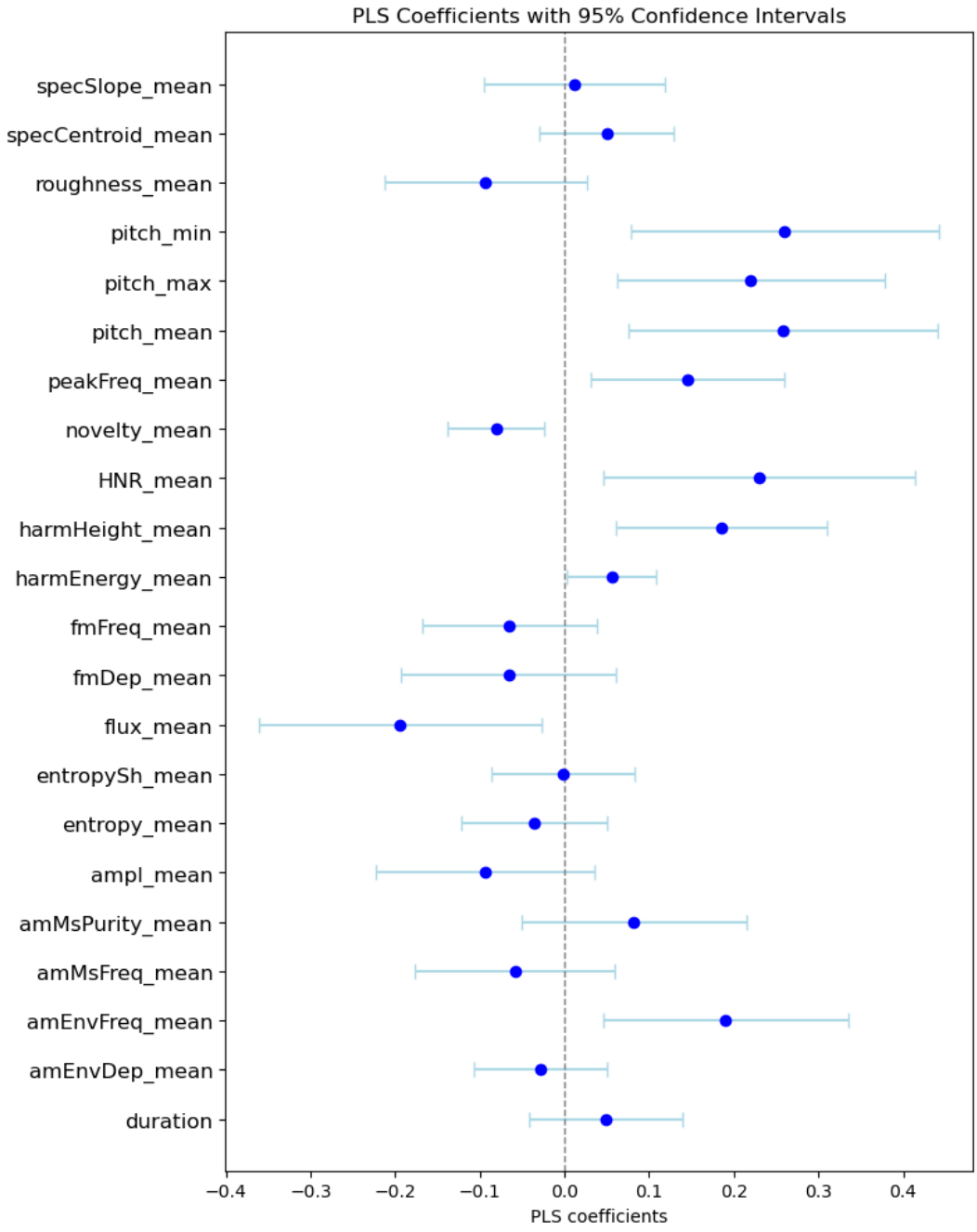


**Figure 4.4** Partial least squares regressions of acoustic predictors of domestic chicks' attentional response to the four musical timbre vocalisations. The statistically significant predictors are those whose bootstrap distribution is above or below zero.

### *3.1.4 Discussion*

The current study found that domestic chicks pay significantly more attention to the fear trill than to any other species-specific vocalisation, suggesting that this call possesses a biological significance that conveys a sense of increased urgency and arousal, conveyed by acoustic features to which chicks pay more attention, such as higher duration, entropy and spectrum variation, and low change in acoustic features such as pitch, amplitude and harmonicity. Another interesting aspect is the fact that our results indicate that, in absolute terms, domestic chicks pay little attention to distress calls: this result is consistent with previous findings in the scientific literature indicating that young birds tend to ignore distress signals emitted by siblings (Collias and Collias, 1956; Thorpe, 1961; Collias, 1962; Heinz, 1973), suggesting that this signal has the mother as its main recipient. Surprisingly, the maternal cluck also elicited a poor attentional response, suggesting that although this vocalisation has acoustic properties that make it attractive to domestic chicks, is not particularly attention-grabbing in a foraging context such as that of our experiment, where the chick is already consuming food resources and is therefore not motivated to attend to and/or reach for the maternal call indicating the presence of food. However, an alternative explanation cannot be ruled out either, namely that maternal cluck was not interesting to the participants because it was not recognised as coming from their mother.

As far as the use of musical timbres is concerned, our experiment shows that domestic chicks pay significantly more attention to the fear trill recreated with a trumpet timbre than to any of the other stimuli tested. This is because the aforementioned timbre quality associated with the fear signal enhances acoustic features such as high harmonic-to-noise ratio and harmonic energy, as well as pitch, but also a low rate of change in these acoustic features, similar to what occurs with species-specific timbres. Thus, it appears that applying the same timbre to different acoustic signals results in different variations in acoustic properties, which

would explain the limited attentional capture exerted by, for example, the distress call recreated with a trumpet timbre.

Overall, our results imply that domestic chicks have different ways of processing and perceiving sounds with distinct timbres. Specifically, when it comes to the typical timbres characterising the natural calls of their own species, our animal model seems to have an innate predisposition to pay more attention to those sounds - such as the fear trill - that are marked by greater unpredictability and complexity - two features that reduce the likelihood of habituation - but also have clear tonal elements, making them more recognisable and easier to process. Conversely, when it comes to musical sounds - which were completely unfamiliar to the animals tested - there is a noticeable shift towards paying more attention to features related to both harmonicity and pitch. This shift may be due to the fact that these features give the sound a more 'voice-like' acoustic structure, which is most sought after by animals when they are in a context where they are exposed to unfamiliar sounds and at the same time motivated to rejoin a conspecific.

These results open the door to further investigation of the effects of timbre on auditory perception in different animal species, particularly in relation to attentional responses, which may also be related to the detection of animacy through sound. More specifically, in addition to investigating this phenomenon in a wider range of species, future research should compare behavioural responses to a wider range of musical timbres, with the expectation, for example, that the timbre of wind instruments may better match the natural behaviour of the animals tested, as they have a sound production system more similar to that of biological entities capable of vocalisation. In addition, future studies should also investigate which parameters underlying the differences in timbre are responsible for eliciting more or less strong attentional responses in different animal taxa, for example by disentangling the contribution of harmonics from that of the envelope. Finally, the last question worth exploring is whether

there is a relationship between timbre preferences and survival in different socio-ecological contexts in different species, e.g. whether sounds with richer harmonic content and more stable spectral features are generally preferred when searching for conspecifics.

# Chapter 5

## General discussion and concluding remarks

How can animals detect animate organisms through sound? The answer to this question is the common thread that unites the studies presented in this thesis. Focusing our attention on the domestic chick, a naïve animal model belonging to a phylogenetically ancient group of birds that is particularly suitable for our purposes, we have investigated those abilities that may underlie the perception and production of auditory animacy, characterising them as innate acoustic predispositions and thus constituting the so-called core knowledge of sounds.

In particular, in Chapter 1 we examined the acoustic features that underlie the detection of animate beings, highlighting the multicomponency of auditory animacy, the perception of which is not based on a single phenomenon but, similarly to the visual domain, is composed of different aspects of sound such as voicelikeness, consonance and acoustic motion. The list of animacy cues may be extended in future research as other promising candidates are identified, such as voice modulations used to express emotional cues in vocalisations or the fractal structure in animal call sequences. We have also reviewed the abilities related to the perception and production of sound in the *Galloanserae* group, to which our model species belong, focusing in particular on those mechanisms and behaviours that are present from the first days of life, thus constituting innate acoustic predispositions; then we have looked at the complexity of communication in this group of animals, noting the interaction between genetic and learned aspects; finally, we have examined the natural responses of both embryos and adults to music, since this acoustic phenomenon contains features that are common to animal communication systems and are therefore also related to the perception of animacy through sound.

In Chapter 2, we focused our attention on those characteristics that can be considered hallmarks of animacy in the auditory sense and that are common to multiple animal species. In particular, we investigated whether the vocalisations of one-day-old domestic chicks exhibit long-term correlations, and thus a fractal structure common to many animal taxa, or whether they are characterised by short-term correlations. If the acoustic signals tend towards a fractal structure, this would indicate that this feature is an innate component of vocalisations and can therefore be considered as a potential auditory animacy cue. Surprisingly, however, our results contradict what has been reported in previous literature, which shows a predominance of short-term correlations, suggesting that fractal structure may be a feature of acoustic signals that emerges with brain maturation or as a result of learning or vocal accommodation. By comparing these findings with the multicomponent view of auditory animacy described in Chapter 1, we can conclude accordingly that while some animacy cues may be present from birth, others - such as fractal structure - might require a longer time span to fully develop and emerge.

In Chapter 3, we examined the auditory innate predispositions in domestic chicks, particularly exploring those aspects related to vocal production that can also signal the presence of an animate being due to the fact that they are dynamic, adjustable features in acoustic events which are not present in sounds characterising non-living things. The first study described in this chapter showed that one-day-old domestic chicks are able to adjust certain acoustic features of their voice - such as the intensity of their distress calls - in response to increased background noise, suggesting that vocal plasticity, at least in the form of the Lombard effect, is an innate trait that is essential for effective communication from birth and that helps to distinguish a creature that is emitting a signal from an environmental noise that is unable to adjust any feature of the sounds it produces. Moreover, the fact that other forms of vocal adaptation, such as temporal and spectral modifications, were not detected in our

study suggests that they may develop at later stages of development, but it is still not known whether this is due to brain maturation or a learning process. This prompts further questions about the relationship between genetic predispositions and environmental shaping in the emergence of adaptive vocal behaviours, positioning this phenomenon within the nature-versus-nurture debate in animal communication research. In the second study, instead, we found that one-day-old domestic chicks produce vocalisations containing nonlinear vocal phenomena (NLPs), and that these acoustic features are more frequent in negative emotionally valenced distress calls than in positive emissions, suggesting that NLPs are an innate feature - probably evolutionarily conserved across avian species - whose function is to signal negative emotional states. In addition, NLPs can also be seen as an aspect of acoustic events that can add 'colour', making them more unpredictable and emotionally charged, thus resulting in a more ‘lifelike’ sound. However, the role of NLPs in evoking animacy perception remains to be explored, although it may be a promising avenue.

In Chapter 4, we investigated whether domestic chicks have innate preferences for specific acoustic properties and how these preferences are affected by changes in timbre. Using a head orientation paradigm and measuring latency to resume feeding, we conducted two experiments with three-day-old domestic chicks. In the first experiment, we presented natural conspecific vocalisations, including distress calls, fear trills, brood calls, food calls and maternal clucking. We found that domestic chicks paid significantly more attention to the fear trill, a negatively valenced call associated with high urgency and arousal, than to other calls. Acoustic analysis showed that chicks' attentional responses were predicted by specific features such as high duration, entropy and spectral variation, and low flux in pitch, amplitude and harmonicity. In the second experiment, we altered the timbre of the distress call and fear trill using musical instrument timbres (trumpet and flute) via synthesis software. Domestic chicks showed an increased response to the fear trill with trumpet timbre, suggesting that

certain timbral qualities can enhance attentional responses even when the calls are altered. These results demonstrate not only that three-day-old domestic chicks have innate auditory predispositions to pay more attention to certain acoustic properties that may be evolutionarily prioritised to enhance survival by drawing attention to signals associated with potential threat, but also that these preferences can be modulated by changes in timbre. When connected back to the previous chapters, these results suggest that innate auditory preferences are not static, but they interact dynamically with acoustic properties like timbre, influencing the behavioural responses of tested animals.

Further studies are needed to increase the number of species studied in the context of auditory animacy and innate predispositions, to explore the features shared across taxa and those unique to each species, in order to phylogenetically reconstruct the evolution of the behavioural traits underlying the perception of animacy in the auditory sense. To this end, a series of experiments, not described in this thesis, were conducted using humans and nocturnal birds of prey as study species. Specifically, the aim of the first study was twofold: (1) to investigate whether the perception of auditory animacy is correlated with fundamental frequency modulation; (2) to investigate whether there is any correlation between the perception of animacy and both the emotional valence and pleasantness of the sounds experienced. Regarding the first research question, the results showed that even minimal frequency modulation is sufficient to induce a significantly greater perception of animacy compared to a monotone sound, i.e. one without modulation. Regarding the second issue, the emerging results - which deserve further investigation in more detail and with a larger sample of participants - concern the fact that the more an acoustic stimulus was perceived as emotionally positive or pleasant, the greater the level of perceived animacy, suggesting an as yet unexplored link between the emotion evoked by sounds and the perception that the given sound was produced by a living being. On the other hand, the research carried out on nocturnal

birds of prey, in particular on the European Scops Owl (*Otus scops*) and the Eurasian Long-eared Owl (*Asio otus*), focused on the analysis of their vocal repertoires in order to investigate whether the acoustic signals emitted in a low-visibility and ecologically very different context from that of the other animals studied so far have a greater consonant preponderance, similar to what has already been observed in other bird species, both songbirds and non-songbirds. In particular, using the same approach as Maldarelli et al. (2024), the fundamental frequency of the calls of the species studied was analysed and the consonance index was calculated for each of them. The results obtained suggest a more complex picture, in which the calls of these species show a dissonant preponderance, possibly due to the fact that they are territorial calls with a deterrent rather than an attractive function.

In light of all the findings presented in this thesis, several key conclusions can be drawn. First, it should be noted that prior to this work, knowledge of auditory animacy was largely speculative and unsystematic. The aim of this thesis, therefore, was to provide a theoretical organisation of this data, while at the same time demonstrating that animacy in the auditory sense is a multidimensional concept that encompasses different features, each of which contributes differently to the perception that a sound has been produced by an animate being. Secondly, the experimental work on domestic chicks presented in this thesis allows us to conclude that innate acoustic predispositions are fundamental, and in particular to demonstrate that the brains of these animals are not born without any innate ability or preference when it comes to producing vocalisations - as in the case of the Lombard effect and non-linear vocal phenomena - or perceiving sounds - as in the case of timbre perception. A third key conclusion that emerged from the study of the innate nature of vocal plasticity in domestic chicks is that not all of these acoustic predispositions are fully mature at birth, but rather that there are some auditory building blocks that are present from the earliest hours of life, while others emerge at later stages of development, probably as a result of neural

maturation or learning. A fourth major conclusion from this thesis is that, as explored in the experiment described in Chapter 4, timbral qualities modulate responses to innate preferences in domestic chicks: in other words, although a species may have tendencies to prefer some acoustic features over others, these are not fixed aspects of perception, but interact with the timbral quality of the sound. Finally, the last conclusion that can be drawn, albeit more speculative, concerns the fact that the emotional charge of a sound may lead to an enhancement of the perception of animacy, as suggested, for example, by the perception of natural vocalisations by domestic chicks - who pay significantly more attention to an emotionally imbued call such as the fear trill - and by the human study briefly described in the previous paragraph.

Taken together, these insights open new research directions. In particular, the study of auditory animacy cues should be extended to species belonging to different animal classes, taking into account both closely related taxa, such as primates, and more distantly related animal groups, such as arthropods, for which there is already evidence for the presence of visual animacy perceptual abilities (De Agrò et al., 2024). Furthermore, auditory animacy should be studied by comparing individuals of the same species at different ontogenetic stages, in order to reconstruct its development and distinguish those aspects that are innate - taking care, as suggested by Sosa (2024), to explore the underlying causes of innateness - from those that are learned. Finally, extending this line of research to other animal species would also make it possible to reconstruct how many auditory animacy cues exist, the relationships between them, and how many of them are shared between species or unique to certain taxa.

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# List of figures