Chapter 1
Acoustic Coding Strategies Through the Lens of the Mathematical Theory of Communication

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Abstract The Mathematical Theory of Communication predicts how the amount of information of a signal is transmitted from an emitter to a receiver after propagation through the environment. This theory can be applied to explain the principles of animal communication and can be, in the acoustic domain, a strong framework to explore crucial questions on communication strategies such as which code for which environment, which code for which social life, how the information is decoded at the receiver's level, how physiological mechanisms constrain the information coding. Such an approach encompasses all aspects of the acoustic communication process, including its dynamic dimensions.

In 1949, Claude Shannon & Warren Weaver published their seminal book *The Mathematical Theory of Communication* in which they define the chain of events supporting the transmission of information: an emitter codes a message into a signal, which propagates through a transmission channel to a receiver, who decodes it to formalize a message (Shannon and Weaver 1949). Primarily devoted to engineers involved in technologies supporting human communication, the Mathematical Theory of Communication aimed at predicting the amount of information transferred in a message. By its ability to encompass all aspects of a communication chain, this theory goes far beyond the technical aspects of human communication and was rapidly adopted by other fields. As stated by Weaver himself in the first part of *The Mathematical Theory of Communication*: "This is a theory so general that one does not need to say what kinds of symbols are being considered—whether written letters

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or words, or musical notes, or spoken words, or symphonic music, or pictures. The theory is deep enough so that the relationships it reveals indiscriminately apply to all these and to other forms of communication." Animals routinely produce, acquire, process, and store information, and information is central to biological systems at every scale (Maynard Smith 2000): organisms are information processing units and the Mathematical Theory of Communication is thus the prerequisite for biologists to understand the principles of animal communication. It will be the philosophy of this book.

We will focus on one subphylum, the vertebrates, and one mode of communication, the acoustic, in which a sound signal is coded by an emitter, then propagated through a channel—air, water, or solid—and finally decoded by one or several receivers. This process corresponds to the transmission of acoustic information. At the receipt of information and as a consequence of the signal emitted, the receivers generally react by modifying their behaviors and consequently by sending back new information. This exchange of information constitutes a communication process. To understand this process, it is primordial to study each step of the transmission chain. For example, if one undertakes to study individual vocal recognition between members of a given species, it is not sufficient to identify through signal analysis the idiosyncratic acoustic parameters likely to carry the vocal signatures. It has indeed been demonstrated that some of these parameters may not necessarily be used by individuals to vocally identify the individual identity of their conspecific. To detect what is really used by animals, it is mandatory to question them through experimental protocols such as playback experiments aimed at testing the importance of each individual acoustic feature. Identifying acoustic coding strategies thus relies on the experimental approach.

According to the Mathematical Theory of Communication, an emitter sends a signal with a finite amount of information which transmits through the channel and the receiver collects only a part of this amount. The loss of information is due to the noise (in the Theory of Communication sense of the word) that takes place at different levels of the chain: at the coding level (e.g., bad motor control during vocal production), at the channel transmission level (the "channel capacity," i.e., the maximum rate at which information can be reliably transmitted over a channel), and at the decoding level (e.g., through the filtering of received signal by sensory organs, errors of meaning interpretation during cognitive processing of information). As a consequence, the emitted and the received messages will differ. In a study investigating how a tropical bird's song transmits information, we showed that the efficiency of a sound communication system results from a coding/decoding process well-tuned to the acoustic properties of the environment (Mathevon et al. 2008; Aubin et al. 2014). Using sound analysis combined to propagation and playback experiments, we demonstrated that the white-browed warbler *Basileuterus leucoblepharus* extracts various information from a received song such as the species and individual identities of the emitter as well as its location in the environment. Strikingly, we found that species information is encoded in acoustic features resistant to propagation changes while individual identity is supported by features that degrade quickly. In their chapter, Ole Larsen et al. provide a thorough review of these communication strategies that allow "public" or "private" signaling. They describe how signals are subjected to attenuation and various other modifications during propagation through the environment that decrease the reliability of information transfer, and how senders can evolve signals within these propagation constraints to match the function of the signal. A sender may choose acoustic behaviors that will help to increase the active space of its signal by overcoming the limitations of the environment, e.g., by increasing the intensity of signal, switching to specific frequency bands, or choosing a singing post. On the other hand, for private signaling, the sender may make its signals more subject to propagation constraints. The efficiency of these strategies depends ultimately on the level of masking background sounds, including sounds generated by physical processes, like wind, rain, and sounds produced by other species. Abiotic and/or biotic environmental noises jam the signal and modify its spectral and temporal characteristics, limiting the ability of receivers to detect it or to discriminate between signals. This is particularly obvious during the dawn chorus of birds whose origin and function are discussed by Diego Gill and Diego Llusia. During the dawn chorus, singing birds are themselves responsible for adding noise to the transmission channel and thus, according to the Mathematical Theory of Communication, for diminishing the volume of coded information which can be transmitted.

At the level of the emitter, the challenge is to transmit to receivers precise and reliable information through an environment that can be constraining for acoustic signals and despite the biomechanical constraints related to anatomo-physiological factors that may affect voice production. In his chapter, Julien Meyer shows how humans shift from "normal" speech to shouting, whistling, and drumming to secure the information when the emitter–receiver distance increases. Indeed, normal speech does not project beyond circa 30 m and the three other registers help to circumvent these constraints. Shouted speech is performed by increasing energy power of the signal which then can transmit information up to a few hundred meters. Whistled speech relies on the whistlers' selection of salient features of a given language and enables people to communicate over 2 km. Drummed speech—which consists in using a musical instrument (drums) to produce sounds mimicking salient cues of spoken languages can extend this range up to 20 km! Whistling and drumming represent simpler coding strategies which keep the same encoded messages as their spoken equivalent. These coding strategies fit perfectly with one prediction of the Mathematical Theory of Communication: the information coding strategy has to be adapted to the capacity of the transmission channel. As stated by Weaver (1949): "The best transmitter, in fact, is that which codes the message in such a way that the signal has just those optimum statistical characteristics which are best suited to the channel to be used."

Which information can be coded in acoustic signals? During animal communication, a part of the information carried by acoustic signals is borne by "static" cues that can be markers of individual idiosyncratic characteristics (e.g., body size, sex, age, identity, etc.). Focusing on terrestrial mammals, Benjamin Charlton and his co-authors illustrate how static vocal cues supporting identity, sex, or body size information depend on the biomechanical constraints applied to the vocal tract of the emitter. Using the source–filter framework, they show that two distinct acoustic features of mammals' voice—the fundamental frequency (driven by the larynx) and the formants (linked to the vocal tract)—have the potential to independently code for this "static" information. Besides its "static" components, part of the information carried by animal acoustic signals is dynamic and related to the current emotional and physiological states of the emitter. This other informative facet of acoustic signals is of major importance because it allows senders to modulate—voluntarily or not—the biological meaning of their signaling. In her chapter, Elodie Briefer focuses on the coding of emotions in acoustic vocalizations. Although the expression of emotions by animals and humans has been of interest since a long time (Darwin 1872), it is now scrutinized in the context of animal welfare and Briefer's review pinpoints the recent increase of our knowledge in this domain. She firstly reports that animals code their emotional state by varying the different dimensions of their vocalizations (signal intensity, spectral content, and temporal dynamics). She then suggests that coding emotional states results from a complex combination of features predicted by motivation-structural rules (the motivational state of the emitter), emotion-dimension rules (valence and arousal), and characteristics of the social links between the emitter and receiver. Finally, she suggests that vocal expression of emotional arousal has been conserved throughout evolution in mammals and maybe in birds.

Besides its sound transmission properties, the environment can impact communication through seasonal-induced modulation of signal production mechanisms. Manfred Gahr's chapter focuses on seasonal singing activity in songbirds, examining the relationships between seasons, hormonal levels, and neural control of song production. Gahr firstly emphasizes that song production is not restricted to males in many songbirds, and that seasonal impact varies among species. He then examines the hormonal systems that support song production. Finally, Gahr discusses the evidence for neural mechanisms of hormone-dependent seasonal song structure. His review emphasizes the urge for developing field studies of female and male singing behavior, hormone production as well as molecular approach of hormones' roles to fully understand the proximate mechanisms of seasonal singing.

At the receiver's end, the challenge is to extract information from signals degraded by transmission through the environment: information has to be decoded and this process ultimately lays on neuronal activity. In her chapter, Solveig Mouterde investigates both sides of the information transmission chain, examining how the "individual identity" information is coded in a songbird's call at the emitter's level, how these vocal signatures are degraded along with sound propagation through the environment, and how the relevant information is received and processed at the receiver's neuronal level. Importantly, Mouterde's chapter underlines the importance of looking at the whole picture, i.e., the whole chain of transmission of information, from information coding in the original sound signal, propagation-induced degradation, to how receivers deal with decoding this altered information at the auditory cortex level. By promoting a quantitative approach of information transfer, Mouterde's chapter provides a nice demonstration of how the Mathematical Theory of Communication can help in fully deciphering a communication strategy.

In the real world, the exchange of information occurs in a network rather than in a "one emitter–one receiver" dyad, with a social environment implicating simultaneously several signalers and receivers. Although this aspect was largely ignored by the Mathematical Theory of Communication, this theory easily extends to communication networks (McGregor 2005). Communication is the glue that holds animal groups or societies together and, in general, sociality goes hand in hand with sophisticated communication systems. In her chapter, Isabelle Charrier investigates mother–offspring acoustic recognition in pinnipeds, a group of mammals with a large diversity of social structures, from solitary to highly colonial species. Through playback experiments, she demonstrates that species with high selective pressures for mother–pup recognition show the most reliable recognition systems, with high vocal stereotypy, a rapid onset of vocal recognition and a multi-parametric vocal signature mainly based on amplitude and frequency modulation features. Through the lens of the Mathematical Theory of Communication, the work of Charrier demonstrates that when noise and risk of confusion between different individuals are significant, the emitted individual information is secured through adapted coding strategies such as redundancy. Moreover, the pinnipeds' data reported by Charrier underline the importance of comparative and large-scale studies of communication systems throughout clades of animals which experience different types and levels of constraints.

Experimental field research that combines sound analysis with elegant playback experiments is a prominent tool to understand how coding of information in vocalizations is related to constraints imposed by animal's social organization and ecology. While this approach can be used to compare information coding strategies in different species as in Charrier's chapter, it can also serve to finely decipher the dynamics of an acoustic communication network within a given species. In her chapter, Caroline Casey reports such approach with another pinniped species, the Northern elephant seal *Mirounga angustirostris*. This species constitutes a remarkable biological model to understand how the complexity of social relations can interfere with information coding in acoustic signals. Casey and her collaborators firstly analyzed the information contained in the calls males and then set up playback experiments with both natural and synthetic signals. By showing that elephant seal males may vary their behavioral response to other male's calls depending on their past experience with the emitter, Casey provides evidence for the importance of learning in the ability of individuals to use this information.

A network environment provides opportunities to multiple receivers to eavesdrop on signals exchanged (interception of communication). Eavesdropping occurs in a situation in which one or more observers (eavesdroppers) extract information from a signaling interaction between others. For example, in numerous bird species, females sample males' song to asses various male quality traits such as age, dominance rank, paternal ability, parasitic load, etc. This situation is developed in the chapter by Nina Bircher and Marc Naguib. Songbirds have been from many years a choice model to investigate questions revolving around acoustic communication. However, most of the effort has been put on how males code for information in their songs and how same-sex competitors interpret it. Deciphering how females decode information related to "quality," motivation, resource holding potential or personality of individual males' signals is thus mandatory to get a whole picture of males' communication strategies.

Social eavesdropping among communication networks occurs not only in intraspecific communication but also between species. Some signals, such as alarm calls, are particularly subject to heterospecific eavesdrop, as illustrated in the chapter by Robert Magrath and his co-authors. Alarm signals are of widespread ecological importance because many birds and mammals give alarm calls when they detect predators or other threats, and have thus been used as classic models for understanding signal design and the evolution of communication. Magrath et al. firstly consider the information conveyed by alarm calls and how it is encoded. They then propose different scenarios that could explain the evolutionary history of information coding in these particular signals. They tell how social eavesdropping by other species can lead to interspecific communication, deception, or suppression of information. They also consider the potential mechanisms involved in the ability of social eavesdropping the alarm calls of a different species, and emphasize the role of learning. Magrath et al.'s chapter however underlines that we still know little about the evolutionary history of alarm coding and about the combined importance of acoustic structure and learning in the development of responses to heterospecific alarm calls.

The presence of social eavesdroppers within a communication network can increase the costs associated with signaling. For the emitter, a possible mechanism for balancing costs and benefits is to engage more than one of the receiver's sensory channels (Smith et al. 2011). These multimodal signals increase the complexity of the communication process, especially when this process is interspecific. In the final chapter of this book, Alexis Billings and Daniel Blumstein emphasize that the use of multimodal signals can be explained by two main hypothesis: the multiple messages hypothesis and the backup signals hypothesis. Multimodal signaling encompasses two different coding strategies: either the addition of another communication channel to acoustics will serve to increase the information content, or it will allow increasing the robustness of information transmission. Both strategies had been suggested by the Mathematical Theory of Communication. Moreover, Billings and Blumstein's chapter goes far beyond intraspecific multimodal communication by developing a framework to understand interspecific multimodal signaling systems. They underline that, while conspecifics usually share similar sensory systems and thresholds, different species may not necessarily have the same sensory systems, the same sensory sensitivity, the same cognitive abilities, or the same information processing abilities. They suggest that interspecific multimodal communication is accomplished through the coevolution of senders and receivers or through sensory exploitation. Their chapter emphasizes that investigations on coding strategies in acoustic communication should now be integrated in a more general framework encompassing other communication channels and not be restricted to interspecific interactions [in this perspective see the recent study on birds-of-paradise by Ligon et al. (2018)]. Here the Mathematical Theory of Communication could be of great help. An important step will be to quantify the information brought by each transmission channel, and to calculate the global information that emerges from this multisensory communication.

Overall, the present book encompasses all aspects of the communication chain, as defined by the Mathematical Theory of Communication. While the past years have witnessed divergences about the nature of communication systems—and especially on the definition of what is information (Bergstrom and Rosvall 2011; Rendall et al. 2009; Sterner 2014; Stegmann 2017), all chapters will emphasize the strength of Shannon and Weaver's approach. Although the Mathematical Theory of Communication is often erroneously called a mathematical theory of information, it is however true that information is one of its core concepts. Minimizing the role of information thus brings a serious risk of misunderstanding the basic principles of animal communication (Seyfarth et al. 2010; Stegmann 2013). While we acknowledge that the term "information" can be ambiguous, since it is often used in the metaphorical sense of *meaning* (Rendall and Owren 2013), this does not justify the abandonment of the term as long as it is correctly defined following the Mathematical Theory of Communication, i.e., as *uncertainty reduction*. Thus, Weaver (1949) states that "this word information in communication theory relates not so much to what you *do* say, as to what you *could* say." By reducing uncertainty, information helps an individual to adapt to its environment, and although information has no universal meaning since it depends on who receives it, it is an embedded characteristic of any signal (van Baalen 2013). According to the Mathematical Theory of Communication, the amount of information can be calculated in *bits*. Calculating this amount of information can help making predictions about the efficiency of a communication system. For instance, Garcia et al. (*in prep*) calculated the amount of information related to species identity in the drumming signal of woodpeckers using measured acoustic parameters from recorded sounds, and found through playback experiments that this mathematical calculation predicts well the performance of birds to discriminate between species. Information is also a powerful concept to compare between different signals. Seminal studies on swallows by Beecher (1982, 1989) used information calculation to demonstrate that the degree of individuality in calls depend on the species' degree of coloniality. This path has been followed by numerous studies that used information calculations to predict the number of individuals that can be potentially discriminated on the basis of their calls [e.g., in penguins, Aubin and Jouventin (2002) and Searby et al. (2004); in hyenas, Mathevon et al. (2010)]. Lengagne et al. (1999) showed that wind limits the amount of information related to individual identity in penguins' calls and further demonstrated that these birds increase the number of calls emitted and the number of syllables per call, using redundancy to maintain the efficiency of communication as the Mathematical Theory of Communication would have predicted. Recently, Elie and Theunissen used information theory to conduct a deep exploration of the call repertoire of zebra finches *Taeniopygia guttata* in order to establish an acoustical and functional classification of this bird's vocalizations: their study is a nice illustration of how a non-supervised approach following the Mathematical Theory of Communication can help interpreting behavioral observations (Elie and Theunissen 2016). Besides, these authors showed that the information theory is of primary interest to explore the neural correlates of acoustic signals at the receiver's level (Elie and Theunissen 2019). They also investigated the information related to individual identity in the zebra finch calls: they found that distinct signatures differentiate zebra finch individuals for each call type, and that birds memorize these multiple signatures (Elie and Theunissen 2018). All these studies (along with many others) demonstrate the utility of an approach based on information in the sense of the Mathematical Theory of Communication. Above all, this approach is a powerful tool to make hypothesis that can be tested through observations or experiments. Besides, and conversely to what is sometimes argued, the Mathematical Theory of Communication is not a reductionist theory that would for instance ignore the psychological dimension of emitters and receivers. It represents a framework which welcomes all aspects of the communication process, including its dynamic dimensions. As stated by Weaver (1949): "The word communication will be used here in a very broad sense to include all of the procedures by which one mind may affect another." He even proposes to use "a broader definition of communication … which could include the procedures by means of which one mechanism affects another mechanism." A few paragraphs later, he insists on the fact that the Theory does not restrict to the engineering of a communication system (what could represent, in the context of animal acoustic communication, the design of sound production organs, signal features, and sensory systems), but contains "most if not all of the philosophical content of the general problem of communication" including the "capacity of the audience." In the context of animal acoustic communication, we assume that this encompasses all the physiological and psychological aspects of both the emitters and receivers. Communicative intentions and mental state attributions are part of the story: when a human being shifts from normal speech to whistling speech, he or she does so with the intention of communicating at long distance, demonstrating that he or she has integrated the channel constraints. Our growing knowledge about animal intentional cognitive abilities provides objective reasons to think that some species are able to behave similarly. For instance, the choice of a song post by a bird to optimize the active space of its vocalizations could result from the cognitive processes supporting efficient communication behavior. Besides, it is often said that the semantic and the pragmatic levels of communication are not concerned by the Mathematical Theory of Communication which would be interested only in the engineering problem of sending information through a transmission channel (Sterner 2014). Yet, Weaver clearly stated that among the three levels of communication problems ("Level A: the technical problem," "Level B: the semantic problem," and "Level C: the effectiveness problem"), "any limitations discovered in the theory at level A necessarily apply to levels B and C," and that level A "overlaps the other levels more than one could possibly naively suspect": "The theory of Level A is, at least to a significant degree, also a theory of levels B and C." Recent philosophical advances are now recognizing the strength of the Mathematical Theory of Communication on all these aspects (Lean 2014). However, there is still one issue that the Mathematical Theory of Communication does not deal with: it is the information quality. In other words, the theory does not distinguish between relevant and irrelevant information (since it was built to only deal with relevant information).

While the field of behavioral ecology usually focuses on this problem by measuring information in terms of fitness consequences (Donaldson-Matasci et al. 2010), it is not fully satisfying if we want to measure the total amount of information coded in a signal, whatever its fitness consequence. Neurobiologists routinely use this approach when measuring, without any assumptions, the information sent and received by neurons (Reinagel 2000; Mouterde, Chap. 8). Although this question goes beyond the aim of the present book, we think that a full understanding of coding strategies would require such a holistic approach.

What is next? Our knowledge about the acoustic coding strategies developed by animals to communicate has considerably increased during the past 40 years. Although quantitative approaches of communication have been developed in the past, they seem to attract less interest nowadays. Yet, we are still lacking quantitative calculations of the quantity of information coded by emitters and decoded by receivers, especially for acoustic signals having complex spectro-temporal dynamics. These calculations will be even more challenging in the context of multimodal signaling, with signals using in parallel different transmission channels (e.g., acoustics, visual, chemical, etc.). Recent papers advocated for a system approach of animal signaling systems, supporting the idea that we now need to think of animal signals as complex dynamic systems (for details see Hebets et al. 2016; Patricelli and Hebets 2016). To understand how multiple signals using various transmission channels support information coding, transfer, and decoding, we will have to quantify, analyze, and compare sets of communication signals that vary in time and space. We believe that such an approach, driven by the concepts of the Mathematical Theory of Communication, are more than ever needed if we want to have a comprehensive understanding of the mechanisms and evolution of complex animal communication systems.

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