

# Animal vocal communication: function, structures, and production mechanisms

# Maxime Garcia and Livio Favarob

<sup>a</sup>ENES Lab, NEURO-PSI, CNRS UMR 9197, Université Lyon/Saint-Etienne, France, and <sup>b</sup>Dipartimento di Scienze della Vita e Biologia dei Sistemi, Università degli Studi di Torino, Italy

\*Address correspondence to Maxime Garcia. E-mail: maxime.garcia@ymail.com and Livio Favaro. E-mail: livio.favaro@unito.it.

#### Introduction

Understanding the processes involved in how and why animals communicate has long been fascinating to scientists (Darwin 1871). This endeavor plays a key role in the pursuit of reaching a better comprehension both of the rules involved in organizing the animal societies around us (Freeberg et al. 2012) and of the evolutionary bases underlying our own vocal communication system: human language (Fitch 2010). Moreover, in recent years, the type and function of information conveyed by animal vocalizations have also attracted research interest in the field of ecology (see Sueur and Farina 2015). While these fields certainly still have room for developing new concepts and methods in order to improve our appreciation of animal vocal communication, to date, 3 main approaches have been applied which have greatly contributed to advance our knowledge on the question.

First, extensive research has attempted to examine and describe the vocalizations used in various contexts and various model species. Very early in the history of bioacoustics, this has led scientists to describe and classify calls into vocal repertoires, trying to identify which classes could best characterize the vocal systems in place within a given species (e.g., Collias 1963; Winter et al. 1966). More recent work has, however, highlighted the limitation of applying humanbased evaluation of vocal repertoire (Range and Fischer 2004). This is partly due to the dichotomy between graded and discrete signaling (i.e., whether acoustic signals are well delimited from one another or rather form a continuum; Marler 1975), which is itself partly related to the presence of nonlinear phenomena in vocalizations (Wilden et al. 1998). As the tools allowing deeper acoustic analyses become more powerful and accessible to a broader community, new concepts and analysis techniques have been developed to circumvent or help dealing with these issues (e.g., acoustic gradation: Wadewitz et al. 2015; nonlinear phenomena: Fitch et al. 2002; Herbst et al. 2013), illustrating the constant scientific improvement in the field.

Second, investigations of the function of animal vocalizations have emphasized the connection that exists between the structure of acoustic signals and their function, such as the behavioral context in which signals are used (e.g., Seyfarth and Cheney 2010). This led to

the emergence of various theoretical frameworks which have been explored by an impressive diversity of empirical paradigms. For instance, the mathematical model of communication by Shannon and Weaver (1949) has paved the way for evaluating the potential information encoded within the vocalizations produced by the emitter and the corresponding decoding processes used by the receiver (Hailman 2008). The motivational-structural rules outlined by Collias (1960) and Morton (1977) have generated considerable research relating acoustic signals structure to the corresponding behavior adopted when producing a signal. Finally, since its inception (and originally applied to human speech), the source-filter theory (Fant 1960) has raised abundant empirical work investigating the usage of either source of filter components of the voice in multiple behavioral contexts such as antagonist interactions, individual recognition, and sexual selection. In all of the above cases, various methods, such as playback experiments and signals modification, conditioning, cognitive experiments, and decision-making choice tasks have been applied successfully (e.g. Kick 1982; Hulse et al. 1984; Cheney and Seyfarth 1988; Aubin et al. 2000; Zuberbühler 2002; Boeckle et al. 2012). Along with a much broader literature, these studies markedly furthered our insight into the functional relevance of vocal signals and their importance in regard to speciesspecific ecological factors.

The third and last approach to carrying out research on animal vocal communication is to look at the production mechanisms involved in this process. Early anatomical descriptions (Harrison 1995 and references therein; Warner 1972) have been made on the sound producing organs, laying the basis for understanding how sound was generated and shaped in the different animal taxa. However, in-depth studies examining the anatomical and physiological determinants of vocal features have only recently been properly considered, probably because of the methodological limitations met when trying to study this aspect of vocal communication. With the recent advances made, for example, with excised larynx (see Brown et al. 2003; Herbst et al. 2012) and syrinx experiments (Elemans et al. 2015), connecting anatomical structures to acoustic

characteristics has become available. This evaluation of the physiological and anatomical constraints acting on sound production provides a critical advance in that it allows (1) identifying the determinants of acoustic signal structure and (2) connecting these structures to physiological states which are intimately related to behavioral contexts, including the emotional state (Briefer 2012).

The 3 key approaches outlined above are all necessary and thus complementary aspects to get a full picture of how a given vocal communication system works. One should note that neuroanatomical approach is also a crucial component of this puzzle, and has been used extensively at first (e.g., Jürgens and Ploog 1970), but less so nowadays because of ethical concerns, rising as our understanding of animal's mind and emotions get deeper.

## Contributions to this issue

The introduction above highlights the substantial advances that have been made in the study of animal vocal communication. The manuscripts in this issue intend to provide a representation of some of the current approaches and questions applied to the study of this research strand (let aside neuroanatomy for the reason aforementioned).

Landgraf et al. (2017) present a study linking acoustics and ecology. The paper examines the selective forces applied in nightingale reproductive strategies. It focuses on extra-pair copulation behavior, and discusses the mechanisms that might explain the evolution of female mate choice in songbirds.

Rogers (2017) discusses the role of underwater breeding calling in the leopard seal as an indicator of male quality. Animal vocalizations are energetically demanding and thus can be considered as costly signals. This paper underlines how breeding calls can be used in sexual selection, and should represent an honest pathway to communicate fitness information to conspecifics.

Filippi et al. (2017) take a psychoacoustics approach to examine humans' perception of emotional arousal in vocalizations of silver foxes. This paper emphasizes the importance of interspecific communication and contributes to the understanding of shared mechanisms of vocal emotional communication in human and non-human animals.

Ravignani et al. (2017) investigate the anatomical determinants of sound production in harbor seal pups. By contrasting their results with acoustic data available on the study species, this article highlights the potential importance of the source- and filter-related components of seals vocalizations for transmitting information about body size (i.e., provide insight into the allometric relationship of harbor seals body size and calls).

Gamba et al. (2017) demonstrate that morphological variation of the vocal tract shapes individual distinctiveness of the vocal utterances, and also provide further evidence that computational approaches can lead to a better understanding of the relationship between information encoding through individual signature and vocal anatomy.

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