Entropy **2010**, *12*, 127-135; doi:10.3390/e12010127

OPEN ACCESS

entropy

ISSN 1099-4300

www.mdpi.com/journal/entropy

Article

Arguments for the Integration of the Non-Zero-Sum Logic of Complex Animal Communication with Information Theory

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Received: 27 September 2009; in revised form: 28 December 2009 / Accepted: 20 January 2010 / Published: 21 January 2010

Abstract: The outstanding levels of knowledge attained today in the research on animal communication, and the new available technologies to study visual, vocal and chemical signalling, allow an ever increasing use of information theory as a sophisticated tool to improve our knowledge of the complexity of animal communication. Some considerations on the way information theory and intraspecific communication can be linked are presented here. Specifically, information theory may help us to explore interindividual variations in different environmental constraints and social scenarios, as well as the communicative features of social *vs*. solitary species.

Keywords: animal communication; communication noise; entropy; game theory; information theory; non-zero sum

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1. Non-Zero Logic of Animal Communication

Non-zero refers to the concept of the *non-zero-sum* that originates from game theory. It attempts to capture mathematically behaviours in strategic situations, when an individual's success in making choices also depends on the choices of others. Non-zero-sum games are ‘strategic scenarios’ in which some outcomes have net results greater or less than zero. Informally, in non-zero-sum games, the gain of one player does not necessarily correspond to another’s loss. In this context, the dynamics of non-zero-sum may be considered as a kind of force that has crucially shaped the way animals communicate today [1], allowing individuals to establish some form of equilibrium among them, which may determine different sorts of social communications. In fact, during non-zero-sum interactions, individuals have to act together to make relations stronger and communication efficient. Since sophisticated forms of communications among players are not necessarily performed to win contests where the gain of one player means another's loss, communication facilitates non-strictly competitive relationships. Players engaged in a non-zero sum conflict have some complementary and some completely opposed interests. Therefore, signalling is the main tool that allows individuals to establish game relationships to solve conflicts and achieve advantages. Consequently, animal communication can be considered one of the most striking results of the many relationships of non-zero sum among individuals. Considering the logic of the non null additivity as the main force engendering and shaping communication, the impressive amount of non-zero sum relationships that continuously occurs among individuals has determined an amazing development of animals' communication in so many and complex ways (e.g., visual, vocal, chemical) [1].

The complexity of animal communication, which is a direct consequence of non-zero sum logics, may have been developed because conspecifics are involved in a sort of arms race evolutionary process, in which (a) the better the communication tools, the better the fitness (mainly intended as the probability to reproduce), (b) the more efficient the signal(s), the clearer and easier the message will be perceived by conspecifics (e.g., a mate, subordinate individuals, members of a clan or a group). More efficient signals are also supposed to improve communication under different constraints, the noise surrounding both sender and receiver being one of the most common negative factors influencing the efficacy of sending information.

2. Information Theory in the Context of Animal Communication

Information theory, in its original applications [2,3], has been previously proven to represent an essential quantitative tool for examining and comparing communication systems across species (see [4] and references therein), being mainly used to explore communicative interactions (as well as characteristics and structures of signalling) among individuals. The statistical information provided by information theory allows analysing communicative repertoires of unknown structure or function objectively, and also assists the transition from signals to meaning by measuring what could be said with a given communication system. Moreover, since this statistical characterization is independent of the type of communication system, information theory allows a comparative examination of the complexity of vocal repertoires and their organization. One of the most powerful applications of information theory, however, is the possibility to examine mathematically the channel capacity and the structure and organization of communication systems [4]. In a way, information theory may be assimilated to a modern *King Solomon's ring* 'the magical signet ring said to have given King Solomon the power to understand the language of animals'. Actually, such an analysis of animal communication may be applied to sequential signalling by individuals as a means for *deciphering* the structure and organization of a species' communication system. Accordingly, by applying the information theory to our researches on animal communication we have the ability to describe how, when and where individuals communicate but, also, to delve deeper into their signalling to try to understand the overlooked aspects. Evidently, large sample sizes are essential to make use of the full potential of the analytical capabilities of the information theory (see [4] for acoustic data), and collecting large samples represents the most challenging constraint we are faced when studying animal communication. This is because a bottleneck for decoding animals' signals is low repeatability of standard living situations, which could give keys for "cracking" animals' species specific codes [5]. Animals tend to behave similarly in repeatable situations, and if these repeatable behaviours are elicited by the distinctive repeatable signals, these behaviours can be used as keys to decode the function and meaning of communication in the wild.

But the interest of information theory goes beyond these premises. One of the first remarks that can be made is that, by referring to the term information in animal communication, we add an important specification to one of the most typical and adaptative definition of animal communication. According to one of the best known adaptative definition of animal communication [6], we can define a signal as any act or structure which alters the behaviour of other individuals. But as noted by Scott-Phillips [7], this definition does not mention the information, when the concept of information and signals are intrinsic components of animal communication [8], communication being considered as the completion of corresponding signals and responses [7]. In this perspective, I consider especially appropriate Vauclair's [9] definition of communication as the following: "*Communication consists of exchanges of information between a sender and a receiver using a code of specific signals that usually serve to meet common challenges (reproduction, feeding, protection) and, in group-living species, to promote cohesiveness of the group*". If information can also be considered as a reduction of uncertainty, (because an effective message reaches the receiver from the sender), then information represents a major source of data that should not be overlooked in studies on animal communication. In the context of animals' communication systems, information theory may answer the question of whether animals can exchange meaningful messages, the complexity of their communication being connected with high levels of sociality and cooperation in animals' societies [1,10,11].

By including information in our connotation of animal communication, we introduce the possibility of unreceived signals, meaning the possibility that signalling could be conditioned, for example, by the quality of displays during vocal performances or the negative effect of noise. Noise represents an important concept in animal communication, and also in information theory. Social communication requires signals to be detected by receivers. Research on communication has been so far focused on how animals are able to minimize the effects of environmental degradation on signal propagation [12], which is often crucial to the understanding of the way animals communicate and interact with each other (e.g., [13,14,15]). However, communication on noisy environments has not been adequately approached using the principles of communication theory. Since simple signal components suffer lower rates of environmental attenuation than more complex, information-rich components [16], future investigations should combine the effect of noise with the real information transmitted by senders. Not only focus on the ways animals may reduce noise during communication. As information theory may enable us to detect the deepest information of signalling, the study of what part of this information (and not the information as a whole) can be lost during transmission might offer new insights into animal communication, especially on the evolution of signal designs. This is especially important when considering that, recently, several studies (reviewed in Ord and Stamps [12]) have showed that many species change the way acoustic signals are delivered in noisy environments. Basically, species are able to alter the design of vocal signalling (e.g., by adjusting the dominant frequency of vocal signals, the speed or the duration of visual displays): if individuals can adapt the type of components included in a signal as conditions affecting signal detection fluctuate, information theory may quantitatively inform us on the characteristics of such changes and how this affects the meaning of the information senders want receivers to perceive. Moreover, because some species can omit conspicuous elements of their communication signals when they are in the presence of predators [17,18], information theory may highlight "pleonastic" elements in signalling that can be omitted in risky situations without altering the main message significance. As stressed by Ord and Stamps [12] in the specific context of alert calls, we should also focus our attention to the possibility that information theory could verify if changes in information due to the noise are similar across animal systems. If they are, this strategy might represent an example of functional convergence in animal communication crossing signal modalities and taxonomic boundaries. This novel approach promises to be one of the most intriguing for the future exploration of animal communication that information theory offers, and should not be overlooked by behavioural ecologists. The application of information theory's ideas and methods has already helped to demonstrate that species or groups of species have very intricate and frequently overlooked forms of animal communication [5,19].

Finally, a complementary way to approach biological signalling using information theory has been recently suggested by Reznikova [5]. By measuring the time that the animals spend on transmitting messages with desired conditions, we can judge the potential of their communicative system. In this perspective, Reznikova and Ryabko [19−21] applied ideas and methods of information theory to focus on the process of transmission of a measured amount of information and, consequently, to evaluate the potential power of the examined 'language'.

3. Shifting From Social to Solitary Contexts

Although rarely applied to the study of animal communication [4,5,22–25 and references therein], information theory has generally been applied to the communication in social species. Undoubtedly, social species have the potential to have an immediate impact on researchers interested in animal communication because of the evident need that grouped individuals have to communicate amongst them. As underlined before, non-zero-sum dynamics of highly social species may be regarded as the force that determines the way animals communicate. However, if the concept of animal grouping entails the concept of individual signalling, we cannot forget the importance of social communication in more solitary and territorial species, meaning those species that only share their vital space with a unique mate and their own descendants, (only until they become independent). We cannot overlook the application of information theory to other contexts. More solitary species, in fact, sometimes rely on very sophisticated forms of communication to declare their territory (*i.e.*, the defended area within home ranges), to demark their home range (i.e. the vital space in which they move and feed), to avoid intrusions, to escalate towards or to avoid fights, as well as to find a mate or to reinforce mating relationships. Finally, more than one way of communication may exists for the same species, as recently observed in nocturnal species for which both vocal and visual signals play an important role [26−31]. One of the future tasks of information theory should also be to focus on these 'lone' species, both diurnal and nocturnal, in order to improve our understanding of communication among not-strictly social species (which may reveal a previously missed form of signalling). A communication network of territorial individuals defending their resources and an alpha individual maintaining its relationships within the pack should be considered equally interesting in the perspective of information theory.

4. Social Environments Shape the Features of Communication

When referring to: (a) game theory as a possible theoretical framework for the study of animal communication rules, and (b) information theory as a tool to gain a deeper understanding of individual signalling, it is essential to highlight the importance of individual experience. Although it is obvious that individuals differ in their social experiences, much of the theoretical and empirical behavioural ecology does not take this into account [32]. For example, simple game theory models generally assume that all individuals interact with all others in the population. However, individuals often interact only with a subset of the overall population, and they might thus vary substantially in their social experiences. Therefore, social dynamics should also depend on the patterns of interactions. Can this factor engender significant and detectable differences during communication? Depending on very different, not-mutually exclusive factors, it is plausible that each individual (or the pool of individuals within a population) may develop, within a common basis of communicative tools typical of its own species, a 'vocabulary' based on personal experiences [33]. High density of conspecifics, for example, could not only shape the rates of communication among neighbours but, depending on continuous exchanges of information due to individual crowding, may more easily or quickly determine the raising of specific 'words' or peculiar sequences allowing them to send information more efficiently. More isolated individuals or populations may remain more linked to the species specific background of communication simply because they are involved less frequently in a communication network. If this is true, the intrinsic properties of the analysis procedures of information theory may represent, in my opinion, a nice way to quantitatively highlight possible differences in communication 'styles' due to personal experiences. Actually, the features of information theory make it a wonderful tool to characterise communication individually, as well as the strength of adaptive behaviours under changing conditions. Similarly, keystone individuals (e.g., the alpha individual in a group) that have a disproportionately large effect on the overall group's dynamics or functions [23], may also develop a peculiar communication vocabulary which can be brought to light by information theory. The development of specific communication cues should not surprise us, considering that relevant examples in animals exist of how social learning and specific constraints or needs may engender the emergence of song learning and tutoring, mate copying, learning of competitive styles, eavesdropping, dialects, public information and spread of innovations (revised in Sih *et al.* [34]). Such an approach also has the advantage of linking information theory with an area of growing interest in behavioural ecology, the existence and importance of personalities or behavioural syndromes (i.e. individuals show consistent differences in behavioural types [34,35]).

5. Zipf's Law & Shannon Entropic Orders

Under such a perspective, I consider it important to underline the potential of the first-order entropic analysis known as *Zipf's law* [36], as well as of the *Shannon entropic orders*, successfully used in several case study on bird communication [37–41,42]. Let me explain. Zipf's statistic may help in evaluating the structure of a vocal repertoire by examining the frequency of use of different signalling elements in relationship to their ranks (i.e. first, second, third *vs.* most-to-least frequent; for a more detailed explanation of the Zipf's law and Shannon entropies see McCowan *et al.* [4]). However, as Zipf's statistic only allows us to examine the structural composition of a repertoire, and not of its higher-order entropies (i.e. how this composition is organized within the repertoire), we need the Shannon entropic orders to determine the signal sequences within a repertoire. High order entropies measure the communication system complexity by examining how signals interact within a repertoire at different sequence levels [4]. Zipf's statistic is generally used to compare complexity among different species or age stages. Nevertheless, since this method has been shown to represent an important comparative measure of repertoire complexity and learning within a species [4], then this same procedure may also allow us to quantify differences in individual vocal repertoires within and among (meta)populations (thus taking into account the effect of local conditions and constraints). With these tools we may quantitatively evaluate different animal vocal communication systems on a statistically comparative scale, i.e. Zipf's Law & Shannon entropic orders have the potential to allow for comparisons among species and/or individuals of a same species, also under different ecological/behavioural conditions and/or constraints. As stressed by McCowan *et al.* [4], such an approach to the study of animal communication will allow us to determine how predictions of information theory measures fit within the comparative frameworks of behavioural ecology and evolutionary theory.

6. On the Importance of Marginal Details

As stressed by Gherardi and Pieraccini [43], information theory revolutionized the field of communication studies and approaches by providing a solid method for quantifying the amount of information that can be exchanged. Because of the difficulty due to the observer's inability to recognize all of the signals and their different sensorial components, as well as of correctly perceiving the receiver response, few researches have been able to apply information measures to animal signalling in order to decipher the structure and organization of communication systems at the individual, population or species level. Moreover, as also well highlighted by Gherardi and Pieraccini [36], one additional reason for the few attempts to apply this theory to the field of animal communication is that the original information measure (entropy) refers to the uncertainty resulting from the transmission of a message, and not to its significance for the receiver. However, we have previously seen that the entropy of a process can also be viewed as the amount of information in the process at increasingly complex levels of signalling organization [4,44]. Several properties of information theory make it useful to study animal communication. One of the most intriguing aspects is that the complexity of information transfer can be reliably measured in narrow, easily perceived communication systems [43]. Thanks to the insights that information theorists have gained within the past 50 years, good samples of signalling interactions among individuals can be well quantified and appropriately classified into discrete categories, a decisive step towards an improved know-how of the complex reality of animal communication.

To conclude, I would like to adapt the comparison between the 'route' followed by physics and geographic explorations made by Freeman Dyson [45], and the study of animal communication in the perspective of information theory. At the beginning, when most of the Earth had still to be discovered, the most 'exceptional' objectives were exclusively represented by the aims of explorers. For George Everest, to be the first to reach the top of this mountain was his sole objective, whereas the rivers, forests and plains between him and the top of the mountain were mere obstacles. In the same way, the study of animal communication at its beginning, because of lack of information, needed 'big' objectives such as the detection and understanding of main ways and patterns of communications. But now, more and more frequently, new achievements in science (and in our understanding of the natural world) are a matter of minute and overlooked details, which really make the difference between a novel and a mediocre science. Therefore the ensemble of those elements and details that could have seemed minor or marginal before, i.e. the still unexplored rivers, forests and plains, represent now the most fertile and still unknown fields of our investigation. Information theory undoubtedly represents one of these quite overlooked fields, and it is in such a direction that we need to focus our future interest on animal communication.

Acknowledgments

The author wishes to thank four anonymous referees for their very helpful comments. Their insights were greatly appreciated and significantly improved this paper. The work was granted by a research project of the Spanish Ministry of Science and Innovation (CGL2008-02871/BOS) and by the Spanish Secretaría General de Universidades, Ministry of Education (Salvador de Madariaga Program).

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