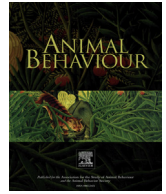




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Special Issue: Communicative Complexity

Structural variability and communicative complexity in acoustic communication

Julia Fischer^{a, b, c, *}, Philip Wadewitz^a, Kurt Hammerschmidt^{a, c}^a Cognitive Ethology Laboratory, German Primate Center, Göttingen, Germany^b Georg-August-University Göttingen, Göttingen, Germany^c Leibniz ScienceCampus Primate Cognition, Göttingen, Germany

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The notion that social complexity may drive communicative complexity has invigorated the research interest in the question of how to assess the structural features of a species' communication system. This applies to both the level of the signal repertoire and the level of potential rules governing the succession of elements. This review first provides an overview of some of the most influential studies in the realm of acoustic communication, before turning to a key problem at the foundation of many analyses. Many biological signal repertoires reveal intermediate forms between specific signal types as well as variation within signal types. Therefore, it is often difficult to identify the specific number of signal types (and consequently, their sequential relationships). Nevertheless, subjective classification or 'hard clustering' approaches force items into specific categories. Yet, given the graded nature of many repertoires, it may be more appropriate to measure the degree of differentiation within a repertoire, instead of the number of call types, which may also be strongly affected by sampling artefacts. 'Fuzzy clustering' provides measures to capture the overall structural variability of a repertoire, i.e. whether they are rather graded or discrete. Because with fuzzy clustering it may also be difficult to identify a single best cluster solution, methods are needed that transcend the number of clusters identified with the cluster analysis. One such approach is the assessment of the distribution of typicality coefficients, which are derived from fuzzy clustering. For the time being, these provide an alternative route to quantitatively test hypotheses regarding the evolution of signal repertoires. Future research should aim to establish a solid mathematical foundation to link the properties of graded repertoires to measures derived from complexity theory. Until then, the notion of complexity to describe the structure of a repertoire should be used with caution.

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Why do some birds just produce three or four different song types, and others more than 200? Why do some monkey species mainly grunt, scream and bark, while others evolved an intriguing variety of twitters, whistles, caws and shrieks? Numerous researchers have aimed to provide answers to such questions, and have invoked habitat characteristics, predation pressure, sexual selection and more recently social complexity as key drivers of vocal complexity (Bradbury & Vehrencamp, 2011; Freeberg, Dunbar, & Ord, 2012). An unresolved issue, however, is that for a formal test of any of the hypotheses put forward to explain variation in signal repertoires between species, we need to develop

better ways to quantitatively capture communicative complexity, so that it can be estimated reliably across species and signal modalities, for use in comparative analyses.

In this paper, we focus on the acoustic domain and largely restrict ourselves to the question of how to quantify vocal complexity in nonhuman primates. Nonhuman primates (hereafter: 'primates') provide particular challenges because most species' repertoires can be considered as graded, with substantial variation within and between call types, such as in Japanese macaques, *Macaca fuscata* (Green, 1975), Barbary macaques, *Macaca sylvanus* (Hammerschmidt & Fischer, 1998), rhesus macaques, *Macaca mulatta* (LePrell, Hauser, & Moody, 2002), chimpanzees, *Pan troglodytes* (Crockford & Boesch, 2005), as well as gorillas, *Gorilla gorilla gorilla* and *Gorilla beringei beringei* (Hedwig, Robbins, Mundry, Hammerschmidt, & Boesch, 2014). This probably also

* Correspondence: J. Fischer, Cognitive Ethology Lab, German Primate Center, Kellnerweg 4, 37077 Göttingen, Germany.

E-mail address: jfischer@dpz.eu (J. Fischer).

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holds for the majority of other terrestrial mammals, due to the sound production mechanism in these taxa (Fitch & Hauser, 1995). We therefore assume that the core findings apply to a broader range of study species, and may also be valid in other communicative domains, such as facial expressions (Parr & Waller, 2006; Scheider, Liebal, Oña, Burrows, & Waller, 2014) or gestures (Hobaiter & Byrne, 2014; Pika, Liebal, Call, & Tomasello, 2005).

We begin this review by summarizing different approaches that have been taken to conceptualize vocal complexity, and stress the importance of clarifying the level of analysis. We then provide an overview of the results of some of the most influential studies, before we turn to our own attempt to characterize the structure of primate vocal repertoires, paying particular attention to the issue of graded versus discrete repertoires. Finally, we suggest a novel method to capture the structural variability of repertoires, to complement (or replace) previous attempts to settle on a specific number of call types.

MEASURING COMMUNICATIVE COMPLEXITY

There are different levels at which communicative complexity can be captured, with increasing difficulties in terms of operationalization. Specifically, one needs to distinguish between the identification of elements on the one hand and analyses of higher-order relationships between elements that appear in succession (sequence analyses) on the other. At the level of the elements, this would amount to the identification of the number of call types in the repertoire (Kershenbaum, Freeberg, & Gammon, 2015). Previously, a higher number of different call types had been equated with a higher degree of complexity (e.g., McComb & Semple, 2005). The central issue here, as we show below, is that the identification of the number of units in a signalling repertoire can be extremely challenging when intermediates between different signal types exist. The problem of identifying the number of units or call types is further exacerbated because other factors, such as individual signatures or variation in signaller quality or state add to the structural variability in the repertoire.

Another way to measure vocal complexity is based on information theory (Shannon & Weaver, 1949). Information theory provides a formal approach to characterize a communicative event in terms of its statistical properties. A key measure in information theory is entropy, which provides an estimation of the amount of uncertainty in a communicative system (Shannon & Weaver, 1949). The greater the variation within a signal space, the greater the uncertainty. Information theoretical concepts, such as Zipf plots, have been used to describe the structure of vocal repertoires based on the frequency of occurrence of different elements in a repertoire (McCowan, Hanser, & Doyle, 1999). The Zipf statistic is derived from a log–log plot of the frequency of occurrence of signalling units against their rank order (Zipf, 1949). In many communication systems, an approximate slope of -1 emerges (Zipf's law), and there is considerable debate about the significance of this relationship (see McCowan, Doyle, Jenkins, & Hanser, 2005 for a summary). Others have used information theoretical approaches to analyse the sequential composition of communicative signals (Freeberg & Lucas, 2012; Hailman, Ficken, & Ficken, 1985; Kershenbaum, 2014; Ord & Martins, 2006). Importantly, information theoretical approaches also rely on an estimation of the number of different units in the system, and thus require a solution to the problem of identifying the number of call types in the repertoire.

To make a full estimate of the communicative complexity of a species requires one to take into account the way variation in signals affects the behaviour of receivers (Freeberg et al., 2012). There are a number of major problems associated with estimating complexity at this level, because responses to signals are not only

affected by signal variation but also by other available information, such as contextual cues and signaller identity, among others (Fischer, 2013; Wheeler & Fischer, 2012). In addition, it is known that receivers may recode graded variation into discrete categories (see Fischer, 2006 for a review). Therefore, for both practical and conceptual reasons, a quantitative assessment of communicative complexity that includes both signaller and receiver characteristics can be achieved for a limited selection of an entire repertoire, at best.

When applying measures derived from information theory, it is important to consider in which way statistical information is related to biological information. Statistical information is maximized when signals are maximally diverse and/or when sequences are truly random (Shannon & Weaver, 1949). Communication systems, however, require a balance between redundancy and diversity (see McCowan et al., 1999). But there is more to consider than redundancy and diversity. As analyses of the evolution of communication have revealed (Dawkins & Krebs, 1978; Maynard Smith & Harper, 2003), signallers are selected to produce signals that serve their own best interests, and that are sufficiently cheap. At the same time, signals only evolve when receivers respond to them (Fischer, 2013; Maynard Smith & Harper, 2003; Scott-Phillips, 2008). For this, signals need to be sufficiently informative, in the sense that they either correlate with a specific state, e.g. resource-holding potential, or can be used to predict upcoming behaviours or events, such as imminence of attack, so that it pays the receiver to attend to them (Bradbury & Vehrencamp, 2011). Correspondingly, two affordances of a communication system emerge, namely a sufficient degree of consistency of signal occurrence with a specific state or context and sufficient capacity to encode as much (potential) information as possible (for an in-depth discussion of the term information, see Fischer, 2013).

DRIVERS OF REPERTOIRE STRUCTURE

Habitat

Several factors have been assumed to impact the structure of a species' vocal repertoire. Peter Marler suggested that in species that live in habitats with poor visibility between signaller and receiver and/or high background noise such as dense rainforests, discrete repertoires should be favoured, because a clear discriminability of call types facilitates signal recognition (Marler, Kavanaugh, & Cutting, 1975). In contrast, in species that live in open habitats with visual access to each other, graded repertoires with variation within and between call types should be favoured because they have a higher capacity to encode potential information, as calls may vary with regard to arousal level. Furthermore, in case of ambiguity, visual information can be used to disambiguate the situation. Similarly, Marler assumed that within a species' repertoire, gradation was more likely to occur in close-range signals, whereas long-distance signals should be more distinct (Marler, 1967).

Others have made more specific predictions regarding the acoustic features of long-distance calls in relation to habitat. It has been proposed that in closed habitats longer signals, signals with a lower repetition rate, a lower frequency modulation and a lower frequency range should be favoured (see Ey & Fischer, 2009 for a review). While the vocalizations of Japanese macaques conformed to the predictions (Sugiura, Tanaka, & Masataka, 2006), this was not the case in other species (e.g. in marmosets: Daniel & Blumstein, 1998). A study of the loud calls given over long distances of four sympatric primate species on Siberut Island also provided only mixed support for the above-mentioned predictions (Schneider, Hodges, Fischer, & Hammerschmidt, 2008). Although all four species concentrated most of the energy (amplitude) of their loud calls

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