Efficiency of coding in macaque vocal communication

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A key characteristic of human language efficiency is that more frequently used words tend to be shorter in length—the ‘law of brevity’. To date, no test of this relationship between frequency of use and length has been carried out on non-human animal vocal communication. We show here that the vocal repertoire of the Formosan macaque (*Macaca cyclopis*) conforms to the pattern predicted by the law of brevity, with an inverse relationship found between call duration and rate of utterance. This finding provides evidence for coding efficiency in the vocal communication system of this species, and indicates commonality in the basic structure of the coding system between human language and vocal communication in this non-human primate.

Keywords: Formosan macaque; communication; language; coding; primate

1. INTRODUCTION

In human language, there is an inverse relationship between word length and frequency of use—the ‘law of brevity’ (Zipf 1936). This relationship can be interpreted as a sign of compression, or optimization of coding (Shannon & Weaver 1949; Cover & Thomas 1991). In a recent study of dolphin surface behavioural patterns, Ferrer-i-Cancho & Lusseau (2009) provided the first evidence from a non-human animal for a similar relationship between signal ‘size’ and rate of use. These authors divided these behavioural patterns—some of which appear to have an important communicative function (Lusseau 2006)—into their component units, and found a negative relationship between the number of such units employed in a pattern and the frequency at which the pattern was seen. This provided strong evidence for coding efficiency in the surface behaviour patterns of this species.

To date, no analysis has been carried out to test for a relationship between signal length and frequency of use among the vocalizations of a non-human animal. Such a relationship might be strongly expected, owing to the costs associated with vocal communication (reviewed by Bradbury & Vehrencamp 1998). Production of vocal signals can be costly, for example, owing to the energetic demands of production (Ward *et al.* 2003),

because these signals increase conspicuousness to predators (Ryan *et al.* 1982) or because they alert potential prey (Deecke *et al.* 2005). Other things being equal, shorter calls will be associated with reduced costs of each of these kinds.

Here, we investigate whether an inverse relationship between signal duration and frequency of use is found in the vocal communication system of a non-human primate, the Formosan macaque (*Macaca cyclopis*). There is great interest in exploring the similarities and differences between human language and the vocal communication of non-human animals, particularly primates (Snowdon 2001; Cheney & Seyfarth 2007). Our analyses test whether the vocal communication systems of humans and a non-human primate share commonality in the rudimentary structure of their coding system.

2. MATERIAL AND METHODS

The Formosan macaque is endemic to Taiwan and lives in social groups of between 9 and 86 individuals, with these groups typically being composed of adult and subadult males and females, as well as juveniles and infants (Hsu & Lin 2001). Hsu *et al.* (2005) classified the vocal repertoire of this species on the basis of calls’ acoustic structure, and furthermore described call types in terms of the behavioural context in which they are given and their probable function. The repertoire was found to consist of 35 distinct call types, although not all of these were given by all age classes in the population. For each call type in the repertoire, Hsu *et al.* (2005) provide data on call duration and the number of calls that were analysed in the study. Vocalizations were collected during 375 h of field recording, of which 320 h were focal watches and 55 h scan samples. As such, the number of calls analysed provides a robust measure of the frequency of utterance of each call type. At worst, calls of shorter duration were perhaps more likely to be missed during sound recording, which would be conservative with respect to the hypothesis being tested here. The data in Hsu *et al.* (2005) were collected and analysed blind to the current study’s aims and we can think of no way in which systematic biases likely to lead to type I error would be present in this dataset.

To investigate the relationship between call duration and frequency of usage, we first used bivariate Spearman’s rank correlations, as data were not normally distributed. We then confirmed results with Pearson’s correlations, with data having been log transformed to meet assumptions of normality. The first analyses included all 35 call types in the repertoire. As some calls may be rare as a result of only being given by a subset of individuals, we then repeated these analyses, including only the 17 call types given by members of all four age classes (adult, subadult, juvenile and infant). It should be noted that these latter analyses also exclude all call types—such as female copulation calls and infant ‘geckers’—that are only given as components of a ‘phrase’ (following the terminology of Struhsaker 1967).

3. RESULTS

There was a significant negative correlation between call duration and frequency of use (Spearman’s rank correlation: $r_s = -0.429$, $n = 35$, $p = 0.010$; Pearson’s correlation: $r = -0.424$, $n = 35$, $p = 0.011$), and this relationship remained significant after the calls not given by members of all age classes were removed (Spearman’s rank correlation: $r_s = -0.569$, $n = 17$, $p = 0.017$; Pearson’s correlation: $r = -0.524$, $n = 17$, $p = 0.031$; figure 1).

4. DISCUSSION

Our analyses indicate that the vocal repertoire of Formosan macaques conforms to the pattern predicted by the law of brevity, with more frequently uttered calls being shorter in duration. This provides, to our knowledge, the first evidence of such a pattern in the

Figure 1. Relationship between call unit duration and frequency of use for the vocal repertoire of the Formosan macaque, *M. cyclopis*. Black circles indicate calls given by members of all four age classes (adult, subadult, juvenile and infant); open circles are all other calls in the repertoire.

vocal communication system of a non-human animal. While there are clear and fundamental differences between human language and the vocal communication of other primates (Pinker 1995; Bickerton 2003), our findings tentatively suggest important shared ground between these communication systems in terms of the basic rules governing signal length and frequency of use. Moreover, our results suggest that similar evolutionary forces may have acted to increase the efficiency of coding in both human and non-human primate vocal communication, or that common self-organization principles (Köhler 1989) underlie these different communication systems.

Previous attempts to explain variation in the form of calls within vocal repertoires have often focused on the information content of these signals, for example, investigating how internal factors such as motivational state may affect the spectral characteristics of vocalizations (Morton 1977; Hauser 1993). Other studies have explored how call structure, including call duration, reflects adaptation to reduce signal distortion in specific environments (e.g. Ey *et al.* 2009). Our findings indicate the importance of also considering coding efficiency as a force shaping the temporal characteristics of calls. Simultaneously investigating the information content of vocalizations, their degradation within the species' 'acoustic habitat' (Brown & Gomez 1992) and their coding efficiency may prove to be a useful approach in understanding the selective forces shaping the size and structure of animal vocal repertoires.

It is important to note that the law of brevity explored here is different from Zipf's law (Zipf 1949), which explores the relationship between total frequency of occurrence of signals and their rank order (i.e. first, second, third...most commonly used). While Zipf's law has been more widely applied in studies of animal communication (e.g. McCowan *et al.* 1999; Hanser *et al.* 2004, but see also McCowan *et al.* 2005; Suzuki *et al.* 2005; Ferrer-i-Cancho & McCowan 2009), only the work of Ferrer-i-Cancho &

Lusseau (2009) has previously tested for patterns consistent with the law of brevity in non-human animal communication. Application of this approach to the vocal repertoires of other primate and non-primate species, as well as to other modalities of non-human animal communication, is now needed to investigate the generality of the relationship between signal length and frequency of use.

A valuable extension of this work would be to explore a second, and perhaps equally important, component of the efficiency of the coding system, namely the energetic cost of call production. In addition, it would be informative to explore how call function affects call duration over and above any relationship to frequency of use; alarm calls, for example, may be short not just owing to coding efficiency but also to reduce conspicuousness. Finally, and particularly in light of recent theories surrounding the role of gestural communication in language evolution (Corballis 2003; Arbib *et al.* 2008; Tomasello 2008), it would be informative to test for patterns consistent with the law of brevity in primate gestural repertoires, to see if they too share this fundamental characteristic of human language.

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