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Key issues in the study of primate acoustic signals, an update

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In our earlier review (Gamba & Giacoma, 2005), we highlighted the fact that studies of non-human primate vocal communication would benefit greatly from an in-depth study of phonation processes, and that anatomical evidence from investigations of the vocal apparatus should be considered. This is crucial from the perspective of the evolution of language and would allow an understanding of whether other species can voluntarily produce “new” calls using different combinations of vocal tract configurations, temporal and fundamental frequency patterns, or if they are unable to do so, due to genetic constraints on their communicative abilities. From a behavioural perspective, these communicative abilities can also help in the interpretation of acoustic variability, for instance when similar vocalisations are used in different contexts. In the past few years, studies on primate vocal communication have made several advances, increasing our knowledge of the role played by acoustic variation in providing information about group composition, sex, age and individuality.

Environment-and context-dependent variation

In recent years, as for various other animals, the study of primate acoustic signals has included consideration of those changes animals can introduce to increase the efficiency of transmission of the released output. Among behavioural patterns, three main strategies can be recognised: move to a more suitable position, increase call intensity, and vocalise when background noise is reduced. Previous studies have reported that the loud calls of non-human primates involve lower frequencies

than other calls within their vocal repertoires, which facilitates their transmission over long distances (Mitani *et al.*, 1998). To limit signal degradation in noisy environments, primates can also modify the timing of their calls. In a recent study, Versace *et al.* (2008) demonstrated that tamarins are able to extract acoustic cues from playback noise and to make flexible use of the timing of vocal signals in an artificial, noisy environment.

Changing the perspective from callers to receivers, the transmission of information can be strongly influenced by the context of emission. One of the key questions in primate communication studies still focusses on those utterances that are termed ‘functionally referential’ (Macedonia & Evans 1993). Since the pioneering works of Tom Struhsaker (1967), and Dorothy Cheney & Robert Seyfarth (1990) on vervet monkey alarm calls, it has been shown that non-human primate listeners are able to extract referential information from certain calls within the repertoire of a species, despite the fact that emitters may or may not intend to provide that information. Several studies have shown that context-specific alarm calls lead to different responses in conspecific listeners across various species (e.g. Barbary macaques, Fischer *et al.*, 1995; Diana monkeys, Zuberbühler *et al.*, 1997).

Among lemurs (*Varecia variegata variegata*, Pereira *et al.*, 1988; *Eulemur fulvus rufus*, Fichtel & Kappeler 2002; *Propithecus verreauxi verreauxi*, Fichtel & Kappeler 2002; *Eulemur coronatus*, Gamba & Giacoma, 2007; *Indri indri*, Maretti *et al.*, this issue), there appears to be a shared pattern that alarm calls given in the presence of aerial predators are highly specific, whereas terrestrial alarm calls are usually given in the presence of

terrestrial predators, but also in the presence of human observers, and in a more generalized context of high arousal or non-specific generalized disturbance. Moreover, Fischer and colleagues (1995) demonstrated that predator-type information may also be accompanied by other cues, such as the caller's arousal. Barbary macaques utter alarm calls, the acoustic structure of which varies significantly with predator type (frequency parameters) and with urgency (temporal features). In fact, vocalisations can be highly flexible in regulating social interactions and provide clues to various characteristics of the emitter, such as age, sexual maturity, gender and hierarchical position.

Wild chimpanzees of different social status give acoustically distinct screams during agonistic interactions, and victims appear to provide conspecific listeners with cues about the severity of the attack (Slocombe & Zuberbühler, 2007). Chimpanzees also exhibit a sophisticated understanding of their group's hierarchical relationships, as they can modulate the information provided by their screams depending on the composition of the audience.

Diana monkeys (*Cercopithecus diana*) are predisposed to use vocalisations within their repertoire in context-specific ways, but ontogenetic experience is important in determining how each individual produces utterances in series. In fact, although considered by most researchers to be the most invariable vocalisations, new evidence about the acoustic structure of alarm calls has shown a significant flexibility in relation to predation pressure in terms of how acoustic units are assembled into sequences (Stephan & Zuberbühler, 2008).

These studies show that, despite the limitations of their vocal repertoires, non-human primates can produce calls with a slightly different acoustic structure in different contexts, which may or may not provide listeners with different semantic and/or contextual information.

Individual- and sex-related variation in non-human primate vocalisations

Individuals are exposed daily to large numbers of conspecific vocalisations (Hauser, 1996),

the acoustic structure of which sometimes carries subtle individual-specific cues. Studies have shown that male and female macaques can make different use of similar vocalisations, and the receivers' responses differ depending on the emitter's sex (Whitham *et al.*, 2007; Greeno & Semple 2009; Arnedo *et al.*, 2010). Humans and non-human primates share the ability to identify other individuals from their vocalisations. This ability has direct implications for understanding how speech emerged in humans. Non-human primates also seem capable of misusing some of these vocalisations in order to benefit from the behaviour of conspecifics. Wild tufted capuchin monkeys (*Cebus apella nigrinus*) used functionally deceptive alarm calls to usurp food resources. Production of these calls varied in relation to food contestability, food quantity and the spatial position of the emitter in relation to other group members (Wheeler 2009). In crested macaques (*Macaca nigra*) only males gave loud calls, which showed no difference across different contexts (Neumann *et al.*, 2010), but these vocalizations encoded the caller's dominance rank in the acoustic structure.

In spite of sharing a general structure, vocalizations change during ontogeny in relation to several factors (Gamba & Giacoma 2005, 2007; Pistorio *et al.*, 2006; Gros-Louis *et al.*, 2008). Sex-related differences in the acoustic structure of the clear calls of chacma baboons (*Papio ursinus*) emerge at the onset of sexual dimorphism in body size and body mass (Ey *et al.*, 2007). Indris show sex-related differences in the notes given during the song, with male indris uttering longer notes than females across the whole song and in each of the shared note types (Sorrentino *et al.*, in press; Giacoma *et al.*, 2010).

Species-specific features and the phonatory apparatus

In our earlier review (Gamba & Giacoma, 2005), we reported extensively on the successful application of the source filter model of sound production to interpret vocal variation across

species and sexes. During phonation, resonance properties of the supralaryngeal vocal tract accentuate energy in some frequency regions while attenuating it elsewhere. These resonances, called formants, reflect the characteristics of the cavities of the vocal tract and can be studied to describe variations in the configuration of the oral vocal tract between different calls or different individuals within a species, or to investigate differences between species. In humans, vocal tract filtering was effectively described by computational models that reproduce certain characteristics of the vocal tract and calculate the acoustic responses determined by them. In the past, modelling of the non-human primate vocal tract was primarily aimed at the investigation of vocal abilities (inevitably compared with human vocal abilities) and strictly limited to resonance of the oral tract. The study of primate phonation often led to the conclusion that “simple” vocal tracts could not produce “complex” utterances. This was based on the debate between uniform and non-uniform vocal tracts, the former for a long time being associated with all non-human phonatory systems, and the latter being exclusive to humans. However, this approach led to some misunderstanding and several mistakes, resulting in a simplistic approach to the study of non-human primate vocalisations. A deeper look at the problem revealed a much more complex view of non-human primate phonation and a more interesting picture to investigate.

Different phonatory mechanisms are involved in particular utterances. The most important cavity branching from the oral tract in non-pathological humans is the nasal tract, which was thought to play a minor role in non-human primate phonation. It is now well documented, but for a very limited number of species, that primates can let the column of air coming from the lungs through the larynx resonate into the mouth or into the nose (Fitch & Hauser 1995; Gamba & Giacoma, 2006). Resonance taking place in the oral tract is, in most cases, reproducible by means of a uniform vocal tract of specified length (Lieberman *et al.*, 1969; Lieberman & Blumstein 1988). Resonance in the nasal tract is arguably more complicated to model because the nasal tract consists of various tubes of

different sizes (Gamba *et al.*, in press). The nasal tract in lemurs is longer than the oral tract, providing a resonance system that could potentially transfer acoustic cues about larger body size. At the same time, nasal resonance is not reproducible by means of uniform tube models, but is more reliably replicated by means of concatenated tubes of variable cross sectional areas (Gamba & Giacoma, 2006). However, more data are needed to test the theory that resonance may happen either in the oral or in the nasal tract, depending on the type of vocalisation. In fact, preliminary investigations of the anatomy of the vocal tracts of strepsirrhines have revealed that some species may be unable to separate the two systems (Kovacic *et al.*, 2008).

Another particularly puzzling case for researchers is those species whose vocal apparatus has cavities branching off from the supraglottal vocal tract. Some non-human primates have branching tubes in the form of inflatable or non-inflatable vocal sacs, which can cause an important variation in the formant pattern of the acoustic output. They can primarily change the acoustical properties of the vocal tract or modify the energy transfer at the glottis (Riede *et al.*, 2008). Riede and colleagues (2006) asserted that discontinuities in the Diana monkey's vocal tract could be responsible for the considerable formant shift in their calls. Lieberman (2006) criticised this hypothesis, bringing attention back to the interaction of the vocal sacs. Experimental simulations of various sac models showed that vocal sacs cause minor deviations from the uniform tube models (Riede *et al.*, 2008). However, air sacs can increase vocal variability and extend the frequency range (Riede *et al.*, 2008). They can also play an important role in shifting formant position, especially for the first formant (Riede *et al.*, 2008). In fact, it has been shown that the presence of air sacs results in the addition of extra frequencies to the spectrum of the vocal output (de Boer, 2009).

Future directions

Despite the increase in the number of studies examining vocal communication in primates using

detailed quantitative methods, there is still much that remains unknown or under-explored. Further investigation on the above-mentioned topics can provide valuable insights into the biology of primate species. Further comparative analyses of primate vocal repertoires will provide important data on the parallel evolution of vocal behaviour. The application of the comparative approach in the past was based mainly on data coming from qualitative analyses, but the increase in quantitative studies of primate vocal communication will certainly add new material for future comparative works.

In terms of vocal repertoire size, we encourage researchers to follow the path of those studies investigating the relationship between a vocalisation and the meaning of the utterance depending on the context of emission. This could throw light on, for instance, the effect of sexual dimorphism on the use of certain calls and, possibly, on whether the call system undergoes important modifications during development, and which specific call types are subject to modifications. The literature on great apes is particularly poor on this subject. This is surprising because the relatively limited vocal repertoire of the apes could reveal a much more complex picture if receivers and emitters are studied in the perspective of contextual communication. Some studies do, in fact, provided preliminary evidence on this topic (Slocombe & Zuberbühler, 2006).

Another major area we suggest for future investigation is interpretation of the vocal repertoire in the light of vocal tract morphology. Despite the fact that many diverse of primate species are currently maintained in zoos, and thus potentially available for post-mortem investigations, data on the vocal tract morphology of most species are lacking, including major uncertainties relating to the presence and function of aerial vocal sacs and vibrating structures. Augmenting the information currently available on vocal tract morphology would be the first step towards a better description of primate phonation processes. The application of medical imaging techniques, such as magnetic resonance imaging, would be a further step, which can provide detailed descriptions of specific phonation processes, including laryngeal and velum

movement, and help us understand how these processes contribute to sound production.

The application of vocal tract modelling techniques would be useful for building parametric models capable of reproducing natural sound patterns, and allowing the investigation of how individual characteristics, such as body size and vocal tract length and shape, actually influence the vocal output. Detailed descriptions of vocal tract morphology and anatomy and the collection of data on the luminal dimensions of primate vocal tracts could provide a more equilibrated evaluation of vocal communication and insights into decoding the long evolutionary road from vocalisations to human language.

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