Vocal Communication in Primates

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Abstract

Vocal communication is common in the animal kingdom. Researchers often examine vocal communication in nonhuman primates (primates) with the aim of identifying similarities and differences with human language and speech, in order to trace the evolutionary origins of our complex communication system. Primates can produce distinct calls in response to specific events, such as the discovery of a certain predator, and listeners seem to understand what these calls refer to. Although on the surface there are similarities between this type of communication and human referential words, the mental processes that underlie them may be very different. While in general the flexibility shown by primate receivers may demonstrate some commonalities with humans, there is much more controversy over whether there are similarities between the production of primate vocalizations and language. It is widely accepted that primates, unlike humans, lack the ability to generate new vocalizations. Although this means primates have a closed repertoire of calls that cannot be expanded, primates are capable of combining their existing calls to generate new messages. The degree of voluntary control and intentionality involved in the use of calls is also a matter of debate, with recent evidence on both a neural and behavioral level challenging traditional assumptions that primate vocalizations are used in an automatic, reflexive manner. More research is needed to examine the mental processes underlying communicative behavior in both the producer and the receiver. In the future adopting a more holistic, multimodal approach to studying primate communication is likely to challenge and ultimately improve our understanding of primate communication and the evolution of human language.

INTRODUCTION

Vocal communication is widespread across the animal kingdom and it has been well studied in a number of different species. The foci of such research has been wide ranging, but when studying our closest living relatives, the nonhuman primates (primates), much research has focussed on identifying similarities and differences between primate vocal communication and human language and speech. Such comparative research often aims to help us trace the phylogenetic history of human communicative abilities and to further our understanding of how human language may have evolved.

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The basic logic underlying this approach is that we can try and identify (i) elements of language that are shared with other primates and thus likely evolved in our ancient past, and (ii) elements of language that are uniquely human and thus likely evolved recently and that may represent the crucial elements that allowed our communication system to become so complex and powerful.

While primates, including humans, communicate using vocal, gestural and facial signals, vocalizations have traditionally been studied in isolation from other modalities. The vocal modality has been the most extensively studied in primates (Slocombe, Waller, & Liebal, 2011), and there may be several reasons for this. First, as human language is predominantly expressed through speech, vocalizations may have been the natural place to start to look for similarities between communication systems. Second, there are established methods for identifying, categorzing and analysing vocal behavior from the perspective of both the producer and the receiver: aspects that are much less established for gestures for instance. Lastly, given the visually dense habitat that many primates naturally inhabit, vocalizations seem to be the primary mode of communication in many species.

This review will examine some key similarities and differences that have been highlighted between aspects of primate vocal communication and human language, before outlining some recent cutting edge research which might challenging these traditional views.

FOUNDATIONAL AND CUTTING EDGE WORK

Researchers have identified several important similarities and differences between primate vocal communication and features of speech and language. Perhaps the most famous finding arose from the seminal work of Robert Seyfarth and Dorothy Cheney on vervet monkey alarm calls. Vervet monkeys face a range of predatory threats and they were observed to produce acoustically different alarm calls to different types of predator (Struhsaker, 1967). Seyfarth, Cheney, and Marler (1980) built on these observations to show that listening monkeys acted as if they understood the meaning of the calls. Vervet monkeys react in qualitatively different ways to their main predators (eagles, leopards and pythons) and playback experiments showed that monkeys produced the appropriate anti-predator response when a group member's alarm call was broadcast: the same response they would give if encountering the actual predator. Since this seminal work, further examples of alarm call systems that seem to refer to different predators have been found and evidence that food-associated calls provide listeners with information about the presence or quality of food has been generated (e.g., Hauser, 1998; Slocombe and Zuberbühler, 2005; Zuberbühler, 2000). Indeed, playback experiments have revealed that receivers are highly adept at extracting information about many aspects of their physical and social world from not only the calls of their own group members (Pfefferle, Heistermann, Hodges, & Fischer, 2008; Slocombe, Kaller, Call, & Zuberbühler, 2010), but also those of other species (Seyfarth & Cheney, 1990; Zuberbühler 2002).

Initially the alarm and food calls that provided listeners with information about external events were heralded as semantic and referential in similar way to human words and were seen as an important source of continuity between human and primate communication. There has since, however, been the realization that although these systems may appear similar on the surface, the cognitive mechanisms that underlie them may be very different (Macedonia & Evans, 1993; Rendall, Owren, & Ryan, 2009; Seyfarth & Cheney, 2003; Wheeler & Fischer, 2012). While human words are produced intentionally to inform others about events in the world, with both signaller and receiver sharing the concept associated with the word, this is not necessarily the case in monkeys. For instance, it could be that monkey alarm calls are a product of simple stimulus—response mechanisms, and that listeners have learnt to use these calls as reliable predictors of specific predators and as such are extracting information from calls that the caller may have never intended to provide (Seyfarth & Cheney, 2003). This highlights the importance of understanding the proximate mechanism driving a behavior—be it arousal, innate, or learnt stimulus–response mechanisms, emotional processes, voluntary control and an intention to change the behavior of another or an intention to change the mental states of another. Without probing the similarity of the mental processes that produce the behaviors, we may erroneously identify primate traits as homologous to human traits, when it is in reality two very different mental processes producing similar surface behavior.

Following the seminal work on referential alarm calls, there has been a strong focus in vocal research on understanding the informational content of vocal signals and playback techniques are perfectly designed for pursuing this line of enquiry. This has lead to a historical emphasis on context-specific vocalizations, while more flexible signals, that are given in a variety of contexts and therefore require the receiver to integrate the signal with other contextual information, may have been overlooked (Wheeler & Fischer, 2012). Such flexible signals have been readily identified in great ape gestural communication (Tomasello, 2008) and are argued to be more cognitively demanding on the receiver than signals with a one-to-one mapping between signal and event. Greater parallels are also drawn between such flexible communication and human language, which can be highly ambiguous and requires the receiver to integrate utterances with other contextual knowledge in order to fully understand the meaning (Carston, 2002). In contrast to gestures, there are comparatively few studies that focus on vocal signals being given in a flexible manner across contexts. However, the current lack of evidence for this kind of vocal communication may well reflect the relative absence of research effort in this area, rather than a genuine absence of ability for this type of communication (Liebal, Waller, Burrows, & Slocombe, 2013; Slocombe *et al.*, 2011). Indeed many alarm call systems are relatively nonspecific and given in response to a variety of events and innovative experimental field research by Kate Arnold and colleagues has investigated the processes underlying the interpretation of these more ambiguous calls by receivers. They have shown that female putty-nosed monkeys integrate information from different sources to infer the likely cause of a male's alarm calls, enabling them to react appropriately to these ambiguous calls (Arnold & Zuberbühler, 2013). Further research examining the pragmatic strategies receivers implement to understand flexibly produced calls and the cognitive processes underlying this behavior could reveal more similarities between human and primate communication.

One well-established and important difference between primate and human vocal communication is the ability to generate new vocalizations. Speech relies on the human ability to generate and imitate new vocalizations, however, other primates seem to have little or no capacity to generate new calls. Although reports of whistling orangutans and raspberry blowing chimpanzees (Hopkins, Taglialatela, & Leavens, 2007; Wich *et al.*, 2009), have shown that primates can invent new sounds, comparable evidence of generating new vocalizations that engage the larynx is lacking. Primates, in contrast to humans, have a relatively limited, genetically determined vocal repertoire, where the structure and range of calls an individual can produce is relatively impervious to experience and learning: species typical calls are produced by monkeys reared in acoustic isolation (Winter, Handley, Ploog, & Schott, 1973) and cross fostering experiments have shown that infant macaque monkeys produce calls more similar to their genetic rather than adoptive parental species (Owren, Dieter, Seyfarth, & Cheney, 1993). The fine control over orofacial muscles that humans possess that is vital for the production of the variety of sounds required for speech has been linked to a certain variant of the FOXP2 gene. Comparative research has shown that while primates have a highly conserved version of the gene, humans have a different variant of this gene that stabilized in the human population relatively recently in our evolutionary past (Enard *et al.*, 2002). Wider comparative work examining the function of vocal plasticity that is evident in more distantly related species, such as parrots, passerine birds and cetaceans (Janik & Slater, 1997) may be enable us to understand the evolutionary pressures that may have made the recent evolution of vocal plasticity in humans an adaptive trait.

The inability of primates to expand their vocal repertoire has lead to assumptions that primates have a finite number of "messages" that they can convey and that this limited, closed system is qualitatively different to the open generative human language system. However, the generative power of human language does not just derive from our ability to generate new words: We are able to express an infinite number of messages through the recombination of words into different utterances (Pinker, 1994). Do we see any evidence of anything similar in primates? While gibbons are capable of singing elaborately structured songs (Geissmann, 2002), the relation between the meaning of individual song elements and sequences of elements is unknown. More recent work by Arnold and Zuberbühler (2006) has, however, identified a simple combinatorial system in the forest dwelling Putty-nosed monkeys. Male Putty-nosed monkeys produce two loud calls, pyows and hacks, with hacks given primarily as alarm calls to eagles and pyows given as more general alarm calls to a range of disturbances, including leopards. They also combined these calls into a pyow–hack sequence which careful observational and experimental work has shown initiates travel in the group, in contexts unrelated to predation. Thus this simple combination of meaningful calls allows more messages to be conveyed, within the constraints of a system where new calls cannot be generated. More recent observational work has shown Campbell monkeys produce a number of different call combinations in context-specific ways (Ouattara, Lemasson, & Zuberbühler, 2009), and this may represent a more complex combinatorial communication system, however experiments demonstrating that listeners extract different meanings from these different combinations are still required.

Although many studies of primate vocal communication aim to elucidate the cognition underlying communication, comparably few studies have succeeded in probing the proximate mechanisms underlying the observable behavior. While playback experiments have proved powerful tools to investigate aspects of monkey cognition, such as understanding of hierarchical relationships (e.g., Bergman, Beehner, Cheney, & Seyfarth, 2003), relatively few studies have focussed on understanding the mental processes that underlie natural communication events. Zuberbühler, Cheney, and Seyfarth (1999) sought to do exactly this by using a prime-probe experiment to examine the processes underling receiver responses to predator-specific alarm calls. They tested whether receivers responded to specific acoustic features of the calls in a relatively inflexible manner or whether their responses were more likely mediated by some kind of mental representation. Their findings indicated that Diana monkeys seemed to process the meaning of the sounds they heard, rather than responding directly to the low level acoustic features of the sounds they heard, demonstrating an important aspect of continuity with humans.

In contrast to the cognitive processes identified in call receivers, the production of vocalizations has traditionally been attributed to emotional processes. Neurological studies revealed that in squirrel monkeys call production was triggered by the activity of subcortical brain areas including the limbic system (Jürgens, 1979) and there was no evidence of the direct connection between cortical motor areas and the larynx that characterizes humans. Although some primates have been successfully conditioned to produce vocalizations in response to arbitrary stimuli (Pierce, 1985), this often takes a considerable number of trials, indicating it is not an easy task for them to master. These classic studies have lead to prominent researchers, such as Michael Tomasello describing primate vocal production as automatic, unintentional and reflexive and as such it has been viewed as cognitively uninteresting and very different from human language. More recent, cutting edge research has, however, challenged this view.

From a neurological perspective, advances in technology have meant that the brain areas involved in vocal and gestural production in our closest living relative, the chimpanzee have now been examined and they seem very different from the results obtained from monkeys. Using PET scanners, Taglialatela, Russell, Schaeffer, and Hopkins (2011) have been able to determine that the homologue to Broca's area, that is critical for language production in humans, is active during the production of vocal and gestural signals. Although this cortical activity was present in chimpanzees who produced both vocal and gestural signals, it was absent in chimpanzees who just produced gestures, indicating that this cortical activation is critically associated with the production of vocal signals. The vocal signals studied here were "attention-getting" signals that have been reported to be novel signals invented in captivity to communicate with human experimenters (Hopkins, Taglialatela, & Leavens, 2007). The extent to which these signals engage the larynx is, however, currently unclear. If these imaging techniques can also be used to examine the neural areas underlying the production of species-typical vocalizations that do engage the larynx, it will greatly inform our understanding of the neural mechanisms involved in vocal production in our closest relatives: whether we will see more commonalities between the neural processes in chimpanzees and humans, or chimpanzees and monkeys is an open question and the answer will have important consequences for our understanding of how speech and language might have evolved.

From a behavioral perspective, observational studies have shown that primates are capable of adjusting their vocal production according not only to the presence of an audience, but the presence of certain individuals. For instance, vervet monkeys are more likely to alarm call when kin are present

(Cheney & Seyfarth, 1990a) and female chimpanzees suppress copulation calls when in the presence of high ranking females (Townsend, Deschner, & Zuberbühler, 2008). Recent field experiments have shown that wild male chimpanzees who are feeding silently on their own will start producing food calls if a playback simulates the arrival of an individual who is more dominant and a friend to the feeding male (Schel, Machanda, Townsend, Zuberbühler, & Slocombe, 2013a). These studies indicate that calls are not automatic and can be directed at specific individuals, but there is still debate as to the proximate mechanisms underlying such audience effects. While they might be indicative of voluntary control, other lower level explanations based on associative learning and emotional or arousal processes have also been offered, particularly for the more basic presence/absence audience effects (Hurford, 2007; Liebal *et al*., 2013). Anne Marijke Schel and Katie Slocombe have recently lead a team to rigorously test whether wild chimpanzee alarm call production is intentional (voluntary and goal-directed), using several established criteria for intentional signal production. These criteria of social use, gaze alternation and persistence have been extensively used to identify intentional gesture production in human infants and great apes, but had never previously been applied to a vocal communication system. Chimpanzees were presented with a moving python model and two types of alarm calls met these hallmarks of intentional communicative acts. These calls were more likely to be given in response to the arrival of friends rather than nonfriends irrespective of their rank, calls were accompanied by gaze alternation between the snake and recipient and callers persisted in vocalizing until all group members were aware of or safe from this ambush predator (Schel, Townsend, Machanda, Zuberbühler, & Slocombe, 2013b). There are alternative explanations that do not invoke intentional processes, for each of these individual criteria, however, obtaining convergent evidence from multiple criteria provides more robust evidence that these calls may be produced intentionally (Liebal *et al*., 2013).

Although chimpanzees may produce some calls intentionally, whether they are capable of vocalizing with the goal of manipulating others mental states is an important and open question. While monkeys have failed to inform ignorant offspring about food or predators (Cheney & Seyfarth, 1990b), chimpanzees have been shown to understand knowledge/ignorance states outside communicative contexts (Hare, Call, & Tomasello, 2001; Kaminski, Call, & Tomasello, 2008). One recent field experiment aimed to test if chimpanzees alarm called at a static model snake to warn ignorant, rather than knowledgeable individuals of the danger (Crockford, Wittig, Mundry, & Zuberbühler, 2012). Although callers did call more in the presence of individuals presumed to be ignorant rather than knowledgeable, in this field setting the researchers were unable to rigorously rule out the influence of other factors on calling, such as the caller's own previous knowledge of the snake and the behavior, rather than the mental state, of receivers.

To summarize, traditional views of primate vocal usage being inflexible, reflexive and driven by emotional rather than cognitive processes (Tomasello, 2008) are being undermined by cutting edge neurological and behavioral research. Neuroimaging techniques have revealed cortical involvement in the vocal production of our closest living relative and behavioral research has found that vocal production is mediated by complex social factors and that chimpanzees can produce calls intentionally, potentially to inform others of external events.

KEY ISSUES FOR FUTURE RESEARCH

While vocalizations are a key mode of communication for many animals, including primates, studying them in isolation may ultimately limit our understanding of communication. Communication in primates, including humans, is inherently multimodal, with gestural, olfactory, facial and vocal signals frequently being combined (Liebal *et al.*, 2013). Removing vocalizations from composite multimodal signals to study them in isolation may lead us to incorrect or incomplete understanding of the signal function and the proximate mechanisms underlying it. Currently many cross-modal comparisons are made, particularly between primate gestures and vocalizations, but the different methods, approaches, settings and assumptions that underpin research in different modalities means that these comparisons are likely invalid and many of our characterizations of vocal and gestural signals may be inaccurate (Liebal *et al.*, 2013; Slocombe *et al.*, 2011). Thus it is critical in the future that there is better integration between researchers focussing on different modalities and where possible a more holistic approach to communication is taken and integrated multimodal research is conducted.

More research is also needed to understand the cognitive processes underlying primate communication. When studying our closest living relatives it is often easy to attribute complex mental processes to the communicative behaviours we observe, without explicitly testing those assumptions. We need to design rigorous, ecologically valid experiments to directly test the proximate mechanisms involved and we must actively test alternative explanations. Broader comparative work that identifies communicative behaviour in less intelligent, distantly related species that is similar to that found in primates (e.g., Scott-Phillips, 2014) is particularly valuable for highlighting the need for directly testing the complexity of cognitive processes underlying primate communication. Similar behaviors can be generated by very different proximate mechanisms and so when searching for homologous traits that may have acted as precursors to human language, it is vital we are identifying behaviors that are similar on both the behavioral and cognitive level.

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