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Review article

Bidding evidence for primate vocal learning and the cultural substrates for speech evolution

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ABSTRACT

Speech evolution seems to defy scientific explanation. Progress on this front has been jammed in an entrenched orthodoxy about what great apes can and (mostly) cannot do vocally, an idea epitomized by the Kuypers/Jürgens hypothesis. Findings by great ape researchers paint, however, starkly different and more optimistic landscapes for speech evolution. Over twenty studies qualify as positive evidence for primate vocal (production) learning following accepted terminology. Additionally, the Kuypers/Jürgens hypothesis shows low etymological, empirical, and theoretical soundness. Great apes can produce novel voiced calls and voluntarily control their modification – observations supposedly impossible. Furthermore, no valid pretext justifies dismissing heuristically the production of new voiceless consonant-like calls by great apes. To underscore this point, new evidence is provided for a novel supra-genera voiceless call across all great ape species. Their vocal invention and vocal learning faculties are real and sufficiently potent to, at times, uphold vocal traditions. These data overpower conventional predicaments in speech evolution theory and will help to make new strides explaining why, among hominids, only humans developed speech.

The evolution of spoken language is a long-standing enigma in science (Christiansen and Kirby, 2003a,b; Ghazanfar, 2008). One of the axioms of the problem lays on the apparent lack of advanced vocal faculties in nonhuman great apes (hereafter *great apes*) – our closest living relatives. If present in great apes, it is argued, these faculties ought to allow them to control and modify the production of their vocal output, to expand their repertoire with new calls via vocal invention or vocal (production) learning (e.g. Fitch, 2017), and ultimately, develop vocal traditions (e.g. Bolhuis and Wynne, 2009). A new generation of data providing this exact evidence overturns the conventional axiom.

In this review, I start by briefly introducing some important points in the debate on animal cultures (Galef, 2004; e.g. Laland and Janik, 2006). I explain that the presence of vocal traditions, including in great apes, can be established in a relatively safer manner than other traditions, such as involving the use of tools (e.g. leaves, grassy stalks or wooden sticks, and stones). I then revisit the seminal definition of vocal learning (Janik and Slater, 1997), the capacity upon which vocal traditions rest. I briefly cite approximately twenty primate studies that qualify as positive evidence for vocal learning. These include both the modification of calls in primates in general (Takahashi et al., 2015; e.g. Watson et al., 2015) and the acquisition of new calls in great apes specifically (Lameira et al., 2013b; e.g. Wich et al., 2012).

The acquisition of new *voiced* calls in particular, involving vocal fold regular oscillation (and thus, voice) as sound source, has been presumed to represent the trigger for speech evolution after the split of the human lineage from the other great apes – an idea expressed by the Kuypers/Jürgens hypothesis (Fitch et al., 2010; Fitch, 2017; Fitch and Zuberbühler, 2013). This hypothesis conjectures that the capacity to acquire new voiced calls is absent in great apes due to the lack of a particular single neural wire in the ape brain (Fitch et al., 2010; Fitch, 2017; Fitch and Zuberbühler, 2013). I describe three fallacies in this hypothesis. First, I note how the work of both Kuypers and Jürgens could have never supported the hypothesis formulated under their name. Second, I cite critical studies showing that great apes can, in fact, do what they ought not by prediction under the Kuypers/Jürgens hypothesis (Lameira et al., 2015, 2016). Third, I clarify how the Kuypers/Jürgens hypothesis offers a weak entry point for the study of speech evolution. It tacitly disregards the role of *voiceless* utterances in speech evolution, which manifest (virtually always) as consonants in humans (such as the speech sounds/p/,/t/and/k/), as opposed to vowels, which are characteristically voiced (Lameira, 2014; Lameira et al., 2014).

I then explore why historical great ape language projects may have failed to produce more data, and I touch down on parallel research lines supporting that great ape vocal capacities have hitherto remained

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largely underestimated. Subsequently, I present data of new evidential nature across the entire great ape family to emphasize the significance of voiceless calls as one of the possible means through which great apes expand their call repertoire (besides via new voiced calls). I finalize by laying out the evolutionary implications of the cumulative evidence on primate vocal learning, notably in great apes. In sum, this review seeks to give a voice to great apes in the study of speech evolution.

1. Detecting great ape traditions

Great apes, like humans, are cultural animals (Whiten and van Schaik, 2007). This means two things. First, great apes own sufficient behavioural flexibility to invent new behaviours, i.e. inventions. Second, they can socially diffuse these inventions from informed to naïve individuals (Reader et al., 2011). Inventions become innovations at the moment of diffusion, i.e. new behaviours that have propagated via social transmission (van Schaik et al., 2006). If innovations survive through continuous chains of social transmission, over time and generations, they become local-specific traditions shared among individuals of the same group (van de Waal et al., 2013; Whiten et al., 2005). A particular collection of traditions that a population exhibits constitutes its culture, or cultural repertoire, and the underpinning mechanisms through which it is maintained become an additional means of behaviour inheritance to that of genes (Whiten, 2005). Culture can, thus, be defined as a collection of behaviours that, while spread socially, are resilient enough to be passed down across generations. This definition remains agnostic on whether other complementary cultural processes as seen operating in humans are also present, such as teaching, niche construction, or cumulative culture. In this way, culture is defined allowing operationalization in comparative terms and application to other species (Ramsey et al., 2007).

The detection of animal culture is, however, an empirical minefield (Krützen et al., 2007). One of the largest concerns relates to ruling out with (some degree of) certainty that ecology or genes are not determinants of behavioural differences observed between populations (Laland, 2008; Laland and Galef, 2009; Laland and Hoppitt, 2003; Laland and Janik, 2006). One of the most applied techniques for this has been the “method of exclusion” – if geographic differences in behaviour (namely, presence vs. absence between populations) cannot be attributed to ecology or genes, *then*, their nature can be concluded to be cultural (Laland, 2008; Laland and Galef, 2009; Laland and Hoppitt, 2003; Laland and Janik, 2006). Two examples in chimpanzee literature presented below illustrate the potential uncertainty associated with the method of exclusion, as well as how primatologists have been addressing this issue.

1.1. Ecological pitfalls

Tool use in chimpanzees for ant dipping has highlighted that setting aside ecological causes for “traditions” can be challenging (Humble, 2011). This is a technique to gather army ants from the ground and trees using a stick or stalk tool typically held between the index and middle finger and which, with a back-and-forth movement stimulates the ants to attack the tool. Once the insects climb on the tool, the chimpanzee collects it and ingests them. Chimpanzee populations exhibit differences in ant dipping techniques: some tools for gathering ants are present at some sites, while absent in others (Whiten et al., 1999). Because tool type and shape varied in *seemingly* arbitrary ways between geographic locations of the chimpanzee territory, ant dipping was initially proposed as representing a tradition (Whiten et al., 1999). Posteriorly, however, through the examination of ant behaviour between sites, it was defined that the level of aggressiveness of each ant species consumed by each chimpanzee population differed and could explain the type of tools that ape populations deployed (Mobius et al., 2008; Schoning et al., 2008). More aggressive ant species, for instance, required longer tools by chimpanzees to avert biting (Humble, 2011).

Nevertheless, the same researchers also came upon chimpanzee populations that used different tool techniques to prey upon the same ant species (Schoning and Humle, 2008), and in the meantime, new ant dipping techniques have been observed in other sites (Mugisha et al., 2016). These observations confirmed that chimpanzee culture involves ant-dipping behaviours in chimpanzees, but perhaps along with a smaller geographic range than initially assumed. As we will see later, great ape vocal traditions inherently remove many of the intricacies related to ecological confounds.

1.2. Genetic pitfalls

At the same time, detection of cultures can be affected by genetic factors. After the cataloguing of the putative cultural repertoire of wild chimpanzees (Whiten et al., 1999), it was observed that genetic and behavioural dissimilarity correlated strongly with each other (Langergraber et al., 2011). This relationship meant that genetic divergence could, after all, explain chimpanzee “culture.” In different phylogenetic analyses, however, this correlation did not bear out (Lycett et al., 2011, 2009). Behavioural differences are particularly challenging to explain within subspecies, since genetic differentiation is assumed marginal, returning, thus, support to a cultural explanation. Moreover, genetic correlation is not necessarily genetic causation (Lycett et al., 2007). Regardless the analyses that one favours, ultimately, several behaviours have proven to classify as “authentic traditions” in so far as they do not show genetic underpinnings. Further below, we will observe how genetics represent a less problematic bias in singling out great ape vocal traditions.

1.3. Supplementing the exclusion method

Misclassifying traditions inserts false positives within a species’ putative cultural repertoire. Scientists can, hence, be misled to overestimate a species cognitive and social capacities. To lower this risk, and complement the exclusion method, great ape researchers have gone back to the drawing board and designed experiments in captivity (Whiten et al., 2005; Whiten and Mesoudi, 2008). Captive settings provide a level of control often too challenging or virtually impossible to be achieved in the wild. Experiments in these regulated and supervised settings have now verified whether great ape innovations can, in fact, be passed on within a group. Resorting to “artificial fruits” (i.e. test boxes with more than one possible opening technique to give access to food inside), it has been demonstrated that once a particular innovation (i.e. opening technique) is seeded in a group, it disseminates and is perpetuated in that group (Dindo et al., 2011; Whiten et al., 2005; Whiten and Mesoudi, 2008). Great ape captive experiments with artificial fruits have supplemented, hence, observations made in the wild in a compelling way and in favour of great ape cultures. As we will find out further below, captive tests and diffusion experiments have also brought they weight to bear in great ape vocal research.

1.4. Emulation vs. imitation

The technical distinction of emulation vs. imitation has also been important in the debate of animal cultures (Galef, 2013) and deserves attention as it also brings forth important aspects in the review of great ape vocal traditions, as we will see later. This discussion does not revolve around the misdetection of animal cultures. Instead, it centres on the identification of the cognitive processes that make animal cultures possible. Emulation defines reproducing the results of behaviour, whereas imitation describes copying *the* behaviour (Tomasello, 1994). Each mechanism purportedly involves in this manner different types of cognitive machinery. Before artificial fruits experiments, it was undetermined which mechanism underpinned the diffusion of innovations in great apes. This work in captivity allowed (partly) addressing this weakness. Notably, experiments have provided evidence for imitation

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