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

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Highlights:

. Vocal traditions are more resistant to criticism than other traditions (e.g. tool use)
. Over twenty studies give positive evidence for primate vocal (production) learning
. Great apes produce novel voiced and voiceless calls and control their modification
. All great ape genera invented the same voiceless call independently and repeatedly
. Contra orthodox ideas, great apes make desirable models in speech evolution theory

Abstract (max 170 words)

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; 2003b; 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

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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 Zuberbuhler, 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 Zuberbuhler, 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 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.

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

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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

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presented below illustrate the potential uncertainty associated with the method of exclusion, as well as how primatologists have been addressing this issue.

Ecological pitfalls

Tool use in chimpanzees for ant dipping has highlighted that setting aside ecological causes for "traditions" can be challenging (Humle, 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 (Humle, 2011). Nevertheless, the same researchers also came upon chimpanzee populations that used different tool techniques to prey upon the same ant species (Schoning et al., 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.

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.

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.

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 between individuals (Galef, 2013; Laland and Galef, 2009; Tomasello, 1994; Whiten et al., 2009). The latest support in this favour has been provided by "ghost-demonstrations" of how artificial fruits operate, demonstrations that subjects fail to imitate (Watson et al., 2017; Whiten et al., 2009; Whiten and Mesoudi, 2008). Controversy over this matter is still ongoing in the field, however (Hopper et al., 2015). It is, therefore, safer to observe these data as non-conclusive and watch this space as future research and discussions ensue. It can be said, nonetheless, that much progress has been made in understanding the underlining dynamics of great ape traditions.

Why vocal traditions are different

With the animal cultures debate as backdrop, we can now gear up heuristically and zone in theoretically into the topic of vocal traditions, notably in great apes. Within the broad debate on animal cultures, vocal traditions provide today some of the strongest body of evidence (Laland and Janik, 2006). This may be due, partly, to favourable grounds regarding excluding ecological or genetic causal explanations, as well as issues surrounding the distinction emulation vs. imitation when vocal learning occurs within species.

Vocal traditions are distinct from other types of traditions. Unlike tool use that inherently involves a direct association with the surrounding *physical* environment of a species, vocal signals are primarily social, interactional and inter-organism behaviours. In the absence of any straightforward ecological prerequisite, it is hard to explain the occurrence of a vocal tradition on this basis.

Together with colleagues, we have in fact investigated in detail possibly the single case in primates where this is the case (De Boer et al., 2015; Hardus et al., 2009b; Lameira et al., 2013a). This rare example refers to wild orangutans modifying sound by positioning a hand or by holding detached leaves in front of the lips during vocal production. Only some populations exhibit these behaviours (van Schaik et al., 2003). Despite the dependence on a physical object for the performance of vocal behaviour, no ecological correlates have been identified that could explain the behaviour's occurrence at some sites and not in others (Krützen et al., 2011; Lameira et al., 2013a).

Signals only require a direct association with another animal, the receiver. This is not to say that ecology does not affect primate bioacoustics (Waser and Brown, 1986). There are, however, very few conceivable occasions when the *presence vs. absence* of a particular call across populations (while the remaining of the repertoire remains altered) could be explained by the presence vs. absence of an ecological factor or a stark contrast along an ecological gradient. To my knowledge, neither has such claim been posed to date in primates nor has this feature of vocal traditions been raised in the discussion of animal cultures – vocal traditions are exceptionally immune to misclassification due to ecology.

At the same time, no genetic mutation is known to function as an on/off switch for a particular call (Enard, 2011; Vargha-Khadem et al., 2005). Theoretically, it is therefore unwarranted to advance a genetic explanation for the presence vs. absence of calls across populations. It is even more marginally improbable for a mutation to have an on/off effect *while simultaneously* leaving the remaining of the species' vocal repertoire unaltered. Genetic mutations associated with speech development and accepted to have played a significant

role in the evolution of human language (i.e. mutations linked to the gene encoding the forkhead box protein 2, FOXP2) have been shown to affect the *entire* capacity of sound articulation, production and perception (Enard, 2011; Vargha-Khadem et al., 2005). Failure to express *one single* amino acid substitution in FOXP2 in humans, for instance, results in *total* disruption of vocal maturation and the development of language impairments linked with deficiencies in multiple brain areas (Enard, 2011). In great apes, genetic correlates of vocal traditions have been sought directly, but none were found (Krützen et al., 2011). Mutations, do not directly code, thus, a particular call, making vocal traditions exceptionally immune to misclassification due to genetics.

Vocal traditions are also relatively concern-free regarding the distinction between emulation *vs.* imitation (Tomasello, 1994). In vocal traditions, behaviour and its result are not dissociable. A different vocal behaviour – involving different articulatory manoeuvres – will, as a rule, lead to a different sound in most of the times. (Exceptions are known to occur in humans, enabled by our species' refined vocal control, a phenomenon referred to as motor equivalence (Ludlow, 2005)). This is also the case with gestures, for instance, where a different (e.g. hand) manoeuvring intrinsically changes the gesture, and thus, the function or meaning attributed to that gesture (Hobaiter and Byrne, 2014). Animal vocal articulation goes, to a large extent, hand in hand with acoustics. The distinction between the copying of a behaviour *vs.* its results is, therefore, less meaningful in the diffusion of vocal innovations between conspecifics than of other types of innovations.

The distinction between emulation and imitation is perhaps pertinent *between species*, especially far-related species, and admittedly, the terms may have hitherto been applied too loosely in the literature. For instance, outstanding feats of vocal learning in animals have been described (Ridgway et al., 2012), sometimes designated "imitation," including a remarkable case of human speech copying by an elephant (Stoeger et al., 2012). The sound-producing mechanism used by this individual involved positioning the trunk inside the mouth. Because this mechanism is different from how humans produce speech, this example better classifies, accordingly, as "vocal emulation." Articulation was not similar to the model (humans), and copying was most likely made strictly on the basis of acoustics. Even parrots that "imitate" human speech with astonishing resemblance are known to be anatomically prevented from correctly reproducing some human articulatory manoeuvres (Pepperberg, 2010a). In the technical sense, "vocal imitation" of human sounds is predicted to disproportionally occur more frequently in primates. The homologies between vocal apparatuses allow copying the same articulation (and its respective acoustic output), as it has been described in great apes learning human sounds (Lameira et al., 2013b; Wich et al., 2009).

Altogether, these circumstances are reassuring; vocal traditions sidestep most crucial points in the animal culture debate. Great ape vocal traditions offer, thus, evolutionary continuity to the emergence of human spoken language, at essence a cultural system. Because this possibility carries colossal implications in how we might frame and understand the evolution of our species, it is important to survey the foundations upon which vocal traditions stand upon – the capacity

for vocal learning. In the following section, I revisit the currently accepted definition of the term and I subsequently investigate what may and may not be assumed about great ape vocal faculties in this regard.

Great ape vocal learning faculties

Definitions

Vocal traditions sit on the capacity of *vocal production learning* (sensu Janik and Slater, 1997). Other forms of vocal learning have been classified focusing on perception, instead of production (Janik and Slater, 2000; 1997), and that have been demonstrated in nonhuman primates (Cheney and Seyfarth, 2005; 1992; Lemasson et al., 2013; Zuberbuhler, 2015).

Vocal production learning (hereafter *vocal learning*) defines the capacity of (*i*) modifying voice parameters (Pisanski et al., 2016) (hereafter *vocal learning by call accommodation*), which does not entail expansion of the species-specific call repertoire) and (*ii*) learning new calls (hereafter *novel vocal learning*), which entails call repertoire expansion. Together, these two faculties provide the most fundamental level of social learning necessary for the *maintenance* of vocal cultures.

The *emergence* of vocal traditions depends, however, on processes much less commonly quoted in the literature. Namely, vocal learning by call accommodation entails the accumulation of minute differences in the same call. These differences tend to emerge gradually over time, much like a phenomenon of drift (e.g. Watson et al., 2015). There is, therefore, no precise moment of inception of a vocal tradition through vocal learning by call accommodation. On the other hand, novel vocal learning depends vocal invention, which defines a

clear-cut moment in time. Vocal invention sparks a new call into existence, and novel vocal learning potentially assures its diffusion as a vocal innovation and its maintenance as a vocal tradition over time.

A wealth of data has been notably produced for some bird and mammal lineages regarding vocal learning and vocal traditions (Araya-Salas and Wright, 2013; e.g. Boughman, 1998; Janik, 2014; Jarvis, 2004; Pepperberg, 2010b; Petkov and Jarvis, 2012; Prat et al., 2015; Schusterman, 2008; Soha and Peters, 2015; Wilbrecht and Nottebohm, 2003). The *relative* paucity of similar evidence in primates has been interpreted as absence for vocal learning (Fitch, 2017), and thus, more generally, as lack of cultural precursors within the primate order for the evolution of spoken language (Bolhuis and Wynne, 2009).

The Kuypers/Jürgens hypothesis

The idea that great apes are non-vocal learners and, therefore, incapable of founding vocal traditions, has been formulated under the Kuypers/Jürgens hypothesis (Fitch et al., 2010; Fitch, 2017; Fitch and Zuberbuhler, 2013). It proposes that great apes lack relevant neural connections linking the centre for voluntary control in the primary motor cortex in the hominid brain and the nucleus ambiguous – site of the laryngeal motor-neurons in medulla oblongata enervating the larynx. Once in place, it is argued, these connections would have allowed great apes to exert the necessary level of motor control over vocal fold action to modify and acquire new calls (Fitch et al., 2010; Fitch, 2017; Fitch and Zuberbuhler, 2013; for a review of analogous neural circuitry in birds see: Jarvis, 2007; Nottebohm, 2005). The Kuypers/Jürgens hypothesis has, however, three fatal quandaries: one etymological, one empirical, and one theoretical.

Etymologically, neither Kuypers' nor Jürgens' work put forward the idea of a neural insufficiency for vocal control in great apes. Kuypers, a Dutch neuroscientist, distinguished as a Fellow the Royal Society of London for his microanatomical mappings of primate neuronal networks, observed in fact these "inexistent" connections in one of three chimpanzee subjects (pp. 237; Kuypers, 1958). The pertinent paper by Kuypers seems to be paradoxically used to support its exact opposite. Kuypers' accounts do not even reject the possibility of the presence of these connections in Rhesus macaques (pp. 227; Kuypers, 1958). A possible explanation for this oxymoron may be the fact that the articles formulating the Kuypers/Jürgens hypothesis (Fitch et al., 2010; Fitch, 2017; Fitch and Zuberbuhler, 2013) do not directly refer to the relevant work by Kuypers.

Also, propositions by Jürgens, a German neurobiologist, for a hypothetical uniquely-human neural circuit for vocal control have been rejected (Terao et al., 1997). They do not allow reasonably extrapolating which connections may or may not endow vocal control in the ape brain (comprehensively reviewed in Lieberman, 2012). Additionally, the work by Jürgens cited in the formulation of the Kuypers/Jürgens hypothesis (e.g. Fitch, 2017) never had great apes as study subjects, only monkeys (Jurgens, 2002; Jurgens et al., 1982). There is, therefore, no nexus to attempt upholding the work by Jürgens as a point of reference for what great apes might be able to perform vocally.

Empirically, the Kuypers/Jürgens hypothesis (Fitch et al., 2010) is invalid at two levels. First, multiple evidence for primate vocal learning exist. Vocal learning by call accomodation has been observed in several primate lineages (Tyack, 2008), including New World monkeys (Elowson and Snowdon, 1994; la Torre and Snowdon, 2009; Snowdon and Elowson, 1999), Old monkeys

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(Candiotti et al., 2012; Lemasson et al., 2011), and great apes (Crockford et al., 2004; Kalan et al., 2015; Marshall et al., 1999a; Mitani and Gros-Louis, 1998; Watson et al., 2015). The role of vocal learning has been particularly well demonstrated in captive marmosets (Gultekin and Hage, 2017; Takahashi et al., 2015; Zürcher and Burkart, 2017).

Second, evidence in primates also expands onto vocal invention and novel vocal learning, primarily observed in great apes, thus far (Hardus et al., 2009a; Hopkins et al., 2007; Lameira et al., 2015; 2013b; Watts, 2015; Wich et al., 2009; 2012). Critically, novel vocal learning specifically demanding active vocal fold control has been shown observationally in the wild (Wich et al., 2012) and in captivity (Lameira et al., 2015) (see video here, youtu.be/ab59zcsV35k). Vocal invention entailing vocal fold control has been observed in the wild (Hardus et al., 2009a) and experimentally demonstrated in captivity (Lameira et al., 2016) (see video here, youtu.be/Lg50_1RSc0E). Given that these observations should be entirely *impossible* under the Kuypers/Jürgens hypothesis, this volume of studies has been unexplainably overlooked.

Theoretically, the Kuypers/Jürgens hypothesis presupposes that animals can only expand their call repertoire through vocal fold (or voice) control (Fitch et al., 2010; Fitch, 2017; Fitch and Zuberbuhler, 2013). While such statement is correct for many species (who produce calls that are the product of oscillations of the vocal folds or some analogous structure, such as the syrinx in birds), including human voiced calls (characteristically expressed as vowels) and great ape voiced calls (or "vocalizations"), the statement is incorrect, however, regarding human voiceless consonants (e.g. /p/, /t/ and /k/) and great ape voiceless calls. Hominid voiceless consonant-like utterances neither depend on

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nor involve vocal fold control. They allow, nonetheless, an individual's call repertoire to expand through the voluntary manoeuvring of the lips, tongue, jaw, and/or musculature generating airflow through the vocal tract (e.g. abdominal musculature and diaphragm) for novel sound production (through vocal invention or novel vocal learning). Repertoire open-endedness is a paramount feature of any vocal learning species, and there seems to be no apparent reason to disregard the possible means through which great apes can indeed achieve this.

Moreover, across human populations, voiceless consonants represent the only consonant type that is universal in all of the world's languages (Lameira et al., 2014). There is evidence suggesting that their presence in human speech repertoire dates back to the original language spoken before the exodus of our species out of Africa (Atkinson, 2011; Knight et al., 2003). Accordingly, the ability of great apes to expand their species-typical repertoire with novel voiceless calls cannot be sensibly dismissed in the study of spoken language evolution on the basis that voice control is not involved (Lameira, 2014). Great ape voiceless calls represent a highly desirable and unique model to investigate the evolution of consonants in the hominid lineage (Lameira et al., 2017). To disregard their role as one of the building blocks of speech will undoubtedly hamper the reconstruction of spoken language evolution (Lameira, 2014; Lameira et al., 2014).

Altogether, the Kuypers/Jürgens hypothesis (Fitch, 2017; Fitch et al., 2016) is contradictory in its alias and cannot account for several lines of evidence that have been stockpiling over decades demonstrating primate vocal learning in general, and in great apes in particular. The dissolution of this

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hypothesis and its alleged roadblocks on the path for spoken language evolution along the hominid branch will allow factually appreciating great ape vocal faculties.

Historical great ape language projects

Thus far, the papers mostly quoted as proof for the seeming absence of vocal learning in great apes (and support to the Kuypers/Jürgens hypothesis, (Fitch, 2009)) are those of historical great ape language projects (K. J. Hayes and C. Hayes, 1952; W. N. Kellogg and L. A. Kellogg, 1967; Miles, 1993; Patterson and Linden, 1981; Savage-Rumbaugh and Lewin, 1994). These projects were mainly developed between the 60s and 70s, but some date back to the beginning of the century (Furness, 1916). Many of these projects raised young great apes in "experimental homes" designed to mimic the setting of a child growing up. Sometimes a great ape was simultaneously cross-fostered with a human child (W. N. Kellogg and L. A. Kellogg, 1967). One of the aims of these studies was to assess the extent to which great apes could acquire spoken language. The results are purportedly null because apes failed to produce human words in a recognizable way as a human child would (Fitch, 2017; 2009). However, Furness clearly states that his orangutan learned to produce human words, such as "papa" and "cup" (Furness, 1916). Furness also raised a chimpanzee, and he went so far to mention that, "In the whole, I should say that the orang holds out more promise as a conversationalist than does the chimpanzee" (Furness, 1916). This suggests that the two apes were exhibiting some performance regarding their vocal faculties since a comparison between the two as drawn by Furness would be otherwise senseless. The absence of any media records challenges,

naturally, evaluating the level of vocal achievement of Furness' orangutan and chimpanzee. If anything, however, these pioneer descriptions should be taken as suggesting positive, instead of null, vocal learning capacities in great apes.

Footage of the chimpanzee Vicki is among some of the earliest media records with audio available for great apes involved in language projects (C. Hayes, 1951). She too was reported to say "papa" and "cup," for instance (see video here, goo.gl/ARgndA). While word replication by Vicki was far from perfect, or what one could perhaps expect from a child of her age, she was nevertheless able to learn new, seemingly voiceless calls, expanding her repertoire in this fashion. There is no knowledge of chimpanzees producing voiceless versions of the word "papa" and "cup" in their natural repertoire.

Besides descriptions of word production, there is probably a simultaneous high rate of false negatives regarding other sounds produced by these great apes. Notably, there was virtually no knowledge at the time about the natural great ape call repertoire. Scientists had no means to gauge vocal production by their subjects. The modern description of the wild orangutan call repertoire was catalogued in the early 2000s (Hardus et al., 2009a), following pioneer reports in the 70s (Mackinnon, 1974; Rijksen, 1978). The gorilla call repertoire in the wild was catalogued less than five years ago (Salmi et al., 2013). The bonobo repertoire was described in captivity in the late 80s (de Waal, 1988), but only preliminarily outlined in the wild with the turn of the century (Bermejo and Omedes, 1999). For chimpanzees, some descriptions were produced in the 70s and 80s for the wild (Goodall, 1986; Marler and Tenaza, 1977) but a modern and comprehensive repertoire description is, alas, still missing. Fundamentally, all these works were produced *after* the start of most great ape language

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projects. The extent to which vocal learning capacities actually manifested in great apes involved in language projects remains, hence, an open question.

There are further reasons to remain cautious in the interpretation of historical great ape language projects as null evidence and consider these subjects as representative of their species and respective vocal faculties. BIZZARE settings (Barren, Institutional, Zoo, And other Rare Rearing Environments), for instance, have altering effects on great ape behaviour (Leavens et al., 2010). In what could perhaps represent parallel conditions in humans, children with a history of institutional rearing, such as orphanages, demonstrate low languages scores than children without such history {Spratt:2012hi}. No conclusions may be drawn, therefore, from the null results of great ape language projects before a thorough examination of the possible factors with an attritional impact on the individuals' development.

At the same time, scientists running these experiments were posed with the "first-generation coach syndrome." Besides no knowledge about the natural great ape call repertoire, there was no information about how to train or work with a great ape, and this still largely applies today for researchers working with captive great apes nearly 50 years after. If you, as a first-generation shepherd dog trainer, for example, failed to collect your sheep drove through the help of your dog, it would be most prudent to first appraise your skillset as a trainer and only then the skillset of your dog as a proxy of the entire shepherd dog breed. Some scholars have come to suspect that great apes in language projects may have performed poorly *because* the projects involved training, instead of natural exposure to the behaviours of caretakers without much explicit training or instruction, as it occurs during language development in children. This goes to

show that, due to their own pioneer nature within scientific research, anyone involved in these projects was ill-informed about how to work with great apes and engage them in cooperative communication and effective transfer of vocal skills.

In the reverse setting of great ape language projects, hundreds of human researchers have lived alongside wild great apes. Together, these studies have accumulated centuries of observation time in similar conditions under which infant great ape develop (e.g. Whiten et al., 1999). Nevertheless, the community of primatologists is still endeavouring to grasp the vocal communication system of great apes entirely. It further remains undetermined how good great ape researchers are in producing a great ape call or call combination *in a recognizable way as a great ape would*. In other words, it is superfluous and unhelpful to set up a benchmark for great apes based on the quality of their word imitation skills if humans do not meet the reverse benchmark.

It is understandable that, for some time, while data was scanty, historical great ape language projects served as a bastion in the literature. An important reason that has decisively contributed to the traditional interpretation of "null" results with regards to vocal learning in these great apes is the fact that many of these projects became remarkably successful once researchers shifted from teaching words to teaching gestural sign languages to the subject (R. A. Gardner and B. T. Gardner, 1969; Miles, 1990; Savage-Rumbaugh et al., 1985). This result certainly revealed that manual motor control is far more refined in great apes than vocal control. These results do not, however, warrant blank slating great ape vocal capacities to *zero*. Nor do they justify closing the eyes to the limitations that these studies posed to the subjects, and researchers alike, for reporting

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vocal learning. If anything, historical great ape language projects show that vocal learning is exceptionally difficult to great apes, but *possible* nevertheless. Now that new a generation of studies finally provides much-desired data, we cannot afford to overlook them and remain fixed in the past if we are to advance determinately our understanding of spoken language evolution.

Intentionality

New strides in a parallel research front help to exemplify we are well overdue in recognizing excellent vocal faculties in great apes. Intentionality defines the capacity to behave according to one's representations of others' mental states (sensu Dennett, 1988; Schel et al., 2013b; Townsend et al., 2016). This capacity was first found in gesture communication in great apes (Cartmill and Byrne, 2007; Luef and Liebal, 2012; Tomasello et al., 1985) and initially assumed siloed from vocal production (cf. Moore, 2016; Scott-Phillips, 2015; Tomasello et al., 1989). A new wealth of data has recently demonstrated, however, that this is not the case. Several great ape call types have been shown to be under intentional vocal production by obeying to several communication requisites, such as the monitorization of the receivers' level of information in order to adjust call production (Crockford et al., 2014; Genty et al., 2014; Gruber and Zuberbuhler, 2013; Schel et al., 2013b; 2013a; Townsend et al., 2016). Even though these studies all relate to "when" to call, instead of "how" to call, they show that major cognitive and vocal feats go well beyond what meets the eye. Thousands of hours of great ape behavioural observation are paramount in the endeavour of adequately registering the actual extent of their vocal capacities (De Waal, 2016; van Schaik et al., 2006). This will be the only means through which we will

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understand the full potential of great ape vocal communication as a precursor system for the evolution of spoken language.

New evidence

Shared vocal learning faculties in great apes

To illustrate the fundamental importance of long-term comprehensive empirical effort across *all* living great ape species (in captivity and wild), this section weaves together a collection of studies to demonstrate that a new type of vocal phenomenon occurs in great apes – *one hitherto unknown from any other animal clades*. Namely, these studies show that all great apes have invented the same call independently, providing, possibly, the first example of a *learned* call shared between all living branches of a phylogenetic family.

A recent paper on wild gorillas (Robbins et al., 2016) provided the last token in a logical frame of evidence validating the proposition that our closest relatives can exert advanced vocal invention and novel vocal learning skills. Robbins et al. described a vocal tradition only present in certain *Gorilla* populations but not others – the raspberry – a call consisting of blowing air through pursing lips. Because genetic on/off mutations do not directly map onto the production/preemption of specific calls while leaving the remaining of the repertoire untouched (as discussed above in *Why vocal traditions are different*), and because raspberries show no specific ecological requisites (e.g. presence of a particular tree species, as discussed above), its circumscribed geographic distribution suggests a cultural origin (Robbins et al., 2016). Raspberries were habitual (i.e. observed repeatedly in several individuals) in one population and

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present but less pervasively in another. Raspberries putatively represent, therefore, a vocal tradition maintained by novel vocal learning, which was in turn presumably the result of an event of vocal invention in the past. These data from the wild add to a description of an isolated case of a captive gorilla who also produces raspberries (Perlman and Clark, 2015).

Remarkably, this call type is also known to be produced by *Pan* (Hopkins et al., 2007; Marshall et al., 1999b; Watts, 2015) and *Pongo* (Wich et al., 2012), but, likewise, *only as a cultural call*. In other words, chimpanzees and orangutans produce raspberries in distinct populations where these calls are prevalent while being absent elsewhere in the genus' territory. In *Pan*, one population has been described to produce raspberries (Watts, 2015), with more than 60 individuals producing the call repeatedly. In *Pongo*, raspberries have been observed in separate, unrelated wild populations (Wich et al., 2012), with production being customary (i.e. shown most or all individuals) or habitual (van Schaik et al., 2003). In captive *Pongo* and *Pan*, raspberries have been observed in multiple populations (Hopkins et al., 2007 Lameira pers obs; Marshall et al., 1999b), suggesting general recurrent vocal invention or novel vocal learning by cultural founding effects (i.e. immigration of a raspberry-producing individual followed by novel vocal learning in the host population). Indeed, in captive chimpanzees, novel vocal learning of raspberries across generations has been verified (Taglialatela et al., 2012) in the form of a natural diffusion experiment as those deployed in studies focused on complementing the method of exclusion (as discussed above). In this case, it was shown that raspberries persist as vocal traditions even in captivity (Taglialatela et al., 2012).

While *innate* call types can be shared across closely related phylogenetic branches, including *within* the great ape genera (Davila-Ross et al., 2009), the phenomenon of shared raspberries appears to be an unprecedented case in the natural world of the same cultural call type being shared at a supra-genera level. It should be noted that there is no evidence to date for call homology *across* great ape genera, as it is known to occur in other primate clades (e.g. between *Papio, Theropithecus,* and *Mandrillus*). Even for calls expected to be under strong selective pressures and adaptive inertia, such as reproductive and alarm calls associated with high-risks/high-return fitness, no apparent similarities exist between the calls of *Pongo*, *Gorilla*, and *Pan*. The case for shared raspberries at the family level of Hominidae is, thus, notable.

The idea of a shared signal across great ape species is not surprising to researchers studying gestural communication (Graham et al., 2016; Hobaiter and Byrne, 2013; 2014; 2011; Roberts et al., 2012). Shared gestures, however, are presumed prevalent and customary in virtually all great ape populations, making it indeed difficult to attribute obligatory learning as a mechanism for the emergence of these gestures. Instead, in the case of raspberries, an attempt to explain this call's geographic distribution without invoking vocal learning would have to account for why raspberries are rare and restricted to very few wild populations wherein they are nevertheless prevalent, customary or habitual.

In support of the view that raspberries are the result of voluntary vocal control and novel vocal learning, an outstanding study by Bianchi et al. has shown that raspberry-producing *vs.* non-producing chimpanzees exhibit differences in brain architecture (Bianchi et al., 2016). Critically, the study identified *larger* grey matter in the homologous area to Broca's (specifically in

the ventrolateral prefrontal and dorsal premotor cortices) in the brains of raspberry-producing chimpanzees, but not in those of non-producing chimpanzees. The regions with observed extension in the brains of raspberry-producing chimpanzees are known to be responsible for orofacial motor control (Bianchi et al., 2016). Although these observations are correlational and not causal, they demonstrate that, either individuals required practice and development of enhanced vocal control for the production voiceless calls (which led to brain growth) or that individuals with naturally larger brain areas in said regions where those who better acquired new calls. Moreover, these observations were made across the impressive number of 69 adult subjects (35 raspberry-producing vs. 34 non-producing) across several ages, including both males and females in the two subsets. This means that, neurologically, knowing how to produce raspberries over-expressed beyond whatever brain differences could be expected due to the differential use of innate calls between individuals. In other words, differences in repertoire and call use between young vs. old, female vs. male, and very possibly, low vs. high ranking chimpanzees were not associated with brain differences, but differences regarding raspberries production were. This is strong evidence for a robust difference between calls acquired through novel call learning vs. innately.

Additional evidence for vocal invention and novel vocal learning comes from the context and function of raspberries in differing great ape populations and genera. In captive chimpanzees, raspberries are used at the end of pant hoots displays (Marshall et al., 1999b), or as a human-directed behaviour to gather attention (Hopkins et al., 2007). It also occurs in sanctuary bonobos (Z. Clay, pers comm), and captive orangutans (Lameira, pers obs). In wild

chimpanzees, they are produced during grooming sessions (Watts, 2015), something also observed in captivity (J. Call, pers comm). In wild orangutans, raspberries are emitted during nest construction (Hardus et al., 2009a; van Schaik et al., 2003), while in wild gorillas the context remains unclear, despite frequent observations of grooming and nest building (Robbins et al., 2016). These observations confirm that separate populations of each species had the capacity to invent and learn raspberries but attributed them to independent contexts and putative functions (Lameira et al., 2013a). The only recurring context that crosses genera is for gathering the attention of human caretakers in captivity (Hopkins et al., 2007). Raspberry production in this context is routinely a request for food in human possession. Raspberries hold, therefore, a clear communicative function in this context. These differences in raspberry context and function suggest that it may be meaningful to distinguish signifier (i.e. the signal itself) vs. signified (i.e. the signal's function) in great ape vocal traditions (Lameira et al., 2013a), where individuals must acquire and learn "what" or "how" to articulate a learned call (signifier) and "when" or "why" to produce it (signified) separately.

Significance of culturally universal raspberries across all great apes

Heuristically, this cross-genera evidence constitutes a step-change in understanding the phylogenetic backdrop wherein the evolution of spoken language ensued. Similarly to the general capacity of great apes to produce and use tools and the premise that this skill provided the behavioural basis for the emergence of human material cultures and technology (de A. Moura and Lee, 2004; Kühl et al., 2016; Roffman et al., 2012), there are now grounds to accept a

similar premise with regards to spoken language – at least as null hypothesis for future studies and test hypotheses. The converging research lines reviewed here across all great ape genera indicate they are cognitively and motivationally predisposed to invent and acquire new vocal behaviours through novel vocal learning. This occurs to the extent that one voiceless call, the raspberry, has recurrently emerged and has been maintained as a vocal tradition in the wild and captivity.

Because raspberries are present in some populations but absent in many others of the same species with no apparent genetic or ecological cause, they do not likely represent *per se* a shared *biological* trait. Instead, it is the underlining apt lip and airflow control required for their production, and the drive needed to vocal invention and learning that seems to have been present in an ancestral hominid. This level of socio-motor-cognition has made certain call types particularly likely to emerge as vocal inventions, which subsequently spread as vocal innovations and become part of the cultural legacy of certain populations in the form of a vocal tradition. Raspberries could be, thus, potentially classified as part of great apes' "zone of latent solutions" (Tennie et al., 2009), but some great ape researchers are yet to be fully committed to this concept (Whiten et al., 2009 and respective supplementary material). Great apes produce other voiceless calls (Lameira et al., 2014), but the observation that raspberries have specifically emerged repeatedly within and across genera indicates that the required articulatory and airflow control are well within reach of great apes. Anecdotal observations of a captive orangutan (Lameira, pers obs) and a captive chimpanzee (Lameira & J. Call, pers obs) living at different facilities but producing the same "clocking sound" (produced by the fast-downward release of

the front of the tongue from the hard palate) support this view; the key aspect here is supralaryngeal and air pressure control other than some unique aspect of raspberries in particular.

The natural predisposition to deploy this measure of motor control for sound production may originate from or relate to parallel selection pressures related to extractive foraging and oral "manipulation" of tools. This could help explain why voiceless calls are pervasively observed in great apes, and not in other primate lineages since great apes engage in complex oral processing of concealed foods and the operation of tools with the mouth (O'Malley and McGrew, 2000).

For the reason that raspberries do not rely on vocal fold action as sound source, but rather on supralaryngeal manoeuvring, this new phenomenon of a pancultural great ape call supports the view that voiceless calls were essential elements in the process of spoken language evolution, and that they represent a desirable model of human proto-consonants (Lameira, 2014; Lameira et al., 2017; 2014). Interestingly, monkeys may also produce voiceless calls, namely, lip-smacks that sometimes comprise an acoustic component, even though the signal often is strictly facial/visual (Barraclough et al., 2006). Monkey lip-smacks emerge in infants through similar means as human speech (Morrill et al., 2012) and exhibit the same open-close mouth rhythm as speech (Ghazanfar et al., 2013; Ghazanfar and Takahashi, 2014; Ghazanfar et al., 2012). However, monkey lip-smacks emerge in infants without the need for sensory feedback or experience, therefore, exhibiting signs that they are innately acquired (Ferrari et al., 2006). This contrasts with voiceless calls in great apes that show indications that they are acquired through vocal invention or learning.

Evolutionary implications and the new "ground-zero" for future research

In sum, the body of work above reviewed demonstrates that great apes have a much more sophisticated vocal control than hitherto alleged. They can modify calls that compose their repertoire (e.g. food grunts in chimpanzees). They can also invent and learn new voiced vowel-like (e.g. orangutan wookies) and voiceless consonant-like calls (e.g. raspberries), expanding in this fashion their sound range (much like humans learn new sounds during language development or the acquisition of a second language, even though with much lower ease). This capacity between great ape individuals linked by social transmission allows new variants and new calls to become established as vocal traditions that survive time and cross generations within groups. It is unjustifiable to delay progress in our understanding of the evolution of spoken language by asserted qualitative differences with the vocal and social faculties of our closest living relatives.

The cumulating evidence gathered by great ape vocal research suggests that hominid evolution saw a gradual expansion of vocal control. Namely, data indicate that the evolution of spoken language involved the voluntary recruitment of motor control of prior innate oral behaviours. In other words, voluntary vocal control allowed access to phylogenetically primordial primate behaviours formerly only deployable through reflective neuro-motoric hard-wires. The voluntary control of the jaw, lips, tongue, and airflow allowed the recruitment of innate voiceless calls (Ferrari et al., 2006), as occasionally observed in monkeys (Barraclough et al., 2006), and that express as learned consonant-like behaviours in great apes (Lameira, 2014; Lameira et al., 2015; 2014; 2013b; Wich et al., 2009; 2012). The voluntary control of the jaw allowed

the recruitment of innate speech-like open-close mouth behaviours (Bergman, 2013; Ghazanfar and Takahashi, 2014; MacNeilage, 1998), which express as a learned behaviour in great apes (Lameira et al., 2015). The control of vocal fold action for voice production allowed the recruitment of innate voiced calls characteristic of the primate repertoire in general (Boë et al., 2017; Fitch et al., 2016; Lieberman et al., 1969; Owren et al., 1997), and that can express as learned vowel-like behaviours in great apes (Lameira et al., 2016; 2015; Wich et al., 2012). Given the overwhelming evidence of great ape vocal faculties and the deficiency of traditional hypotheses to properly depict the vocal behaviour of this clade, the premises forwarded here offer a promising foundation and a solid new null hypothesis for fresh progress in the study of language evolution.

This innovative view will also inform language evolution theory in the larger comparative sense. How can we ever hope to understand the confluence of unique selection forces within the hominid lineage and their ensuing idiosyncratic result in our species, if we do not know how great ape vocal faculties *factually* compare with those exhibited by several other lineages, such as birds (Petkov and Jarvis, 2012), cetaceans (Janik, 2014), bats (Boughman, 1998), elephants (Poole et al., 2005), and far related primate species (Snowdon, 2017)? The study of these clades will offer insight into common selective pressures benefitting the use of and progress in vocal communication across living organisms and social systems. Yet, the stark fact remains: spoken language only evolved among hominids. Thus, together with knowledge of selective forces, to solve the puzzle of spoken language evolution will require knowing which anatomical and behavioural structures were targeted accordingly at the basis of our phylogenetic branch.

Decades ago it was supposed that a descended larynx was *the* feature that enabled humans to speak. Since then this idea has been proven incorrect since other species have also a descended larynx (Fitch and Reby, 2001), including great apes (Nishimura et al., 2003). This feature, while important, is now viewed as having contributed secondarily to the faculty of speech (Nishimura et al., 2008). Heuristically, however, incorrect means forward. After the overturn of the idea that "speech follows anatomy," researchers moved ahead theoretically, and come to consider that "speech follows the control over anatomy" (Fitch, 2017). This review shows that this next idea, while incorrect, enables now new progress, fundamentally preserving the momentum of renewal sustained by Fitch about a generation ago (Fitch, 2000). We can now say that, while important, great ape control over anatomy was a very improbable impediment for the emergence of speech in the hominid lineage. History repeats, and with it a much desirable advance of scientific theory.

Concluding remarks

New descriptions – in the wild and captivity – will continue to fill in the gaps of our knowledge about great ape vocal faculties and their potential correspondence with other species. As researchers find the means to overcome logistic (e.g. remote locations), biologic (e.g. slow life history and reproductive rates (Wich et al., 2004)), historical (e.g. continuously decreasing population numbers due to human action, (Marshall et al., 2006; Meijaard et al., 2011; 2010; Wich et al., 2014; 2008; 2016)) and ethical issues (e.g. via non-invasive protocols, (Lameira et al., 2016)) associated with studying (critically)

endangered great apes (IUCN Red List of Threatened Species 2016) (Estrada et al., 2017), these studies will provide a richer overview of the phylogenetic context in which spoken language emergence, as well as its most likely evolutionary trajectories. Given individual and population idiosyncrasies regarding call repertoire composition, future work should preferably comprise several thousands of hours of observation (van Schaik et al., 2006).

Assertions about vocal learning capacities orthodoxly presumed absent in great apes cannot be taken for granted or blindly accepted without proper preceding research effort across all living great ape genera. Existing evidence suggests there was no neurological silver bullet or epiphany for the emergence of spoken language along the human lineage (Ghazanfar, 2008). Great apes exert voluntary control over the primary musculature actions involved in speech production: laryngeal (Lameira et al., 2016; e.g. 2015), supralaryngeal (e.g. Lameira et al., 2015; 2013b) and oscillatory (Lameira et al., 2015). Prospective research may attempt to zoom in what motivates great apes to invent and learn new calls and expand their call repertoire. Such dispositions probably prompted our ancestors to increasingly rely on vocal communication in the course of language evolution. The process of speech evolution involved advances in both the biological and cultural domains that ensued over millions of years (Lieberman, 2015). Using great ape vocal faculties as a time machine back to our last hominid common ancestor will permit recognizing the humble, and yet significant and steady first steps taken towards full-blown language along the phylogenetic branch that would see humans evolve one day.

Acknowledgements

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