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EDITOR'S NOTE

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A translated version, in french, is available online (see Annex).

Une version traduite, en français, est disponible en ligne (voir le document en annexe).

1 Introduction

- 1 In classical philosophy, from Aristotle to Descartes, language is defined as an expression of thought (from greek "logos") that would be specific to humans. In this conception, thought and language are not dissociable and are what distinguishes humans from the other animals. It is difficult to find a single definition of human language that applies to all disciplines. For example, linguistics tends to focus on syntax, and phonology, Sociology insists on a symbolic system through which individuals communicate and through which culture is transmitted, genetics on the genetic foundations of language. Paleoanthropology, archaeology and neurosciences also have their own focus (for reviews see: Fitch, 2010, 2011; Wacewicz & Zywiczyński, 2017). According to the CNRTL ("Centre National de Ressources Textuelles et Lexicales"), language can be considered as a human communication system involving a set of

symbols, and this function is considered by many authors as different from the other animal communication systems (e.g., Hauser *et al.*, 2002; Berwick & Chomsky, 2016). Fitch (2011) uses the term “language” for “any system that freely allows concepts to be mapped to signals, where the mapping is bi-directional (going from concepts to signals and vice versa) and exhaustive (any concept, even one never before considered, can also be mapped)”. In linguistics, language is defined by the properties that characterize it (e.g., arbitrariness, displacement, discretion, etc., see Hockett, 1960).

- 2 In the field of ethology, animal communication can be defined as the transmission of a signal from an individual to one or several others, this signal being selected during evolution for its informative value. The sender produces a signal which is the physical medium of the information and causes a change in the behavior and/or physiological state of the receiver (Shannon & Weaver, 1949). This definition of animal communication is purely mechanistic, compared to that describing human language. Indeed, some researchers do not attribute language-like capacities to non-human animals because they consider that language is part of what makes us unique (e.g., Berwick & Chomsky, 2016; Chomsky, 1966, 2007; Hauser *et al.*, 2002; Lachlan & Feldman, 2003; Martins & Boeckx, 2019). Hence, these researchers defend a discontinuist scenario of language evolution where language is seen as a complex entity, that appeared suddenly and recently during evolution, only in the human lineage. On the contrary, a continuist scenario is also being defended in comparative studies that aims at revealing the structure, function and evolution of some cognitive human features (Fishbein *et al.*, 2020). The continuist position claims that studying homologous cognitive traits in various primate species (including humans) will lead to a better understanding of the evolutionary history of language in *Homo sapiens*. Because of their phylogenetic proximity with humans, non-human primates (NHP) might indeed share with humans some language features that are potentially inherited from common ancestors (for reviews see: Bouchet *et al.*, 2016; Call & Tomasello, 2020).
- 3 In the present article, we will first present some major differences between the discontinuist and continuist approaches and discuss their limitations. Then, in order to establish objective and relevant comparisons between human and non-human primates’ communication systems, we will propose a de-anthropocentric approach of the comparison between communication systems, including ours. We wish to propose a reflection aiming at encouraging future comparative studies to step back from the human language system to look for more general communicative features that are more likely to be shared across primates, including humans.

2 Human language vs. animal communication: a discontinuist approach

- 4 The discontinuist approach not only considers that language is what makes the human species unique, but also that this cognitive function is the result of sudden major qualitative evolutionary changes (see below the Merge model proposed by Berwick & Chomsky, 2016). According to that position, the human species does not share, at least as far as this faculty is concerned, any significant evolutionary heritage with other existing or even extinct species (Chomsky, 2007; Hauser *et al.*, 2002); there are no intermediate states to language (Martins & Boeckx, 2019), and this cognitive function results from a combination of singular genetic mutations and cultural transmission

that occurred only in the human lineage (Lachlan & Feldman, 2003). Although human language could be partly innate (see development timetable - all children go through the same stages of language acquisition, whatever their culture - and genetics, Berwick & Chomsky, 2016; Chomsky, 2007), postulating that humans do not share any language roots with the other species only contributes, we believe, to deepening the mystery of the human exception. Another less radical discontinuist proposal exists, that consists in considering language as the result of an accumulation of minor changes from speech perception to language *per se*, but the faculty of language is still considered unique to humans (Fitch, 2010; Jackendoff & Pinker, 2005; Liberman & Mattingly, 1989).

2.1 “Why only us” (Berwick & Chomsky, 2016)

- 5 The discontinuist / inneist approach gathers evidence proving that we, humans, are different from the other animals. This quest for human unique characteristics is not exclusively focused on language, but this cognitive function remains central in that quest (e.g., our uniqueness could also reside in the weight of the encephalon relative to body mass: Jerison, 1991; Noback, 1975; in the area of the telencephalon relative to the total area of the brain: Finlay & Darlington, 1995; Northcutt & Kaas, 1995; in the cortical thickness: Striedter, 2005; in the size of frontal lobes relative to other lobes: Striedter, 2005; in the length of the vocal tract: Liberman *et al.*, 1969). Hauser and collaborators (2002), for example, defend the idea that language recursion (i.e., the ability to insert repeatedly small language sequences into bigger sequences) is what makes us unique. Berwick and Chomsky (2016) proposed that the human singularity lies in our ability to build syntactic trees which results from one singular genetic mutation in *Homo sapiens*. Indeed, the ability to combine language units in different ways, which allows us to produce an infinite number of communicative sequences or sentences, would be what distinguishes our communication system from that of the other animals. Other features of human language have been proposed as functional candidates for explaining human uniqueness. For example, Tomasello & Moll (2010) have argued that shared intentionality is specific to human communication; Tattersall (2009) explained that symbolic thought and - by extension - language, is only found in humans. Dehaene *et al.* (2022) recently argued that the use of discrete symbols, associated to mental representations, and the composition of these symbols in recursive structures allow our species to build language, as well as music, mathematics, and science. These few examples illustrate the diversity of the characteristics that are supposedly specific to humans and the difficulty ending that quest. Moreover, different contradictions and reformulations of the arguments in these studies show that the hypothesis of a possible co-evolution or combination between these characteristics is ignored, maybe because they are, most of the time, studied in isolation.

2.2 Limits of a discontinuist approach

- 6 In a Philosophy of Science article, Lecointre & Huneman (2020) explain “If this separative (i.e. discontinuist) logic were pushed to its extreme, we would end up isolating each unitary entity. And in biology, this would go as far as each cell, even as far as each protein; to the point where it would be impossible to have words of general scope, and therefore to think.” (p. 79). This citation perfectly illustrates the limits of looking for unique and species-specific characteristics, from the point of view of

biology and classification. Indeed, looking for species-unique features makes no sense in terms of evolution since biological differences, and hence uniquenesses, are at the roots of speciation. Said differently, it is *impossible not to find* differences between two species because speciation (i.e., the very separation between animal groups) is based on differences. For understanding animal evolution and animal phylogenies, we need on the contrary to study general phenomena and nested constructions from the most general to the most precise. Resemblance seems to be the best tool to construct those nested constructions (Lecointre & Huneman, 2020). Moreover, as explained in Darwin's *Origin of Species* (1859), shared characteristics are evidence of ancestry. Thus, looking for homology and analogy appears to be the best way to understand language general phenomena and evolution. Homologous traits found in a variety of species are common traits (e.g., organs, behaviors) due to descent from a common ancestor. Analogous traits (also called convergent traits) correspond to functional resemblances between species that are structurally different and have no common ancestor.

3 Looking for homologies and analogies: a continuist approach

- 7 The continuist approach, that essentially comes from biology and neuroscience, looks for structures and functions shared by humans and NHP to defend the idea of a gradual evolution of language (e.g., Chater *et al.*, 2009). This approach hypothesizes that existing phylogenetically related species confronted to similar selective pressures might share similar cognitive components or properties inherited from their common ancestors. This approach is usually applied to the language components, like semantics, syntax, prosody, etc. (Hauser *et al.*, 2002 ; Masataka, 2003 ; Snowdon, 1997). To illustrate this point, we will detail the results of several studies in NHP that focus on some communicative components that are found in humans and predominant in the NHP literature (for a larger review see Bouchet *et al.*, 2016) : social learning, referential functional communication and combinatoriality. Here we will only be detailing work on vocalizations because this canal of communication represents the vast majority of NHP's communication studies (71 % of the studies in 2022 ; Liebal *et al.*, 2022), although a growing number of researchers are studying NHP communicative gestures (for reviews see : Call & Tomasello, 2020 ; Prieur *et al.*, 2020 ; Tomasello & Call, 2019).

3.1 Social learning

- 8 One of the key properties of human language is that it is acquired by infants through social learning. In ethology, social learning is defined as learning from others: more specifically, "learning that is influenced by observation of, or interaction with, another animal (typically a conspecific) or its products" (Heyes, 1994). Social learning can occur through various specific processes including imitation, local and stimulus enhancement, and teaching (for precise definition see Whiten & van de Waal, 2018). In humans, social tutors (mainly parents) drive the first exchanges of babble, then the first words and later the acquisition in children of the different aspects of language such as prosody, semantics, conversational rules (Masataka, 2003). Indeed, it has been shown for example that prelinguistic infants learn new vocal forms by discovering phonological patterns through their mothers' feedback (Goldstein & Schwade, 2008)

and that children's vocabulary progress is linked to the frequency of mother-child language interactions (Olson *et al.*, 1986). Moreover, infants' pointing elicits more verbal responses from parents, particularly object labels (Wu and Gros-Louis, 2015) and the dyadic combination of infant gaze-coordinated vocalization and caregiver response increase the later vocabulary size (Donnellan *et al.*, 2020). Contrary to human language, NHP communication was first considered as deprived of social learning. Indeed, the pioneering studies of the 1970s-1980s established that the development of vocal communication in monkeys was under the sway of a strong genetic determinism (e.g., Newman, 1985; and more recently Hammerschmidt & Fischer, 2019). For example, Geissmann (1984) realized hybridation studies on the songs of two gibbon species and showed that hybrid individuals produced vocalizations whose structure was intermediate between the two parent species, suggesting a strong genetic determinism on the scale of the overall structure of the song. Later, however, it was shown that there could be maternal influences, at the scale of note details in the song, but not on the overall structure of the song. Koda *et al.* (2013) for example have shown that agile gibbons infants' song acoustically converges, through learning, in terms of rhythm and shape of the notes towards the maternal song. During mother-daughter duet interactions in the first years of life, the daughter learns to synchronize her song and to match the shape of the notes to those of her mother's. Also, the mother uses a stereotype song structure as a possible learning support for her infant daughter. In marmosets, Takahashi *et al.* (2017) have highlighted that infants exhibit vocal production learning via social reinforcement from their parents. This learning is made possible through the experience-dependent increase in the control of the vocal apparatus that allows infant marmosets to more consistently produce phee calls (contact calls). In Campbell's monkeys, Lemasson *et al.* (2011) have shown that acoustic similarity of contact calls between individuals relies on the strength of the social bonds but not on the degree of relatedness between the individuals. The acoustic similarity of females' songs can disappear when the social bond between the females weakens. Finally, in Japanese macaques with despotic societies, acoustic similarity is linked to rank differences: subordinate females tend to copy the vocalizations of the dominant females (Lemasson *et al.*, 2016).

- 9 These few examples show that although the overall vocalization structure of many NHP is mainly genetically constrained, social learning clearly affects the fine structure of vocalizations in many species. Nevertheless, as suggested by Fischer *et al.* (2020), the vast majority of studies that reported positive evidence of vocal learning in NHP observe only minor changes within the species specific range of calls while, in humans, spontaneous imitation of words for example is open-ended. Hence, in most cases vocal convergence in NHP individuals seems to be analog to accent variations rather than to novel phonemes combinations making up new words.

3.2 Referential functional communication

- 10 Human language is also referential and functional. It is characterized by its "semantics" which is the ability to create association of arbitrary signals to convey to meaning, which allows humans to communicate on concrete as well as abstract events, objects (capacity of abstraction), that can be either close or distant in time and space (capacity of displacement)(Hockett, 1960). Playback experiments with calls have revealed that a number of non-human species show evidence of referential communication, defined as

the use of signals that refer to objects or events in the external environment (e.g., Macedonia & Evans, 1993, for NHP). This referential communication has points in common with the notion of semantics, but it lacks detachment from the immediate context, and therefore lacks the capacity for abstraction and the ability to displace, as opposed to human language (Hockett, 1960).

- 11 In their well-known early work (1980), Seyfarth and colleagues have shown that vervet monkeys use three different alarm calls, each one referring to a different predator. The authors proved that vervet monkeys classified alarm calls for leopards, eagles, and pythons. In a similar playback experiment, it has been shown that Diana monkeys also use different alarm calls for different predators (i.e. eagle and leopard), which demonstrates that the communication of these monkeys is referential as well (Zuberbühler *et al.*, 1997). Moreover, it has been highlighted in captivity that several species of primates were able to create new referential calls corresponding to new elements of their environment. For example, Slocombe & Zuberbühler (2006) have described in chimpanzees that rough grunt calls vary in their acoustic structure according to the palatability of the food items encountered. They also showed that particular rough grunts become meaningful labels that refer to specific food items, such as bread or bananas. Those “food-associated calls” were learnt in the context of captivity (bread, for example, is not a resource found in the natural environment) and were used not only by the group of chimpanzees but also by the newcomers in the group. In Campbell’s monkeys, it was found that individuals born in captivity no longer use the alarm calls normally associated with predators, but instead created a new anti-human alarm call (Ouattara *et al.*, 2009a). Altogether, these studies show that NHP can also use referential communication. Crockford *et al.* (2012) showed that the call is not a reflex but is adapted to the degree of knowledge of the conspecifics. Using playback experiments, they have shown that signaling chimpanzees were not only motivated by their own perspective but also took the receivers’ perspective with regard to the threat into account.

3.3 Combinatorial system

- 12 Human language is a combinatorial system: the combination of sound-units without inherent meaning (phonemes) makes elements (morphemes and words), and the combination of these meaningful units makes larger structures (sentences) whose meaning depends on syntactic rules (Hockett, 1960). This language property, which is also named “duality of patterning” (Hockett, 1960) allows humans to generate an infinite number of messages from a finite number of basic elements (Martinet, 1960). There are evidence today that different levels of combinations exist in NHP’s vocal communication (for a review, Zuberbühler, 2015). It should be noted here that many debates are emerging between linguistics and ethology concerning the application of linguistic terms to NHP’s communication systems (Schlenker *et al.*, 2023). In a paper aimed at characterizing the diversity of combinatorial rules found in the vocalizations of non-human animals, Coye *et al.* (2022) suggest that we might go beyond the traditional dichotomy between the articulation of phonemes and morphemes (respectively phonological and lexical syntax), because these sound units are notably difficult to adjust to NHP vocalizations.

- 13 In spite of this difficulty, some evidence of combinatoriality have been found in NHP species, at three levels. A first level is the use of affixation. For example, it has been shown that Campbell's monkeys use affixation to broaden the calls' meaning, by transforming a specific eagle alarm call into a general arboreal disturbance call, or by transforming a specific leopard alarm call into a general alert call (Ouattara *et al.*, 2009b). A second observable level consists of the combination of two simple calls into a complex call. For example, it has been demonstrated in a population of wild chimpanzees that almost half of the vocalizations resulted from combinations of different calls (Crockford & Boesch, 2005; and more recently, Leroux & Townsend, 2020). In this population, each vocalization was used in a specific context, and combined vocalizations had a new function, two pieces of information being conveyed simultaneously. Finally, a third level concerns the call sequences, which can be composed of many different calls. As a noteworthy example, males' alarm calls in Campbell's monkeys result from a complex combinatorial system where information is coded not only in the specific associations but also in the order or succession of the calls (Ouattara *et al.*, 2009b). The combination and order of six different basic calls can potentially convey several pieces of information. The organization of these vocal sequences can be predicted from the context that is given at the beginning of the sequence. Moreover, the rate of emission of the calls within the sequence is also found to be informative: it increases as a function of the imminence of the danger. Thus, a sequence combining different calls, with a precise order and a precise rhythm, can refer to a seen eagle or a leopard, a heard but not seen predator, a tree fall, the presence of another monkey group or it can refer to the departure of the group. This example may be the most complex example of combinatoriality in NHP vocalizations known to date.

3.4 Limits of the continuist approach

- 14 The studies described above completely overturned our knowledge of NHP vocal communication in the past forty years. They question the evolutionary history of language and tend to reduce the gap between human and NHP. Nevertheless, two major critics are usually opposed to that conclusion: first, human grammatical rules give to language combinatorial power that far surpasses the combinatorial evidence observed in NHP, and second, the limited size and closeness of NHP vocal repertoires restrict even more the combinatorial power of NHP vocalizations (Bouchet *et al.*, 2016). We believe however that these critics are weakened by major flawed premises: they result from comparisons and measures of non-human communication systems that use language as the one and only frame of reference. These comparisons preclude non-human communication systems from competing with language on human specific communication features. More problematic, by using a unique frame of reference, the continuist approach suggests implicitly that primates' evolution follows a single direction, towards humanity. In the following, we will question the anthropocentric idea of looking for specific characteristics of our communication system in other species and the use of language as the one and only frame of reference.
- 15 Although a growing number of studies on NHP communication are interested in gestures (e.g., in apes: Heesen *et al.*, 2019; Macaques: Gupta & Sinha, 2019; Baboons: Molesti *et al.*, 2020; Mangabeys: Schel *et al.*, 2022; New world monkeys: Larenas *et al.*,

2023 ; for reviews see: Call & Tomasello, 2020; Hobaiter *et al.*, 2022; Prieur *et al.*, 2020), the majority focus on vocal communication (71% of the studies in 2022; Liebal *et al.*, 2022). This exclusive focus on the oral-auditory communication canal represents only a small piece of the picture and *de facto* excludes primate species that do not vocalize much while interacting extensively. We are convinced the accent that is made on the vocal modality in most inter-specific comparisons results from our anthropocentrism, but fairer comparisons are possible.

4 Broadening the comparative approach

- 16 This section aims at enriching and broadening the continuist approach. We suggest to give-up using human language as the unique frame of reference and instead run comparative studies through the prism of evolutionary processes and interactional complexity, with multimodality as a crucial vector of this complexity. We believe this proposal might positively change our vision of primate communication and its evolution. This suggestion implies first, that we insist on the diversity of environments (social and ecological constraints) in inter-NHP species comparisons, second, that we explore the interactional structure of communication systems, third, that we investigate the role of sociality in the structure and expression of communicative interactions, and finally, that we fully integrate multimodality into comparative studies of NHP communication systems.

4.1 Diversity of primates and evolution

- 17 It is common to study NHP communication in comparison to human language. Although informative, this approach is biologically irrelevant since it compares two entities that cannot be compared: non-humans versus humans, i.e., millions of species vs. one. Within the primate branch, there is a huge diversity of ecologies, social systems and organizations, even within the same phylogenetic branch (for a review see Mitani *et al.*, 2012). In NHP comparisons, this variety offers possibility to investigate the effects of the physical environment (see the ‘efficacy-backup hypothesis’, Fröhlich & van Schaik, 2018; Heberts & Papaj, 2005; Partan & Marler, 2005) and social life (see the ‘social complexity hypothesis’: Dunbar, 2009; Freeberg *et al.*, 2012) on the evolution of communication systems. No need to say that future comparisons between human and NHP need to take into consideration the characteristics of each primate species and renounce to treat laboratory primate species (i.e., mainly macaques and marmosets) as a representative of all NHP.
- 18 As concerns NHP comparisons, recent papers have highlighted the role of evolutionary mechanisms (inertia and divergence) in the specific vocal systems of phylogenetically close species. For example, Coye *et al.* (2022) have shown that predation and social complexity play a major role in the evolutionary divergence of Campbell’s and Diana monkeys’ respective the vocal repertoires, even though these two species possess several homologous vocal units due to phylogenetic inertia. Those two closely related primate species are adapted to different ecological niches within the same habitat. Their respective vocalizations are adapted to these niches in terms of call structure, production patterns, total effective repertoire size and functional diversity of calls. Campbell’s monkeys (the species more exposed to predation) produce more

inconspicuous calls than Diana monkeys, suggesting that predation can influence the evolution of vocal systems. In a similar vein, Gustison *et al.* (2012) compared the evolution of vocal complexity in chacma baboons and geladas, two closely related primates that differ in their ecology and social structures. They identified multiple homologous calls but have also shown that the geladas, that live in complex social groups, have larger vocal repertoires. Geladas aggregate into multi-level, fission–fusion societies with long-term sub-unit “harem-like”, while chacma males primarily form temporary consortships with females. Their need to maintain long-term bonds within the unit seems most important and leader males use derived vocalizations after fights within their sub-unit. Gelada-specific vocalizations may therefore have evolved such as to maintain the relationships within the units. Finally, Rebut *et al.* (2020) compared structural complexity in the vocal communication of intolerant macaques (Japanese and rhesus macaques) vs. tolerant macaques (Tonkean and crested macaques). Within the monophylogenetic group of macaques, social interactions are more ambiguous in tolerant species than in intolerant species. The results of this comparison revealed that, in situations with a greater number of options and consequences (i.e., in agonistic and affiliative contexts), tolerant macaques show higher levels of vocal diversity and flexibility than intolerant macaques. This shows how communication systems can be shaped by the nature of the social ties. Together, these comparative studies highlight the utility of making detailed comparisons among closely related species to understand the evolution of communication systems. The authors were able to examine in detail the function of recently evolved calls and to reveal the role of the social and ecological characteristics of each species in this evolution. Altogether, these results show that focused studies of carefully chosen taxa, using directly comparable measures, allow us to dig the processes of evolution that are involved in the complexity of communication systems.

4.2 Language as a tool in a complex interactional system

- 19 In his paper, Levinson (2019) defends the idea that human language appeared during evolution as a consequence of the strong pre-existing interactional complexity of human societies. Said differently, language did not come first. In a similar vein, Beckner *et al.* (2009) describe language as a complex adaptive system that evolved from our highly interactive social existence. If interactional complexity shaped human language during evolution, then it makes sense to study this general phenomenon in a comparative perspective before, or in parallel with, focusing on the precise mechanisms of language. Looking for points of similarity in the interactional systems of various primate species might help understanding the evolutionary processes and precursors of interactional complexity and, thus, the evolution of language. According to Levinson (2019) and Beckner *et al.* (2009), complexity resides in interindividual interactions *per se* and language is only one of the tools involved in those interactions. According to these authors, human interactional complexity resides in the need for constant adaptations and readjustments, which leads to flexibility. For example, the behavior of human interacting individuals is modulated by their current and past interactions, and based on their socio-ecological experience. During turns of speech, repairing mechanisms can be observed when failures or refusals occur, which demonstrates the existence of adaptation strategies (Beckner *et al.*, 2009; Levinson, 2019). The behavior of interacting humans is also the result of different factors, from

perceptual mechanisms (multimodal signals and information) to social motivation (e.g., through joint attention), and finally, our interactional system is diverse, heterogeneous and in perpetual reorganization (Beckner *et al.*, 2009; Levinson, 2019).

- 20 We believe that this “interaction engine” (Levinson, 2020, 2019) might also be first in other primate communication systems and should be investigated for the sake of interspecies comparisons. Such an approach is beneficial in many aspects. First, it places the comparative cursor on the socio-evolutionary aspects of communication systems rather than on the communicative systems themselves. Second, it addresses the complexity of the interactions and the development of shared cultural communication strategies in a group. Third, it allows us to analyze NHP communication complexity in a broad and integrative way, avoiding the caveat of the human syntax-oriented approach. Fourth, it takes into account the simultaneous use of various communication canals instead of only one, like the vocal/auditory canal. Finally, it can be applied to many primate species while taking into account their biology and socio-ecological context, and therefore ensuring fairer inter-species comparisons.

4.3 Socially guided communication

- 21 The “social complexity hypothesis for communicative complexity” posits that living in a complex social system requires complex communication skills (Freeberg *et al.*, 2012). The sociality of a species would play the role of selection pressure in the evolution of communication. This hypothesis predicts the existence of a direct functional link between patterns of social organization and patterns of communication (Rebout *et al.*, 2020; Thierry, 2022). The effect of social life on primate vocal communication has been empirically validated in several large-scale studies (see Lemasson *et al.*, 2022). Nevertheless, these studies classically compare vocal repertoire sizes and group sizes between species and sometimes forget the interactive (“social”) dimension of communication.
- 22 This is not the case in Pournault *et al.* (2022). In this study, vocal interaction patterns were compared in phylogenetically close species (chimpanzees, bonobos, orang-utans and gorillas) that differ dramatically in terms of sociality. Indeed, these species present very different social lives, in terms of group size, group structure, and social organization. Therefore, they present the perfect profile to study the impact of sociality on “conversational rules” and on the different forms of interactional complexity. Pournault and colleagues (2022) have shown that, while orang-utans used principally isolated calling, chimpanzee, the most competitive species, presented a high proportion of overlapping vocalizations during their close call interactions, at the opposite of gorillas and bonobos, way more tolerant, who presented a predominance of vocal turn-taking. Those results highlight a gradation structure in social–vocal complexity: the most solitary specie, Bornean orang-utans, used isolated calls and showed a poor interactional system. On the other hand, for the three more sociable species, call overlap and turn-taking exchanges may represent two possible vocal alliance strategies, depending on the nature of the social bonds. These results suggest that the social lifestyle of the species has an impact on the interaction patterns, which highlights the importance of further research on the role of sociality on the evolution of communication systems in primates, including humans. Because of our intensive

interaction system, language evolution cannot probably be understood without taking into account its social component (Beckner *et al.*, 2009).

4.4 Reintegration of multimodality

- 23 It is important to note that we use here the term “multimodality” as it is used in comparative psychology, i.e. referring to multimodal signals as being due to simultaneous and sequential integration of the ‘modalities’ vocalization, gesture, and facial expression (Liebal *et al.*, 2014). Nevertheless, as explain by Fröhlich & van Schaik (2018), behavioral ecologists would rather focus on the senses employed to detect signals and thus, distinguish ‘multi-component signals’ if perceived within the same sensory modality, from ‘multimodal’, where components occur in more than one sensory modality (e.g., acoustic, visual, tactile, etc.) (Partan and Marler, 2005).
- 24 As explained by Slocombe *et al.* (2011), only 5% of the studies on primate communication systems consider multimodal signals. Recently, Liebal *et al.* (2022) have shown in a follow-up systematic review that primates communication research is still largely unimodal and that the approaches differ a lot across modalities, which makes it difficult to compare and to pool the data. Plus, the frequent focus on the vocal canal excludes *de facto* NHP species that do not vocalize much, and ultimately prevents us from considering other forms of communication complexity (e.g., combination of modalities, diversity and flexibility of signals). However, a growing number of studies show that the communication of several NHP species involves different types of signals and the combination of different sensory channels (e.g., in chimpanzees, *Pan troglodytes*: Hobaiter *et al.*, 2017 ; Pollick & de Waal, 2007 ; Tagliatalata *et al.*, 2015 ; Wilke *et al.*, 2017 ; bonobos, *Pan paniscus* : Genty *et al.*, 2014; Pollick & de Waal, 2007; howler monkeys, *Alouatta palliata*: Jones & Van Cantfort, 2007 ; crested macaques, *Macaca nigra* : Micheletta *et al.*, 2013). Human communication is also clearly multimodal and several important pieces of information come from gestural signals during conversations (Holler & Levinson, 2019). Indeed, humans frequently combine gestures, body movements, and facial expressions with speech (Ekman, 2004; Goldin-Meadow, 1999; Holler and Levinson, 2019; Iverson & Goldin-Meadow, 1998). Co-speech gestures occur even in the absence of learning (Iverson and Goldin-Meadow, 1998), and preverbal children communicate with combinations of sounds, gestures and facial expressions (Bourjade, 2022; Cochet & Byrne, 2016). Co-speech signals are presumably a way to enhance communication (Wu & Gros-Louis, 2015). An increasing number of studies emphasize the importance of considering multimodality to assess the full complexity of our communication system in the investigations that question the evolutionary origins of human language (Forrester, 2008; Fröhlich *et al.*, 2019; Fröhlich & van Schaik, 2018; Liebal *et al.*, 2014; Waller *et al.*, 2013). The main argument of this line of research is that human and NHP communication systems are multimodal and share numerous features, thought to be essential for human language, such as intentionality, flexibility, and ontogenetic plasticity. It is more and more acknowledged that focusing on a unique modality of signaling prevents researchers from apprehending the whole complexity of primate communication (Liebal *et al.*, 2014; Waller *et al.*, 2013). To study the structure and functions of multimodal signals, and understand the evolutionary constraints that may have shaped primates multimodal communication, including ours (Waller *et al.*, 2013; Liebal *et al.*, 2014; Fröhlich & van Schaik, 2018), it is necessary to formally describe the use of these signals, their modalities, as well as the circumstances leading to such

complex communication (interactional context, social life, physical environment, ontogeny, etc.) in several species (Forrester, 2008). Research on multimodal communication in NHP is starting to grow (e.g., Aychet, Blois-Heulin, & Lemasson, 2021; Aychet, Blois-Heulin, Palagi, *et al.*, 2021; Fröhlich *et al.*, 2019; Liebal *et al.*, 2022) and collaborations between disciplines allow us now to study of interactions in a more holistic way and to export the methods from one discipline to the others (e.g., pragmatics, computational sciences and ethology: Bohn *et al.*, 2022, analyzed signal combinations in chimpanzees through a computational modelling perspective; linguistics and ethology: Mondada & Meguerditchian, 2022, apply a multimodal conversation analytical approach to the study of baboon communication; for reviews see: Fröhlich *et al.*, 2019; Heesen & Fröhlich, 2022). Aychet, Blois-Heulin, & Lemasson, (2021) for example have shown that red-capped mangabeys use different sequences of communicative signals that varied in complexity and multimodal composition depending on social context and signaler characteristics. By taking into account the association of various communication signals (body, facial and vocal) and modalities (visual, audible and tactile), these authors have shown that red-capped mangabey can produce flexible communication sequences.

5 Conclusion

- 25 The present paper aimed at showing that comparative studies on communication evolution would greatly benefit from taking into account the environmental and social specificities of NHP when running comparisons between primates' communication systems. The demonstration of human-like features in the communication systems of NHP has provided insight into the understanding of our communication system's evolution. Nevertheless, it appears essential to make enlarged comparisons that are not only based on human language characteristics. In an egalitarian conception of the comparison between species, human communication shall be conceived as a multimodal and complex interactional system subject to evolutionary pressures. This paper presents theoretical perspectives for which it would be necessary to develop integrative methodologies (i.e., integrating the diversity of environments in inter-NHP species comparisons, the interactional structure of communication systems, the role of sociality in the structure and expression of interactions, and finally, multimodal communication) to facilitate and unify comparative studies.

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Declaration of interest

28 The authors declare no conflict of interest.

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ABSTRACTS

Language, according to classical philosophy, is considered as the expression of thought specific to human. This function is still considered qualitatively different from the rest of animal communication in several fields such as psychology, neuroscience or cognitive science, leading to numerous debates in the scientific community. Many comparative studies have been conducted during the past century, with the aim of revealing the structure, function and evolution of language's components, opposing a discontinuist vision to a continuist vision of this evolution. This article aims at proposing an integrative approach of the comparison between human and non-human primates' communication systems that goes beyond the opposition between discontinuism and continuism. We propose to encourage inter-specific comparisons of communication systems using the point of view of biology that, contrary to the discontinuist position and its quest for human uniqueness, study similarities between species (even non-human) rather than differences. Several works belonging to the continuist approach have shown that some characteristics of language can be found in non-human primates, such as social learning, functional referential communication or even forms of combinatoriality. Nevertheless, by using human language as the one and only frame of reference, these studies might miss some general communicative features that many primates have in common. We propose to enrich the conception of communication systems by considering them as comparable flexible interactional systems that produce a variety of combined multimodal signals, whose organization is strongly shaped by the environmental and social constraints.

La fonction de langage est encore considérée comme qualitativement différente du reste de la communication animale dans plusieurs domaines tels que la psychologie, les neurosciences ou les sciences cognitives, ce qui a donné lieu à plusieurs débats au sein de la communauté scientifique. De nombreuses études comparatives ont été menées au cours du siècle dernier dans le but de

révéler la structure, la fonction et l'évolution des composantes du langage, opposant une vision discontinuiste à une vision continuiste de cette évolution. Cet article vise à proposer une approche intégrative de la comparaison entre les systèmes de communication des primates humains et non humains qui va au-delà de cette opposition. Nous proposons de favoriser les comparaisons interspécifiques des systèmes de communication en utilisant le point de vue de la biologie, qui, contrairement à la position discontinuiste et à sa quête de l'unicité humaine, étudie les similitudes entre les espèces (même non humaines) plutôt que les différences. Plusieurs travaux relevant de l'approche continuiste ont montré que certaines caractéristiques du langage étaient présentes chez des primates non humains, telles que l'apprentissage social, la communication référentielle fonctionnelle voire la combinatorialité. Cependant, en utilisant le langage humain comme seul et unique cadre de référence, ces études pourraient passer à côté de certaines caractéristiques générales de la communication que de nombreux primates ont en commun. Nous proposons d'enrichir la conception des systèmes de communication en les considérant comme des systèmes interactifs, flexibles et comparables qui produisent une variété de signaux multimodaux combinés et dont l'organisation est fortement influencée par les contraintes environnementales et sociales.

INDEX

Keywords: Primate communication, social life, interactional system, comparative research, evolution

Mots-clés: Communication des primates, vie sociale, système interactionnel, recherche comparative, évolution

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