Fagot, J., Boë, L.J., Berthomier, F., Claidière, N., Malassis, R., Meguerditchian, A., Rey, A. & Montant, M. (2018). The baboon: a model for the study of language evolution. Journal of Human Evolution. 126, 39-50

The baboon: a model for the study of language evolution

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Keywords : speech, cognition, cumulative culture, gesture, statistical learning, memory

Abstract

Comparative research on the origins of human language often focus on a limited number of language-related cognitive functions or anatomical structures that are compared across species. The underlying assumption of this approach is that a single or a limited number of factors may crucially explain how language appeared in the human lineage. Another potentially fruitful approach is to consider human language as the result of a (unique) assemblage of multiple cognitive and anatomical components, some of which are present in other species. This paper is a first step in that direction. It focuses on the baboon, a non-human primate that has been studied extensively for years, including several brain, anatomical, cognitive and cultural dimensions that are involved in human language. This paper presents recent data collected on baboons regarding (1) a selection of domain-general cognitive functions which are core functions for language, (2) vocal production, (3) gestural production and cerebral lateralization, and (4) cumulative culture. In all these domains, it shows that the baboons share with humans many cognitive or brain mechanisms which are central for language. Because of the multidimensionality of the knowledge accumulated on the baboon, that species is an excellent nonhuman primate model for the study of the evolutionary origins of language.

Introduction

Theories on the evolutionary origin of language often consider that language has appeared in our species following the emergence of a distinctive morphological or other feature associated with it (e.g., Lieberman et al. 1969; Chomsky, 1988; Hauser et al., 2002). Following this approach, researchers tend to focus their attention on features that are supposed to be unique to humans. For example, Lieberman et al. (1969) claimed that humans are unique among primates in having a low larynx in their vocal tract and assumed that this can explain why humans are the only species to have speech. Another example in the cognitive domain is the claim that only humans have the cognitive capacities for recursion (Hauser et al., 2002) or, more generally, the ability to build and perceive hierarchical sequences (Friederici, 2017), and therefore that the emergence of language in humans is a direct consequence of this unique syntactic-like ability. Such positions on the emergence of language are intuitively appealing, but they raise a series of theoretical and methodological problems. For instance, the fact that our species is unique for a given biological or cognitive trait related to language does not necessarily imply that this trait is at the origin of the emergence of language in humans. Humans are unique in many respects, and therefore focusing on a single dimension to account for the emergence of a complex cognitive function like language might miss the critical role of other, potentially similarly important, uniquely human dimensions. Moreover, theories of human uniqueness can only be proved in studies showing that nonhuman animals do not have the capacity which is considered central for the emergence of language in humans. This position therefore raises the issue of demonstrating the absence of such capacity.

An alternative perspective on the evolution of language is to consider that language did not emerge because of a decisive change regarding a unique factor, such as the position of a low larynx, but that it emerged from a unique assemblage of complementary anatomical (body and brain) and cognitive processes. This perspective requires that the phylogenetic and ontogenetic histories of these components and their combinations are considered. However, following this strategy in many species is almost impossible for two reasons. First, it is technically difficult if not impossible to ensure that the same experimental protocol can be used with different species, due to the potential cognitive/perceptive specificities of the considered species. Second, precise homologies across species between brain structures, and among cognitive functions are difficult to establish (e.g., Marino et al., 2007; Reader, Hager and Laland, 2011), and the variabilities of brain structures and/or cognitive mechanisms inevitably increase with the number of species under study.

In this context, one promising strategy to study the emergence of language could be to focus on many cognitive and anatomical features in a limited number of nonhuman species, and to compare these assemblages to those of humans. Such a proposition protects us from interpretative errors by giving us a more balanced knowledge on the different factors that might have contributed to language evolution. To illustrate this point, consider the finding that a portion of a given sulcus is deeper in the right compared to the left hemisphere in humans, but not in chimpanzees (Leroy et al., 2015). Such asymmetry could be shaped by the evolution of language or the evolution of another function, or it could be the result of some neuroanatomical constraints that have no functional consequence. In the absence of precise knowledge of the role of that sulcus (structure/function relationship) in both species, the explanatory contribution of such human unique feature in language evolution scenarios remains limited. The same reasoning holds in the cognitive domain. Humans have a unique ability to process complex syntactic rules, in comparison to other species, and it was hypothesized that this difference can be explained by the fact that only humans can represent structures in a hierarchical way (Fitch, 2017). However, the fact that non-human primates process sequences of a lower level of complexity than humans might more simply be explained by more limited working memory spans (e.g., Fagot & de Lillo, 2011), preventing processing of the complex sequences. We believe that we could gain greater understanding of language evolution by studying different cognitive processes across species, including domain-general functions, such as memory, that might be at the roots of potential human-nonhuman differences. Fagot et al. (2018) claimed that much can be learned about the evolution of language if domain-general functions are studied in an evolutionary perspective. Their rationale for focusing on domain-general dimensions to study the evolution of language is inspired from the re-use principle of Anderson (2010): because language is a complex and phylogenetically recent ability, it probably results from intense re- use and re- combination of inherited components. More generally, this multidimensional approach of language evolution should also include physical (body), neuroanatomical and cultural dimensions, in addition to the domain-general cognitive dimensions cited above, to better understand how all these features combine, interact, and in what aspects they are truly equivalent to human abilities.

In this article, we bring attention to baboons (*Papio* ssp.) as a potentially interesting animal model to study the emergence of language. There are several reasons for this. First, baboons are phylogenetically close to humans (apes are closer, but they are less abundant and fewer studies of them have been undertaken), and thus humans and baboons share a large number of anatomical, cognitive and behavioral traits. The phylogenetic proximity of baboons and humans limits the number of factors to consider when identifying potentially critical differences that might be at the origins of language. Second, and most importantly, baboon cognition, anatomy, ethology and genetics have been extensively studied during the past decades. The availability of such a large amount of data on the same species allows us to design experiments that fit precisely with the cognitive architecture of the species. Moreover, being able to compare human to nonhuman primates across a number of aspects has the potential to broaden our perspective on the evolution of language. In this context, the main goal of this article is to present a selection of the data collected so far on baboons that, when compared to humans, might inform us about the origins of language. We present what is currently known about a selection of domain general functions in baboons that are of interest for understanding language evolution, before documenting the findings on more language-related functions, such as vocal production, communication through gestures and cultural transmission in the species. It is worth noting that although we focus on baboon research in this article, we do not imply that the baboon is the only valid animal model for the study of language, and this matter is examined further in our Discussion.

Domain-general functions

Domain-general functions correspond to the cognitive mechanisms, such as memory, that apply to a variety of functions beyond language (Saffran and Thiessen, 2008). Domain-general functions have been studied extensively in baboons, in our laboratory and several others. Considering that this article is on the use of baboons as potential animal model to study language and its evolution, we will pay special attention to studies conducted in the domain of short- and long-term memory, and statistical learning, because of their importance for language.

Short- and long-term memory capacities

The concept of short-term memory corresponds to the capacity for holding and maintaining information for a short period of time. This sort of memory is clearly important in language to keep track of the words within a sentence (see below, in the section dedicated to long-distance dependencies), but also for the rapid verbal learning (Kimppa et al., 2015) of the numerous words in a lexicon (Brysbaert et al., 2016). Brain connectivity changes in relation to short term memory in the perisylvian brain region are suspected to have played a major role in the evolution of human language (Schomers et al., 2017), and information about short-term memory capacities in baboons can be found in Fagot and De Lillo (2011), and Rodriguez et al. (2011). Fagot and De Lillo (2011) used an adaptation of the Corsi Block-Tapping test. In this test, the Guinea baboon (*Papio papio*) had to first observe a screen on which several identical squares were progressively added in such a way that the display contained a first square, and then two, and three, and so on, until the full test sequence had been presented. Immediately after that presentation, all the n squares of the sequence were displayed simultaneously on the screen and the baboons had to touch them in the same order as they appeared during the presentation phase. Results of these findings are shown in Figure 1A. The two Guinea baboons tested in this study solved this task with an above chance performance for sequences lengths of three or four items. One of them was above chance with five-item sequences, although its performance was very low (expected probability from chance =0.0014). These results therefore suggest a Corsi-memory span between four and five items in this experiment. Comparison of these results to those of humans tested in the same condition suggests that the short-term memory span is smaller in baboons than in humans (see Fig. 1A). Rodriguez et al. (2011) also measured the durability of the short-term memory system in baboons (but provided no information on the subspecies to which their subjects belonged). Their experiment used a delayed matching-to-sample (DMTS) in which the delay between the presentation of the sample and comparison images varied between 0 and 16 seconds. The performance dropped from nearly 95% correct to 70% correct when the delay increased (data inferred from their Fig. 1A), suggesting that this information can be maintained in the short term in the 0 to 16 seconds range. The above two studies support the claim that the baboon can store a large amount of information in short-term memory, albeit smaller than in humans, and that baboons can maintain this information in short-term memory in a small temporal range.

Insert Fig. 1

Another important ability for language is the capacity to keep a large amount of information in long-term memory. This long-term memory system is crucial for the storage of phonology, semantics, grammatical rules, pragmatics, and many other aspects of language (Greene, 2005). Human adults can, for instance, permanently store the names of objects and draw on a mental lexicon with more than 20,000 entries (Forster, 1976; Nation, 1993).

The ability of Guinea baboons to store the association between items in long-term memory was tested by Fagot and Cook (2006). In this study, these authors presented a randomly selected sample picture on a screen, after which two choice stimuli were displayed on the right and left sides. The correct response to each picture was randomly chosen and permanently assigned at the outset of training, and the database from which the sample image was selected in each trial progressively increased during the three years of the experiments. Therefore, the baboons had to learn and remember each picture and its associated response to be able to select the correct response. This challenging task revealed impressive long-term memory capacities. First, averaged over the last 75 sessions of testing, one baboon was 78% correct with a set size of 5910 pictures, the other was 80% correct with a set size of 6180 pictures. The fact that the performance is still high with a set size of about 6000 pictures suggest that their long-term memory capacity was not even saturated at the end of the experiment, and that they could have probably learned thousands more picture-response associations with prolonged testing. Second, with respect to the issue of forgetting, analyses of the trial performance as a function of the time lag between consecutive presentation of the same picture revealed that the long-term memory of specific items could last over approximately one year and tens of thousands of intervening trials. This study has been replicated in a human subject (Voss, 2009) revealing highly comparable results, regarding both the number of items that the two species can keep in mind, and the rate of forgetting. Taken together, these studies on short and long-term memories therefore suggest that baboons have weaker working-memory capacities than humans, but that the two species have roughly identical long-term memory capacities.

Statistical learning

The ability to detect environmental regularities is a fundamental aspect of human and non-human cognition that has been intensively studied over the last decades (Rey et al., 2018). It is also a central feature of language acquisition and language processing (e.g., Frost et al., 2013; Misyak and Christiansen, 2012). This fundamental ability allows human and non-human animals to detect and encode various kinds of regularities simply by being exposed to or processing these regularities. Because these regularities can be extracted and memorized without any intention, Conway and Christiansen (2006) proposed that the ability to detect these regularities corresponds to an implicit form of statistical learning. The Guinea baboon’s ability to extract regularities has been studied in two domains, the first one focusing on the learning of spatial statistics, and the other more on the learning of temporal statistic inferred from sequence learning.

Spatial statistics To the best of our knowledge, the learning of spatial statistics in baboons has been investigated in two studies. Goujon and Fagot (2013) trained Guinea baboons to detect a T-shaped target on a screen, among various configurations of L-shaped distractors (displayed in different orientations). Two contextual cueing conditions were used in this study. In the first condition, the target was presented on a background of distractors providing no information on the target’s location. In the other, the spatial configuration of the background distractors was predictive of the target location. Baboons quickly demonstrated statistical learning in this task: response times to the cued locations rapidly became shorter, after a few dozens of trials, compared to the non-cued location.

The second study on the learning of spatial statistics in baboons is Grainger et al. (2012). Researchers in this study demonstrated that the Guinea baboon can be trained with touch screens to discriminate real English four-letter words from four-letter strings that are not words and can furthermore successfully categorize novel word and non-word stimuli never seen before, after training (Fig. 2).

Insert Fig. 2

Examination of the baboons’ strategies via a modelling approach (Hannagan et al., 2014) showed that this discrimination between the words and non-words involve the learning of particular bigram or trigrams that were statistically more frequent in the word than the non-word categories. This performance can be accounted for by the baboon’s ability to detect the statistical regularities between and among words, and to develop an open-ended representation of the word and non-word categories on that basis (Fagot, 2017).

Temporal statistics Temporal statistics have mostly been investigated in the human literature by using serial response time paradigms. A method combining the advantages of the artificial language paradigm (Saffran et al., 1996) and the serial response time task (Nissen and Bullemer, 1987) was used in several studies with a group of Guinea baboons. In Minier et al. (2015), Guinea baboons had to touch a red circle appearing at nine possible positions on a touch screen (see Fig. 3). Reinforcement was provided after each series of nine touches. To study the fine-grained dynamics of regularity extraction, three triplets of fixed positions were created and the sequences of nine touches performed by the monkeys corresponded to a random combination of these three triplets. In that situation, within each triplet, the first position was totally predictive of the second, which was also totally predictive of the third. If baboons can learn these regularities, then their response time on the second and third positions of a triplet should decrease over time due to the development of expectations. Minier et al. (2015) indeed observed a progressive decrease in response times depending on the amount of exposure to the regularities and they further observed that responses times on the third position of a triplet decreased faster compared to the second. This last result indicates that monkeys used not only the immediate co-occurring position to predict the next, but they could also use broader contextual information (i.e., the first and second positions) to predict the response on the third position.

Insert Fig. 3

Recently, using the same experimental set up with human participants, Rey et al. (2018) obtained similar patterns of results regarding the evolution of response times for the second and third positions in a regular triplet. However, they also found a striking difference between baboons and humans. Indeed, in that experiment, the three triplets were presented in random order to compose the sequence of nine touches. Response times on the first position of the triplets are therefore not predictable, except for the third and last triplet appearing in the sequence. If participants (baboons or humans) had extracted the more global structure of the experiment (i.e., the fact that three triplets are presented randomly to create the sequence of nine touches), then response times on the first position of the third presented triplet should also decrease over time because, by deduction, it should become progressively predictable. The data revealed that only humans displayed such a decrease in responses times on the first position of the last triplet, suggesting that they not only extracted the local regularities (like baboons) but also the more global regular structure.

Similarly, it has long been thought that non-human animals cannot learn non-adjacent dependencies. Non-adjacent dependencies are constitutive of human language, in particular syntax (e.g., Sandoval & Gomez, 2013). For example, in German sentences the verb is often separated from the subject by a series of words. However, several recent studies have shown that under certain circumstances, non-human animals can extract these regularities (for a recent review, see Wilson et al. [2018]). Malassis et al. (2018) also compared the performance of Guinea baboons and humans in a task in which they had to produce three-target sequences containing regular relationships between the first and last target locations (and no regularity on the second position). In this experiment, both baboons and humans could learn these forms of non-adjacent dependencies (the baboons required a slightly longer training), indicating that there is no fundamental limitation in non-human primates to extract such complex associations.

This difference in the ability to extract complex regularities has also been claimed as a fundamental difference between human and non-human primates. Hauser et al. (2002) have argued that a major difference between human languages and animal communication systems is the presence of complex recursive structures, such as center-embedded structures. However, Rey et al. (2012) demonstrated that baboons can produce center-embedded patterns of responses after being trained to associate pairs of items. The baboons’ responses in this experiment were considered as a by-product of associative learning and working memory constraints. These data indicate that baboons can learn non-adjacent associations. The studies by Rey et al. (2012) and Rey et al. (2018) suggest that the main limitations found in baboons, in comparison to humans, can be accounted by species differences in working memory capacities, which corroborates the conclusions of the first section of the present article.

Category formation

Humans can form categories of various kinds. Categorization is a domain-general ability that is fundamental for a variety of cognitive functions (e.g., inference or decision making). It is also central for the acquisition of language at the structural and semantic level (Rosch, 1978). At the structural level, language uses syntactic categories, such as the noun or verb categories, and knowledge of such categories is at the core of the grammatical structure of any language. At a more semantic level, nouns often refer to categories (e.g., cat referring to the category of cats).

The ability to form categories based on various concrete or more abstract dimensions is widespread in the animal kingdom and baboons are no exception (Herrnstein, 1990). Experimental studies have shown that baboons can categorize visual objects, that is, after being trained they can decide to which category a newly presented exemplar belongs. This has been done in Guinea baboons with alphanumeric characters (Vauclair and Fagot, 1996), word versus non-word four letter strings (Grainger et al., 2012), and even baboon versus human pictures (Malivel and Fagot, 2001). Olive baboons (*Papio anubis*) have successfully sorted real food versus non-food objects in two separate classes (Bovet and Vauclair, 1997). Categorization has also been demonstrated in tasks requiring the consideration of more relational properties among or between items (e.g., Dépy et al.,1999). Thus, Guinea baboons can categorize visual objects depending on the spatial relation they represent (above/below relations: Dépy et al., [1999]; far/near relations: Dépy, et al. [1998]; openess versus closeness relations: Barbet and Fagot, [2011]), and can furthermore process same/different categorical relations in conditional matching tasks (Wasserman et al., 2001).

Insert Fig. 4

An even more abstract form of thinking is analogical reasoning that can be considered as a form of categorization based on abstract relationships. Developmental studies in human children have shown a close relationship between analogical reasoning and the acquisition of linguistic labels (Christie and Gentner, 2013), and it is therefore interesting to investigate if this capacity also exists in nonhuman primates. Several studies were conducted with Guinea baboons in this domain. Analogical studies in baboons used the relational matching task shown in Figure 4 (based on Fagot and Thompson 2011). In this task, the baboon is first shown one pair of objects that are either identical or different. Two comparison pairs are then shown, and the baboon must indicate the stimulus pair showing the same (same or different) relation as the sample pair. This task captures the essence of analogical reasoning because it requires that the subject apprehend the relation between relations. Fagot et al. (2001) were the first to show that two Guinea baboons can solve a version of this task involving arrays of same or different icons as relational stimuli. A more complex version of this task, using pairs of shapes as stimuli, was tested in Fagot and Thompson (2011) and showed that six out of 29 baboons could solve the relational matching task illustrated in Figure 4, and that five of these six monkeys then transferred this ability to novel sets of shapes. This transfer occurred even in trials in which the incorrect pair shared an element with the sample pair with which it was being compared, as illustrated in Figure 4. All these findings show that the baboons have the capacity – which is critical for language – to categorize stimuli considering both concrete and more abstract stimulus dimensions. They can also solve complex tasks requiring the processing of relations between relations.

Communication and language-specific functions

In this section, we discuss some anatomical dimensions linked to the origins of speech (i.e. the vocal apparatus), and to the origins of intentional communication (i.e., communicative gestures) in baboons. We will investigate below the ability of the baboons to produce vowel-like sounds, as well as the presence of human-like brain and gestural asymmetries in that species.

Spontaneous vocalizations and the precursors of speech

Potential precursors of human language found in nonhuman primate vocalizations and gestures could be ancestral to our own communication system (for reviews, see Boë et al., 2017a). Since Lieberman et al. (1969), it has been generally considered that the anatomical configuration of the vocal tract of nonhuman primates makes it impossible for them to produce vowel-like sounds. In contrast to humans, nonhuman primates have a larynx in a low position in the vocal tract which, according to Lieberman et al. (1969) left nonhuman primates unable to modify their vocal tract shape by tongue, lip or jaw maneuvers, restricting them to produce exclusively /ə/ vocalizations expected from the resting configuration of the vocal tract. However, recent discoveries challenge this dominant view that a low larynx is required for vowel systems. For instance, it is now well known that human babies, who also have a high larynx, produce the same vocalic range as adults (De Boysson-Bardies et al., 1989). In addition, low larynxes have been discovered in animal species (chimpanzee, ruminant) with no documented ability to produce systems of vowel-like sounds (e.g., Nishimura et al., 2006)

In one of our recent studies (Boë et al., 2017b), we investigated whether nonhuman primates can produce a much richer set of distinct vowel-like vocalizations than predicted by the descent of larynx hypothesis. We recorded spontaneous vocalizations of 15 adult Guinea baboons, three males (mean age 16 years: range 8–26) and 12 females (13.5 years; range 8–25), living in a social group. Within a corpus about 2000 recordings, we found 13 different vocalizations which were all described in detail in Kemp et al. (2017). Interestingly, these vocalizations recorded in captivity were highly similar to those already described in the wild (e.g., Maciej et al., 2013), suggesting that the individual vocal units were in fact relatively fixed within the species. We however observed a large degree of variability within the call sequences, which concerned the number of grunts within a vocal sequence, F0 and the tempo (Kemp et al., 2017). More extensive studies will be required to indicate if this variability results from random processes and inter-individual variability, or if it reflects some degree of behavioral/cognitive flexibility in the use of these vocalizations.

We also verified which of these vocalizations contained formants and found that the formants were distinctively present in five of them. They included grunts and wahoos (produced mainly by males), barks and yaks (mainly by females), and copulation calls (only by females). Grunts and copulation calls are typically short-distance communications while the wahoos, barks and yaks carry over longer distances (Maciej et al., 2013; Owren et al., 1997).

Insert Fig. 5 here

Acoustical analyses of five types of vocalizations revealed at least five distinct classes of vowel-like segments. These five vowel-like segments, wphich are represented in the left part of Figure 5, correspond to the high central [ɨ], high back [u], mid-high back [o] low front [æ] and low back [ɑ]. Note that these five vowel-like segments cover a large portion of the baboon’s vocal space, in a proportion almost equivalent to that found (for instance) in American-English 12-year-old children. Similarly important, the baboons combined these vowel-like segments in several ways. First, the wahoo call contains two vowel-like segments, namely the low front [æ] and the high back [u] (for more details, see Berthomier et al. [2017]). Second, some vowel-like segments were found in different vocalizations. Hence, the [æ] was present in both the bark calls and the wahoos. In the same way, the vowel-like segment [u] was shared by the male grunts and female copulation calls. All these findings confirm that the baboons can produce contrasting vowel qualities despite a high larynx. This conclusion supports earlier work by Fitch et al. (2016) who found from a modeling approach that the vocal tract of macaques can produce a variety of vowel-like sounds. It is however in sharp disagreement with Lieberman et al.'s (1969) hypothesis that a low larynx is required to produce vowel-like sounds. The consistencies of the results obtained in baboons (Boë et al., 2017) and macaques (Fitch et al., 2016) further suggest that the human phonetic system for speech originates from articulatory features already present in an ancestor that we share with these two species. Although baboons have a small vocal repertoire compared to humans and have, like many other primate species, a relatively inflexible vocal repertoire, the properties of their vocal apparatus and the phonetic structure of their vocalizations show that this species represents an interesting animal model for the study of the origins of speech.

Gestural and brain asymmetries as potential precursors of brain specialization for language

As many cognitive processes, most language functions involve functional hemispheric specialization of the brain, which reflects the better aptitude of one hemisphere over the other for a given function, and/or inter-hemispheric anatomical differences (Josse and Tzourio-Mazoyer 2004). In a large majority of humans, the left hemisphere is dominant for language functions such as phonology, semantics or sentence processing (Vigneau et al. 2006) and the right-hemisphere is dominant for context processing and prosody (Vigneau et al., 2011). Among such a complex lateralized neural network, some perisylvian regions play a key-role. These regions include Broca's area (Inferior Frontal Gyrus, IFG) within the frontal lobe, as well as the Superior Temporal Sulcus (STS) and the Planum Temporale (PT) in the temporal lobe (Cooper, 2006). Interestingly, some of these regions for language show striking structural inter-hemispheric asymmetry in size (i.e., surface, volume or depth of a region greater in a hemisphere in comparison to the other, e.g. Geschwind and Levitsky, 1968; Dubois et al., 2009; Keller et al., 2011). Although their functional role remains unclear (e.g., Dorsaint-Pierre et al., 2006; Keller et al., 2011), these structural asymmetries have been considered unique signatures of brain evolution related to human language (e.g., Crow, 2002; Leroy et al., 2015). However, as demonstrated in the next paragraph, this has been challenged by several studies of nonhuman primates, including baboons (e.g., Meguerditchian et al). Given the phylogenetic proximity between humans and nonhuman primate species, comparative approaches might enable the potential precursors of hemispheric specialization for language in our common ancestors to be detected.

One way to address this topic is to focus on handedness as a landmark of such human’s hemispheric specialization uniqueness. Nearly 90% of humans are right-handed (Annett, 1985) and, from an evolutionary perspective, there is strong debate about whether such population-level right-handedness has precursors in nonhuman primates or is unique and exclusively related to language emergence and brain specialization for language (Fagot and Vauclair, 1991; Bradshaw and Rogers, 1993; Crow, 2002; Corballis, 2002). The latter view has been challenged by two sets of evidence. First, although in a much lower degree than in humans, baboons showed population-level right-handedness for bimanual coordination tasks (Vauclair et al. Hopkins, 2005; Meguerditchian et al., 2011; Molesti et al., 2016), as do many other terrestrial apes and monkeys (Meguerditchian et al., 2013), suggesting that predominance of right-handedness is not unique to human evolution and not specific to language emergence. Second, handedness for manipulation in humans is a poor marker of hemispheric specialization for language, and might be an independent lateralization phenomena (Groen et al., 2013; Mazoyer et al., 2014; Ocklenburg et al., 2014). This view is supported by evidence showing that both right-handed and left-handed individuals showed similar left-hemispheric lateralization for language (Knecht et al., 2000).

Thus, considering that human handedness is independent from language lateralization, a comparative approach of handedness among primates might be irrelevant to investigate the evolution of brain specialization for language. The question remains unanswered: is there any behavioral asymmetry in humans which might better reflect hemispheric specialization for language? Given the strong links between the communicatory gestural and language systems in humans, which are considered as an integrated system dominated in the left hemisphere (Gentilucci and Dalla Volta, 2008), hand preferences for communicative gestures might constitute a better behavioral indication of hemispheric specialization for language (Meguerditchian et al., 2011) than handedness for manipulation. Several findings obtained in baboons support this idea. As found in human children and in chimpanzees (Meguerditchian et al., 2010, 2013), gestural communication in baboons showed specific pattern of manual lateralization (e.g. Figure 6): communicative gestures elicited not only a more pronounced degree of right-handedness predominance but also independent individual hand preferences in comparison to non-communicative actions (Meguerditchian and Vauclair, 2006, 2009). In addition, considering that gestural communication in baboons has intentional properties (Bourjade et al., 2014), these findings speak for a greater dominance of the left-hemisphere in intentional communicative signaling, which might involve a different system from the one related to manipulative functions. This lateralized communicative system in nonhuman primates might be inherited from our common ancestor with Old World monkeys (~25–30 million years ago) and thus might constitute a prerequisite of brain specialization for human language (Meguerditchian and Vauclair, 2008; Meguerditchian et al., 2011).

Insert Figures 6 and 7

A complementary way to explore the evolution of the lateralized communicative system is to investigate in baboons the lateralization of brain structures related to language in humans. Within non-human primates other than the great apes, the baboon is a good model for this comparative approach with human. For instance, in comparison with other Old World monkeys, such as macaques, the baboon brain is not only on average twice as large (Leigh, 2004), but has also a larger brain gyrification, containing the homolog structures of the primary cortices found in humans (Kochunov et al., 2010). These advantages facilitate the identification of similar gross brain structures (e.g., sulci, cortices) in monkeys and humans, and thus make that the baboon is an interesting species to investigate potential continuities pertaining to human brain organization for language. Most studies conducted on non-human primates have focused on great apes, particularly chimpanzees, and have reported human-like leftward structural asymmetries of a key language region, the planum temporale (Gannon et al.,1998; Hopkins et al., 1998). In addition, a contralateral association of asymmetries between (1) inter-hemispheric surfaces of the equivalents of Broca’s and Wernicke's areas (IFG and PT) and (2) the direction of manual preferences (i.e. right versus left hand) for communicative gestures has been found in chimpanzees (Taglialatela et al., 2006; Hopkins and Nir, 2010; Meguerditchian et al., 2012). At least one study found those brain asymmetries to be systematically absent in non-human primates more phylogenetically distant from humans, including Old World monkeys such as macaques (Gannon 2010). This picture changed with the work of Marie et al., (2018) on baboons, in which 96 anatomical T1 MRI cerebral images were analyzed and were used to constitute an averaged brain template (Love et al., 2016). This brain-imaging MRI study revealed a left size-asymmetry of the planum temporale in baboons (Marie et al., 2018, see Fig. 7), in a quasi-identical distribution to the one originally found in humans (Geschwind and Levitsky, 1968). In addition, according to ongoing studies on other sulci of interest in these baboons’ images, a significant neuroanatomical depth asymmetry in favor of the right hemisphere was found in a specific portion of the superior temporal sulcus. The exact same asymmetry described in humans was presented as a human-specific brain landmark of communication and social cognition (Leroy et al. 2015). Interestingly, other preliminary results provide additional support to the idea that communicative gestures in baboons, but not manipulation handedness, might be related to an intentional communicatory lateralized system, homolog to that of human language (Meguerditchian et al., 2013). These further inter-hemispheric sulci analyses in baboons included (1) the arcuate sulcus (in which the ventral portion and its depth delimitate the equivalent of Broca area surface in the monkeys' brain) and (2) the central sulcus (in which a middle portion and its depth delimitate the motor hand area surface, Meguerditchian et al., 2016). Whereas direction of handedness (i.e., left- or right-hand) for manipulation correlated with the contralateral depth asymmetry of the "motor hand area" central sulcus section, communication gestures asymmetries in baboons were rather correlated with the one of the "Broca area" arcuate sulcus portion (Meguerditchian et al., 2016). Altogether, the findings reviewed above support the idea that, regarding key structures of language and gesture, there is a continuum in hemispheric specialization between baboons and humans. This suggests that prerequisites of hemispheric specialization for language might be dated back to the common ancestor of great apes (including humans) and Old World monkeys and be ultimately related to its gestural communication system (Meguerditchian et al., 2013). Gestural production might thus constitute a good candidate for the phylogenetic prerequisite of language.

The cultural evolution of language

One interesting feature of language is that it evolves culturally through time. Children learn a language by being exposed to the speech production of speakers of that language, they then become speakers themselves, and their use of the language serves as new evidence for another generation of language learners. This process of iterated learning (Kirby, 2001) repeats itself every generation, and in every new generation small changes are introduced, which will be passed onto future generations of speakers. If the changes introduced by the learners every generation are independent from the cognitive mechanisms involved in language learning and production, languages across the world would evolve largely independently of each other and adapt to local socio-ecological conditions. On the contrary, if the changes introduced every generation are systematic (if, for instance, they are biased by cognitive mechanisms shared by humans), then languages across the world are going to evolve to reflect these biases (in addition to local socio-ecological conditions). Importantly, if the changes are systematic, the iterated learning process is going to amplify the effect of even small biases that affect language acquisition and production, and what might be considered a small effect when studying language change from one generation to the next generation might become a powerful drive over many generations (Kirby et al., 2007).

Experiments involving transmission chains can capture such process. Kirby et al. (2008) for instance introduced a non-structured language (random associations between a set of visual objects and artificially constructed labels) as input in the transmission chain. Because of the transmission process, they observed that this language became progressively more structured and easier to learn. The idea that weak cognitive biases can shape language evolution across many generations is also supported by empirical evidence showing that certain features that are common across world languages are puzzling without an evolutionary perspective. For instance, there is some evidence that color names across the world share a similar structure that reflect an almost optimal partition of color perception (Regier et al., 2007) and that this structure can emerge through a process of iterated learning. Such experiments using iterated learning to study language are a powerful demonstration of the possible effect of weak cognitive biases on language evolution (Kalish et al., 2007; Cornish et al., 2013). However, one outstanding criticism regarding the importance of weak cognitive biases in shaping language evolution concerns the fact that the humans taking part in these experiments have already acquired a language. That first acquisition will necessarily guide the evolution of the experimental language according to the principles just described (participants will be biased by their first language and will therefore reproduce the structure of that language). Studies on animals, such as baboons, can overcome this difficulty.

Claidière et al. (2014) conducted the first language-like transmission chain experiment among non-human animals. In this study, Guinea baboons used a computerized system to complete a working memory task. Each trial began with the display of a grid made of 16 squares, 12 white and four red (see Fig.8A). After 400 ms, all the red squares became white and, to obtain a food reward, the monkey had to touch the previously red squares, in any order. The trial was complete when four different squares had been touched. After training the baboons to perform this task, the authors implemented a transmission procedure. The first baboon in the transmission chain was exposed to 50 randomly chosen patterns and the computer recorded the responses to each of the pattern. Once the first subject had been tested, its behavioral output (the actual pattern of squares touched while attempting to reproduce the observed patterns) on these 50 trials was randomly reordered (the order of the 50 trials was shuffled) and became the set of target patterns shown to the next individual in that chain (Fig. 8B).

Insert Fig. 8

In the Claidière et al. (2014) study, the behavioral response of the baboons evolved to exhibit the three fundamental properties of human language. Because of the transmission process, the behavioral responses of the baboons became progressively (1) structured (grids developed a rare but highly salient structure of four connected squares (colored in Fig. 8C), (2) systematic (the response of the baboons to one grid depended on other grids in the set), and (3) lineage specific (different reproductions of the experiment converged on different distribution grids). These results therefore suggest that iterated learning, in the absence of an already acquired language, can generate typically linguistic features (structure, systematicity, and lineage specificity). This first study therefore shows the potential of using iterated learning experiments with nonhuman primates, such as baboons, to understand the effect of pre-linguistic cognitive mechanisms on language evolution.

Discussion

Many perspectives on language evolution claim that language emerged because of a decisive change in one critical and uniquely human feature (e.g., Lieberman et al., 1969; Chomsky, 1988; Hauser et al., 2002). These classical approaches have promoted comparative studies focused on the evolution of such key features, with the aim of documenting potential qualitative differences between humans and the other animals. Our article follows a different perspective. We consider instead that language resulted from the evolution of a unique combination of both domain-general (cognitive) and more specialized (anatomical and cultural) components, and therefore that understanding the evolution of language requires that we consider and compare as many of these components as possible across species. We propose that, to be successful, this multicomponent approach requires researchers to focus their efforts on a small number of animal models that can be compared to humans. We further propose that baboons can be used as a nonhuman animal model to study the origins of language.

The main reason to choose baboons as an animal model in this context is that researchers have now collected a substantial amount of information on a broad range of language related cognitive domains in these species. Baboons have been studied in research on perception (Barbet and Fagot, 2011), statistical learning (Fagot, 2017; Rey et al., 2018), short-term memory (De Lillo and Fagot, 2011), long-term memory (Fagot and Cook, 2006), categorization (Dépy et al., 1988), concrete and abstract reasoning (Fagot and Thompson, 2011), and cumulative culture (Claidiere et al., 2014). These cognitive mechanisms were explored here because of their relevance for the emergence of language. The many other contributions of this volume further demonstrate that much is known about the evolutionary origins and genetics of baboons, and their natural behavior in the wild. Of course, other animal species can be similarly interesting in this context, including chimpanzees, macaques, capuchins and marmosets, which have also been extensively studied in both laboratories and in the field. Nevertheless, it remains that for questions related to language evolution, very few non-human primate species have been studied as thoroughly, and with such diverse perspectives, as baboons.

The second reason for choosing baboons as model species to study the evolutionary origins of language is the fact that most of the studies show that baboons share with humans both domain-general mechanisms, such as the properties of their long-term memory system (Fagot and Cook, 2006), and more specialized language-related anatomical or functional properties, like the basic phonological properties of the vocal tracts (Boë et al., 2017b), lateral asymmetries in the brain structures (Meguerditchian et al., 2013) and some aspect of cultural transmission (Claidière et al., 2014). Given that baboons and humans diverged approximately 25–30 million years ago, together these results suggest that there is more continuity between humans and other primates than was previously thought, especially regarding language evolution (see also Seyfarth and Cheney, 2017). Noticeably however, quantitative differences between baboons and humans can be striking. For instance, working (short-term) memory seems to be limited in baboons compared to humans (Fagot and de Lillo, 2011) and more studies are needed in this domain, in baboons and in other species, to understand the functional consequences of such differences better.

To sum up, we believe that a promising strategy for future studies on language evolution would be to focus on a limited number of species, including baboons, to compare which of the mosaic of different (domain-general and more language-related) functions is present or absent in the considered species, and then try to explain the steps during evolution that account for the differences between these configurations. This approach can reveal the mechanisms that can be accounted for by convergent evolution. To illustrate this point, it is interesting to highlight one of the potential limits of the baboon as a model to study language evolution: like chimpanzees, baboons have a relatively simple vocal repertoire, vocal control and flexibility in comparison to arboreal primate species such as the marmoset (e.g., Agamaite et al., 2015; Choi et al., 2015). Given that chimpanzees and baboons are phylogenetically closer to humans than marmosets, this finding suggests that the size and flexibility of the vocal repertoire can be the result of convergent evolution in marmosets and humans, and hence provides little information about the origins of language if considered in isolation. Finally, another limitation of the baboon model is that we are still missing important information on critical language-related information, as related to the syntax, semantics, pragmatics and much more. However, future research can address this limitation, providing an even more extensive perspective on the evolution of language.

Acknowledgments

This work, carried out within the Labex BLRI (ANR-11-LABX-0036) and the Institut Convergence ILCB (ANR-16-CONV-0002), has benefited from support from the French government, managed by the French National Agency for Research (ANR) and the Excellence Initiative of Aix-Marseille University (A*MIDEX). This research was also supported by the Premilang2 ANR-project (#ANR-13-BSH2-0002) and the Chunked ANR-project (#ANR-17-CE28-0013-02).

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Figure captions

Figure 1. Short-term memory in baboons. A Corsi memory span measured in both Guinea baboon and humans in Fagot and De Lillo (2011, redrawn from their figure); B Accuracy in the delayed matching-to-sample task in juvenile baboons, as a function of the interval between the sample and comparison displays (redrawn from Rodriguez et al., 2011, one distractor condition).

Figure 2. A. Learning curves in baboons for words and non-words as a function of the number of training sessions. B. Scores of correct responses at the first presentation of a new non-word (dark grey) or at the first and subsequent presentations of a new word (light grey). The difference in bigram frequency between words and non-words seems to provide evidence that baboons can correctly categorize words and non-words at first sight (redrawn from Grainger et al. 2012's data).

Figure 3: A: In the serial response time task, the nine possible positions are divided in three triplets (4-7-3, 1-9-6, 5-8-2). B: Mean Response times (RT) in milliseconds (ms) for the first (RT1), second (RT2) and third (RT3) positions of the triplets and for each block of training (one block is composed of 400 trials). Error bars correspond to standard errors. Redrawn from the data of Minier et al. (2015).

Figure 4. Illustration of the relational matching task used in baboons by Fagot and Thompson (2011). A. In this task, the subject must process the same or different relation between the shapes composing the sample pair (shown on the top) and select the comparison pair (bottom) instantiating the same relation as the sample. B. In this second version of the task, the foil pair to avoid shares one item with the sample pair (cross-mapped condition).

Figure 5: Comparative data on the production of vocalic sounds by humans and baboons. The left part figure shows the different vowel-like sounds produced by baboons in Boë et al.

(2017b). The gray shading corresponds to the maximum acoustic space inferred from modeling. The right part of the figure shows findings from American-English speaking children (inferred from Peterson and Barney, 1952). Note the strong similarities between the two species, suggesting a phylogenetically ancient origin of the vowel systems of humans Adapted from Figure 3 of Boë et al. (2017b), published with permission.

Figure 6. *Communicative gesture performed by a male baboon. A young baboon intimidates a human observer by quickly slapping his right-hand on the ground while staring at him/her. Time in milliseconds (ms).*

Figure 7. *Quantification of asymmetry in the baboon planum temporale. a) Three dimensional render of a baboon brain and its delineation of the left planum temporale surface area (red). b) Overview of the coronal section per coronal section tracing method, one individual coronal section with overlay of left (red) and right planum tracing (green). c) Oblique section oriented along both planum temporale of a baboon brain (left planum in red, right planum in green) with a clear leftward asymmetry of surface area. d) Number of left-biased, non-biased and right-biased baboons for the planum temporale surface area according to classification of individual asymmetry quotients (AQ). Redrawn from Marie et al. (2018).*

Figure 8: A: Trial timeline: a first screen appears with 12 white squares and four red ones. After 400ms the red squares disappear, and the baboon can touch the previously red squares. B: Transmission procedure: the responses of one baboon, the square touched by baboon N when exposed to the stimuli, become the stimuli for the next baboon, the squares that baboon N+1 must memorize. C: Evolution of the baboons' responses across generations in three different replications of the experiment (chain 1-3): the initially random grids (Left) become

structured across many events of transmission (responses with four connected squares are colored; all the squares were red in the experiment).