Evolution of brain and language

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Introduction

Language is one of the most important behavioral adaptations of the human lineage. Clues to the evolution of language are evident in the fossil endocranial record, particularly when placed in the context of comparative analyses of primate brains. Brain size evolution itself is associated with several important behavioral dimensions central to language. In addition to dimensions related to the complexity of the social environment, it is less well-recognized that brain size increases also suggest a dramatic increase in the richness of conceptual understanding. The importance of this for language evolution is that it underlies the usefulness of enhanced communication: Our ancestors had increasingly interesting things to talk about. Clues about language evolution are also evident in the endocranial surface in the vicinity of Broca's cap in the left hemisphere, which overlies areas relevant to language processing in modern humans. Asymmetries in this region on fossil endocasts suggest a deep ancestry to enhanced communication in our lineage. Finally, a key question in brain and language evolution involves why Broca's region in particular became co-opted for language, given that it appears to substantially predate the human lineage (and therefore language itself). One hypothesis is that it evolved to pay special attention to any kind of sequential pattern information in the environment. Research probing this hypothesis in humans and great apes will be discussed.

The question of the origins of language is one of the most interesting in human evolution. An evolutionary perspective suggests that this system was built up from cognitive abilities (and the circuits underlying them) that pre-existed language itself, and were modified in some ways to allow for language. The question here is exactly what pre-existing abilities actually underlie language. We can get clues about this from a couple of sources. One way is to study brain structure and function of our closest living relatives, particularly to look at what sorts of abilities they have that could plausibly have been elaborated for language in our own lineage. But another interesting avenue to pursue is to assess the non-linguistic functions of modern human language areas, as these may well be clues to the original functions of the circuits now used for language. In addition, we must ask why our ancestors found the need to communicate so elaborately at all?

It is obvious that language is currently used as a communication system. Although there are some linguists who believe language is actually not really for communication primarily, and instead is a kind of tool used for thought (e.g., Chomsky, 2002), this perspective is deeply problematic. It ignores the question of why humans would need a new « tool for thought » independent of a need for communicating with others, given that the social world has likely been the most important selective environment of our species for a very long time (Holloway, 1975; Humphrey, 1984). Furthermore, given that language functions now as a communication system, we would still need to explain why there would be a usefulness of early hominins to communicate at all. I have long argued that the existence of a communication system implies that there is some sort of a shared understanding of the world among those that are communicating (Schoenemann, 1999). The existence of a communication system means there is some kind of a shared code for communicating thoughts of various kinds. So the question is, what is it that would have driven our species to elaborate communication systems to the extent that you see today, creating modern human language?

Evolution of conceptual complexity

Extensive work has been done attempting to train chimpanzees, bonobos, and other apes to communicate using symbols analogous to human language. One of the most

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famous is a bonobo named Kanzi. Videos of tests of his abilities are available online (e.g., https://youtu.be/2Dhc2zePJFE). This particular video is a replication of an extensive published study of his abilities in which Kanzi was given 660 novel commands and then assessed on his comprehension based on his responses (Savage-Rumbaugh *et al.*, 1993). The sentences used in this experiment were specifically selected to be odd, and unlikely to have ever been asked of him before. For example, the caretaker (Sue Savage-Rumbaugh) asks Kanzi at one point: "Will you put some soap on your ball?" Another example is: "Can you put the pine needles in the refrigerator?" By asking him to do a number of odd and peculiar things, Savage-Rumbaugh was probing whether he had just learned meaningless associations between sounds and simple behaviors by rote, or whether he actually has some understanding of the meaning of the words and how they're put together.

Experiments like this on Kanzi, as well as other studies on other apes (e.g., Gardner and Gardner, 1994; Premack and Premack, 1972) show that ape brains do have the basic abilities to learn to harness the meanings of words (abstract symbols) and at least some simple arbitrary syntactical rules. It is true that you have to put an ape in a very unusual (i.e., human-like) developmental situation in order to get them to do this, but the critical point is that they can do it given the right environment.

However, there is a difference – an interesting difference – between what apes have been able to do vs. what humans do. This is highlighted in an interesting quote in a review of language abilities of non-human animals by Charles Snowden (1990):

> "Although the abilities of Kanzi and his companions are remarkable and come very close to some of the capacities shown by young children, there still appear to be limitations. Bonobos [pygmy chimpanzees] and chimps *appear to be more limited in the topics that they find interesting to communicate about.*" (p. 222, italics added)

This raises the question of whether this limitation in topics might be the result of apes having a fundamentally more limited inner mental world as compared to humans. Consistent with this is the fact that the number of words learned by a typical ape subject in such studies is in the neighborhood of about 400. By contrast, typical American high school students learn something like 40,000 words (actually dictionary entries, which are arguably more complex than the words ape language subjects use; Miller and Gildea, 1991). This suggests a huge, ~100-fold or more difference in the richness in humans compared to apes. I have long argued that this is a fundamentally critical difference, and that it indicates a tremendous elaboration of the inner mental worlds of hominins, which has thereby given our lineage the impetus to develop such an elaborate communication system (Schoenemann, 1999, 2010, 2012).

These behavioural differences are actually predicted quite nicely by what we know about brain evolution. Cranial capacity increased over time dramatically, starting somewhere between two and three million years ago (fig. 212), and a strong argument can be made that this reflects at least partly a tremendous increase in conceptual complexity of the inner mental world of our ancestors (Schoenemann, 2012). The argument for this can be summarized as follows: First, the evidence from research on brain structure/function indicates that concepts themselves are based on complex neural networks connecting different brain regions. Second, the size of cortical and sub-cortical areas, both within and between species, are proportional to the degree of elaboration functions. Third, increasing brain size across primates – and mammals generally – leads to increasing specialization of brain regions. Thus, larger brains have the possibility of more complex neural networks, both because specific regions are processing information in more complex ways, as well as the fact that there are more specialized ways in which information itself can be processed.

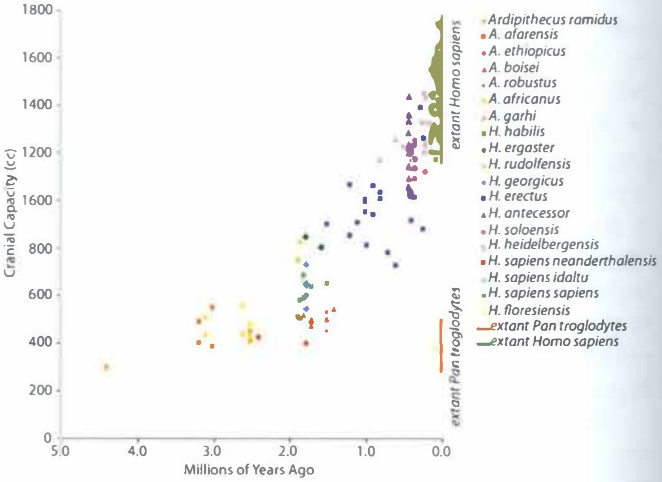

Figure 212: The fossil record of hominin brain evolution. Data primarily from Holloway et al. (2004); see Schoenemann (2013) for additional sources.

A concept is typically composed of many different cognitive dimensions or sensations. For example, the concept embodied by the word "coffee" incorporates a distinctive smell, the typical sense of warmth coming off of a fresh cup, the feeling that you get from drinking it (e.g., caffeine), the sounds associated with making and drinking it, the color of the brew, and so forth (Damasio and Damasio, 1992). Processing of these different kinds of sensations is known to involve very different parts of the brain. To be connected in some way to a single mental concept of "coffee," they obviously have to be physically connected in some way. The actual neural network connecting and integrating them together is either literally the instantiation of the concept itself, or is a key part of the instantiation of the concept. In either case, the more complex the possible networks, the more complex the possible concepts.

We also know that the amount of neural resources devoted to a task are proportional to the degree of elaboration of function of that task. This can be seen clearly comparing cortical maps of species with very different behavioral repertoires. For example, more than half of the cortex of the ghost bat is devoted to processing auditory information, which supports its highly advanced echolocating abilities (Krubitzer, 1995). The star-nosed mole, by contrast, spends most of its time underground feeling for grubs to eat in the dark with its very sensitive finger-like projections on its nose. Its cortical map contains only a tiny primary visual area, but a correspondingly huge area devoted to somatosensory processing of its nose projections (Krubitzer, 1995).

Though it is not often pointed out, this pattern is also evident within human brains as well.

This is graphically illustrated in sensory and motor "homunculi" in which the size of different parts of the body are drawn to be proportional to the amount of total sensory or motor cortical representation devoted to that part of the body. These show that we have, for example, much more cortical representation for lips and fingers than we do for our calves, even though the surface area of the former is much smaller than that of the latter. The amount of cortex that is devoted to particular areas is proportional to the degree of sensitivity and/or our ability to manipulate that part of the body.

It has also been shown that larger brains have greater numbers of cytoarchitecturally distinct cortical areas (presumably these are functional, although for many of these areas we do not know exactly what their function is). Changizi and Shimojo (2005) showed that there was a positive relationship between brain volume and number of distinct cortical areas across species that had been cortically mapped. Using this data they estimated that humans should have approximately 150. For chimpanzees, the estimation is around 100. Not only does there appear to be more cytoarchitecturally (and presumably also functionally) distinct areas, but equations in Changizi and Shimojo (2005) suggest that individual areas in humans are 2.3 larger on average in absolute terms. This suggests that the processing complexity within areas is significantly greater as well, leading to even greater conceptual complexity in humans (Schoenemann, 2017).

Furthermore, individual areas in larger brains are less directly interconnected than corresponding areas in smaller brains (Ringo, 1991). This means that processing in given areas in larger brains can occur with greater independence from other areas than is likely the case for smaller brains, which means we expect greater functional independence (and/or specialization) of areas as the brain gets bigger. All of these patterns predict greater conceptual complexity in human brains as compared to other primates.

More generally, larger brained creatures will be expected to have a richer internal conceptual world. What's going on in our heads is much richer than what's going on in a typical primate brain, including those of chimpanzees.

At the same time, larger brains are associated with more complex social lives. The idea that the social world played a key role in molding human cognition is often associated with Humphrey (1984), though Holloway has often made this point, specifically with respect to human brain evolution (e.g., Holloway, 1975). Empirical work showing that brain size is significantly associated with social group size in primates was done first by Sawaguchi and Kudo (1990) and shortly thereafter by Dunbar (1992). This has recently been confirmed in much larger datasets for absolute brain size (DeCasien, Williams, and Higham, 2017; Powell, Isler, and Barton, 2017). Fig. 213 shows the relationship for data from the latest dataset to date (Powell *et al.*, 2017):

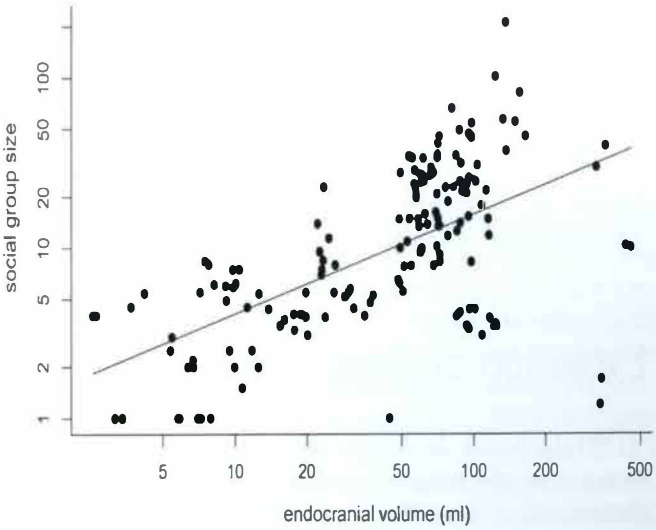

Figure 213: Relationship between endocranial volume (a close proxy for brain size) and average social group size across 154 primate species (data from: Powell et al., 2017). Regression line: log(social group size) = 0.58893 x (log(endocranial volume)) + 0.06005 (r = 0.60, p < 0.0001).

Thus, in the largest dataset to date, representing about half of all primate species, 36% of the variation in social group size is associated with variation in brain size. Social group size is in fact by far the strongest behavioral correlate of brain size so far established. Furthermore, it is important to understand that primate sociality is intrinsically interactive. Unlike, for example, schools of fish, primates do not congregate solely to decrease the likelihood of being preyed upon. Their interaction is inherently communicative: They exchange information in various forms.

This means that larger brains lead *both* to an increasing richness, subtlety, complexity of conceptual understanding of the world, but also to a bias towards an increasingly interactive social existence (in primates at least). When we consider the likely outcome of both of these tendencies, the need to develop some sort of a system to allow increasingly efficient communication would seem inevitable in our evolutionary history. This in turn would lead to the development of increasingly complex and useful syntax and grammar (Savage-Rumbaugh and Rumbaugh, 1993; Schoenemann, 1999).

There has been a fair amount of work attempting to model computationally such a transition (e.g., Christiansen and Chater, 2008; Christiansen, Reali, and Chater, 2006; Kirby, 2002; Kirby, Cornish, and Smith, 2008; Smith, Kirby, and Brighton, 2003), and it is not at all clear that such a transition would require genetic changes specific to language syntax (as opposed to elaborating pre-existing domain-general abilities), contrary to perspectives of those committed to a strongly formalist model of language (e.g., Berwick, Friederici, Chomsky, and Bolhuis, 2013; Chomsky, 1972; Jackendoff, 2002; Pinker, 1994). In any case, increasing conceptual complexity is likely to be one of the important foundations driving the evolution of language in the human lineage. It provides an explanation for why enhanced communication would have been useful in the first place, thereby providing a key foundational explanation for the evolution of language.

Evolution of language areas

While brain evolution strongly points to both an increase in the range of potentially interesting things to communicate, as well as an increasingly intensive interactively-social existence during human evolution, it is likely that language evolution also required at least some changes in neural organization relevant to language production and perception. This can be inferred from the differences between apparent ape abilities and human abilities, as judged from studies of apes like Kanzi. An evolutionary perspective tells us that neural control for any new behavior will occur through the modification of pre-existing areas, and not through the de novo evolution of completely new ones (Schoenemann, 1999). Whether or not any of these changes were solely specific to human syntax, however, is unclear, and also not evolutionarily likely *a priori*.

It turns out that there are, in fact, homologous areas to human language areas in the brains even of monkeys (and possibly other mammals, though this has not been investigated to date). One area of particular interest for language evolution is Broca's region, usually defined as incorporating Brodmann areas 44 and 45 on the left hemisphere. Broca's region in monkeys is quite a bit smaller than in humans (which almost surely has behavioral consequences), but it nevertheless exists (Petrides and Pandya, 1999; Schenker *et al.*, 2010; Striedter, 2005). Given that these homologs exist in Old world monkeys (inferred from the work on Rhesus macaques) and in apes, this suggests that the origin of Broca's region circuitry goes very far back into primate evolution (fig. 214). Given that it is ~5-6 times larger in humans than in apes (Keller, Roberts, and Hopkins, 2009; Schenker *et al.*, 2010), it is likely that some additional functional elaboration occurred during human evolution. Exactly what this change involved is not clear (see below), but knowing what its original function might have been is an important part of the puzzle, and will give us clues about what changes in actual function (if any) were necessary for human language.

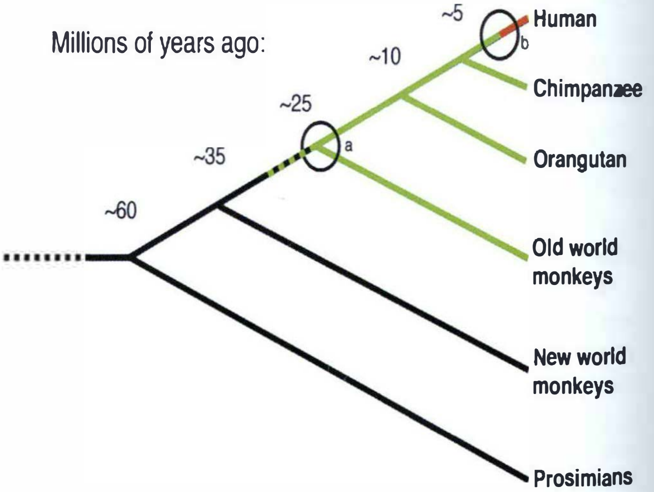

Figure 214: Phylogenetic history of Broca's region, as inferred from studies of living primates studied to date. The green lineages likely had Broca's homologs. The circle labeled "a" indicates the likely most recent possible origin of Broca's region (if New world monkeys and prosimians also turn out to have Broca's homologs, the origin would be even older). The circle labeled "b" indicates the possible elaboration of Broca's in human language evolution.

Is it possible to map the evolutionary history of this area using fossil evidence? First, it is important to keep in mind that language processing for most people is primarily does in the left hemisphere. Figure 215 illustrates the results of a meta-analysis I conducted with Ralph Holloway of 11406 fMRI studies illustrating the cortical areas most strongly associated with language (Schoenemann and Holloway, 2016). The map is a reverse inference map, indicating the probability that the term "language" is used in high frequency in fMRI studies that report activation at a given location. Note that the left hemisphere (leftmost image in fig. 215) shows much more extensive activation than the right. Also note that significant activation is seen in the cortical area that lies under the area known as "Broca's cap" of an endocast (endocranial surface of the braincase). This feature is often prominent in fossil endocasts.

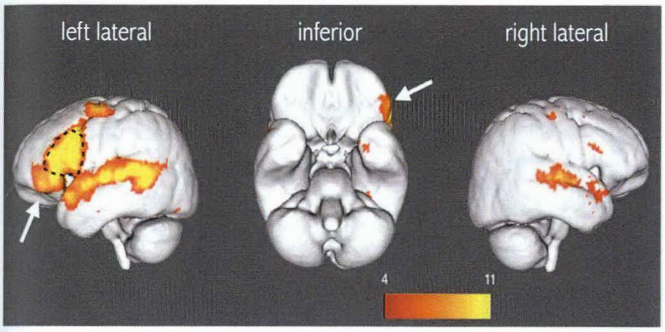

Figure 215: Cortical areas most strongly associated with language. A meta-analysis of 11406 fMRI studies indexed by neurosynth.org. Color values are z-scores indicating the likelihood that the word "language" is used in an fMRI study given the presence of reported activation at a given voxel (i.e., P(Term"language"|Activation), a reverse inference map), thresholded for multiple comparisons using a false discovery rate (FDR) criterion of .01. The black dotted line outlines Broca's region, and the arrows point to the cortical area underlying "Broca's cap" on an endocast.

Furthermore, left Broca's region is physically larger than the right in modern human brains (Foundas, Eure, Luevano and Weinberger, 1998). An unpublished study from my lab carried out by Lindsey Kitchell and myself, of 72 scans of modern human brains, found that a portion of Broca's region is ~20% larger on the left compared to the right (based on morphing the right hemisphere into the left). Given the anatomical asymmetries of modern human brains and the associations with language, this suggests that fossil endocasts (braincases) may leave evidence of changes relevant to language evolution.

In their encyclopedic review of all fossil hominin endocasts then available, Holloway, Broadfield, and Yuan (2004) specifically report asymmetries in Broca's cap. Many specimens are missing either the right or left Broca's caps (or both), so asymmetry cannot be assessed in all specimens. However, for the 21 (pre-anatomically modern) specimens for which both sides can be assessed in this region, 17 (over 80%) were judged qualitatively more prominent on the left compared to the right. Another 2 were judged possibly left-biased, and only 2 (relatively recent Neanderthal; less than 10%) were judged clearly right-biased. Figure 216 plots the cranial capacity and age of all these specimens.

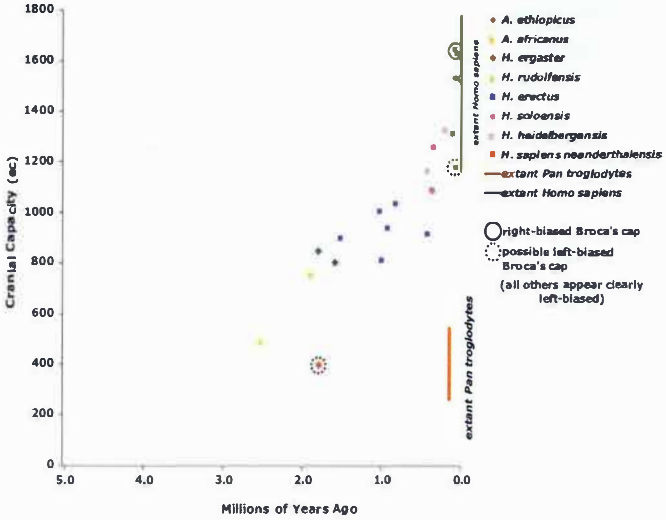

Figure 216: Broca's cap asymmetries in fossil hominins. Based on analyses reported by Holloway et al. (2004). Unless circled, all specimens appear to be clearly left-biased.

This suggests that an interesting asymmetry in an area overlying what today is a language area goes very far back in our species' evolutionary history. This in turn suggests that, at the very least, some kind of enhanced communication has a very deep ancestry. Whether such enhanced communication should be called "language" two millions years ago is a good question, but it is clearly suggestive evidence for language evolution.

Studies of endocranial features suggestive of gyri and sulci in Broca's region have been reported for some fossil specimens. Falk (1983) argued that the endocast of the early *Homo* KNM-ER1470 (*Homo rudolfensis* on figures 216 and 217) more closely matched the human pattern than it did any of the great apes in the left inferior frontal region, approximating where Broca's region would be underneath the endocranial surface. Falk's analysis of endocranial surface morphology was qualitative and subjective, but it is possible to mathematically calculate the curvature at each point on the surface (based on a small local patch), and display this data color-coded in such a way as to illustrate surface morphology objectively. Figure 217 shows this analysis for KNM-ER-1470 (created using a CT scan of a research-quality endocast of the original fossil specimen made by Ralph Holloway). For comparison, surface curvature maps of modern human and modern chimpanzee brains are included. The pattern in the left inferior frontal (LIF, inside the cyan circles) for KNM-ER-1470 does indeed look more similar to the modern human pattern than it does to the modern ape. Exactly what this means with respect to language is unclear, but it does strongly suggest that changes had occurred in that region by that time (~1.88 MYA).

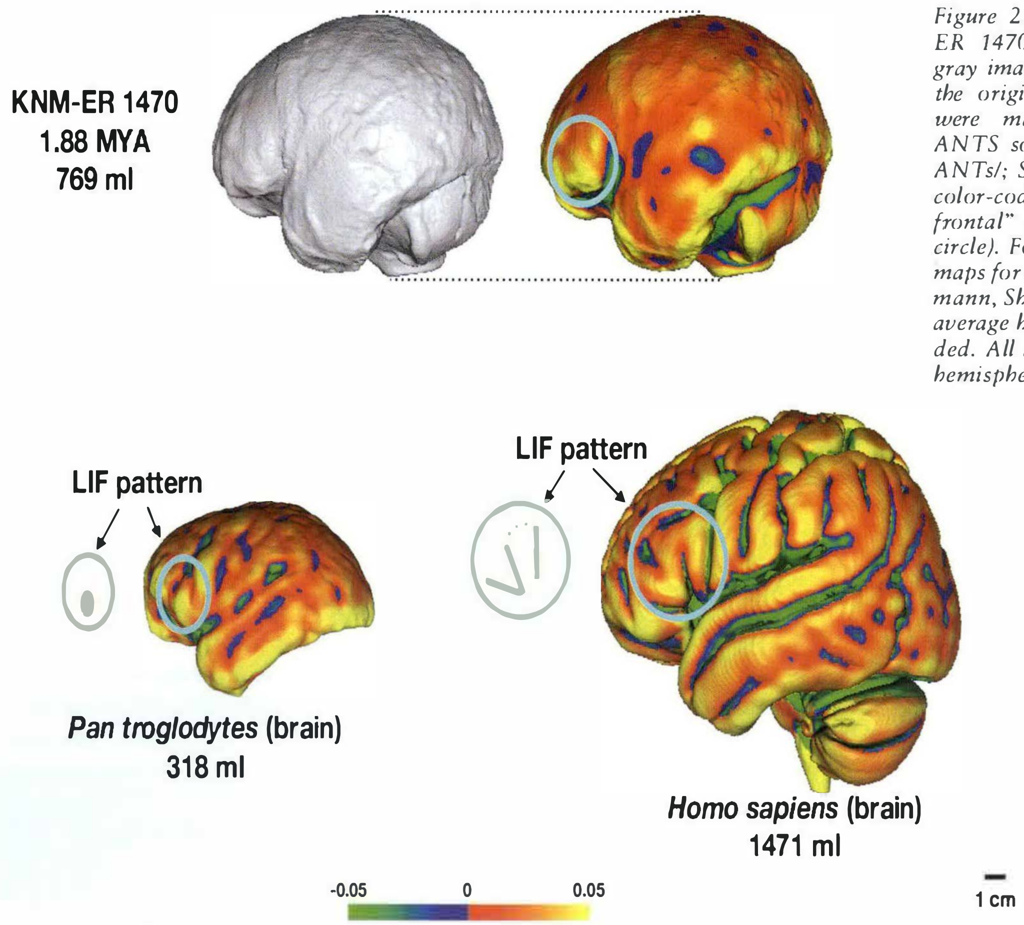

Figure 217: Surface curvature of KNM-ER 1470 fossil hominin specimen. The gray image represents a 3D rendering of the original endocast. Curvature values were mathematically calculated using ANTS software (https://stnava.github.io/ANTs/; SurfaceCurvature algorithm) and color-coded. LIF refers to "left inferior frontal" (this area is identified by a cyan circle). For comparison, surface curvature maps for an average chimp brain (Schoenemann, Sheehan, and Glotzer, 2005) and an average human brain (MNI152) are provided. All images are oriented with the left hemisphere displayed.

This sort of analysis has not yet been done systematically for all fossil hominins. However, Holloway (1983) believes other early *Homo ergaster* specimens KNM-ER 3733 (1.78 MYA) and 3883 (1.57 MYA) had « true » Broca's caps. The *Homo erectus* specimen KNM-ER 15000 (1.5 MYA) has "inflated" gyri over Broca's area (Begun and Walker, 1993). The Daka *Homo erectus* specimen (1.0 MYA), has a strong left Broca's cap protrusion (though convolutional details are lacking according to Gilbert *et al.*, 2008). Later specimens that preserve LIF morphology are generally consistent with the view that Broca's region had undergone substantial change from the presumed ancestral ape condition. This is true, for example, of the *Homo antecessor* specimens from Atapuerca, Spain (0.43 MYA), judging from published images in Poza-Rey *et al.*, 2017. This suggests a very old ancestry for enhanced communication, at least with respect to the processing that relies on circuits in Broca's region.

Why is Broca's region involved in language processing?

Another key part of the puzzle is to determine why Broca's region evolved to be involved in language processing at all? A simplistic explanation is that because language needs particular types of processing, Broca's region evolved specifically to fill this need. However, we know it cannot be this simple because homologs of

Broca's region exist in other species, as outlined above. These species don't have language – or at least human language – so language behavior selecting for certain kinds of processing abilities, and Broca's region evolving to fill these needs, cannot be the explanation for the origin of Broca's region. Instead, it must have been that the circuits in this region originally evolved to process non-linguistic information in ways that happen to (later) be particularly useful to language behaviour. This realization leads to the conclusion that the usefulness (genetic adaptedness) of enhanced communication drove early hominins to use whatever pre-existing circuits were useful for this purpose. This is consistent with the proposal by Christiansen and Chater (2008) that language adapted to the human brain more so than that the brain adapted to make language possible. The question then becomes: What exactly was the original, non-linguistic function of the circuits in Broca's region?

There are two predictions that follow from the realization that Broca's region had pre-linguistic functions. One is that non-linguistic – *but potentially language-useful* – processing likely occurs in Broca's region homologs in non-human primates today. Probing what non-human primates are using their Broca's regions for will be critical for understanding how it came to become involved in language processing in humans. Some work has been done on this question in monkeys, showing that homologs of Broca's region contain mirror neuron circuits (Arbib, 2005; Rizzolatti and Arbib, 1998), as well as circuits that are involved in recognition of species-specific calls (Gil-da-Costa *et al.*, 2006), orofacial motor sequencing (Petrides, Cadoret and Mackey, 2005), and the retrieval of visual and spatial information (Petrides and Pandya, 2009). Intriguingly, Broca's region in chimpanzees seems to be specifically activated during the production of communicative gestures (Taglialatela, Russell, Schaeffer and Hopkins, 2008). These all have possible usefulness with respect to language, and further research is needed to probe exactly why and how Broca's region circuits are involved in these tasks, as well as if and how they could have formed the foundation for the processing of language grammar and syntax in Broca's region in humans.

Another prediction is that in modern humans circuits in Broca's region likely retain the original non-linguistic, yet "language-useful" functions. This follows from the recognition that human behavior is largely added on top of – and not a wholesale replacement of – primate behavior. It is likely that the original functions of these circuits are still important for humans, and haven't simply been replaced. This is of course an empirical question that will await detailed understanding of what these circuits are doing in non-human primates.

So what non-linguistic functions are modern human Broca's region circuits involved in? One particularly intriguing finding is that this region seems to be critical for implicit learning of non-linguistic sequential patterns. This stems from work originally explored by Reber (1967), who showed that human subjects appeared to learn rules about non-linguistic sequences simply by being exposed to them, even though they were never told to pay explicit attention to the sequences, nor even that the sequences followed any rules at all. More recent work has shown that Broca's aphasics do not show implicit learning of these sequential patterns (Christiansen, Kelly, Shillcock and Greenfield, 2010), as well as that in healthy subjects Broca's region shows significantly greater activation to ungrammatical non-linguistic sequences after first being exposed to grammatical sequences for 20-40 minutes (Petersson, Folia and Hagoort, 2012).

This suggests an intriguing hypothesis: Broca's region evolved to extract (learn) sequential pattern information of all kinds from an individual's environment. It is not hard to think of possible benefits of this ability to an individual: It allows better predictions about patterns of social behavior, of food/resource availability, and of sounds associated with danger vs. benefit. It would make possible the learning of patterns of tool creation and use, for example: termite "fishing" using simple preformed stick tools by chimpanzees.

We are probing this hypothesis in two ways. First, we are assessing whether orangutans at the Indianapolis zoo show the same pattern of implicit learning of sequential patterns simply from exposure. The plan is to employ a serial reaction time paradigm in which the subject simply presses buttons that follow sequential rules. Pilot studies in my lab indicate that humans get faster following the sequences over successive training blocks, and further, show faster reaction times to new grammatical sequences (that they haven't been exposed to before) compared to ungrammatical sequences (that are closely matched for simple bi-gram and tri-gram pattern frequencies, but nevertheless break some aspect of the grammar). The beauty of this paradigm is that subjects are not aware they are even taking a test block, which makes it very easy to apply to non-human primates, since they only have to learn that the task involves following sequences on a screen. If orangutans, and other primates, show the same pattern as humans with this task, and given that it activates Broca's region in humans, the next step will be to find out how the brains of non-human primates do this. It is possible that they are doing it with different circuits than humans, but this would be extremely unlikely from an evolutionary perspective. The work of Wilson and colleagues (Wilson *et al.*, 2013, 2015) has made great headway in this regard, showing both that monkeys can learn simple artificial grammars simply through exposure, as well as that they show overlap with humans in the specific parts of the brain that are involved in processing these sequences, using fMRI methods. They have not, however, shown activation in Broca's region proper in either humans or monkeys for their simple artificial grammar – in constrast to the findings for functional studies of Reber's (1967) grammar in humans (Christiansen *et al.*, 2010; Petersson *et al.*, 2012). For this reason we are currently exploring implicit learning of sequential tasks in non-human primates that are known to activate Broca's region in humans.

The second way we are probing this hypothesis is to explore within humans the overlap of this implicit non-linguistic sequential processing with actual language grammar processing. The question here is to explore the extent to which there really is any language-specific modifications in Broca's region for this kind of information. There are three basic possibilities: 1) non-linguistic sequential pattern processing is done in Broca's region in humans because this area evolved circuits specifically for human language grammar, and because of the overlap in requirements, both tasks now activate this language-evolved circuitry. 2) non-linguistic sequential processing is accomplished in an older, evolutionarily-conserved portion of Broca's region, and language grammar is processed in evolutionarily new, language-specific areas. 3) There is one domain-general sequential processor, which both language grammar and non-linguistic sequential pattern processing both use, and which is evolutionarily conserved. Determining the overlap of function for these functions in human Broca's region will be an important first step in teasing apart these possibilities.

This work will help us better understand how the brain makes language, and how evolutionarily old circuits may have been repurposed to create a new behavior so fundamental to the human condition. Understanding what processing is going on in Broca's region in non-linguistic primates, and how it relates to human language processing, will be critical to our ability to understand how our species got language.

Conclusion

Increasing brain size tells us two important things relevant to language: First, it led to increasing conceptual complexity and richness, thereby giving hominins increasingly interesting things to potentially communicate about. Second, it brought increasing social complexity and richness of social interactions, thereby making increasingly sophisticated communication adaptive for hominins. These two are likely interrelated, and may well simply represent two sides of the same process. Both were surely critical influences driving the evolution of language. The fossil record of endocasts contains suggestive clues about an important language area, Broca's region, in the left inferior frontal, pointing to changes in this area dating as far back as the earliest *Homo*, close to 2 MYA. Furthermore, work so far done exploring what Broca's region does in modern humans, both linguistically and non-linguistically, is consistent with the evolutionary theoretical expectation that language was built through modifying pre-existing circuits. The suggestion outlined here is that Broca's region circuits originally evolved to extract useful sequential information from the organism's environment, which made them attractive targets for the evolution of language syntax in our lineage. Future work exploring the current functions of Broca's region circuits in non-human animals, with a focus on the sequential pattern processing tasks known to involve Broca's region circuits in humans, as well as the degree of any overlap of linguistic and non-linguistic processing in Broca's region in modern humans, will allow us to piece together a coherent explanation for how the human brain acquired the abilities for language.

Références bibliographiques

ARBIB M. A. (2005): From monkey-like action recognition to human language: An evolutionary framework for neurolinguistics. *Behavioral and Brain Sciences*, 28(2), pp. 105-124.

BEGUN D. and WALKER A. (1993): The endocast. *The Nariokotome Homo Erectus Skeleton*, pp. 326-358.

BERWICK R.C., FRIEDERICI A.D., CHOMSKY N. and BOLHUIS, J.J. (2013): Evolution, brain, and the nature of language. *Trends in Cognitive Sciences*, 17(2), pp. 89-98.

CHANGIZI M.A. and SHIMOJO S. (2005): Parcellation and area-area connectivity as a function of neocortex size. *Brain, Behavior and Evolution*, 66(2), pp. 88-98.

CHOMSKY N. (1972): *Language and Mind (Enlarged)*. New York: Harcourt Brace Jovanovich, Inc.

CHOMSKY N. (2002): *On nature and language*. Cambridge University Press.

CHRISTIANSEN M. H. and CHATER N. (2008): Language as shaped by the brain. *Behavioral and Brain Sciences*, 31, pp. 489-509.

CHRISTIANSEN M.H., KELLY M.L., SHILLCOCK R.C. and GREENFIELD K. (2010): Impaired artificial grammar learning in agrammatism. *Cognition*, 116(3), pp. 382-393.

CHRISTIANSEN M.H., REALI F. and CHATER N. (2006): The Baldwin effect works for functional, but not arbitrary, features of language. In A. Cangelosi, A. Smith, and K. Smith (Eds.), *Proceedings of the Sixth International Conference on the Evolution of Languag*. pp. 27-34. World Scientific.

DAMASIO A.R. and DAMASIO H. (1992): Brain and language. *Scientific American*, 267(3), pp. 89-95.

DECASIEN A.R., WILLIAMS S.A. and HIGHAM J.P. (2017): Primate brain size is predicted by diet but not sociality. *Nature Ecology and Evolution*, 1, 0112.

DUNBAR R.I.M. (1992): Neocortex size as a constraint on group size in primates. *Journal of Human Evolution*, 22(6), pp. 469-493.

FALK D. (1983): Cerebral cortices of East African early hominids. *Science*, 221, pp. 1072-1074.

FOUNDAS A.L., EURE K.F., LUEVANO L.F. and WEINBERGER D.R. (1998): MRI asymmetries of Broca's area: the pars triangularis and pars opercularis. *Brain and Language*, 64(3), pp. 282-296.

GARDNER B.T. and GARDNER R.A. (1994): Development of phrases in the utterances of children and cross-fostered chimpanzees. *In* R.A. Gardner, B.T. Gardner, B. Chiarelli, and F.X. Plooij (Eds.), *The Ethological Roots of Culture* (pp. 223-255). Dordrecht: Kluwer Academic Publishers.

GILBERT W.H., HOLLOWAY R.L., KUBO D., KONO R.T. and SUWA G. (2008): Tomographic analysis of the Daka calvaria. *Homo erectus: Pleistocene Evidence from the Middle Awash, Ethiopia*. University of California Press, Berkeley and Los Angeles, pp. 329-347.

GIL-DA-COSTA R., MARTIN A., LOPES M.A., MUNOZ M., FRITZ J.B. and BRAUN A.R. (2006): Species-specific calls activate homologs of Broca's and Wernicke's areas in the macaque. *Nat Neurosci*, 9 (8), pp. 1064-1070.

HOLLOWAY R.L. (1975): *The role of human social behavior in the evolution of the brain*. New York: American Museum of Natural History.

HOLLOWAY R.L. (1983): Human paleontological evidence relevant to language behavior. *Human Neurobiology*, 2 pp. 105-114.

HOLLOWAY R.L., BROADFIELD D.C. and YUAN M.S. (2004): *The Human Fossil Record, Volume 3. Brain Endocasts – The Paleoneurological Evidence*. Hoboken: John Wiley and Sons.

HUMPHREY N. (1984): The social function of intellect. *In Consciousness Regained* (pp. 14-28). Oxford: Oxford University Press.

JACKENDOFF R. (2002): *Foundations of Language: Brain, Meaning, Grammar, Evolution*. New York: Oxford University Press.

KELLER S.S., ROBERTS N. and HOPKINS W. (2009): A comparative magnetic resonance imaging study of the anatomy, variability, and asymmetry of Broca's area in the human and chimpanzee brain. *J Neurosci*, 29(46), pp. 14607-14616.

KIRBY S. (2002): Natural Language From Artificial Life. *Artificial Life*, 8(2), pp. 185-215.

KIRBY S., CORNISH H. and SMITH K. (2008): Cumulative cultural evolution in the laboratory: An experimental approach to the origins of structure in human language. *PNAS*, 105(31), pp. 10681-10686.

KRUBITZER L. (1995): The organization of neocortex in mammals: are species differences really so different ? *Trends in Neurosciences*, 18(9), pp. 408-417.

MILLER G.A. and GILDEA P.M. (1991): How children learn words. In W.S.-Y. Wang (Ed.), *The Emergence of Language: Development and Evolution* (pp. 150-158). New York: W. H. Freeman.

PETERSSON K.-M., FOLIA V. and HAGOORT P. (2012): What artificial grammar learning reveals about the neurobiology of syntax. *Brain and Language*, 120(2), pp. 83-95.

PETRIDES M., CADORET G. and MACKEY S. (2005): Orofacial somatomotor responses in the macaque monkey homologue of Broca's area. *Nature*, 435(7046), pp. 1235-1238.

PETRIDES M. and PANDYA D.N. (1999): Dorsolateral prefrontal cortex: comparative cytoarchitectonic analysis in the human and the macaque brain and corticocortical connection patterns. *The European Journal of Neuroscience*, *11*(3), pp. 1011-1036.

PETRIDES M. and PANDYA D.N. (2009): Distinct Parietal and Temporal Pathways to the Homologues of Broca's Area in the Monkey. *PLoS Biology*, 7(8), e1000170.

PINKER S. (1994): *The Language Instinct: How the Mind Creates Language*. New York: Harper Collins Publishers, Inc.

POWELL L.E., ISLER K. and BARTON R.A. (2017): Re-evaluating the link between brain size and behavioural ecology in primates. *Proceedings of the Royal Society B: Biological Sciences*, 284(1865), 20171765.

POZA-REY E.M., LOZANO M. and ARSUAGA J.L. (2017): Brain asymmetries and handedness in the specimens from the Sima de los Huesos site (Atapuerca, Spain). *Quaternary International*, 433, pp. 32-44.

PREMACK A.J. and PREMACK D. (1972): Teaching language to an ape. *Scientific American*, 227(October), pp. 92-99.

REBER A.S. (1967): Implicit learning of artificial grammars. *Journal of Verbal Learning and Verbal Behavior*, 6(6), pp. 855-863.

RINGO J.L. (1991): Neuronal interconnection as a function of brain size. *Brain, Behavior and Evolution*, 38, pp. 1-6.

RIZZOLATTI G. and ARBIB M.A. (1998): Language within our grasp. *Trends Neurosci*, 21(5), pp. 188-194.

SAVAGE-RUMBAUGH E.S., MURPHY J., SEVCIK R.A., BRAKKE K.E., WILLIAMS S.L. and RUMBAUGH D.M. (1993): Language comprehension in ape and child. *Monographs of the Society for Research in Child Development*, 58(3-4), pp. 1-222.

SAVAGE-RUMBAUGH E.S., and RUMBAUGH D.M. (1993): The emergence of language. *In* K. R. Gibson and T. Ingold (Eds.), *Tools, Language and Cognition in Human Evolution* (pp. 86-108). Cambridge: Cambridge University Press.

SAWAGUCHI T. and KUDO H. (1990): Neocortical development and social structure in Primates. *Primates*, 31(2), pp. 283-289.

SCHENKER N.M., HOPKINS W.D., SPOCTER M.A., GARRISON A.R., STIMPSON C.D., ERWIN J.M. and SHERWOOD C.C. (2010): Broca's area homologue in chimpanzees (Pan troglodytes): probabilistic mapping, asymmetry, and comparison to humans. *Cerebral Cortex*, 20(3), pp. 730-742.

SCHOENEMANN P.T. (1999): Syntax as an emergent characteristic of the evolution of semantic complexity. *Minds and Machines*, 9, pp. 309-346.

SCHOENEMANN P.T. (2010): The meaning of brain size: the evolution of conceptual complexity. *In* D. Broadfield, M. Yuan, K. Schick, and N. Toth (Eds.), *Human Brain Evolving: Papers in Honor of Ralph Holloway*. Bloomington, Indiana: Stone Age Institute Press.

SCHOENEMANN P.T. (2012): Evolution of brain and language. In M.A. Hofman and D. Falk (Eds.), *Progress in Brain Research* (Vol. 195, pp. 443-459). Amsterdam: The Netherlands: Elsevier.

SCHOENEMANN P.T. (2013): Hominid Brain Evolution. *In* D. R. Begun (Ed.), *A Companion to Paleoanthropology*, pp. 136-164. Chichester, UK: Wiley-Blackwell.

SCHOENEMANN P.T. (2017): A complex-adaptive-systems approach to the evolution of language and the brain. *In* S. S. Mufwene, C. Coupé, and F. Pellegrino (Eds.), *Complexity in Language: Developmental and Evolutionary Perspectives*, pp. 67-100. Cambridge University Press.

SCHOENEMANN P.T. and HOLLOWAY R.L. (2016): Brain function and Broca's Cap: A meta-analysis of fMRI studies. *American Journal of Physical Anthropology*, 159 (S62), p. 283.

SCHOENEMANN P.T., SHEEHAN M.J. and GLOTZER L.D. (2005): Prefrontal white matter volume is disproportionately larger in humans than in other primates. *Nature Neuroscience*, 8(2), pp. 242-252.

SMITH K., KIRBY S. and BRIGHTON H. (2003): Iterated learning: a framework for the emergence of language. *Artificial Life*, 9(4), pp. 371-386.

SNOWDON C.T. (1990): Language capacities of nonhuman animals. *Yearbook of Physical Anthropology*, 33, pp. 215-243.

STRIEDTER G.F. (2005): *Principles of Brain Evolution*. Sunderland, MA: Sinauer Associates.

TAGLIALATELA J.P., RUSSELL J.L., SCHAEFFER J.A. and HOPKINS W.D. (2008): Communicative signaling activates "Broca's" homolog in chimpanzees. *Curr Biol*, 18(5), pp. 343-348.

WILSON B., KIKUCHI Y., SUN L., HUNTER D., DICK F., SMITH K. and PETKOV C.I. (2015): Auditory sequence processing reveals evolutionarily conserved regions of frontal cortex in macaques and humans. *Nature Communications*, 6, p. 8901.

WILSON B., SLATER H., KIKUCHI Y., MILNE A.E., MARSLEN-WILSON W.D., SMITH K. and PETKOV C.I. (2013): Auditory Artificial Grammar Learning in Macaque and Marmoset Monkeys. *Journal of Neuroscience*, 33(48), pp. 18825-18835.

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