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# The evolution of enhanced conceptual complexity and of Broca's area

## Language preadaptations

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Evolutionary change occurs most often through the modification of pre-existing structures. What were the pre-existing circuits in our primate ancestors that paved the way for human language, and how did they change in the lineages leading to our present condition? Among the neural modifications that were critical for human language, there are two of special interest: The origin and evolution of the remarkably rich conceptual world that humans share to the exclusion of other primates (which made possible increasingly sophisticated communication systems), and the origin of neural circuitry that underlies various sequential and hierarchical aspects of language, as utilized for example in syntax and word morphology. The fossil record of brain evolution and the archaeological record provide intriguing clues about these processes.

**Keywords:** conceptual complexity, Broca's, brain evolution, language evolution, syntax, sequential processing, endocasts, fossils

### Introduction

Evolutionary biological theory holds that evolutionary change is most likely to occur through the modification of pre-existing structures (Bock, 1959; Jacob, 1977). This follows from the recognition that biological change itself is often driven by behavioral change (Mayr, 1978). Individuals in any given generation are inevitably constrained to use their pre-existing biology to fill whatever behavioral needs they have. Assuming some behavior is adaptive for them, even using an existing imperfect circuit to approximate the adaptive behavior is necessarily going to be better than not attempting the behavior at all (Schoenemann, 1999). As a consequence, evolutionary modifications of these inferior circuits will always be *more likely* than the evolution from scratch of entirely new complex circuits. Note that this logic remains even though human brains seem to have many more uniquely definable

cortical areas than other primates (Changizi and Shimojo, 2005; Fan et al., 2016). Detailed studies of exactly what these “new” areas do differently in humans is in its infancy, but work to date suggests they are subdivisions (and specializations) of pre-existing functional areas, and not completely unrelated functional areas (Mars et al., 2013; Uylings and Van Eden, 1990).

Given this, a complete understanding of language evolution requires the identification of relevant precursor neural circuits as well as an explanation of how they were modified to subservise language today. Although there are many behavioral domains that are important to language evolution, the focus here will be on two of particular interest: (1) conceptual understanding, and (2) the identification and processing of sequential pattern information. In part this focus stems from the recognition that clues about their evolution are potentially identifiable in the fossil record, as will be reviewed below. In particular, the enhancement of conceptual understanding can be indexed by brain size increases, and enhanced sequential processing appears to depend at least partly on the elaboration of circuits involving Broca's area, which may leave impressions on fossil skulls. Sequential processing involving (but not limited to) Broca's may have originally evolved to track and predict sequential patterns in the organism's environment, preadapting this circuitry for the cultural evolution of language grammar. It will be argued that enhanced social complexity was both the driver of – and being driven by – the evolutionary enhancement of both of these sets of circuits.

### Conceptual complexity

Language presupposes that individuals share a significant degree of overlap in their conceptual understandings of the world, not just because it makes symbolic reference possible, but also because it makes communication useful in the first place (Schoenemann, 1999). That species appear to differ in the richness of their conceptual world is typically overlooked in models of language evolution. However, several lines of evidence point to a dramatic increase in conceptual richness during the evolution of the genus *Homo* (Schoenemann, 2012). Put in the context of evidence for a co-evolving, increasingly complicated interactive social existence, this increasing conceptual richness was likely a major reason for increasing communicative complexity. In turn, increasingly complex communication would have encouraged increasingly complex social interactions, thereby further increasing the usefulness of richer conceptual understanding. Given that concepts are instantiated as brain network activation states, it is also likely that the enhancement of circuits used in communication would have itself enhanced conceptual complexity.

Other animals besides humans have concepts – at least in a broad sense of the term – even though they are likely not nearly as rich and complex as those

humans have. In order for monkeys to respond reliably to alarm (Seyfarth et al., 1980) and other social calls, the calls must make salient some conceptual category in most individuals' minds. Baboons respond differentially to sequential patterns of calls depending on whether or not they match their prior expectations of dominance positions (Bergman et al., 2003). This indicates that they have separate conceptualizations of each individual in their social group, the idea of higher and lower dominance, and hierarchical social groups (families). Ape language studies demonstrate that apes have (or can learn) the concepts labeled by symbols. Work with the bonobo Kanzi, for example, demonstrates that he knows several hundred English words (Savage-Rumbaugh et al., 1993). Concepts in monkeys and apes are likely not identical to human variants with respect to their semantic coverage (as is true between individual humans, and groups of humans). The critical point is that non-human primates do organize sensory and other information into conceptual categories, that they can in at least some instances code symbolically. Suggestions to the contrary (e.g., Berwick et al., 2013) simply misunderstand a degree of difference for a degree of kind.

The difference is therefore not that monkeys and apes lack concepts or the ability to code them symbolically. It is instead a difference in quantity, complexity, subtlety, and richness. Snowdon (Snowdon, 1990) notes "Bonobos and chimps appear to be more limited in the topics that they find interesting to communicate about." (p. 222). Ape language research studies typically report vocabulary sizes of only a few hundred symbols, whereas estimates for humans are ~40,000 (Miller and Gildea, 1991).

This difference is directly predictable from a consideration of human brain evolution. Concepts appear to either be – or be dependent on – patterns of neural activation. Even seemingly simple concepts involve activation of many brain areas. The concept 'red' depends on unique activation of particular sets of cone cells in the retina, retinal ganglion activation, lateral geniculate nucleus, primary visual cortex (V1), and secondary visual areas V2 and V4 (and likely others; Bramão et al., 2010). More abstract concepts like 'love' are presumably based on even more complex and subtle sets of neural activation.

Larger brains have the potential for a larger range of unique network activation states. Not only are individual areas often larger in humans than in apes (e.g. Broca's area is ~5–6 times larger in humans than in apes: Keller, Roberts, & Hopkins, 2009; Schenker et al., 2010), but in addition, larger brains seem to have larger numbers of uniquely definable cortical areas (Changizi and Shimojo, 2005). Recent estimates suggest humans have over 200 (Fan et al., 2016) – more than twice what can be estimated for chimpanzees (Changizi and Shimojo, 2005), though these appear to be specialized subdivisions of areas found in smaller brained primates. Because the number of potential unique subsets of areas and

their interactions increases geometrically as the total number of areas increases, this can at least theoretically translate into many orders of magnitude difference in unique network activation states (Schoenemann, 2017). This is consistent with Jerison (1985): "Grades of encephalization presumably correspond to grades of complexity of information processing. These, in turn, correspond in some way to the complexity of the reality created by the brain..." (p. 30). When combined with the recognition that areas become increasingly specialized as brain size increases, the likely increase in conceptual complexity further magnifies.

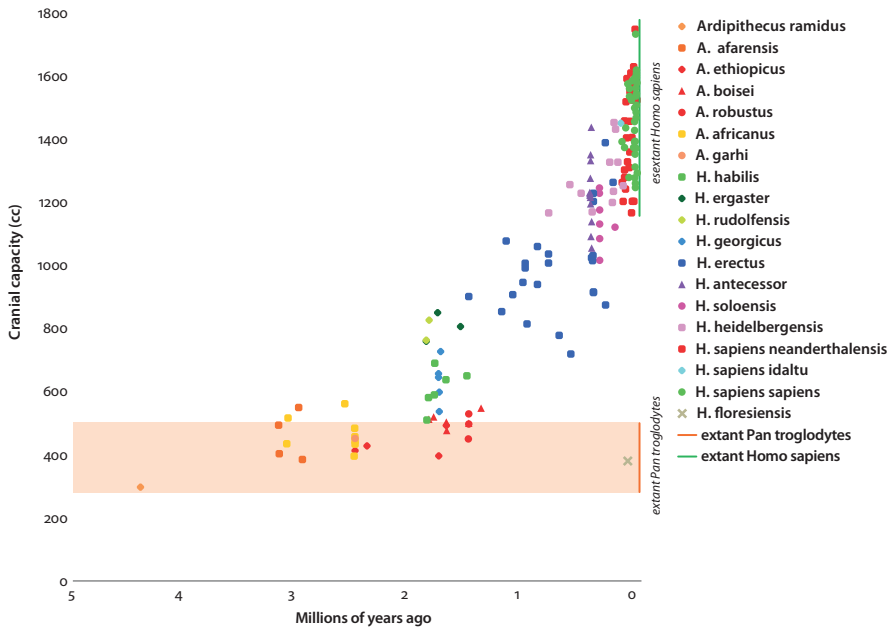
The existence of mirror neurons, allowing the individual to recognize which actions of others are the same as its own, is also relevant to conceptual richness (Arbib, 2016). Being able to have categories of types of action that include one's own behavior – which are critical for complex social interactions – would require a mirror neuron system. Arbib (2017) argues that "complex action analysis, the ability to recognize another's performance as resembling an assemblage of familiar actions," along with imitation – both of which depend on a mirror system – are fundamental to the elaboration of meaning expression (p. 234).

It is important to note that the full expression of all the possible network activation states will depend crucially on the neural developmental context. In humans, this developmental context critically includes the social environment, which includes cultural influences (see Sinha, this volume). Thus, a key component of language evolution is cultural evolution.

This all suggests increasing brain volume is an approximate index for the evolution of conceptual complexity. Cercopithecoid monkeys average brains that are about 1/4th the size of modern chimpanzees (Stephan et al., 1981). However, the fossil record of the transition from the last common ancestor we share with these monkeys (LCA-m) to that which we share with chimpanzees (LCA-c) for brain size is very spotty (Begun and Kordos, 2004; Schoenemann, 2013).

Modern chimpanzees in turn have brains ~1/3rd the size of modern humans. The earliest hominin brains were about the same size as modern chimpanzees, but starting sometime between 2–3 million years ago, a dramatic increase begins, and appears to accelerate up until the last ~100 KYA (Figure 1).

Intriguingly, although stone tools have been reported between 3.3 and 2.6 MYA (Harmand et al., 2015; Semaw et al., 2003), stone tools are not consistently found before ~2 MYA (Nicholas Toth, personal communication). Research on what stone tools might tell us about the evolution of cognition has recently focused on the cognitive neuroscience of stone tool manufacturing (Putt et al., 2017; Stout and Chaminade, 2012; and Putt and Stout in this volume). With respect to the question of increasing conceptual complexity, stone tool technology shows both an increase in tool types – from just a few basic types in the earliest Oldowan technology to an extensive range of special purpose tools made from multiple



**Figure 1.** The fossil record of hominin brain evolution. Data Holloway et al. (2004) and Schoenemann (2013). The orange band represents the range for modern human chimpanzees. Note that the range of hominins even ~3 MYA is shifted higher compared to modern chimps

materials in the Upper Paleolithic – as well as increasing standardization of forms (Isaac, 1976). Toth & Schick (2009) argue there is a >4-fold increase in the number of cognitive decisions required to make the earlier Oldowan as compared to later Acheulean technology (which first occurs ~1.7 MYA but becomes fully mature ~0.7 MYA). In addition, Increased visuomotor coordination, possible changes in hand shape, improved imitation ability and possibly teaching (see Stout, this volume) would be required. Consistent with this, cranial capacity increases seen during the Acheulean technological tradition are substantial (Figure 1).

What might have caused such an increase in conceptual complexity? Humphrey (1984) proposed that increasing intellect was an adaptation to social living, and that tools were made possible by this (when combined with a grasping hand). Consistent with this, brain size in primates is associated with social group size (Dunbar, 2003). Although DeCasien et al. (2017) and Powell et al. (2017) report *relative* brain size does not correlate with social group size in primates, both datasets show a robust correlation with *absolute* brain size. Increasing brain size over time predicts increasing social complexity as well as increasing conceptual richness.

There are two ways in which social complexity would likely induce conceptual richness. First, social complexity would have spurred the elaboration and

refinement of conceptual understanding. Understanding increasingly subtle patterns of social signals would select for finer conceptualization of social behaviors generally. As social interactions become increasingly complicated, conceptualizing the difference between Machiavellian strategic behavior vs. that of a truly reliable ally would be critical. Individual behaviors themselves might be the same, but subtle differences in context could signal extremely important underlying differences in long-term commitment.

At the same time, increasing social complexity would lead to the elaboration of cultural learning generally: More individuals doing more things leads to increasing technological elaboration, thereby selecting for the ability to conceptualize the world in increasingly rich, subtle, and creative ways. Increasing technological complexity also dramatically increases the ways individuals can interact with the world. This suggests a dynamic, positive feedback effect on cultural complexity that would select for increasing neural elaboration underlying conceptualization. Consistent with this, Powell et al. (2009) show it is possible to model dramatic changes in technological innovation (e.g., the transition to the Upper Paleolithic ~45,000 years ago) using demographic changes alone.

The evolution of increasing conceptual richness in the context of an increasingly socially-interactive existence would have been a powerful spur to enhanced communication. The positive-feedback nature of this interaction over evolutionary time would have led inevitably to selection for increasingly elaborate modern human language systems.

## Sequence processing

Language grammar and syntax rely partly on sequence processing. Since an evolutionary perspective predicts this circuitry most likely occurs through the modification of pre-existing circuits, we should expect that modern language circuits have precursors of some kind in non-human primates. Any particular aspect of language processing likely involves complex interactions of circuits from many different brain areas, of course, and not simply neural circuits localized in one area alone. The focus here will be on a subset of circuits relevant to sequential processing, which are depend in part the cortical region known as Broca's area. This focus is partly because Broca's has such a long and important history in neurolinguistics studies, but also because – as a cortical as opposed to subcortical area – it stands a better chance of leaving imprints on fossil endocrania, and thereby suggesting the time-course of aspects of language evolution. Studies of Broca's aphasia, Parkinson's disease, and Huntington's disease indicate the critical involvement of subcortical structures such as the basal ganglia also (Lieberman, 2000). Nevertheless, functional brain imaging studies show Broca's area plays a role in

grammar (Grodzinsky, 2000; Thompson-Schill et al., 1997), and gray matter loss in Broca's is correlated with the degree of deficits in syntactic comprehension and production (Wilson et al., 2011). The 5–6 fold difference in size in Broca's area (Keller et al., 2009; Schenker et al., 2010) between humans and chimpanzees tells us there has been particularly strong selection in hominin evolution on this region.

What, then, is the evolutionary history of Broca's area? Because homologs of Broca's area have been found in both apes and monkeys (Schenker et al., 2010), the precursors of human language circuits there must have evolved for purposes other than language. Homologs of Broca's area in monkeys has been shown to contain mirror neuron circuits (Arbib, 2016), is active during the recognition of species-specific vocal calls (Gil-da-Costa et al., 2006), is involved in orofacial motor sequencing (Petrides et al., 2005), and the active controlled retrieval of visual object and spatial information (Petrides and Pandya, 2009). Chimpanzee Broca's homolog is active during the production of communicative gestures (Tagliatela et al., 2008), consistent with the proposal that mirror neurons in Broca's area form an important foundation for language (Schenker et al., 2008).

Another avenue for obtaining clues about the original function of Broca's is to ask what non-linguistic functions are still evident in human Broca's area? These may represent ancient functions of the original Broca's area circuits in earlier monkeys and apes. Although they may simply represent secondary uses of circuits that evolved specially for language in humans, this can be ruled out if Broca's homologs in modern monkeys and apes also have these functions. One intriguing set of studies shows that Broca's is important for implicit learning of non-linguistic sequential patterns or "rules" (Christiansen et al., 2010; Petersson et al., 2012). This suggests an intriguing hypothesis: Circuits in Broca's originally evolved to 'extract' or learn sequential pattern information (predictions about what sequences are likely) from the organism's environment. In hominins they would have been an attractive substrate for the evolution of syntax (and grammar), as well as the ability to distinguish words based on different patterns of phonemes.

Such sequence-pattern-sensitive circuits would be useful for all sorts of reasons, including a connection with mirror neuron mediated action recognition. An action typically involves some number of parts or 'sub-actions', which are sequenced in a specific way. For example: the action: [grabbing an object] involves first extending the arm towards the object, and then closing the fingers around it. By contrast, the action: [punching an object] involves first closing the fingers around themselves (to make a fist), and then extending the arm (rapidly) towards the object. Recognizing these as distinct actions requires being sensitive to the particular sequence of sub-actions that they entail. Being able to quickly differentiate between a someone punching vs. grabbing you would be extremely useful in a complex social environment.



Sequential patterns of sounds – rather than the individual sounds themselves – are of course the key to differentiating individual words. "Cat", "tack", and "act" are distinguishable not because of the basic sounds they contain, but rather the order in which the sounds appear. Much of grammar involves sensitivity to different orders of words in a sentence. Although not all languages use word order to mark argument structure, there is no language for which word order is truly meaningless (William Wang, personal communication). For all languages, some circuitry is needed that is sensitive to differences in sequential ordering of constituents.

Understanding the evolutionary history of sequential processing requires assessment of the degree of overlap (if any) between linguistic vs. non-linguistic sequential processing. Fedorenko et al. (2012) do report somewhat distinct (though highly individually variable) linguistic and nonlinguistic functional regions of Broca's area, but their tasks did not assess sequential processing particularly well. Differential localization of linguistic vs. non-linguistic processing within Broca's also does not demonstrate that humans evolved unique language-specific circuitry there. Such differentiation could be entirely developmentally induced. The degree of individual variability found by Fedorenko et al. (2012) makes any suggestion of a genetic hard-wiring unlikely.

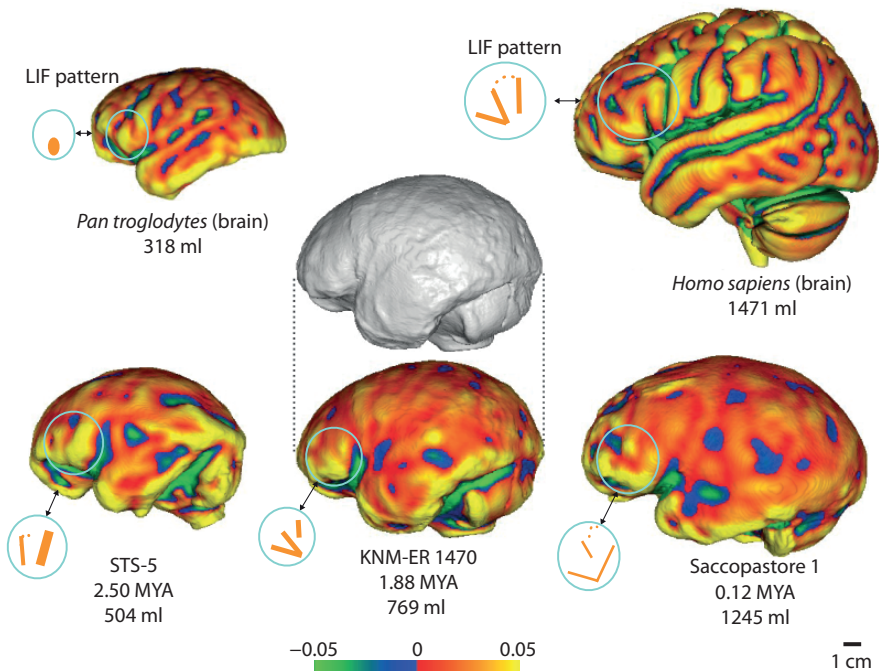
Because of the non-linguistic nature of the sequential processing tasks probed by Christiansen et al. (2010) and Petersson et al. (2012), it is possible to probe whether or not non-human primates also demonstrate implicit learning of sequential patterns, and if so, whether their homolog of Broca's is also involved. Recent studies with simpler patterns suggest they do (Wilson et al., 2015; Wilson in this volume, 2013), and we are pursuing similar work.

Evidence of brain evolution in the fossil record provides tantalizing clues about the evolution of Broca's area (Holloway, 1983). Given that in modern humans left Broca's is more active during language processing, and that Broca's tends to be larger on the left than on the right, asymmetries in Broca's cap of fossil endocasts are of particular interest (Holloway, 1976). While Broca's cap only partially overlies Broca's area (Falk, 2014), it does overly area intensively involved in language processing (Schoenemann and Holloway, 2016). Holloway et al. (2004) report subjective assessments whether left Broca's cap is larger than the right in the 19 pre-anatomically modern specimens for which both left and right Broca's caps are preserved. The majority (almost 80%), going back >2 MYA, show the left protruding more than right, and only two show a clear right bias.

Assessments of fossil endocast sulcal/gyral patterns overlaying Broca's area also suggest changes occurring >2 MYA. The earliest fossil suggesting a difference from the basic chimpanzee pattern in the left inferior frontal (LIF) is an *Australopithecus africanus* specimen, STS-5 (~2.5 MYA from Sterkfontein, South Africa; Figure 2). This specimen also displays a left-biased Broca's cap (Holloway et al., 2004).

Even more suggestive is a 1.8 MYA early *Homo* specimen, KNM-ER 1470. Holloway (1976) noted the endocranial gyral/sulcal impressions in the area overlying the LIF were clearly larger than in earlier hominins. Falk (1983) argued its convolitional detail was more consistent with a human-like Broca's. The curvature pattern confirms a more modern-human-like LIF (Figure 2).

Early *Homo ergaster* specimens KNM-ER 3733 (1.78 MYA) and 3883 (1.57 MYA) had "true" Broca's caps (Holloway, 1983), although surface morphology is not described. 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), displays strong left Broca's cap protrusion similar to modern humans. Gilbert et al. (2008) report it lacks convolitional details, but images of the



**Figure 2.** Top row: Chimpanzee brain (average of 3 male and 3 female; Schoenemann, Sheehan, & Glotzer, 2005); Human brain (Grabner et al., 2006). Bottom row: Endocrania of 3 hominin fossils: STS-5, KNM-ER 1470, and Saccopastore 1. Color coding corresponds to the average curvature of the surface at each point, calculated following Avants et al. (2005) and Avants & Gee (2003). An image of the virtual endocranium of KNM-ER 1470 without curvature coding is included for comparison. For each image, the LIF area overlying Broca's area is enclosed by a cyan circle, and a matching circle highlighting the basic pattern for that endocranium appears just to its lower left. Typical pattern of the LIF for modern chimp and human are indicated for comparison. Note that the fossil endocranium LIF patterns are more similar to the modern human brain

endocast indicate a more complicated morphology than is typical for chimpanzees. The Ngandong (Solo XI) *Homo erectus* specimen (Indonesia, 0.34 MYA) has a well-developed Broca's area (Holloway, 1980).

Later hominins appear to retain this characteristic. *Homo antecessor* specimens from Atapuerca, Spain (0.43 MYA), appear to be more modern-human-like in the LIF, judging from published images (Poza-Rey et al., 2017). Curvature analysis of the Saccopastore 1 (0.12 MYA) Neanderthal specimen suggests the same for this group as well (Figure 2).

This suggests significant changes in Broca's area go back at least to early *Homo*, and possibly earlier. Though tantalizing, what exactly these changes reflect neuroanatomically and linguistically are not clear. Because Broca's area is known to have non-linguistic functions it is possible these inferred changes in Broca's area only reflect increasing tool use, pantomime (or both), and not something about language directly.

The archaeological evidence of tool use is much richer than the fossil evidence of brains. Sites that contain only stone tools vastly outnumber those with hominin fossils. What these stone tools may tell us about cognitive evolution, and language in particular, is an area of intense interest (Morgan et al., 2015; Putt et al., 2017; Stout and Chaminade, 2012). Although left hemisphere Broca's area does not appear to be particularly active in these studies, its role in sequential processing and hierarchical representation of motor actions nevertheless suggests it was relevant to stone tool manufacturing. The archaeological record indicates increasing sophistication of technology over time, and the earliest evidence of stone tool manufacturing approximates when the earliest suggestions of changes in Broca's area occur in the hominin fossil record. These changes in tool complexity are consistent with both an elaboration of conceptual complexity, as well as enhanced sequential processing ability.

## Toward a new road map

The fact that conceptual complexity and sequential processing have been highlighted here should not be taken to mean that these are the only important components to the story. The arguments here are meant to suggest important considerations for ongoing research. Some intriguing directions to pursue include:

- How are the homologs of modern human language circuits functioning in nonhuman primates? Investigation should not just Broca's area, but also its connections with posterior areas and the basal ganglia, Wernicke's area, and mirror neuron circuitry. Which circuits are specifically involved with sequential information? We are currently working with Robert Shumaker, Indianapolis Zoo, to assess implicit learning of nonlinguistic sequential rules

in orangutans. Which of these homologs also process information about hierarchical social relationships (Wilkins and Wakefield, 1995)? Hierarchical relationships make predictions about what sequential patterns are likely in social environments. The relationship between sequential processing and hierarchical processing should be explored fully. Sequential processing in monkeys is known to activate premotor and supplementary motor areas (e.g., Nakajima et al., 2013), but exactly what role Broca's area might play in monkeys, and how this was elaborated over time, has not been extensively probed. The possible role of increasing social and technological complexity in enhancing the usefulness of the ability to identify and reconstruct sequential patterns (in many domains) deserves particular attention.

- Is there direct evidence of increasing conceptual richness going from monkeys to apes to humans? One idea: use the oddball paradigm with EEG (Picton, 1992). A smaller difference between oddball vs. expected stimuli should show larger ERP's for larger brained species (Mark Liberman, personal communication).
- What connections exist between conceptual richness, sequential processing, and hierarchical processing? How might these covary across primates of varying brain sizes?
- What is the relevance of sequential processing to mirror neuron activity in nonhuman primates? Does the later depend on the former? Are mirror neuron circuits used in processing non-human primate communicative/social/gestural behavior?
- Evidence suggests that language-trained apes do have limited syntactic understanding (e.g., "Rose is gonna chase Kanzi" vs. "Kanzi is going to chase Rose Savage-Rumbaugh et al., 1993, p. 95). What circuits are they using for this?
- Assuming that sensitivity to sequential processing critically underlies grammar and phonology, what then, if anything, has to change in this circuitry to support grammar (syntax and semantics) or phonology? Or can a system that extracts sequential patterns from the environment be harnessed for grammar directly?
- What quantitative evidence can be obtained for changes in fossil endocranial morphology that might be relevant to language? Research on endocranial form suggests the parietal was also important (Bruner et al., 2016). Exactly how much can we predict about a hominin brain from its skull alone? We are currently obtaining brain and for skull data from the same human and ape subjects to directly assess this.
- Exactly what cognitive functions are necessary for the transitions between stone tool types documented in the archaeological record, and are these correlated with changes in endocranial morphology?

- Lastly, further elaboration of dynamic models of the co-evolution of language and neurobiology would be useful (Gong et al., 2014). For example, is it possible to marry socially-interactive agent-based models with models of brain function, e.g., those outlined in Arbib (2016)? To what extent might syntactic complexity be a cultural evolutionary byproduct of increasing conceptual complexity (Schoenemann, 1999; Smith et al., 2003)? If so, can one directly model the expanding spiral of influences (e.g., Arbib, 2016)? Can the elaboration of language and technology seen in the archaeological record be modelled?

## Acknowledgements

This research was supported in part by grant 52935 from the Templeton Foundation titled: “What Drives Human Cognitive Evolution?” N. Toth, K. Schick, C. Allen, P. Todd, P.T. Schoenemann, co-Principle Investigators. The paper was prepared for a workshop funded by NSF Grant No. BCS-1343544 “INSPIRE Track 1: Action, Vision and Language, and their Brain Mechanisms in Evolutionary Relationship,” (M.A. Arbib, Principal Investigator). I thank Ralph Holloway for insights on the endocranial evidence, allowing his endocast of KNM-ER 1470 to be scanned, and for his copy of Giorgio Manzi’s virtual endocast of Saccopastore 1. The endocast of STS 5 was derived from CT scans of the original. I also thank the reviewers.

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