The importance of exploring non-linguistic functions of human brain language areas for explaining language evolution

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Abstract

The evolution of language is a special case of the evolution of behavior. Evolutionary biologists have long recognized that behavioral change drives biological change, rather than the other way around (Mayr 1978). This has recently been highlighted specifically with respect to language evolution (e.g., Christiansen and Chater 2008). In the context of human evolution, this means that cultural evolution will, to a large extent, drive biological evolution. The transition from quadrupedalism to bipedalism, for example, was driven by behavioral changes (Hunt 1994). We didn't evolve bipedal anatomy first, only to stumble upon its usefulness later. The spread of agriculture lead to selection for sickle-cell alleles (Livingstone 1958). The domestication of dairying animals lead to selection for continued lactase production (Durham 1991). Applying this logic to language evolution, for every generation in which greater facility at communication was adaptive, individuals would have used pre-existing cognitive abilities to communicate as best they could. Genetic changes would have therefore been strongly biased towards those that modified pre-existing abilities, rather than entirely new neural circuits devoted exclusively to language. This also means that we should expect homologs of human language circuits in non-human primate brains (Schoenemann 1999). Homologs of Broca's and Wernicke's areas have in fact been located in primates (Striedter 2005), and finding out what they use them for is critical to understanding the coevolutionary process that lead to language in humans. One fruitful approach is to identify non-language abilities that are also processed in human language areas. Broca's area in humans has been implicated in non-linguistic sequential processing (Petersson et al. 2004), hand/tool manipulation (Higuchi et al. 2009), and non-verbal auditory processing (e.g., Muller et al. 2001). Because these are non-linguistic, their functional localization can also be explored in non-human primates. If they also activate Broca's area homologs, this would support the view that language adapted to pre-existing cognitive architectures, rather than requiring the creation of completely new, language-specific brain areas.

Behavior drives biological evolution, not the reverse

The evolutionary process is iterative, with behavioral changes occurring *within* each generation driving the system. Biological changes between generations are the *result*, not the cause, of evolutionary change. The evolutionary logic is as follows:

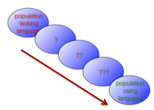


Figure 1: Evolutionary change occurs through successive modifications of a series of populations, with selection operating among individuals within each population. Individuals will always adapt behaviorally if they can, since their biology is generally less flexible. This inevitably biases the process towards modifications of pre-existing abilities (Schoenemann 2009)

1) For a complex adaptation to evolve (biologically) it must be beneficial, and this must be true within each generation (at least on average) during the transition from incipient to full-blown adaptation.

2) Individuals are not able to change their genes to be more adaptive, but they may be able to change their behavior. Some species (especially primates) are inherently more behaviorally flexible than others (e.g., reptiles).

Given this, individuals within each generation will always be expected to use whatever pre-existing cognitive circuitry they have available (point 2) to better accomplish the (by definition) beneficial task (point 1).

The evolutionary process is fundamentally biased towards modifying pre-existing abilities

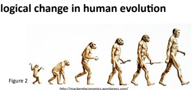
If there is any way for existing circuitry to be harnessed towards a new task, even if this is clearly suboptimal in some absolute engineering sense, the evolutionary process will necessarily follow this path. Models that rely on the evolution of completely new dedicated circuitry are flawed. If there is even the *slightest* possibility that pre-existing circuitry can be utilized to accomplish a task just a tiny bit better than previously, the system will capitalize on this.

Evolutionary biology has long recognized these as central principles of evolutionary change

> **"There is little doubt that some of the most important events in the history of life, such as the conquest of land or of the air, were initiated by shifts in *behavior*."** (Mayr 1978, p. 55, emphasis added)
>
> **"Evolution does not produce novelties from scratch. *It works on what already exists*, either transforming a system to give it new functions or combining several systems to produce a more elaborate one,"** (Jacob 1977, p. 1164, emphasis added)

There are many examples of behavioral change causing biological change in human evolution

- Increasing behavioral adoption of bipedal locomotion (which is possible, but not comfortable, in other apes) led to selection for a suite of anatomical changes in the pelvis, knee, foot, and cranial base (Figure 2). Our ancestors did not evolve these first, and adopt bipedalism later. (e.g., Hunt 1994).

Figure 2

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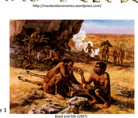
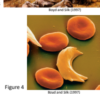
- Cultural changes spurred by technology (stone tools, fire) lead to significant increases in the density of nutrients (through the incorporation of meat and animal fat, cooking of food), which in turn led to selection for smaller dentition, smaller jaws and associated musculature, gut proportions favoring the small intestine (which is specialized for high-nutrient-density foods), and arguably an inability to survive on raw vegetable diets alone (Figure 3; Wrangham 2009).

Figure 3

Boyd and Silk (1997)

- The cultural adoption and spread of agriculture led to selection for sickle-cell alleles: agriculture created the perfect conditions for spread of the mosquito responsible for spreading malaria, to which sickle-cell is an adaptation (Figure 4; Livingstone 1958).

Figure 4

Boyd and Silk (1997)

- The domestication of milk-producing animals (initially in parts of Europe and Africa) led to selection for lactose tolerance in adulthood (a genetic change still rare in many parts of the world, and unknown in non-human mammals; Figure 5; Durham 1991).

Figure 5

http://sites.google.com/a/palaeome.org/leche/Home/fellows/roz-gillis-1

Thus, our starting expectation for language should be:

Selection for changes in brain circuitry subserving language was driven by behavioral changes emphasizing increased communication.

The evolution of completely new language-specific circuitry is inherently unlikely

An evolutionary approach requires that we explore all possible models that emphasize the modification of behavior - and hence, pre-existing neural circuitry - that could conceivably allow individuals to accomplish tasks more effectively (even if only minutely so) within each generation. These models are inherently more likely than explanations postulating evolutionarily-novel innate circuitry devoted solely to language (let alone grammar).

Note that "arguments from personal incredulity" (to borrow a phrase from Richard Dawkins) are not convincing refutations (many people still cannot personally imagine how biological evolution itself could be valid). Actually testing models is what needs to be done.

There have been a number of discussions of language evolution that are consistent with the idea of behavioral change driving biological change: e.g., Sampson (1979), Lieberman (1984), Savage-Rumbaugh and Rumbaugh (1993), Christiansen (1994), Schoenemann and Wang (1996), Deacon (1997), Gibson and Jessee (1999), Schoenemann (1999), Kirby (2000), Christiansen and Chater (2008), Higuchi et al.(2009). The metaphor of language as an organism adapting to the human brain, rather than the brain adapting to language (e.g., Christiansen and Chater 2008) is inherently more consistent with basic evolutionary principles, than models postulating completely new circuitry (e.g., Bickerton 1990; Chomsky 1972; Hauser et al. 2002; Pinker 1994; Pinker and Jackendoff 2005).

Bibliography

Bickerton D. 1990. *Language & Species*. Chicago: University of Chicago Press.
Boyd R, and Silk JB. 1997. *How Humans Evolved. New York: W. W. Norton.*
Chomsky N. 1972. *Language and Mind*. New York: Harcourt Brace Jovanovich, Inc.
Christiansen MH. 1994. *Infinite Languages, Finite Minds: Connectionism, Learning and Linguistic Structure* [Unpublished PhD dissertation]. Edinburgh, Scotland: University of Edinburgh.
Christiansen MH, and Chater N. 2008. Language as shaped by the brain. *Behavioral and Brain Sciences* 31:489-509.
Deacon TW. 1988. Human brain evolution: I. Evolution of language circuits. In: Jerison HJ, and Jerison I, editors. *Intelligence and Evolutionary Biology*. Berlin: Springer-Verlag. p 363-382.
Deacon TW. 1997. *The symbolic species : the co-evolution of language and the brain*. New York: W.W. Norton.
Durham WH. 1991. *Coevolution : genes, culture, and human diversity*. Stanford, Calif.: Stanford University Press.
Gibson KR, and Jessee S. 1999. Language evolution and expansions of multiple neurological processing areas. In: King BJ, editor. *The Origins of Language: What Nonhuman Primates Can Tell Us. Santa Fe, New Mexico: School of American Research Press. p 189-227.*
Hauser MD, Chomsky N, and Fitch WT. 2002. The faculty of language: what is it, who has it, and how did it evolve? *Science* 298:1569-1579.
Higuchi S, Chaminade T, Imamizu H, and Kawato M. 2009. Shared neural correlates for language and tool use in Broca's area. *Neuroreport*.
Hunt KD. 1994. The evolution of human bipedality: ecology and functional morphology. *Journal of Human Evolution* 26(3):183-202.
Jacob F. 1977. Evolution and tinkering. *Science* 196:1161-1166.
Kirby S. 2000. Syntax without natural selection: How compositionality emerges from vocabulary in a population of learners. In: Knight C, Studdert-Kennedy M, and Hurford JR, editors. *The Evolutionary Emergence of Language*. Cambridge: Cambridge University Press. p 303-323.
Lieberman P. 1984. *The Biology and Evolution of Language*. Cambridge, Massachusetts: Harvard University Press.
Livingstone FB. 1958. Anthropological implications of sickle cell gene distribution in West Africa. *American Anthropologist* 60:533-562.
Mayr E. 1978. Evolution. *Scientific American* 239:47-55.
Muller RA, Kleinhans N, and Courchesne E. 2001. Broca's area and the discrimination of frequency transitions: a functional MRI study. *Brain and Language* 76(1):70-76.
Petersson KM, Forkstam C, and Ingvarc M. 2004. Artificial syntactic violations activate Broca's region. *Cognitive Science* 28:383–407.
Pinker S. 1994. *The Language Instinct: How the Mind Creates Language*. New York: Harper Collins Publishers, Inc.
Pinker S, and Jackendoff R. 2005. The faculty of language: what's special about it? *Cognition* 95(2):201-236.
Rilling JK, Glasser MF, Preuss TM, Ma X, Zhao T, Hu X, and Behrens TE. 2008. The evolution of the arcuate fasciculus revealed with comparative DTI. *Nature Neuroscience 11(4):426-428.*
Sampson G. 1979. A non-nativist account of language universals. *Linguisitics and Philosophy* 3:99-104.
Savage-Rumbaugh ES, and Rumbaugh DM. 1993. The emergence of language. In: Gibson KR, and Ingold T, editors. *Tools, Language and Cognition in Human Evolution*. Cambridge: Cambridge University Press. p 86-108.
Schoenemann PT. 1999. Syntax as an emergent characteristic of the evolution of semantic complexity. *Minds and Machines* 9:309-346.
Schoenemann PT. 2009. Evolution of Brain and Language. *Language Learning 59(s1):162-186.*
Schoenemann PT, and Wang WS-Y. 1996. Evolutionary principles and the emergence of syntax. *Behavioral and Brain Sciences* 19(4):646-647.
Striedter GF. 2005. *Principles of Brain Evolution*. Sunderland, MA: Sinauer Associates.
Wrangham RW. 2009. *Catching Fire: How Cooking Made Us Human*. New York: Basic Books.

Non-human primates have homologs of supposed 'language' areas

If language adapted to the human brain, there should be evidence of pre-existing neural architecture that would have been fertile ground for appropriation and modification by language. In fact, anatomical, cytoarchitectural, and connectivity data show that apes and monkeys possess homologs of human language areas and circuitry (Deacon 1988; Striedter 2005; Rilling et al. 2008). This includes Broca's area, Wernicke's area, and the arcuate fasciculus (the major connective pathways between them).

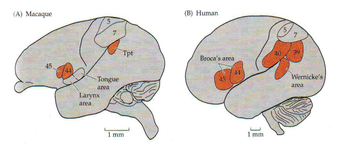


Figure 6: Cytoarchitectural areas 44 and 45 correspond to Broca's area; area Tpt in macaques is likely homologous to Wernicke's area, and/or areas 39 and 40 (Striedter 2005)

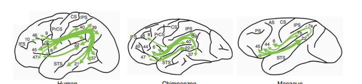


Figure 7: The arcuate fasiculus connecting Broca's and Wernicke's areas in humans also connects the homologous areas in chimpanzees and macaques (Rilling et al. 2008)

The existence of these areas in non-human primates should concern those arguing that language evolution required the evolution of entirely new, language-specific, even grammar-specific circuits. One defense might be to argue that Broca's area, Wernicke's area, and the arcuate fasciculus are *not* the required new circuits. However, one should then easily be able to point to other areas of the brain that are active specifically during human language, but for which other primates do not have homologs. This has not been done, nor has the issue even been addressed (as far as I am aware).

The existence of these 'language' areas in other primates, on the other hand, are exactly what would be predicted if language adapted to the human brain, rather than the reverse. These areas came to be used by language specifically *because* they had already (before language) evolved to process information in ways that would ultimately be useful for language.

The existence of these 'language' areas in non-human primates indicates they must necessarily have evolved for non-language purposes. Finding out what functions they serve in these other species is an important step in evaluating models of language evolution.

Why does Broca's 'language' area have non-linguistic functions in humans , if it evolved only for language?

A useful approach is to assess any explicitly non-linguistic functions that are processed in Broca's area in humans. If the 'language as shaped by the brain' model is correct, these brain areas would be expected to continue to process this non-linguistic information in humans today. We should be able to find residues of the putative original non-linguistic functions of these language areas.

Broca's area in humans has in fact been implicated in a number of non-linguistic tasks. These include: processing non-linguistic sequential information to extract implicit structure and patterning of stimuli (Petersson et al. 2004), sequential patterns of hand/tool manipulation (Higuchi et al. 2009), and non-verbal auditory processing (e.g., Muller et al. 2001). Each of these involve basic abilities that: 1) are not explicitly linguistic, but 2) involve circuits nevertheless clearly useful to language, and likely foundational for it.

However, how can we exclude the possibility that these basic abilities are solely secondary manifestations of the evolution of new language areas? Perhaps human 'language areas' only *inadvertently* process these non-linguistic functions, but not because they actually were their initial functions. There are two ways to rebut this position.

First, why should we believe that non-language functions could be processed by putative 'language areas' in modern humans, when it is claimed language itself could not possibly use pre-existing circuits? Why would language be different from other cognitive functions in this respect? An answer to this question – that does not rely on an "argument from personal incredulity" – has never been offered.

Directly testing the respective models: What do non-human primates do with their 'language' area homologs?

Since these abilities are non-linguistic, it should be possible to assess their functional localization in non-human primates. If it could then be shown that these abilities are also processed in their Broca's area homologs just as they are in humans, it would completely undercut the argument that Broca's area evolved specifically for language. Instead, it would support the view that language adapted to pre-existing cognitive architectures, rather than requiring the creation of completely new, language-specific brain areas.

Conversely, if it turns out that these abilities are *not* processed in their Broca's area homologs as in humans, then it would support the view that completely new circuitry would have been necessary.

Conclusion

An evolutionary perspective requires us to take seriously the view that behavioral change within generations drove biological evolution between them. This makes the likelihood of modification of pre-existing circuitry inherently more likely than the evolution of completely new, language-specific (let alone grammar-specific) circuits. These two models, however, can in principal be directly tested. Given that:

1) Human Broca's area subserves non-linguistic functions that nevertheless appear to be foundational for language.
2) Being non-linguistic, it should be possible to assess their functional localization in non-human primates (at least in principle).
3) Non-human primates have clear Broca's area homologs.

If these non-linguistic – but language-foundational – functions are also processed in non-human primate Broca's area homologs, it would support the view that completely new circuits were not necessary. Conversely, if they are not processed in non-human primate Broca's area homologs, then the view that new circuits were required for language evolution would be supported. The same approach can and should be applied to all putative 'language' areas in humans (e.g., Wernicke's, the arcuate fasciculus, etc.)