

Evolution of Brain and Language

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The evolution of language and the evolution of the brain are tightly interlinked. Language evolution represents a special kind of adaptation, in part because language is a complex behavior (as opposed to a physical feature) but also because changes are adaptive only to the extent that they increase either one's understanding of others, or one's understanding *to* others. Evolutionary changes in the human brain that are thought to be relevant to language are reviewed. The extent to which these changes are a cause or consequence of language evolution is a good question, but it is argued that the process may best be viewed as a complex adaptive system, in which cultural learning interacts with biology iteratively over time to produce language.

A full accounting of the evolution of language requires an understanding of the brain changes that made it possible. Although our closest relatives, the apes, have the ability to learn at least some critical aspects of language (Parker & Gibson, 1990), they never learn language as completely or as effortlessly as do human children. This means that there must be some important differences between the brains of human and nonhuman apes. A fair amount is known about the ways in which human brains differ from the other apes, and we know

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much about specific functions of different parts of the brain. These two fields of study, combined with an understanding of general evolutionary processes, allow us to draw at least the broad outlines of the evolutionary history of brain and language.

There is a complex interplay between language evolution and brain evolution. The existence of language presupposes a brain that allows it. Languages must, by definition, be learnable by the brains of children in each generation. Thus, language change (a form of cultural evolution) is constrained by the existing abilities of brains in each generation. However, because language is critical to an individual's adaptive fitness, language also likely had a fundamental influence on brain evolution. Humans are particularly socially interactive creatures, which makes communication central to our existence. Two inter-related evolutionary processes therefore occurred simultaneously: Language adapted to the human brain (cultural evolution), while the human brain adapted to better subserve language (biological evolution). This coevolutionary process resulted in language and brain evolving to suit each other (Christiansen, 1994; Christiansen & Chater, 2008; Deacon, 1992).

The coevolution of language and brain can be understood as the result of a complex adaptive system. Complex adaptive systems are characterized by interacting sets of agents (which can be individuals, neurons, etc.), where each agent behaves in an individually adaptive way to local conditions, often following very simple rules. The sum total of these interactions nevertheless leads to various kinds of emergent, systemwide orders. Biological evolution is a prime example of a complex adaptive system: Individuals within a species (a "system") act as best they can in their environment to survive, leading through differential reproduction ultimately to genetic changes that increase the overall fitness of the species. In fact, "evolution" can be understood as the name we give to the emergent results of complex adaptive systems over time. One can also view the brain itself as a complex adaptive system. This is because brain circuits are not independent of each other. Processing in one area affects processing in connected areas; therefore, processing changes in one area—whether due to biological evolution or learning—influence (and select for over evolutionary time) changes in other areas.

A number of neural systems relevant specifically to language interact with and influence each other in important ways. Syntax depends fundamentally on the structure of semantics, because the function of syntax is to code higher level semantic information (e.g., who did what to whom). Semantics in turn depends on the structure of conceptual understanding, which—as will be reviewed later—is a function of brain structure. These structures are in turn the result

of biological adaptation: Circuits that result in conceptual understanding that is relevant and useful to a given individual's (ever-changing) environmental realities will be selected for and will spread over evolutionary time.

For some species (e.g., primates, in general, and humans, in particular) the relevant selective environment for biological evolution is largely a function of the behavior of other individuals within one's social group. This means that the adaptiveness (reproductive benefit) of an individual's particular behavior at any given moment in time depends crucially on the flexible responses of others in the group, who are at the same time attempting to behave in an adaptive manner in response. Language, in its role as a communication system, is a prime example of such an interactive, adaptive set of behaviors. Because an individual's linguistic ability is a function of (and is constrained by) their own brain circuitry, understanding language evolution (and language itself) ultimately involves understanding how the repeated complex communicative interactions of individuals influences not only cultural change but also biological change. The evolution of brain circuits, therefore, cannot be understood independent of the evolution of language, and vice versa, which means the coevolution of brain and language—and, in fact, language itself—can be understood as a complex adaptive system.

By its very nature, language evolution constrains changes in both brain and language in predictable ways. Because the evolutionary benefits of language for an individual are not independent of that individual's existing social environment, language evolution is therefore inherently more complex than the typical evolutionary scenarios for physical characteristics. Natural selection involves the biased survival of individuals who have some variation (mutation) that benefits them in their environment. Biologists therefore speak of the environment "selecting for" certain traits (e.g., longer thicker fur in cold environments). Because the relevant environment doing the "selecting" for language is not something external to and independent of the species, but rather the social group itself, the benefit of any particular mutation affecting linguistic ability is therefore dependent on the existing cognitive abilities of others in one's social group. Being "better" than others linguistically is not an evolutionary benefit if it means that others cannot understand you as well. Changes are adaptive only if they increase your ability to make maximal advantage of the preexisting abilities of others. This is unlike having thicker fur in a cold environment, in which the advantage to an individual is independent of the fur thickness of others.

It is possible for mutations relevant to language evolution to be adaptive strictly at the individual level (and therefore spread) even if they are not

immediately useful for communication, but only if they are beneficial for some other reason. In this case, they would simply be *inadvertently* useful for future changes in the communication system. For example, it might be that mutations responsible for circuits involved in increasing recursion, types of memory, or concept-symbol mapping abilities were initially selected for because of their usefulness for some nonlinguistic cognitive functions, perhaps by making reasoning or thought more efficient or useful. In this case, however, these circuits would necessarily be nonlinguistic (and noncommunicative), initially. Once they spread sufficiently throughout the population, language could evolve (through cultural evolution) to make use of them. This would represent a case of preadaptation, in which language adapted to preexisting brain circuitry, rather than causing the creation of wholly new language-specific circuitry.

Therefore, language evolution itself will be strongly constrained by preexisting cognitive abilities within each generation. Changes affecting the perception of linguistically relevant signals would have been favored only to the extent that they increase the individual's ability to perceive and rapidly process the acoustic signals *already used by others for language*. Changes affecting the production of linguistically relevant signals would be favored only to the extent that they could be understood by the preexisting perceptual abilities of others. Signals too complicated or subtle for others to process would not be adopted and, hence, mutations influencing them would not likely spread.

The fact that language evolution is constrained by the preexisting abilities of individuals in the population means that any changes in brain circuitry relevant to language in a given generation would likely consist of slight modifications of circuits that already exist, rather than major changes in the ways language is processed by the brain. Because this would be true for every generation, language evolution in the long run would necessarily be continually biased toward the modification of preexisting mechanisms, rather than the accumulation of wholly new components (Schoenemann, 2005). As a consequence, we should expect language circuits in modern humans to show extensive homologies with preexisting systems in closely related animals. Even if language evolved to use circuits not originally linguistic in function, these hijacked circuits would likely also represent modifications of nonhuman-specific circuitry. Thus, studying brain and behavior in nonhuman primates is actually central to understanding human language evolution.

What changes in the brain itself are likely the result of this coevolutionary process involving both language and brain? Inferences about these changes are constructed from knowledge of how language is processed in the brain,

combined with knowledge of how our brains are different from those of our closest evolutionary relatives. To the extent that a particular area relevant to language appears to have changed significantly, we are justified in inferring that this area was important for language evolution. It is possible for the area to have evolved for other reasons, only to be co-opted later for (or by) language—particularly to the extent that language has adapted to the human brain. Evolutionary inferences will also involve thinking about the interplay of different behavioral abilities over our history. Both evolutionary and complex adaptive systems perspectives predict that language evolution is not independent of the evolution of other aspects of cognition.

Language processing does not appear to be highly compartmentalized into unique circuits independent of those serving other behavioral functions but instead depends heavily on the integration of a large number of abilities that are processed in widely dispersed circuits across the brain (Damasio & Damasio, 1992; Mueller, 1996). Therefore, assessing the coevolution of language and brain requires a broad focus on a number of brain regions.

Interpreting Evolutionary Changes in Size

In order to properly understand the significance of changes in the human brain, it is important to recognize that there must have been some sort of benefit to increasing amounts of neural tissue. There are very high evolutionary costs to maintaining large brains. The human brain accounts for about 20% of the total basal metabolic resources in adults and up to approximately 50% for young children (Hofman, 1983). Larger brains are also associated with longer maturation periods in primates (Harvey & Clutton-Brock, 1985), which—everything else being equal—means fewer offspring per unit time. Because of these evolutionary costs, increases in neural resources would not be selected for unless there were clear counterbalancing benefits (Smith, 1990).

There are several kinds of comparisons one can make between species with respect to their brains. The simplest involves simply comparing absolute size differences of either the whole brain or some specific part of the brain. Because brain size varies with the size of the body across mammals (and other groups of animals), various indexes of relative brain size have been proposed to attempt to take account of body size difference—the most commonly used being Jerison's (1973) "encephalization quotient" (EQ; a ratio of a species actual brain size to the average brain size for a mammal that size). The problem with measures like EQ, however, is that their behavioral relevance is ambiguous (Schoenemann, 2006; Striedter, 2005). Larger bodies, having greater muscle mass, presumably

require greater neural connectivity to these muscles, but it is not clear why we should expect a greater muscle mass to *also* require more neurons for nonmotor cognitive tasks, such as logical reasoning or language. It seems more reasonable to suppose that more neural tissue allows for more complex processing—regardless of the size of the body. A number of empirical studies show that relative brain size is not as good a predictor of behavioral differences as absolute brain size (reviewed in Schoenemann, 2006). Intriguingly with respect to language evolution, this is also true for various types of learning tasks, including “transfer learning,” in which the subject is required to generalize a task away from a specific context (Beran, Gibson, & Rumbaugh, 1999). The importance of learning to human evolution in general, and language in particular, is discussed further below.

Although absolute amounts of neural tissue are likely behaviorally important, this does not mean that relative increases (i.e., controlling for body size) are therefore *irrelevant*. Both types are potentially important.

Evolutionary Changes in the Brain Relevant to Language

Overall Brain Size

At approximately 1,350 cc, human brains are about five times as large as one would expect for the average mammal of our body size (i.e., $EQ = \sim 5$) and are about three times as large as they are in the average primate of our body size (including our closest relatives: chimpanzees and gorillas; reviewed in Schoenemann, 2006). Focusing solely on overall brain size is an oversimplification, however. Some parts of our brain are larger than expected and others smaller (although some controversy exists about specific areas; Deacon, 1988; Rilling, 2006; Schoenemann, 2006; Semendeferi, Armstrong, Schleicher, Zilles, & Van Hoesen, 2001). Nevertheless, there are some interesting correlates of overall brain size that are likely relevant to language evolution.

Not only does brain size correlate strongly with length of maturation (Harvey & Clutton-Brock, 1985), but it also correlates with overall life span (Allman, McLaughlin, & Hakeem, 1993). This means that the larger the brain, the greater the potential for behavioral learning to be a central part of the organism’s behavioral repertoire. Larger brained animals do in fact tend to rely on learning much more so than smaller brained animals (Deacon, 1997), and larger brained primates do better at a variety of experimental learning tasks (see above).

Given the large increase in brain size during human evolution, we should expect learned behavior specifically to have played an important role. Although

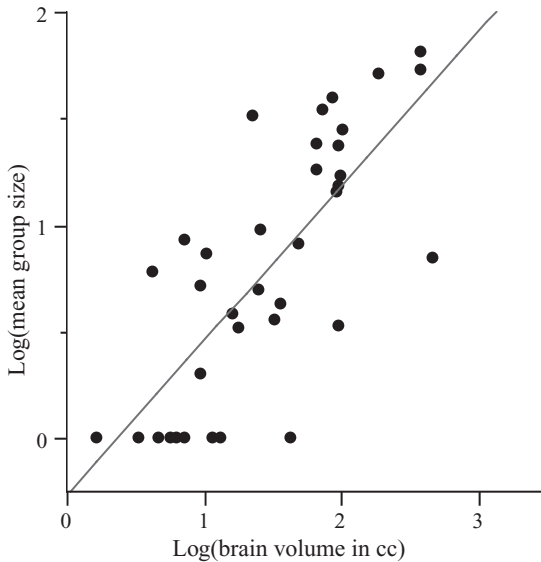


Figure 1 The relationship between brain volume and mean group size in primate species. $N = 36$, $r = .75$, $p < .0001$. Data from Dunbar (1995).

learning can be biased in particular ways by evolved innate influences, human behavioral evolution is better characterized by increasing behavioral flexibility rather than greater numbers of hardwired, innate circuits. Learning language obviously depends on being able to understand changing, fluid contingencies between constituents and meaning. Because language is fundamentally creative, it would be impossible to learn it solely through stimulus-response associations (as Chomsky has long argued, e.g., Chomsky, 1959). To the extent that language depends on learning, as well as that learning itself can be facilitated by language, the extensive changes in brain size made language increasingly possible.

Larger brained animals also show a strong tendency toward interactive sociality (Dunbar, 2003). Brain size across primates correlates strongly with the size of a species' typical social group (Figure 1), which is assumed to be an index of the complexity of the species' social existence. Larger social groups have increasingly complicated social interactions, and successful social living depends on learning how best to navigate them. Human social complexity appears to be particularly complex. Given that language is an inherently social activity, the usefulness of language (its selective value) would be greatest in the human species.

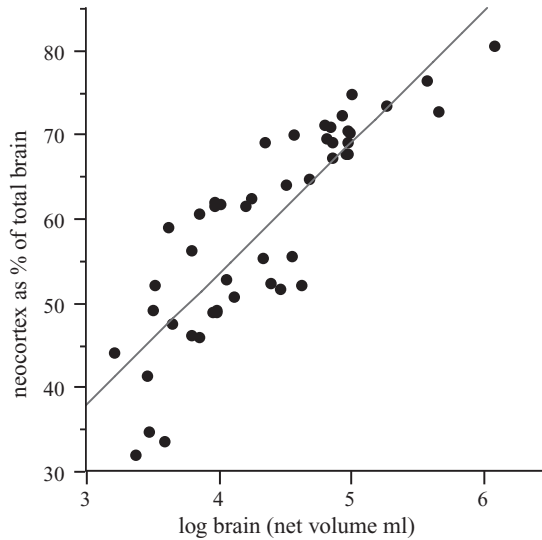


Figure 2 The relationship between log brain volume and proportion of total that is neocortex in primate species. $N = 48$, $r = .85$, $p < .0001$. Data from Stephan, Frahm, and Baron (1981).

Larger brains are also associated with disproportionate increases in the size of the neocortex, which plays a key role in conscious awareness generally, as well as mediating a number of complex cognitive functions, including language (Figure 2). Over 80% of the entire human brain is neocortex; in smaller brained primates, it averages about half that.

Furthermore, the areas of the neocortex directly devoted to the primary processing of sensory information, as well as the conscious control of muscle movement, make up a *decreasing* proportion of the entire neocortex as it increases in size (Figure 3, from Nieuwenhuys, 1994). Proportionately more of the neocortex is devoted to integrating different types of information. The larger these “association areas” are, the greater the likely potential for increasingly complex types of integrative processing (Schoenemann, 2009).

Furthermore, these association areas are composed of numerous relatively specialized processing areas. Larger brains have greater numbers of identifiably distinct cortical areas (Changizi & Shimojo, 2005; Northcutt & Kaas, 1995). This turns out to be a predictable consequence of increasing brain size: Specific areas of the neocortex tend to be less directly connected to each other in larger brains than they are in smaller brains (Ringo, 1991). This means that areas are

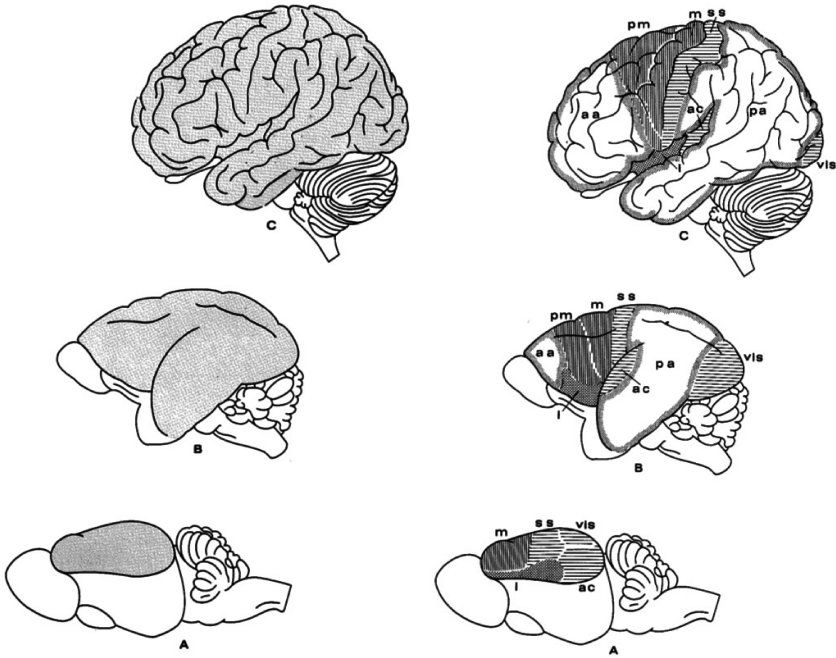


Figure 3 Size of “association” cortex in mammals of different brain size. These drawings represent lateral views of the cortex of hedgehog (A), galago (prosimian primate) (B), and human (C). The gray area of the figures on the left identify the cortex as a whole; the white areas of the cortex in the figures on the right identify “association” cortex, which is not devoted to processing primary sensory or motor (muscle movement) information. **aa**, anterior association cortex; **pa**, posterior association cortex; **pm**, premotor area; **m**, primary motor area; **ss**, somatosensory area; **vis**, primary visual area; **ac**, primary auditory area; **I**, insula. From Nieuwenhuys (1994), used with permission.

able to carry out tasks increasingly independently of each other, leading easily to increasing functional localization.

This has obvious implications for the development of language areas in humans, but there is a more interesting (and potentially more important) consequence: Greater numbers of specialized processing areas will result in richer, more complex, more subtle conceptual understanding (Gibson, 2002; Schoenemann, 1999, 2005). Because language semantics require a conceptual structure for words and grammar to map onto, a rich conceptual world translates into the potential for more complicated language. The functional neuroanatomy of conceptual understanding is, therefore, fundamental to understanding language evolution.

In fact, much of the brain appears to be involved with processing conceptual information (Damasio & Damasio, 1992; Schoenemann, 2005). When a subject imagines an object that is not actually present, similar areas of their brain are activated as when the object *is* being viewed (Damasio et al., 1993; Kosslyn et al., 1993). Different kinds of sensory inputs—visual, auditory, olfactory, taste, somatosensory (touch, temperature, pain, body position)—are processed with different neural pathways. Whereas some basic concepts involve only a single sensory modality (e.g., [red], or [rough (texture)]), most concepts require the integration of more than one sense. For example, the concept [coffee] typically invokes not just a particular taste, but also a smell, a visual image of a mug, the sensation of warmth, and so forth (Damasio & Damasio, 1992). For these sensory impressions to be bound in some way into the concept [coffee], the different areas that process these impressions must be connected. A complete list of areas that are relevant to just the basic features of conceptual awareness would be very long, involving all the visual (color, shape, motion, etc), spatial, auditory, temporal organization, olfactory, taste, somatosensory, and limbic system (emotion) areas.

Given that conceptual awareness forms the very foundation of language (Hurford, 2003a), that larger brains appear to give rise to more complex conceptual universes (and, hence, more interesting things to communicate about), and that humans are intensely socially interactive, increasing brain size is likely a good proxy for language evolution (Gibson, 2002; Schoenemann, 1999, 2005).

Classical Language Areas

Broca's and Wernicke's areas were the first cortical regions to be associated with specific linguistic abilities. Broca's aphasics display nonfluent, effortful, and agrammatical speech, whereas Wernicke's aphasics display grammatical but meaningless speech in which the wrong words (or parts of words) are used (Bear, Connors, & Paradiso, 2007; Damasio et al., 1993). Broca's area is located in the posterior-inferior frontal convexity of the neocortex, whereas Wernicke's area is localized to the general area where parietal, occipital, and temporal lobes meet. For most people, these areas are functional for language primarily in the left hemisphere.

Additional areas, adjacent to, but outside these classic language areas, appear to be important for these aspects of language processing as well. Broca's and Wernicke's aphasias (i.e., the specific types of language deficits themselves) are not exclusively associated with damage to Broca's and Wernicke's cortical areas (Dronkers, 2000). Damage to the caudate nucleus, putamen, and internal

capsule (structures of the cerebral hemispheres that are deep to the cortex) also appear to play a role in Broca's aphasia, including aspects of syntactic processing (Lieberman, 2000).

The evolutionary histories of these areas are quite curious, as homologues to both Broca's and Wernicke's areas have been identified in nonhuman primate brains (Striedter, 2005). Exactly what function they play in other species is not currently known, but an evolutionary perspective would predict that they likely process information in ways that would be useful to language (Schoenemann, 2005), consistent with the view of language adapting to the human brain by taking advantage of circuits that already existed. The presence of these areas in nonlinguistic animals is a glaring anomaly for models that emphasize the evolution of completely new language-specific circuits in the human lineage (e.g., Bickerton, 1990; Pinker, 1995). In any case, although detailed quantitative data on these areas in nonhuman primates have not been reported, it does appear that they are significantly larger both in absolute and relative terms in humans as compared to macaque monkeys (Petrides & Pandya, 2002; Striedter, 2005).

Given that Broca's and Wernicke's areas mediate different but complementary aspects of language processing, they must be able to interact. A tract of nerve fibers known as the arcuate fasciculus directly connects these areas (Geschwind, 1974). The arcuate fasciculus in humans tends to be larger on the left side than on the right side, consistent with the lateralization of expressive language processing to the left hemisphere for most people (Nucifora, Verma, Melhem, Gur, & Gur, 2005).

The arcuate fasciculus appears to have been elaborated in human evolution. The homologue of Wernicke's area in macaque monkeys does project to prefrontal regions that are *close* to their homologue of Broca's area, but apparently not directly to it (Aboitiz & Garcia, 1997). Instead, projections directly to their homologue of Broca's area originate from a region just *adjacent* to their homologue of Wernicke's area (Aboitiz & Garcia, 1997). Thus, there appears to have been an elaboration and/or extension of projections to more directly connect Broca's and Wernicke's areas over the course of human (or ape) evolution. Recent work using diffusion tensor imaging (which delineates approximate white matter axonal connective tracts *in vivo*) suggest that both macaques and chimpanzees have tracts connecting areas in the vicinity of Wernicke's area to regions in the vicinity of Broca's area (Rilling et al., 2007). However, connections between Broca's area and the middle temporal regions (important to semantic processing; see below) are only obvious in chimpanzees and humans and appear to be most extensive in humans (Rilling et al., 2007).

Presumably these connections were elaborated during human evolution specifically for language (Rilling et al., 2007).

Prefrontal Cortex

Areas in the prefrontal cortex (in addition to Broca's area) appear to be involved in a variety of linguistic tasks, including various semantic aspects of language (Gabrieli, Poldrack, & Desmond, 1998; Kerns, Cohen, Stenger, & Carter, 2004; Luke, Liu, Wai, Wan, & Tan, 2002; Maguire & Frith, 2004; Noppeney & Price, 2004; Thompson-Schill et al., 1998), syntax (Indefrey, Hellwig, Herzog, Seitz, & Hagoort, 2004; Novoa & Ardila, 1987), and higher level linguistic processing, such as understanding the reasoning underlying a conversation (Caplan & Dapretto, 2001).

There appears to have been a significant elaboration of the prefrontal cortex during human evolution, with cytoarchitectural data pointing to an approximately twofold increase over what would be predicted for a primate brain as large as ours (Brodmann, 1909; Deacon, 1997). Recent comparative studies using magnetic resonance imaging to quantify volumes generally support these older data although there is still some debate (reviewed in Schoenemann, 2006). Our own study found that connective tracts (white matter areas composed mostly of axons) seem to account for the lion's share of the increase (Figure 4, Schoenemann, Sheehan, & Glotzer, 2005). The degree to which language was specifically and directly responsible for these changes is not clear, because the prefrontal also mediates other important nonlinguistic behavioral dimensions that likely also played a key role in human behavioral evolution, such as planning, maintaining behavioral goals, social information processing, temporary storage/manipulation of information ("working memory"), memory for serial order and temporal information, and attention (see Schoenemann, 2006, for references). Teasing out the relative contributions of these various behavioral domains (including language) to prefrontal elaboration during evolution will likely be very difficult, in part because they almost surely all contributed as part of a complex adaptive system involving many aspects of human behavior.

There are two specific areas of the prefrontal for which we have comparative information: Area 13 (involved in processing information relevant to the emotional aspects of social interactions) and area 10 (involved in planning and organizing thought for future actions) differ with respect to their apparent degrees of evolutionary modification. Area 13 seems to have lagged behind the overall increase in brain size, being only approximately 1.5 times larger than the average ape (pongid) value, whereas the brain as a whole is approximately 3 times larger (Semendeferi, Armstrong, Schleicher, Zilles, & Van Hoesen,

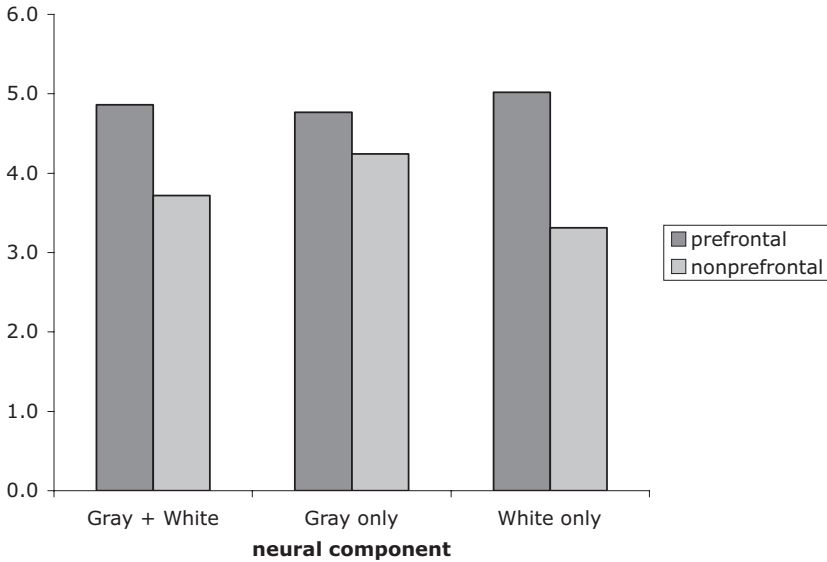


Figure 4 Ratio of the size of prefrontal cortex (anterior to the corpus callosum) between human and chimpanzee (average of common and bonobo chimps, *Pan troglodytes* and *Pan paniscus*). Prefrontal areas are disproportionately larger than nonprefrontal areas in humans, particularly for white matter (primarily connective fibers). Data from Schoenemann, Sheehan, & Glotzer (2005).

1998). However, the fact that it is absolutely larger in humans likely requires a functional explanation, presumably related to the elaboration of social complexity in humans.

Area 10, which also shows activity in linguistic tasks that require selection of appropriate words given a specific semantic context (Gabrieli et al., 1998; Luke et al., 2002), is approximately 6.6 times larger than the corresponding areas in pongids (Semendeferi et al., 2001). Although this increase is actually close to what one would expect given how this area seems to scale with the size of our brain as a whole (Holloway, 2002), it is difficult to believe that this increase did not also have functional implications for language evolution.

Concepts and Semantic Processing

Connecting conceptual understanding to specific linguistic codes is obviously central to language. As discussed earlier, conceptual understanding itself appears to depend on a wide network of many different areas of the brain. Humans (and primates generally) are particularly biased toward visual

information, which, as a consequence, forms an important component of conceptual understanding for most people (blind people being an exception). Visual information processing starts in the retina of the eye and is transferred through intermediate nuclei to the primary visual cortex, located in the occipital lobe, where it first becomes available to conscious awareness (Bear et al., 2007). Visual information is subsequently processed along two major pathways: the dorsal stream (extending up into the parietal lobe), which processes information regarding the location and motion of an object, and the ventral stream (extending to the anterior tip of the temporal lobe), which processes information regarding the characteristics of the objects themselves independent of their location and motion (e.g., shape, color, etc., Bear et al., 2007). Because of this functional distinction, the dorsal stream is often referred to as the “where” pathway, and the ventral stream as the “what” pathway (Bear et al., 2007). Thus, broadly speaking, these two pathways correspond to objects (which get mapped as nouns) and actions/orientations/directions (which are central to concepts mapped as verbs) (cf. Hurford, 2003b).

Within the “what” pathway, the understanding of proper nouns appears to depend on anterior and medial areas of the temporal lobe, whereas understanding common nouns appears to depend on the lateral and inferior temporal lobes (Damasio & Damasio, 1992). These areas have been elaborated during human evolution. Overall, the human temporal lobe is 23% larger than predicted based on how large our brain is, and it is almost four times larger in absolute volume than the temporal lobe of chimpanzees (data from Rilling & Seligman, 2002). The difference appears greatest for the portions corresponding to connectivity (i.e., white matter axonal tracts; Rilling & Seligman, 2002), consistent with the fact that concepts critically depend on interconnectivity with other cortical areas.

The primary auditory cortex of the temporal lobe (where conscious awareness of auditory information first occurs) appears to be only approximately 6% larger than predicted based on our overall brain size. Immediately adjacent areas also involved in processing auditory information appear to be only approximately 17% larger (Deacon, 1997). In absolute terms, these areas would still be more than three times larger than the equivalent area in apes, however. Thus, it seems likely that important enhancements occurred with respect to auditory processing. Because these auditory areas are a subset of the entire temporal lobe, the rest of the temporal lobe (important to the semantics of nouns) must have increased even more than the approximately 23% for the temporal lobe as a whole. This points, again, to the elaboration of circuits involved

in conceptual and semantic processing and suggests that this was particularly important during our evolution.

One area of the temporal lobe that has been of particular focus has been the planum temporale, located in the superior portion of the temporal lobe (just posterior to the primary auditory cortex). Studies showing a tendency for the planum temporale to be larger on the left side (e.g., Geschwind & Levitsky, 1968) were initially assumed to reflect a functional anatomical correlate of language evolution (the expressive parts of which are usually localized to the left hemisphere). However, it turns out that apes show a similar asymmetry in this region also (Gannon, Holloway, Broadfield, & Braun, 1998). Exactly what the asymmetry indicates is not clear, but it obviously cannot be specific to language. It may be that it has a general role in processing auditory information for communication (not just language). If so, it would be yet another example of brain preadaptations for language.

With respect to the “where” pathway, which likely grounds concepts central to most verbs, there is some indication of an evolutionary expansion of this area during human evolution, based on analyses of brain endocasts of fossil hominins (Bruner, 2004). Detailed comparative anatomical studies among primates have not been reported, however. The semantic generation of verbs (the actual words themselves) seems to involve Broca’s area (Damasio & Damasio, 1992; Posner & Raichle, 1994), which also appears to have been elaborated during human evolution, as discussed earlier.

Right Hemisphere

Although the cortical language areas discussed so far are localized to the left hemisphere in most people, there is substantial evidence that the right hemisphere also contributes importantly to language. The right hemisphere understands short words (Gazzaniga, 1970) and entertains alternative possible meanings for particular words (Beeman & Chiarello, 1998), suggesting that it is better able to interpret multiple intended meanings of a given linguistic communication. The right hemisphere also plays a greater role in a variety of types of spatial processing in most people (Tzeng & Wang, 1984; Vallar, 2007), thus presumably grounding the semantics of spatial terms. The right frontal lobe mediates aspects of prosody (Alexander, Benson, & Stuss, 1989; Novoa & Ardila, 1987), which is critically important to understanding intended meaning (consider sarcasm, in which the intended meaning is directly opposite the literal meaning).

There are, however, no comparative analyses of right versus left hemisphere differences across primates that I am aware of, so the extent to which there has

been biased evolutionary changes for one or the other hemisphere is not known. The right hemisphere in humans is not significantly different in size than the left (Allen, Damasio, & Grabowski, 2002), suggesting that it probably has increased approximately threefold along with the cortex as a whole.

Basal Ganglia

Although the cortex is heavily involved in language processing, cerebral nuclei deep to the cortex also appear to play important roles. A group of interconnected nuclei, collectively known as the basal ganglia, participate in an important circuit loop that functions in the selection and initiation of willed movements (Bear et al., 2007). The circuit starts with signals from a variety of areas of the cortex that are sent to the putamen and caudate nucleus (part of the basal ganglia). These, in turn, connect to the globus pallidus (another part of the basal ganglia), which then connects to the thalamus (ventral lateral nucleus), which finally send signals back up to the cortex (Bear et al., 2007). A variety of studies have implicated these circuits not just in language production (which makes sense given that language requires willed movements) but also in language comprehension (see references in Hochstadt, Nakano, Lieberman, & Friedman, 2006). Diseases affecting the basal ganglia, notably Parkinson's and Huntington's, result not only in motor (muscle movement) problems but also in problems understanding complicated syntax (e.g., center-embedded clauses), as well as processing semantic information (Hochstadt et al., 2006). As mentioned above Broca's aphasia (the behavioral syndrome) can be caused by damage not just to Broca's area (as was traditionally held), but also to areas deep to it, likely including circuits involving the basal ganglia (Lieberman, 2002).

Comparative studies of the relative size of the basal ganglia in humans suggest that these nuclei are only about 65% as large as predicted for a primate brain as large as ours (Schoenemann, 1997; Stephan et al., 1981). However, they are still about twice as large in absolute terms as predicted based on body size. If the basal ganglia were solely involved in motor functions, we would expect them to scale closely with overall body size. Because they are significantly larger than this and because humans do not appear to have significantly more sophisticated motor abilities than apes (with the exception being those related to vocalization), it is reasonable to suggest that the increase in absolute size of the basal ganglia indicates an important role supporting higher cortical functions like language.

Cerebellum

The primary function of the cerebellum was long thought to be monitoring and modulating motor signals from the cortex (Carpenter & Sutin, 1983).

However, more recent work has implicated the cerebellum in a whole range of higher cognitive functions, including goal organization and planning, aspects of memory and learning, attention, visuo-spatial processing, modulating emotional responses, and language (Baillieux, De Smet, Paquier, De Deyn, & Marien, 2008). The cerebellum appears to play a role in speech production and perception, as well as both semantic and grammatical processing (Ackermann, Mathiak, & Riecker, 2007; Baillieux et al.; De Smet, Baillieux, De Deyn, Marien, & Paquier, 2007). The cerebellum also seems to play a role in timing mechanisms generally (Ivry & Spencer, 2004), which may explain its functional relevance to language (given the importance temporal information plays in language production and perception).

Comparative studies suggest that the human cerebellum overall is slightly smaller than one would predict for how large our brain is (Rilling & Insel, 1998), but is approximately 2.9 times larger than predicted based on our body size (the largest increase of all brain regions besides portions of the neocortex). The higher cognitive functions of the cerebellum appear to be localized specifically to the lateral hemispheres (lobes) of the cerebellum, which are more evolutionarily recent (although present in primates; MacLeod, Zilles, Schleicher, Rilling, & Gibson, 2003). The lateral hemispheres of the cerebellum appear to have undergone a significant shift in proportions in apes and humans (hominoids) compared to monkeys: These areas are 2.7 times larger in hominoids than in monkeys, based on the size of the (evolutionarily older) cerebellar vermis region (MacLeod et al., 2003). Humans fall comfortably with apes in this measure, however, but they do differ significantly from apes with respect to overall body weight (human lateral cerebellar hemispheres are approximately 2.9 times larger than predicted based on body weight; MacLeod et al., 2003). These increases in cerebellar size therefore cannot be explained by, for example, greater muscle mass in humans, and as a consequence must result either from some sort of tight developmental linkage relative to the rest of the brain or from selection specifically for behavioral abilities that rely on the cerebellum. Given its role in language processing, this increase (however explained) may be relevant to language evolution.

Vocalization

The muscles responsible for vocalization are directly innervated by nuclei in the brainstem, which relay signals from midbrain and higher cortical areas. The nucleus ambiguus controls the muscles of the vocal folds and is therefore responsible for producing and changing the pitch of the primary vocal signal. This signal is then filtered in various ways by manipulations in the shape of

the supralaryngeal vocal tract before it exits the mouth and nose (Denes & Pinson, 1963). The vocal tract is affected by the shape and position of the tongue (whose muscles are controlled by the hypoglossal nucleus and nucleus ambiguus), lower jaw (trigeminal nucleus), and the lips (facial motor nucleus). This whole system depends on the maintenance and manipulation of air pressure in the lungs, which is accomplished by the muscles of the chest and abdomen (innervated by anterior horn areas along the spinal cord; Carpenter & Sutin, 1983).

Even though vocal production has clearly been important to language, these brainstem nuclei do not appear to be particularly enlarged. The hypoglossal nucleus in humans is large, on average, but shows substantial overlap with apes, whereas the human trigeminal and facial motor nuclei completely overlap in size with those of the great apes (Sherwood et al., 2005). Thus, there is little evidence that language evolution substantially modified these nuclei.

Because conscious muscle movement depends on the cerebral cortex, deliberate communication requires direct connections from the cortex to these brainstem nuclei. In humans there are also indirect connections to the vocal folds, tongue, and mandible routed through the reticular formation of the brainstem and to the muscles of respiration routed through the nucleus retroambiguus of the brainstem (Striedter, 2005). An additional indirect pathway starts in the cingulate gyrus of the cortex and routes through the periaqueductal gray area of the midbrain and mediates involuntary vocal responses to pain or strong emotions (Striedter, 2005).

Comparative studies of these cortical-to-brainstem language pathways are, unfortunately, lacking. Nonhuman primates do have indirect connections to the brainstem nuclei involved in vocal production (Jurgens, 2002; Jurgens & Alipour, 2002), allowing them a variety of emotionally mediated vocalizations. However, nonhuman primates have weak direct connections to the brainstem nuclei that control the tongue and respiration muscles and completely lack direct connections to the larynx (Jurgens, 2002; Jurgens & Alipour, 2002). This suggests that the evolution of language encouraged the evolution of at least some new direct cortical pathways to the brainstem specifically for deliberate conscious vocalization.

Auditory Perception

For conscious awareness of sounds, auditory information must be relayed from the cochlea (where sound is translated into neural signals), through a series of intermediate nuclei in the brainstem and midbrain, on the primary auditory cortex located in the temporal lobe. Comparative mammalian data on the size

of intermediate auditory nuclei along these auditory pathways suggest that humans have somewhat smaller auditory nuclei than expected for our brain weight, although the difference is not statistically significant (Glendenning & Masterton, 1998). In absolute terms, our auditory nuclei are reasonably large, although not dramatically so (total for all auditory nuclei volumes in humans is 187 mm³, compared to 104 mm³ for domesticated cats, which weigh only approximately 3 kg). These data suggests only modest changes in these nuclei during human evolution.

Conclusion

Many evolutionary changes in the brain appear to have relevance to language evolution. The increase in overall brain size paved the way for language both by encouraging localized cortical specialization and by making possible increasingly complicated social interactions. Increasing sociality provided the central usefulness for language in the first place and drove its evolution. Specific areas of the brain directly relevant to language appear to have been particularly elaborated, especially the prefrontal cortex (areas relevant to semantics and syntax) and the temporal lobe (particularly areas relevant to connecting words to meanings and concepts). Broca's and Wernicke's areas are not unique to human brains, but they do appear to have been elaborated, along with the arcuate fasciculus connecting these areas. Other areas of the brain that participate in language processing, such as the basal ganglia and cerebellum, are larger than predicted based on overall body weight, although they have not increased as much as a number of language-relevant areas of the cortex. Finally, little evidence suggests that significant elaboration of the auditory processing pathways up to the cortex has occurred, but direct pathways down to the tongue and respiratory muscles have been strengthened, with new direct pathways created to the larynx, presumably specifically for speech.

These findings are consistent with the view that language and brain adapted to each other. In each generation, language made use of (adapted to) abilities that already existed. This is consistent with the fact that the peripheral neural circuits directly responsible for perceptual and productive aspects of language have shown the least change. It makes sense that languages would evolve specifically to take advantage of sound contrasts that were already (prelinguistically) relatively easy to distinguish. This perspective is also consistent with the fact that Broca's and Wernicke's areas are not unique to humans. Differences in language circuits seem mostly to be quantitative elaborations, rather than completely new circuitry.

Three major factors seem to have conspired to drive the evolution of language: first, the general elaboration of—and increasing focus on—the importance of learned behavior; second, a significant increase in the complexity, subtlety, and range of conceptual understanding that was possible; and third, an increasingly complex, socially interactive existence. Each of these is reflected by a variety of changes in the brain during human evolution. Because language itself facilitates thinking and conceptual awareness, language evolution would have been a mutually reinforcing process: Increasingly complicated brains led to increasingly rich and varied thoughts, driving the evolution of increasingly complicated language, which itself facilitated even more complex conceptual worlds that these brains would then want to communicate (Savage-Rumbaugh & Rumbaugh, 1993; Schoenemann, 2009). The interplay between internal (conceptual) and external (social) aspects of human existence that drove this coevolutionary process highlights the usefulness of thinking about language evolution as a complex adaptive system. The extent to which increasing conceptual complexity itself might have driven language evolution represents an intriguing research question for the future.

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