Brain Evolution Relevant to Language

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1. Introduction

The evolution of language obviously presupposes a brain that made language possible. At the same time, given the fundamental importance language has to the human condition, a critical driving force of the evolution of the human brain must have been language. Given that language is at least as much a cultural/behavioral phenomenon as it is a biological one, it is clear that language has adapted itself to the human brain as much as the human brain has adapted itself to language (Christiansen 1994). This view suggests a coevolutionary process in which both language and brain evolved to suit each other (Deacon 1992). One important window into language evolution therefore involves the study of how our brain changed over our evolutionary history.

Our understanding of exactly what changes occurred is derived from research highlighting the ways in which our brains differ from those of our closest primate relatives. The details surrounding the evolutionary timing of most of these changes (what occurred when) are not known with a great degree of confidence, however, because brains do not directly fossilize, and we are left trying to infer neural structure of fossil hominids solely by studying the inside surface of the braincase ('endocast'). The present article will focus instead on specific differences between our brains and those of other primates that appear to be most relevant to the evolution of language. An understanding of these changes provides an important grounding for models of language evolution. Given that there is one actual evolutionary history to be explained, the many pieces of evidence for it—whether biological, neurological, behavioral—must necessarily ultimately point towards the same explanation (or sets of explanations).

In order to assess which evolutionary changes in the brain where most relevant to language evolution, it is first necessary to review how modern human language is processed in the brain today—or more appropriately: how language uses the brain. We may then profitably explore the ways in which these areas may have changed. If we can show that particular parts of the brain that are heavily used by language have, at the same time, also changed substantially during our evolutionary history, this is suggestive evidence that the anatomical changes were spurred by the language evolution. Such an assessment is only correlative, and as such cannot be seen as conclusive evidence for co-evolution. However, it does give us an essential foundation upon which to build our understanding of the evolution of language.

2. Functional neuroanatomy of language

Determining what parts of the human brain are most relevant to language evolution is complicated by the fact that, in actuality, a great many areas of the brain appear to be important for successful language processing. Language is not a singular, unitary cognitive ability, processed in a single place in the brain, but instead depends on the successful integration of a number of separate abilities. Language, of course, makes use of conventionalized patterns of sounds (or other types of signals) to code for conceptual information. Some of this information is encapsulated in relatively short sequences of sounds called ‘words’. The rules governing the patterning of sounds are the focus of phonology. The ways in which words connect to particular conceptual meanings is the domain of semantics. Conventionalized patterns of these words in turn convey ‘higher-level’ conceptual information, such as the argument structure of the intended message (‘who did what to whom’), the temporal context (when something happened), and so forth. These regularities are referred to as the grammar and syntax of a language. The brain's ability to both produce and decode these conventionalized patterns of sounds—at the word, sentence, and discourse levels—depends on a wide range of cognitive circuits, involving many parts of the brain.

Control of muscles critical for vocal language

At the most basic level, the muscles involved in directly creating the sounds (in the case of verbal language) that make up an utterance are directly controlled by neuronal fibers originating in nuclei in the brainstem (not the higher cortical areas or even the midbrain areas). The most important of these brainstem nuclei for spoken language include the nucleus ambiguous (for muscles controlling the vocal folds, as well as one of the muscles of the tongue), the hypoglossal nucleus (for the rest of the muscles of the tongue), the trigeminal nuclei (for the muscles of the lower jaw, or mandible), the facial motor nucleus (for the muscles of facial expression, including those responsible for lip movements), and anterior horn areas along the spinal cord (for muscles involved in adjusting air pressure in the chest) (Carpenter & Sutin 1983).

Because conscious awareness appears to be a function of the cerebral cortex, deliberate communication using language therefore requires that cortical areas somehow communicate with these lower motor nuclei. In humans, these nuclei receive both direct (straight from the cortex) and indirect (routed through intermediate brain nuclei) connections from the cortex (Butler et al. 2001, Striedter 2005). The indirect connections for the muscles of the vocal folds, tongue, and mandible are routed through a structure of the brainstem known as the reticular formation, which is involved in maintaining body posture, in addition regulating sleep and wakefulness) (Li et al. 1995, Striedter 2005). The indirect connections for respiration are routed through the Nucleus Retroambiguus of the brainstem (specifically, the medulla) (Striedter 2005).

There is an additional pathway for all these language-relevant muscles that starts in the cingulate gyrus of the cortex (a phylogenetically older part of the cortex than the neocortex), which then routes through an area of the midbrain known as the periaqueductal gray (which plays a role in processing somatic pain sensations) (Striedter 2005). This pathway mediates the involuntary vocal responses to, e.g., pain or other strong emotional responses (we are conscious of these responses, but they are involuntary in origin).

Perception of auditory information

Sound pressure waves are transduced into neural signals in the cochlea of the inner ear (Denes & Pinson 1963). These signals are passed up to the primary auditory cortex in the temporal lobe through several intermediate auditory nuclei in the brain stem (Denes & Pinson 1963). Conscious awareness of sound requires that the sound reach the cortex for further processing (e.g., phonemes to words to sentences to discourse).

Cerebellum

One area that has recently become of interest with respect to language is the cerebellum, which is part of the hindbrain connected to the back of the pons. Traditionally, its primary function was thought to be the monitoring, modification, and modulation of motor (muscle movement) signals from the cortex (Carpenter & Sutin 1983). However, more recent functional imaging studies have shown that the cerebellum is also active during a number of higher cognitive processes, including language related tasks. Specifically, it appears to play a role in the production of speech sounds, the perception of durational aspects of speech and non-speech acoustic signals, and possibly even the processing of grammatical information (Ackermann et al. 2007). The extent to which the cerebellum plays a central role in higher level language (and non-language) cognitive processes is not clear. It might be that these processes simply rely critically on intact 'silent speech' muscle organization of the cerebellum, or it might be that processes such as timing are actually fundamental to the circuit. This is currently an area of particular interest in brain and language studies.

Classical language areas

The classic language areas of the cortex, Broca's and Wernicke's, are located in the left hemisphere of most people (Figure 1). Broca's area is localized to the left posterior-inferior frontal convexity, while Wernicke's area is localized to the general area in which the parietal, occipital, and temporal lobes meet. These areas were originally delineated by mapping the overlap of lesions of individuals sharing similar characteristic linguistic deficits. Broca's aphasics display non-fluent, agrammatical speech, whereas Wernicke's aphasics display grammatical but meaningless speech (Bear et al. 2007). Thus, Broca's area is involved not only in the construction of speech 'rhythms' (Damasio et al. 1993), but also in syntax and grammar. Wernicke's

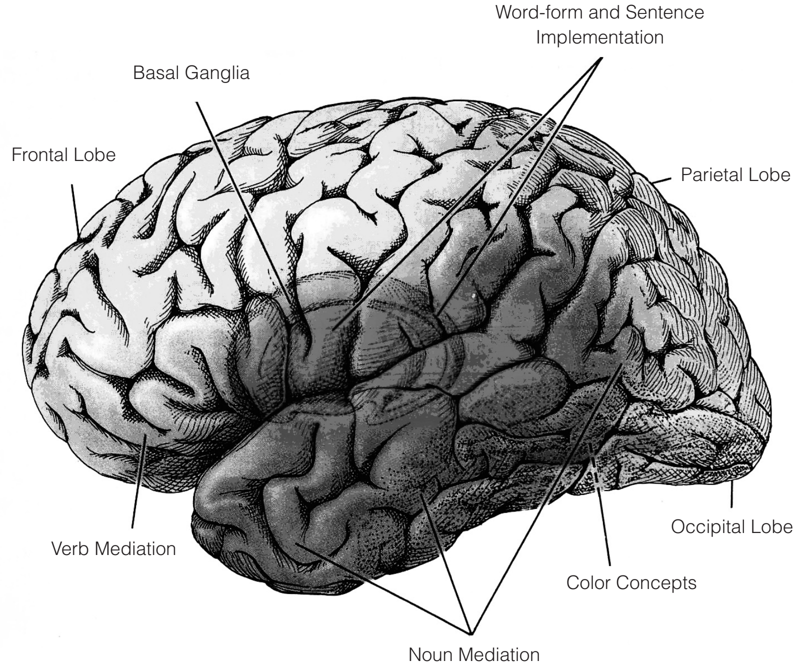

Figure 1. Important brain regions involved in processing language. Broca's area is colored light blue; Wernicke's area is the posterior third of the region colored red. Note that the basal ganglia are structures deep to the cortex (not visible from the surface). Figure from Damasio and Damasio (1992). [IMAGE USED WITH PERMISSION]

area, by contrast, appears to be critical for the selection of noun words (and even parts of words).

However, it has increasingly become clear that the behavioral symptoms defining Broca's and Wernicke's aphasia are not tightly associated with damage to Broca's and Wernicke's cortical areas themselves: a significant number of Broca's aphasics do not have damage to their Broca's areas, and damage to Broca's area does not inevitably result in the symptoms of Broca's aphasia, and the same seems to be true for the connection between Wernicke's aphasia and Wernicke's area (Dronkers 2000). It appears likely that deep cortical areas (underlying Broca's and Wernicke's areas) play a key role in what have come to be called (unfortunately and confusingly) Broca's and Wernicke's aphasia. In particular, damage to the deep cortical structures including the basal ganglia (Figure 1) and internal capsule (which is composed mostly of white matter fibers connecting cortex to deep cortical nuclei and lower areas of the brain) have been shown to produce symptoms similar to Broca's aphasia (Lieberman 2000). These structures also appear to be part of the circuitry involved in syntactic processing (Lieberman 2000).

In order for language to be processed appropriately, it stands to reason that Broca's and Wernicke's areas need to communicate with each other. There are many pathways by which this is possible, but the most direct is a fiber tract (composed of myelinated axons) known as the arcuate fasciculus. Consistent with the fact that, for most individuals, the classical language areas are lateralized to the left hemisphere, the arcuate fasciculus appears to be larger on the left side than the right (Nucifora et al. 2005).

Prefrontal cortex and language

In addition, other areas in the prefrontal cortex besides Broca's area appear to play critical roles in language processing. Several studies suggest the prefrontal cortex is involved in organizing semantic information (Gabrieli et al. 1998), assessing grammatical and semantic acceptability of language (Luke et al. 2002), processing contextual (semantic) clues relevant to interpreting language (Kerns et al. 2004), acquiring semantic information (Maguire & Frith

2004), the retrieval of abstract semantics (Noppeney & Price 2004), verbal fluency (Gaillard et al. 2000), and the selection of semantically appropriate words (Thompson-Schill et al. 1998). In addition, the prefrontal appears to play a role in processing syntax (Novoa & Ardila 1987), as well as higher level linguistic processing, such as understanding the reasoning underlying a conversation (Caplan & Dapretto 2001).

Right hemisphere language processing

Although the cortical language areas discussed so far are most often (but not always) localized to the left hemisphere, there is substantial evidence that the right hemisphere plays critically important roles in language processing. The right frontal lobe, and particularly the prefrontal (most anterior) portion, seems to pay a critical role in prosody, which is critical for the proper use and understanding of such things as sarcasm, non-literal verbal humor, irony, indirect requests, intended affect, and so forth (Alexander et al. 1989, Novoa & Ardila 1987). Sarcasm in particular highlights the critical importance of prosody to effective language use, since the actual intended meaning of a sarcastic comment cannot be derived solely from an understanding of the meanings of words and of the grammar and syntax. In addition, patients with damage to the right hemisphere frontal areas often lack the ability to reproduce musical melodies (Alexander et al. 1989).

There is also evidence that the right hemisphere has a separate but parallel function to the left hemisphere for interpreting word meanings. It has been clear for a long time that the right hemisphere has some non-trivial language abilities. Experiments from split-brain patients, in which the left and right cortical hemispheres have been disconnected by severing the corpus callosum, show that the right hemisphere can understand short words, even though it lacks the ability to produce linguistic output (Gazzaniga 1970). Recent experiments have also suggested that the right hemisphere entertains a broader range of possible meanings for particular words in a sentence than does the left hemisphere (Beeman & Chiarello 1998). The right hemisphere is therefore likely better able to interpret multiple intended meanings of a given linguistic communication.

In addition, the right hemisphere plays a greater role in a variety of types of spatial processing. 'Spatial neglect', for example, in which a patient appears to ignore one side of their body, is more common after right hemisphere damage than left (Vallar 2007). Tzeng and Wang (1984), using an ingenious experimental testing paradigm in which the subject's response indicated whether they had perceived tachistoscopically presented letters in a temporal or spatial manner, showed that there was a right hemisphere (left visual field) bias for spatial perception, and a left hemisphere bias for temporal perception. Given that language is often used to convey spatial information, the right hemisphere therefore plays an important role.

Conceptual and semantic understanding

The semantic structure of language fundamentally depends on there being a conceptual structure for words (and grammar) to map on to. A strong argument can be made that much of the brain is involved, in one way or another, with in the construction and understanding of concepts and their inter-relationships (Damasio & Damasio 1992, Schoenemann 2005). Concepts appear to be instantiated as webs of interconnectedness among different brain regions. This interpretation is consistent with the finding that imagining an object (that is not present) activates the same areas of the brain as when the object is present (Damasio et al. 1993, Kosslyn et al. 1993). In particular, primary cortical areas involved in the initial basic cortical processing of visual information show activation even if simply imagining an object.

It appears likely that even simple concepts involve a network of activation across a wide variety of areas. For example, the concept 'cat' may bring to mind fur, purring, claws, etc. 'Fur', 'claws' and 'purring' are of course themselves concepts, which in turn have visual and tactile (in the case of 'fur' and 'claws') and auditory (in the case of 'purring') components. Visual, tactile, and auditory information are processed in separate cortical areas, and this means that the concept 'cat' must, at a minimum, activate a network connecting these areas. A complete list of areas that are relevant to basic features of conceptual awareness would be very long, involving at a minimum all the visual areas (including those responsible for color, shape, motion, etc), spatial areas, auditory areas, temporal organization areas, olfactory areas, taste areas, somatosensory areas, limbic system components (which provide emotional valence), and so on.

Visual information processing has been particularly well studied. It proceeds along two major pathways, often referred to as the dorsal and ventral streams (Bear et al. 2007). The dorsal stream moves from the primary visual cortex in the posterior occipital lobe (in the most posterior part of the brain) up into the adjacent parietal cortex, and is involved in processing visual information regarding the location and motion of an object. The ventral stream, which proceeds from the primary visual cortex through to the anterior tip of the temporal lobe, is involved in processing visual information regarding objects themselves (independent of their location and motion). Because of the functional distinction between the dorsal and ventral streams, they are often referred to as the 'where' and the 'what' visual pathways. Since language codes these aspects of our conceptual world, these areas are therefore fundamental to language even though they are not specifically 'language' areas.

The specific ability to connect concepts and conceptual understanding to specific linguistic codes appears to depend on a number of cortical areas. Connecting specific concepts to specific nouns appears to depend on the temporal lobes. A variety of studies suggest that anterior and medial areas of the temporal lobes are critical for the understanding of proper nouns, whereas the lateral and inferior temporal lobes appear to be critical for common nouns (Figure 1, Damasio & Damasio 1992). The generation of appropriate verbs, however, does not depend on the temporal lobe, and instead seems to involve Broca's area (Damasio & Damasio 1992, Posner & Raichle 1994). The extent to which this reflects a grammatical or semantic role (or some combination) for Broca's area is not clear, however.

Summary of brain areas relevant to language

Thus, it is clear that language relies on a large number of distributed areas across the brain. Although the left hemisphere seems to play the major role in expressive language for most people, the right hemisphere is also clearly involved in important ways. If one is concerned with the question of meaning, it would appear that much of the brain is involved at a key level. In addition, all these areas need to be interconnected in order for language to be maximally effective. Exactly how do human brains differ from those of other primates, specifically with respect to key aspects of language processing?

3. Comparative evolutionary assessments of the human brain

Brain size

The most obvious difference in the human brain in comparison to the brains of our closest living relatives, the primates, is in overall brain size. In absolute terms, human brains are about 3 times larger than those found in apes. Although brain size varies with body size across mammals, the human brain nevertheless exceeds mammal predictions (based on body size) by ~5 to 7 fold, and exceeds primate predictions by ~3 fold (see Schoenemann 2006 for a review). Interpreting this increase with respect to its relevance to behavior is difficult, however. It is clear that the human brain is not simply an isometrically scaled-up version of an ape brain, though there is some controversy about which subdivisions have undergone disproportionate changes (Deacon 1988, Rilling 2006, Schoenemann 2006, Semendeferi et al. 1998, 2001). Evolutionary changes in specific areas relevant to language will be reviewed below, but first it is important to point out some interesting correlates, both behavioral and structural, of general increases in brain size that are likely of importance.

The brain is clearly not a single, undifferentiated set of processors, and as such, overall brain size is unlikely to have a single function. However, there are a number of important behavioral features—many highly relevant to language—that are correlated with overall brain size. First, brain size correlates strongly with lifespan (Allman et al. 1993, Hofman 1983). This means, among other things, that the bigger the brain, the greater the opportunity for learning to be an effective and important part of an organisms behavioral repertoire. Larger brained animals do in fact tend to rely on learning much more so than smaller brained animals (Deacon 1997). To the extent both that language depends partly on learning, as well as that learning itself can be facilitated by language, the extensive increase in brain size in the human lineage probably made language that much more likely.

In addition, larger brained primates excel particularly at what may be called ‘transfer learning’, which can be distinguished from simple stimulus-response learning. For some animals, the better they learn a particular simple stimulus-response association, the harder it appears to be for them to learn a new, different one. Other animals display the opposite pattern: the better they learn the first association in a series—the better they are at learning subsequent associations. They appear to learn the general intent behind particular learning paradigms, rather than fixate on specific, particular associations. In a human context, we think of this as ‘learning to learn’. In turns out that brain size is the best neuroanatomical predictor of whether an animal excels at transfer learning: the larger the brain, the better they are at it (Beran et al. 1999). The relevance to language is that learning language depends on being able to understand changing, fluid contingencies between constituents and meaning. In addition, language is fundamentally creative. It would be impossible to learn a human language solely through stimulus-response associations, because it affords no room for creativity (this is one of the contributions of Chomsky and his followers).

Another behavioral dimension associated with brain size is the degree of interactive sociality displayed by the species. The strongest correlate of brain size across primates is the size of a species typical social group (Figure 2). Because larger social groups involve increasingly complex patterns of social interaction, including various kinds of complex contingencies, successful social living selects for increasingly sophisticated learning capabilities. Thus, brain size can be seen as a proxy for the degree of social interactivity within a species. Given that language is an inherently social activity, the usefulness of language (and hence, likelihood that competence in it would be selected for) would be greatest in the human species.

There are some important structural correlates of increasing

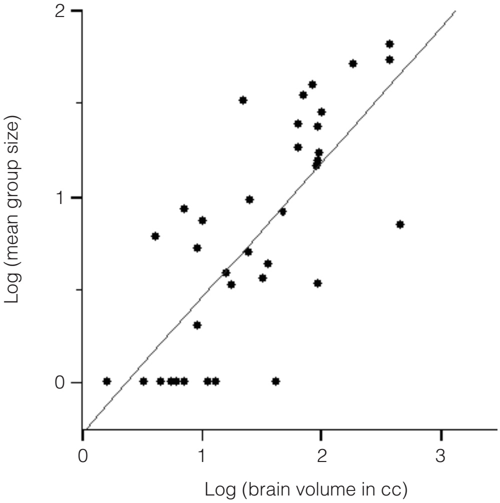

Figure 2. The relationship between brain volume and mean group size in 36 primate species. N = 36, r = .75, p <. 0001. Data from Dunbar (1995).

brain size that likely contributed to language evolution as well. In primates, there is a disproportionate increase in the size of the neocortex as brain size increases. In humans, the neocortex makes up over 80% of the entire brain, whereas in smaller brained primates it can account for less than 35% (Figure 3). The neocortex, found only in mammals, appears to be the most recent evolutionary addition. It is responsible (in humans at least) for conscious awareness, and appears to play a key role in many types of complex, higher cognitive abilities, including language. It is not presently known how much of this pattern of increasing predominance of the neocortex is traceable directly or indirectly to some inherent structural biases. However, the result of this effect is that the very areas that in humans play a central role in language are also ones that are increasingly elaborated in larger brained primates.

In mammals generally, portions of the neocortex are devoted to the primary processing of basic sensory information (e.g., vision, audition, sense of touch, taste, etc.), as well as the direct conscious control of muscles. In larger brained mammals, however, these areas

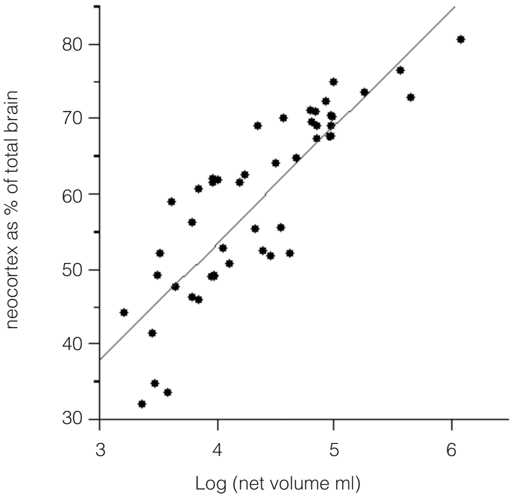

Figure 3: The relationship between log brain volume and proportion of total that is neocortex in Primates. N = 48, r = .85, p < .0001. Data from Stephan et al. (1981).

make up a decreasing proportion of the entire neocortex. This means that an increasingly large proportion of the neocortex is devoted to more complex and interesting kinds of processing: the integration and combination of basic sensory information in ever-increasing degrees of sophistication. These areas are commonly referred to as 'association areas' because of this. The larger the amount of association cortex in a brain, the greater the potential for increasingly complex and subtle types of integrative processing. It turns out that larger association cortices are not undifferentiated, but are instead composed of numerous relatively specialized processing areas. This in turn is predictable from some consideration of the ways in which brain regions are connected.

Brains are networks of neurons. The connections between groups of neurons are as important as the groups of neurons themselves. It doesn't actually make any sense to talk about groups neurons strictly in isolation (when this happens, we refer to it as 'brain damage'). Given this, how this might neuronal connectivity predictably change as the number of neurons is increased? In a small brain, it is physically easier for any given neuron (or functional sets of neurons called nuclei) to be more directly connected to other neurons or nuclei, for the simple reason that there are fewer other neurons and nuclei to connect to (Ringo 1991). To take a simple example, if two neurons are reciprocally interconnected, there are two processes connecting them (one from each neuron to the other). If another neuron is added and becomes equally well connected to the existing neurons, there must now be six processes connecting them (three neurons each with two connections to the other ones). Adding one neuron requires adding four additional connections, if that neuron is to be equally well connected with the existing neurons. It is easy to see that the number of interconnections will need to increase exponentially if the degree of interconnectivity is to be maintained as neurons are added.

There is evidence that, in real brains, there is a tradeoff between numbers of neurons and degree of interconnectivity. Though counting individual neurons and their interconnections is not currently feasible because of the immense number of neurons and connections in mammal brains, it is nevertheless possible to make gross assessments. Longer distance connections are accomplished through neuronal processes called axons. These axons are often (though not always) covered with specialized sheaths knows as myelin, which allow the neuronal signals to travel much faster. Because myelin appears lighter in color than neurons and other support cells, areas with large numbers of axons appear whiter in appearance, and so are referred to as white matter areas (the areas where the neuron cell bodies are located are gray in appearance, and is known as gray matter). It is possible to quantify white matter vs. gray matter and use this comparison as a proxy for the degree of interconnectivity between neurons. Data on real brains indicate that the proportion of white matter increases as brains get larger, but not nearly fast enough to suggest that equal interconnectivity is maintained (Ringo 1991, Striedter 2005). One illustration of this can be seen by plotting of corpus callosum cross-sectional area vs. brain volume. The corpus callosum is band of connective tissue that is made up of axons connecting the two cerebral hemispheres. As can be seen from Figure 4, relative corpus callosum size (the ratio of corpus callosum area to total brain volume) actually decreases as brain size increases.

This means that as brains increase in size, there are relatively fewer connecting axons through the corpus callosum per unit volume: groups of neurons therefore become less directly connected to other groups of neurons. The significance of this is that functional localization (specialized processing carried out in specific areas) would appear to be a natural consequence of increasing brain size. Consistent with this, Changizi and Shimojo (2005) have shown that the number of identifiably different cortical areas increases to the 1/3rd power of neocortex area.

Thus, larger brains have disproportionately larger neocortices, with the lion's share of these increases devoted to more and more complex kinds of specialized information processing in localized areas. While this is critically important to the evolution of language, it does not mean that language was therefore a necessary

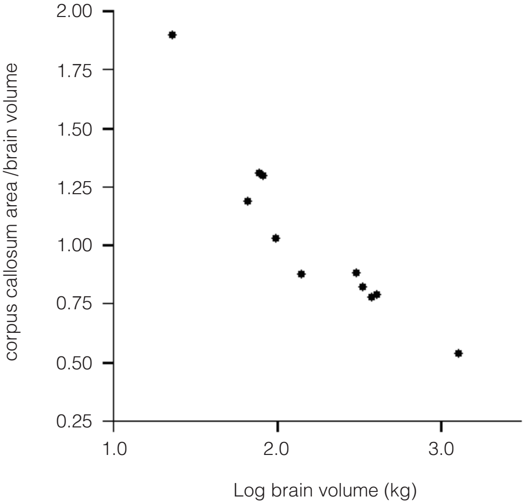

Figure 4: Ratio of corpus callosum area (mm3) to log brain volume (kg) in 11 primate species. Data from Rilling & Insel (1999a). Strictly speaking, neocortical surface area would be a better measure, but this was not reported. Since surface area scales almost 1:1 with brain volume (Jerison 1982), the general finding of an inverse relationship between the relative size of the corpus callosum and the areas it connects is still valid. See also Striedter (2005) for a plot of relative corpus callosum area to log neocortex surface area showing the same negative relationship.

consequence or byproduct of increasing brain size. Rather, it shows that it would be easier to mold a set of semi-independent specialized language processors from a larger brain than it would be in a smaller brain. At a minimum, the likely effects of these general changes would be towards enhancing the subtlety and complexity of our inner mental world, and thereby giving us much more to talk about with others (Schoenemann 1999, 2005).

Brain size and body size

Before assessing the evolutionary changes of specific regions and subdivisions of the brain that may be relevant to language, a few comments should be made about how to interpret changes in size. Such changes can be assessed relative to body size, or to the size of the brain itself, or to some other subcomponent. It has long been recognized that brain size is correlated with body size in mammals (and other groups of animals). This has led to the creation of various indices which allow one to assess brain size relative to expectations based on body size. The most commonly used such measure is Jerison's Encephalization Quotient {often designated: EQ), which is simply the ratio of a species absolute brain size divided by the average brain size of a mammal of that body weight (Jerison 1973). For humans, this value is about 5–7, depending on the estimation of the average mammal brain/body relationship (Jerison 1973, Martin 1981)}. This measure is often used as if it were the most behaviorally relevant variable describing brain differences between species. A strong argument can be made that absolute brain size changes actually have profound behavioral consequences, regardless of any concomitant changes in body size (Schoenemann 2006). Similarly, one can scale parts of the brain to brain size itself, so as to determine whether some parts of the human brain appear to have been more highly elaborated than others over our evolutionary history. As will be clear below, some parts do appear to have increased more than others. However, when we assess these changes, we need to be careful not to assume that changes in relative size are more important than changes in absolute size. So, for example, when we see that the cerebellum has increased in size—but at a rate less than that seen in the neocortex—it is a mistake to assume that there cerebellum increase was therefore unimportant, behaviorally meaningless, or (even worse) somehow indicative of a decreased importance relative to the neocortex. Because of the very high metabolic demands of neural tissue (Hofman 1983), it is extremely unlikely that any increases would occur in some neural component if they did not provide counterbalancing benefits. Absolute changes in size of some component are likely important regardless of what other changes might also be occurring. With this in mind, what changes in brain subcomponents are known that might be relevant to the evolution of language?

Connections between the cortex and the midbrain

Non-human primate brains share with human brains the indirect connections between the larynx, tongue, and trunk areas of the neocortex and the brainstem motor nuclei that directly control muscles involved in vocal production (Jurgens 2002, Jurgens & Alipour 2002). The indirect connections include the pathways discussed above that route through the reticular formation (for laryngeal and tongue control) or nucleus retroambiguous (for chest muscles). There are also even more indirect routes, from the anterior cingulate (mesocortex, which is older than the neocortex) to a midbrain region known as the periaqueductal gray area, and then on to either the reticular formation or nucleus retroambiguous.

Non-human primate brains differ with respect to the degree of direct connections from the neocortex to the brainstem motor nuclei. Only weak direct connections are known in non-human primates to the brainstem motor nuclei that control the tongue and respiration muscles, and apparently no direct connections exist from the neocortex to the larynx (Jurgens 2002, Jurgens & Alipour 2002). This is consistent with the extensive conscious control of vocalization displayed by humans using language, as compared to other non-human primates who instead seem to vocalize primarily in highly emotional situations.

The size of the pathways leading back from the cochlea to the primary auditory cortex in the temporal lobe (where conscious awareness of sound occurs, and speech processing begins) have apparently not been quantified across different species. However, the sizes of numerous intermediate auditory nuclei (where signals undergo intermediate processing before being passed on to subsequent nuclei) have been assessed in mammals. The volume of these nuclei tend to vary strongly with overall brain weight (Glendenning & Masterton 1998). If one scales the sum of all the auditory nuclei together against overall brain weight, humans fall somewhat below the average for a mammal with our brain weight, but still comfortably within the 95% confidence intervals (N = 53). However, perhaps because our overall brain weight is so large, in absolute terms the total size of our auditory nuclei was actually the largest represented in Glendenning's study (at 187 mm^3). Nevertheless, this is only a bit larger than the total value for deer (175 mm^3), even though the overall body size for deer is only 2/3rds the body size of humans. Perhaps more impressive are domesticated cats, which weigh only ~3 kg, but have auditory nuclei totaling 104 mm^3. The closest primate in the sample was a lemur (a prosimian very distantly related to humans—no apes were included in the sample unfortunately), weighing 2 kg and having auditory nuclei totaling ~24 mm^3. Thus, the size of the auditory nuclei in humans do not appear to be particularly impressive with respect to either body or brain weight, though they are reasonably large in absolute terms. As has been argued above, absolute differences are not irrelevant, though the lack of ape data for comparison hampers a clear-cut interpretation. If we take seriously the perspective that language adapted itself to the human brain, we should expect that it would make use of pre-existing auditory processing abilities. That is, languages would evolve specifically take advantage of sound contrasts that were already (prior to language evolution) relatively easy to distinguish innately. We might tentatively conclude from this that greater evolutionary change has occurred in the sound production pathways than the sound perception ones.

Cerebellum

With respect to overall brain size, the human cerebellum is slightly smaller than one would predict based on cerebellum/brain size scaling in primates, though not significantly so (Rilling & Insel 1998). However, with respect to body size, the human cerebellum is ~2.9 times larger than predicted (Schoenemann 1997). It shows the greatest disproportion of any brain region other than the neocortex (which is ~3.3 times larger, as mentioned above). As discussed above, the cerebellum does seem to be involved in language processing, specifically with respect to the production and perception of speech sounds (Ackermann et al. 2007). The fact that it does not scale directly with body size—suggesting that it doesn't get bigger solely because proportionately more muscle fine-tuning is needed by bigger bodies—and given its varied cognitive contributions, this suggests that it likely isn't bigger in humans simply because the whole brain is bigger. Its increase suggests functional implications.

Deep cortical nuclei

Unfortunately, I am aware of no comparative studies of the size of various deep cortical nuclei, such as the basal ganglia. As discussed above, these appear to form an important part of the circuitry involved in syntactic processing. The extent to which these areas have been elaborated is therefore not currently known.

Neocortical areas

It is apparent that, although the neocortex in humans is large and has increased proportionately more than the brain as a whole (as predicted by the biased increase in neocortex with increasing brain size across primates), not all parts of the neocortex underwent equivalent increases. Several areas, for example, appear to have undergone proportionately much less increase than the neocortex as a whole. The primary motor cortex (where direct cortical control over muscles originates) is only ~33% as large as predicted given how large our neocortex has become, based on non-human primate scaling trends, and the premotor cortex (where complex muscle movements are coordinated and planned) is only ~60% as large (Blinkov & Glezer 1968, Deacon 1997). Similarly, the primary visual area of the neocortex (where visual information is first processed on a conscious level) is only 60% as large as predicted based on non-human primate scaling trends (Holloway 1992). Given that the neocortex as a whole increase 3.3 times over primate body size scaling expectations (Schoenemann 1997), these findings show that, in terms of the absolute volumes, the primary motor cortex stayed relatively constant in size, while the premotor and primary visual cortex underwent modest increases over that found in apes. This is a good example of how an emphasis on relative component size would lead to potentially misleading assumptions about behavior, as there is no evidence that humans have particularly poor abilities in the visual domain (which would be predicted if relative decreases in visual cortex size were behaviorally meaningful).

With respect to the dorsal and ventral visual streams (which, as discussed above, are central to the perception of different kinds of visual information), there is apparently no quantitative primate data on this score (but see discussion of the temporal lobe—through which the ventral stream runs—below).

Given that the primary motor, premotor, and primary visual cortical areas lagged behind the overall increase in neocortical size, there must necessarily have been areas that increased to a proportionately greater extent (such that overall the increase was ~3.3-fold, Preuss 2000, Schoenemann 2006). One area that appears to have undergone a relatively greater increase is the temporal lobe. Overall, the human temporal lobe is 23% larger than predicted based on overall brain volume scaling trends in our closest relatives, the apes (neocortex-only scaling was not reported unfortunately, Rilling & Seligman 2002). The difference from expectations appears greatest for white matter volume, suggesting that connectivity with other cortical areas was particularly important for this cortical area. Given that the temporal lobe plays a central role in the understanding of nouns, as discussed above, this is suggestive of selection for increased processing of conceptual information.

The primary auditory cortex itself (a very small subset of the temporal lobe cortex, located on the superior temporal gyrus) appears to be only ~6% larger than predicted, and immediately adjacent areas in the superior temporal lobe appear to be only ~17% larger (Deacon 1997). Since these are a subset of the entire temporal lobe, it would appear that the rest of the temporal lobe (i.e., those areas not directly involved in processing of sound) have increased by a greater amount than the 23% estimated for the temporal lobe as a whole. The fact that the human disproportion increases the farther one gets from the primary processing of auditory information fits with the suggestion that the elaboration of circuits involved in conceptual and semantic processing have been particularly important in driving language evolution (Deacon 1997, Schoenemann 1999, 2005). It is important to keep in mind, however, that, in absolute terms, even the primary auditory cortex is still ~3 times larger than the equivalent area in apes. This is important because there are good reasons to believe that absolute increases in amounts of cortical tissue—not just increases in amounts over that predicted based on brain size scaling trends—are behaviorally relevant (for discussion see: Schoenemann 2006, Striedter 2005). Thus, one can make a compelling argument that important enhancements likely occurred with respect to auditory processing as well, even if the greatest elaboration appears to have occurred in the non-auditory regions of the temporal lobe.

One area that has been of particular focus is the planum temporale. This area is located in the superior portion of the temporal lobe, hidden in the sylvian fissure, just posterior to the primary auditory cortex, and is generally considered part of Wernicke's language area in humans. In a classic autopsy study by Geschwind and Levitsky (1968), this area was found to be asymmetrical, with 65% of the cases showing a left hemisphere bias, and only 10% showing a right hemisphere bias. Given that the processing of the expressive aspects of language typically are also left hemisphere lateralized, this suggested there the planum temporale asymmetry might be an anatomical marker of this language processing bias. Unfortunately, it has recently been shown that a similar asymmetry exists in the planum temporale of apes (Gannon et al. 1998), which means that asymmetry in this region does not constitute evidence of language specialization. Exactly what it does indicate is not clear, but it is possible this area is involved in communication generally, and is an example of an area preadapted to language

Another area that appears to have increased substantially is the prefrontal lobe. Allometric analyses of cytoarchitectural data collected by Brodmann (1909) suggest the human prefrontal is ~200% as large as would be predicted on the basis of the size of the rest of the brain (Deacon 1997). Recent comparative studies using MRI to quantify volumes generally support these older data (Schoenemann 2006, Schoenemann et al. 2005), though one study suggested that the entire frontal lobe (of which the prefrontal is only a subset) was not larger than predicted allometrically (that is, in relative terms, Semendeferi et al. 2002). However, given that other portions of the frontal lobe appear to be significantly smaller than predicted (i.e., the primary motor and premotor areas discussed above), the prefrontal must necessarily be larger than predicted (Schoenemann 2006). Because the prefrontal does not have clearly defined sulcal boundaries on the surface of the cortex, it cannot be unequivocally delimited using MRI, and proxy measures must be used instead. Our own study found that, whereas the non-prefrontal portions of the human brain were 3.7 times larger than the average for the two chimpanzee species studied, the prefrontal portion was 4.9 times larger (Figure 5, Schoenemann et al. 2005). A number of other studies also support this contention, including assessments of the degree of folding in different areas of the cortex (prefrontal regions showing the greatest amount, Armstrong et al. 1991, Rilling & Insel 1999b), and assessments of the degree of localized distortion necessary to 'morph' non-human primate brains into human brains (Avants et al. 2006, Van Essen 2005, Zilles 2005), consistently show significant prefrontal elaboration in humans.

What is particularly intriguing is the finding that the difference was greatest for white matter (Figure 5, Schoenemann et al. 2005). Given the prefrontal's general executive role coordinating and monitoring activity in posterior brain regions, and given the increase in distinct cortical areas in the human brain overall (predicted by the increase in brain size as discussed above), connectivity to and from the prefrontal would be expected to be particularly enhanced in humans. This would explain why the prefrontal seems to increase in size faster than the rest of the cerebrum as brain size increases (known as 'positive allometry').

Within the prefrontal there are several different regions that can more or less be distinguished with respect to function, but not all of

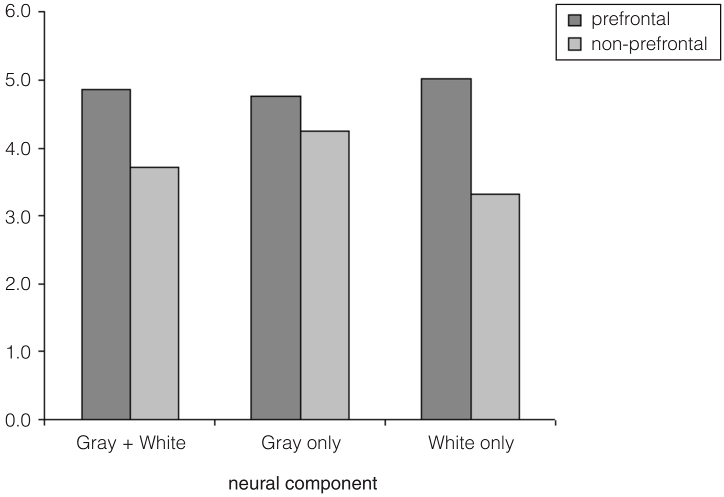

Figure 5: Difference in absolute size of the prefrontal vs. non- prefrontal areas of the cerebrum of humans compared to chimpanzees (Pan troglodytes and Pan paniscus). Gray matter is primarily neuron cell bodies, dendritic connections, and their glial support cells, whereas white matter is primarily long-distance connections between regions.

these have been compared across primates. Area 13, which appears to be involved in processing information relevant to the emotional aspects of social interactions, seems to have lagged behind the overall increase in brain size, being only ~1.5 times larger than the average ape (pongid) value (Semendeferi et al. 1998). By contrast, area 10, which is involved in planning and organizing thought for future actions, is ~6.6 times larger than the corresponding areas in pongids (Semendeferi et al. 2001). This increase is close to what one would expect given the positive allometry shown by this area with respect to the brain as a whole (Holloway 2002). With respect to language, area 10 appears to be involved in the selection of appropriate words given some semantic context (Gabrieli et al. 1998, Luke et al. 2002).

Classical language areas

Homologous regions to human Broca's and Wernicke's language areas have been identified in non-human primate brains (see references in Striedter 2005). Exactly what these areas are doing in other these other species is not clear, though an evolutionary perspective predicts that they process information in ways that made them likely candidates for usurpation by evolving language behavior in the human lineage (Schoenemann 2005). Assessing the function of these areas in non-human primates would provide an empirical assessment of the extent to which human language required the evolution of completely new circuits. This would appear to be a fruitful avenue for future research. Given the difference in degree of language-like behavior displayed by humans and non-human primates, however, it is clear that some non-trivial elaboration of function has occurred in these areas in our lineage. Quantitative data on the relative size of the homologs of Broca's and Wernicke's areas in a wide range of non-human primates have not been reported, but qualitative assessments suggest that these areas are significantly bigger both in absolute and relative terms in humans as compared to macaque monkeys (e.g., see Figure 6 and diagrams in Petrides & Pandya 2002).

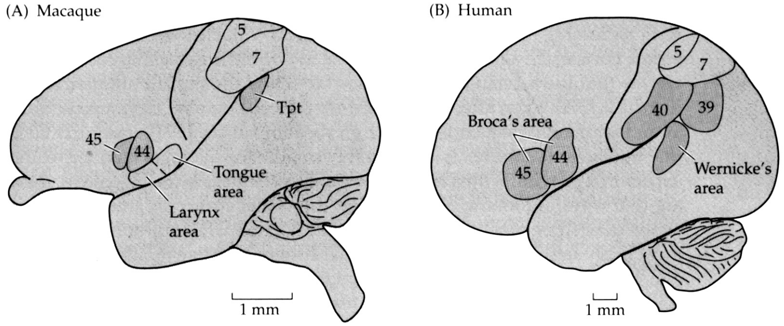

Figure 6: Broca's and Wernicke's areas in the human brain and their apparent homologs in Macaque monkeys (from Streidter 2005, [IMAGE USED WITH PERMISSION]). Area Tpt is thought to be homologous to Wernicke's area. The extent to which Brodmann's areas 40 (supramarginal gyrus) and 39 (angular gyrus) are unique in humans is not clear. Both these latter areas play a role in semantic processing in language, and variously have been included as being part of Wernicke's area by some researchers (Tanner 2007).

There does appear to be a difference between humans and non-human primates in the degree to which the arcuate fasciculus connects Broca's and Wernicke's regions. It appears that in macaques the homolog of Wernicke's area, Tpt, does project to prefrontal regions, but not directly to the presumed homolog of Broca's area (areas 44 and 45). Instead projections to these areas stem from an adjacent area in the parietal lobe: area 7 (Figure 7, see Aboitiz & Garcia 1997). This would suggest that there has been an extension of projections more directly to Broca's area over the course of human (or ape) evolution (no tracer data currently exist for chimpanzees because of their endangered status, so we can't rule out the possibility that some of this evolutionary change occurred prior to the human lineage). Recent MRI imaging techniques that can estimate white matter axonal tracts, known as Diffusion Tensor Imaging, have been applied to this question. Using this method, macaques and chimpanzees both appear to have tracts connecting the posterior temporal areas in the vicinity of Wernicke's area to the inferior frontal regions in the vicinity of Broca's area. However, only chimpanzees and humans have obvious connections between

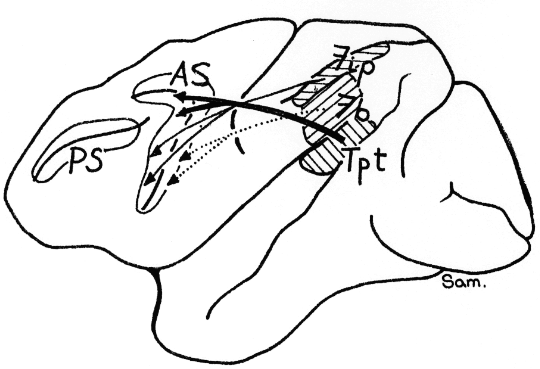

Figure 7: Projections from the Macaque homolog of Wernicke's area, region Tpt, to prefrontal regions. The putative homolog of Broca's area is along the inferior extent of the arcuate sulcus (labeled AS). Tpt seems instead to project to the superior areas of the AS. From Aboitiz and Garcia (1997) [IMAGE USED WITH PERMISSION]

the middle temporal regions important to semantic processing and Broca's area. In addition, humans are reported to have the most extensive of such connections (Rilling et al. 2007). This suggests that these connections were significantly elaborated during human evolution, presumably for language.

Conclusion

Language depends critically on a large number of areas and circuits in the brain. In addition to the classical language areas, Broca's and Wernicke's, language depends on extensive areas in the prefrontal cortex (semantic processing, discourse planning and construction, working (immediate) memory), and temporal lobe (connecting words to concepts, decoding speech information). In addition, the right hemisphere appears to play important roles as well, particularly with the processing of prosody, alternative semantic interpretations, and spatial conceptualization. These cortical areas also have to both receive information from the ears (in the case of speech) as well as send signals to muscles that allow speech to be performed.

Many changes in the brain appear to be relevant to language evolution. Overall brain size increases had many effects that paved the way for language in fundamentally important ways, particularly by making localized cortical specialization increasingly likely, and by encouraging (or making possible) the increasing intensity of social interactions, thereby providing the very reason for the existence of language in the first place. Specific areas of the brain that are directly relevant to language also appear to have been particularly elaborated, including the temporal lobe (especially areas relevant to connecting words to meanings and concepts), and prefrontal cortex (especially with respect to its connections to other areas). There appear to be homologs of Broca's and Wernicke's areas in non-human primate brains, but they are smaller (both relatively and absolutely) than in humans. The connections between these areas, contained in the arcuate fasciculus, do not appear to be as substantial as those in the human brain. Further, the human brain appears to have more connections between Broca's area and temporal lobe areas adjacent to Wernicke's (specifically, the middle temporal gyrus—an area that mediates word-meaning pairings). Finally, it appears that although it is unclear whether there was any significant elaboration of the auditory processing pathways up to the cortex, direct pathways from the cortex down to the tongue and respiratory muscles were strengthened, and new direct pathways were created to the larynx. These presumably facilitated the conscious control of speech.

Given that concepts area instantiated as webs of connectivity across a variety of brain regions and processing areas, the changes in the human brain outlined here all point to a significant increase in the complexity, subtlety, and range of concepts that our brain is capable of. The fact that there are more distinct cortical areas in the human brain than any other primate brain (Changizi & Shimojo 2005), the fact that the temporal lobe and particularly the prefrontal cortex have become so elaborate, and the fact that overall neural connectivity has increased dramatically (albeit to a predictable amount given our overall brain size), all support this view. Placed in the context of an intensely socially-interactive existence, as was the case for our earliest (non-linguistic) ancestors, this elaboration of conceptual complexity would almost certainly have played a central role in driving the evolution of language. Given the way language itself can facilitate thinking and conceptual awareness, it seems likely this would have been a mutually reinforcing process: Increasingly complicated brains would have increasingly complicated thoughts to express, thereby encouraging the evolution of increasingly complicated language, which would itself facilitate increasingly complex conceptual worlds that these brains would then want to talk about. Deacon's (1997) ideas about the origin and elaboration of symbolic thought dovetail nicely with such a model, and suggest a way in which such a self-reinforcing process might occur. The extent to which increasing conceptual complexity itself could drive language evolution represents an intriguing direction for future research.

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