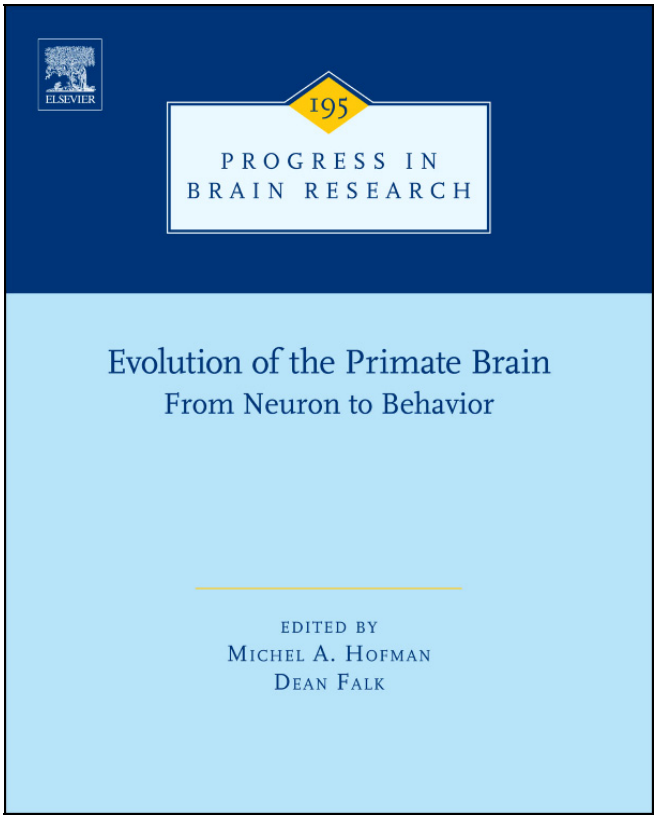
Provided for non-commercial research and educational use only.
Not for reproduction, distribution or commercial use.

This chapter was originally published in the book *Progress in Brain Research,* Vol. 195, published by Elsevier, and the attached copy is provided by Elsevier for the author's benefit and for the benefit of the author's institution, for non-commercial research and educational use including without limitation use in instruction at your institution, sending it to specific colleagues who know you, and providing a copy to your institution's administrator.



All other uses, reproduction and distribution, including without limitation commercial reprints, selling or licensing copies or access, or posting on open internet sites, your personal or institution's website or repository, are prohibited. For exceptions, permission may be sought for such use through Elsevier's permissions site at:
http://www.elsevier.com/locate/permissionusematerial

From: P. Thomas Schoenemann, Evolution of brain and language. In Michel A. Hofman, Dean Falk, editors: *Progress in Brain Research,* Vol. 195, Amsterdam: The Netherlands, 2012, pp. 443-459.
ISBN: 978-0-444-53860-4
© Copyright 2012 Elsevier B.V.
Elsevier

Author's personal copy

M. A. Hofman and D. Falk (Eds.)
Progress in Brain Research, Vol. 195
ISSN: 0079-6123
Copyright © 2012 Elsevier B.V. All rights reserved.

CHAPTER 22

Evolution of brain and language

P. Thomas Schoenemann*

Department of Anthropology, Indiana University, Bloomington, IN, USA

Abstract: In this chapter evolutionary changes in the human brain that are relevant to language are reviewed. Most of what is known involves assessments of the relative sizes of brain regions. Overall brain size is associated with some key behavioral features relevant to language, including complexity of the social environment and the degree of conceptual complexity. Prefrontal cortical and temporal lobe areas relevant to language appear to have increased disproportionately. Areas relevant to language production and perception have changed less dramatically. The extent to which these changes were a consequence specifically of language versus other behavioral adaptations is a good question, but the process may best be viewed as a complex adaptive system, whereby cultural learning interacts with biology iteratively over time to produce language. Overall, language appears to have adapted to the human brain more so than the reverse.

Keywords: coevolution; conceptual complexity; communication; cortex; Broca's area; Wernicke's area; comparative primate; brain scaling.

Introduction

Among all the behavioral changes made possible by human brain evolution, language is arguably the most critical to defining the human condition. Other animals communicate, but none do so with the richness and complexity of human language. This means that there must be some important differences between the brains of humans and other animals in areas relevant to communication. Comparative studies of the brains of humans and other animals, combined with an understanding of the different functions of specific brain regions, and considered within a realistic evolutionary perspective, allow a reasonable sketch of the evolution of brain and language.

Languages must 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. 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

*Corresponding author.
Tel.: +1-812-8558800; Fax: +1-812-8554358
E-mail: toms@indiana.edu

DOI: 10.1016/B978-0-444-53860-4.00022-2

Author's personal copy

creatures, which makes communication central to our existence. Two interrelated 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 and Chater, 2008; Deacon, 1992).

The coevolution of language and brain can be understood as a complex adaptive system (Beckner et al., 2009). 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, system-wide order. With respect to the coevolution of brain and language, a number of language-relevant neural systems interact with and influence each other in important ways. Syntax depends fundamentally on the structure of semantics, since the function of syntax is to code higher-level semantic information. Semantics in turn depends on the structure of conceptual understanding, which—as will be reviewed below—is a function of brain structure. These structures are in turn the result of biological adaptation: circuits that result in conceptual understanding that is useful to a given individual's environmental realities will be selected for.

In general, the selective environment for primate species is largely a social one. 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 also attempting to behave in an adaptive manner in response. Understanding language evolution ultimately involves understanding how the repeated complex communicative interactions of individuals result in cultural change in languages, and how these changes in turn influence biological change in the long term. The evolution of brain circuits cannot be understood independent of the evolution of language, and vice versa.

Because the evolutionary benefits of language to an individual would always have been dependent on the preexisting cognitive abilities of others, language evolution is inherently constrained. New genetic variants enhancing 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*. Similarly, 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.

It is possible for some new variant to be adaptive strictly at the individual level (and therefore spread) even if it was not immediately useful for language, but this could only be true if they were beneficial for some other reason. In this case, however, it would not be a "language" variant. If it spread wide enough (for nonlinguistic reasons), it might later be co-opted for language. This would not result in the evolution of highly language-specific circuits.

For these reasons, any adaptive changes in language circuitry occurring during a given sequence of the evolutionary process will be biased toward slight modifications of preexisting circuits, and away from major changes in the ways communication is processed by the brain (Schoenemann, 2005). Language circuits should show extensive homologies with preexisting systems in closely related animals. These hijacked circuits would, by definition, be domain general (contra Tooby and Cosmides, 1992).

Inferences about evolutionary changes in the brain relevant to language are derived from knowledge of how language is processed in the brain, combined with knowledge of how our

Author's personal copy

brains are different from those of our closest evolutionary relatives. To the extent that a particular area known to be relevant to language appears to have also changed significantly, we are justified in inferring that this area was important for language evolution, though whether it increased specifically for language will be difficult to determine. Evolutionary inferences will also involve thinking about the interplay of different behavioral abilities over our history. Both an evolutionary perspective and a complex adaptive systems approach predict that language evolution occurred hand in hand with the evolution of other aspects of cognition. Language processing depends heavily on the integration of a large number of abilities that are processed in widely dispersed circuits across the brain (Damasio and Damasio, 1992; Mueller, 1996). Assessing the coevolution of language and brain therefore requires a broad focus on a number of brain regions.

Evolutionary changes in the brain relevant to language

Knowing how different language-relevant brain areas have changed over our evolutionary history is central to understanding the coevolution of brain and language. However, it is not clear what counts as significant change: increases relative to brain size, body size, or simply absolute size independent of either brain or body? Because of the evolutionary costs to increasing the absolute numbers of neurons (Hofman, 1983), changes in absolute size of an area *independent* of body or brain increases are likely to be behaviorally relevant. Further, there are many examples of changes that appear to be unrelated to either body or brain size increases. The olfactory bulb (responsible for sense of smell) has actually decreased in size (being half that found in chimpanzees; Stephan et al., 1981), the primary motor cortex (Brodmann area 4) has apparently not increased at all in absolute size (Blinkov and Glezer, 1968), and premotor cortex (Brodmann area 6) and primary visual cortex (Brodmann area 17) appear to have lagged significantly behind the increase in overall brain size (Deacon, 1997; Schoenemann, 2006). Thus, brain evolution is remarkably plastic over the long term (contra Finlay et al., 2001). It is true that brain size correlates with body size across major groups of animals, which in turn has led to the use of relative brain size measures when comparing species (e.g., the encephalization quotient or EQ; Jerison, 1973; see also Chapter 20). However, this association does not require that relative brain size is behaviorally relevant. It likely just represents an inevitable tradeoff between the utility of brains and their disproportionate metabolic costs: larger brains may always be useful, but only larger animals can afford to pay for them metabolically (e.g., Martin, 1981). In fact, absolute brain size is empirically a much better predictor of species differences in behavior than is relative brain size (Deaner et al., 2007; Gibson et al., 2001; for a discussion see Chapter 15). For this reason, any changes in brain anatomy are therefore potentially of behavioral importance.

One caveat that needs to be stated; however, we do not know the details of exactly how different areas of the brain actually process information. We lack the neural equivalent of a circuit diagram for anything larger than the 302 neuron brain of the worm *Caenorhabditis elegans* (White et al., 1986; Chapter 17). Because of this, we cannot be sure that a fourfold increase in one area has greater behavioral implications than a twofold increase in some other area. Nevertheless, any increase would seem to be important, given the costs of maintaining excess neurons.

Overall brain size

Human brains are about three times larger than that found in our closest relatives, the African apes (even taking body size into account; Jerison, 1973).

Author's personal copy

Exactly what behavioral implications this has is a matter of debate, but given the importance of language to the human condition, it is reasonable to believe that at least part of this increase is due to language. The idea that the evolution of brain size and language are related is an old one going back at least to Darwin (1882), who argued there was likely a "...relation between the continued use of language and the development of the brain..." (p. 87). Because different parts of the brain have changed in different ways, focusing solely on overall brain size is an oversimplification. However, there are some interesting correlates of overall brain size that are likely relevant to language evolution.

First, as pointed out above, absolute brain size is empirically behaviorally relevant. Overall brain size also correlates strongly with both length of maturation (Harvey and Clutton-Brock, 1985) and overall lifespan (Allman et al., 1993; Hofman, 1993). This means that the bigger the brain, the greater the potential for behavioral learning to be a central part of the organism's behavioral repertoire. Larger brained animals rely on learning more than do smaller brained animals (Deacon, 1997), and larger brained primates do better at a variety of experimental learning tasks (Deaner et al., 2007).

A great deal of modern human behavior (including language) depends critically on learning. While 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. The increasing behavioral flexibility and reliance on learning made possible by the increase in brain size, therefore, made language increasingly possible, if not inevitable.

Primates as a group are particularly interactively social, and interactive sociality is a particularly complicated niche (Holloway, 1975; Humphrey, 1984). The size of the typical social group has been shown to be associated with various measures of brain size (including absolute brain size) in primates (Fig. 1; Dunbar, 1995; Reader and Laland, 2002). Social group size is a reasonable proxy for the complexity of one's social existence. Human social networks appear to be particularly complex, and given that language is an inherently social activity, the selective value of language is likely greatest for humans.

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, appears to be strongly associated with overall brain size (Hofman, 1985). The neocortex makes up over 80% of the entire human brain, which is the highest value among all primates. The corresponding values for apes (who have the next largest brains among primates) range from ~76% to 73%, while particularly small brained monkeys range down to 59%, and the smallest brained primate of all, the mouse lemur (*Microcebus murinus*), has a neocortex that takes up only 44% of its brain (Hofman, 1985, 1988;

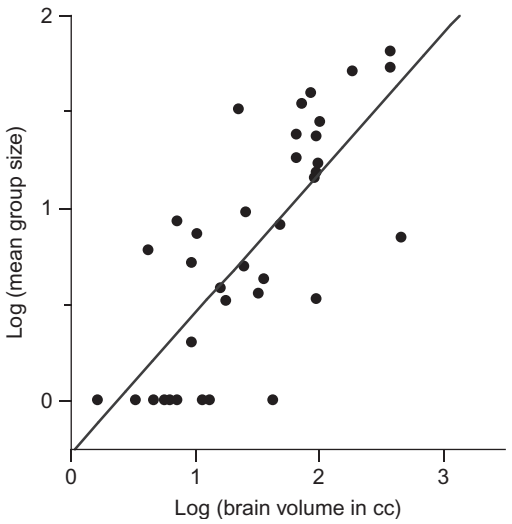


Fig. 1. The relationship between brain volume and mean group size in primate species. N=36, r=0.75, p<0.0001. Data from Dunbar (1995).

Author's personal copy

Stephan et al., 1981). This would suggest that as brains get larger, conscious behavior becomes increasingly important.

In addition, as the neocortex increases, areas of it that are devoted specifically to integrating different types of information (so-called association areas) increase disproportionately, at the expense of areas devoted either to the processing of sensory information from a single modality (such as the primary visual or primary auditory cortices) or to the conscious control of muscle movement (Fig. 2). The larger these "association areas" are, the greater the likely potential for increasingly complex types of integrative processing (Schoenemann, 2010).

Further, as these association areas expand, they appear to evolve increasing numbers of relatively specialized processing areas. Larger brains have greater numbers of identifiably distinct cortical areas (Changizi and Shimojo, 2005; Northcutt and Kaas, 1995). This turns out to be a predictable consequence of increasing brain size: any given area of the neocortex will tend to be less directly connected to other areas in larger brains compared to smaller brains (Ringo, 1991). This means that areas are able to carry out tasks increasingly independent of each other, leading predictably to increasing functional localization.

An fundamentally important consequence of this that it allows for the formation of richer, more complex, and more subtle conceptual understanding (Gibson, 2002; Schoenemann, 1999, 2005). Much of the brain appears to be relevant to concept formation (Barsalou, 2008; Damasio and 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 basic sensory input—visual, auditory, olfactory, taste, and somatosensory (touch, temperature, pain, body position)—are processed in different areas. While some basic concepts involve only a single sensory modality (e.g., [green] or [smooth (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 and 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. These are processed using extensive regions of the parietal, occipital, and temporal lobes (Fig. 3b).

Given that conceptual awareness forms the very foundation of language (Hurford, 2003a), and given that larger brains appear to give rise to more complex conceptual universes (and hence more interesting things to communicate about), and given that humans are intensely socially interactive, increasing brain size itself should be seen as an excellent 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 et al., 2007; Damasio and Damasio, 1992). Broca's area is located in the posterior–inferior frontal convexity of the neocortex, while Wernicke's area is localized to the general area where parietal, occipital, and temporal lobes meet (Fig. 3d). For most people, these areas are functional for language primarily in the left hemisphere. However, it turns out that Broca's and Wernicke's aphasias (the specific types of

Author's personal copy

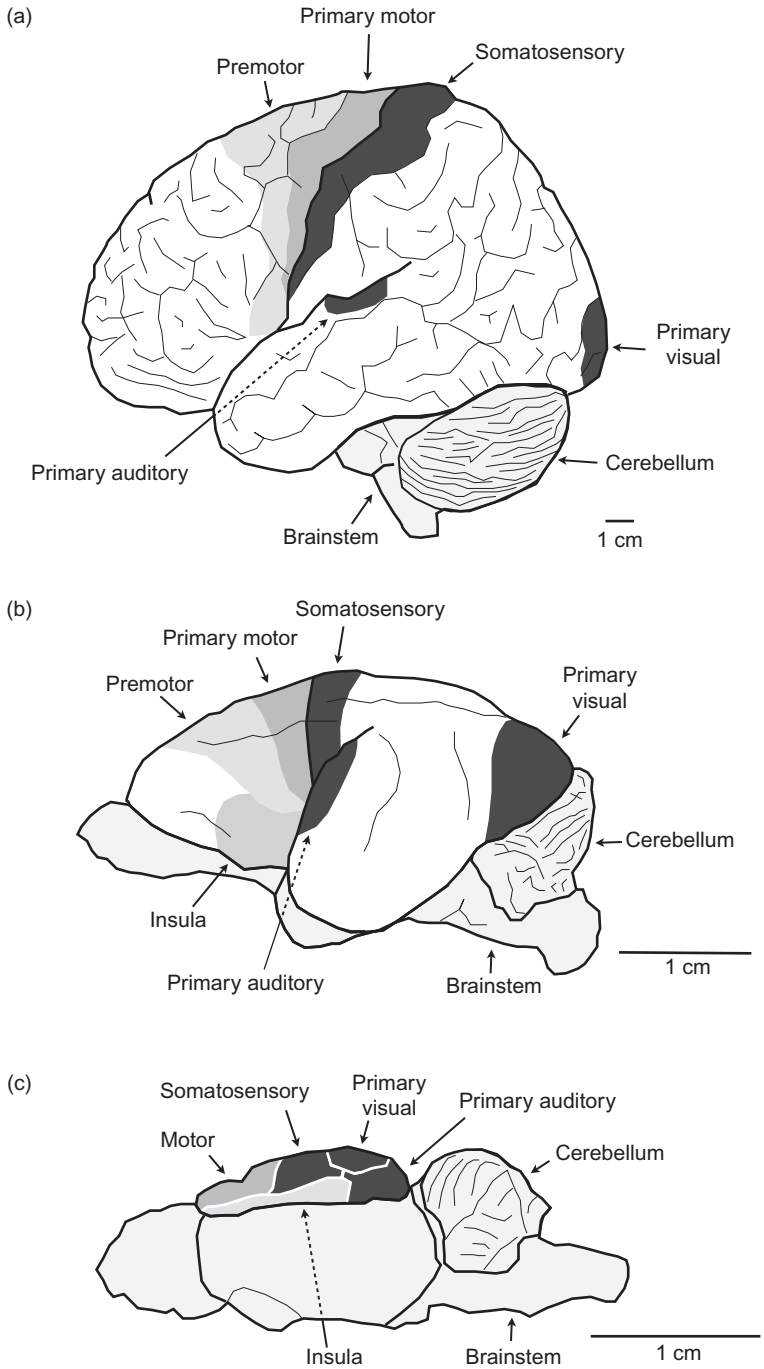


Fig. 2. Size of "association" cortex in mammals of different brain size. Lateral line drawings of the cortex of human (a), galago (prosimian primate) (b), and hedgehog (non-primate mammal) (c). Images are not to scale (note 1cm scale bars for each image;

Author's personal copy

language deficits) 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). It is clear that a simple model of language being processed solely in Broca's and Wernicke's areas is too simplistic (Poeppel and Hickok, 2004), though these areas are clearly relevant.

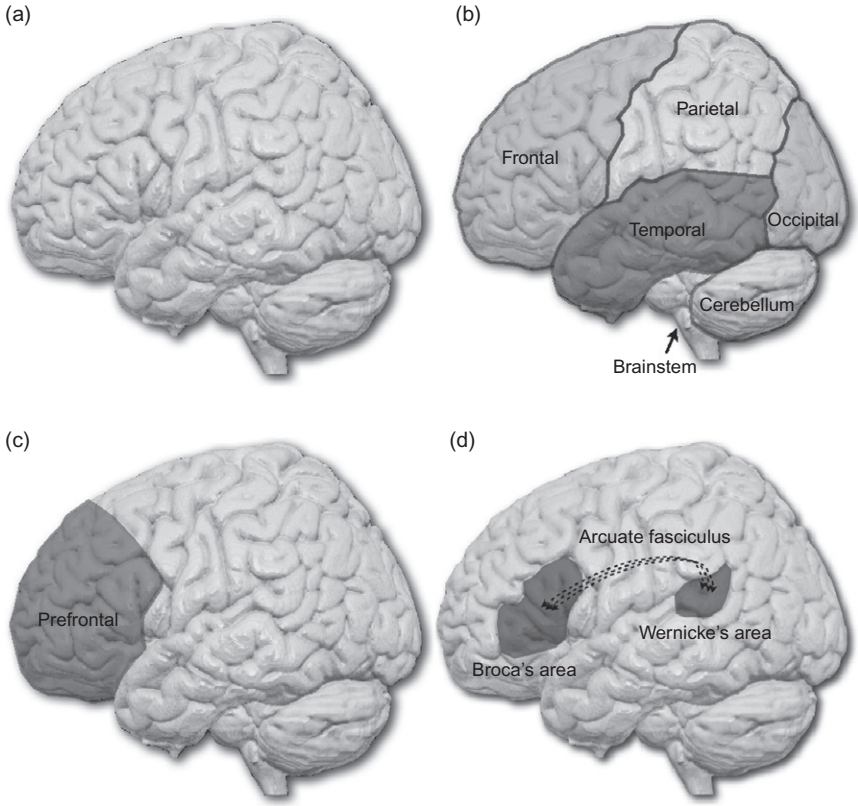


Fig. 3. Major regions of the brain. (a) Lateral view of the brain. (b) Lobes of the cortex, with cerebellum and brainstem indicated. (c) Prefrontal cortex. (d) Classical language areas. The arcuate fasciculus is a connective pathway deep to the cortex. The brain image is a 3D rendering of an average of 27 MRIs of the same individual from Holmes et al. (1998), used with permission.

corresponding volumes: hedgehog: ~3ml, galago: ~10ml, human: ~1350ml). The white regions represent cortical areas that are devoted to processing information *other* than primary sensory or motor (muscle movement) information. They function to integrate information in various interesting ways. Hedgehog brains have essentially no association cortex, whereas human brains have significantly more association cortex than other primates, both absolutely and proportionately. The human insula is not visible on the surface, being buried deep to the Sylvian fissure (which separates the temporal lobe from the frontal and anterior parietal lobes). The human brain was drawn from a 3D rendering of an average of 27 MRIs of the same individual (Holmes et al., 1998, used with permission). Galago and hedgehog brains were drawn from images at http://www.brains.rad.msu.edu, and http://brainmuseum.org, used with permission. Functional areas are mapped following Nieuwenhuys et al. (2008).

Author's personal copy

The evolutionary histories of Broca's and Wernicke's areas are quite intriguing, since homologs to both of these areas have been identified in nonhuman primate brains (Striedter, 2005). These species lack human language capabilities, of course, so these areas must have evolved originally for other purposes. An evolutionary perspective would predict that in nonhuman primates these areas likely process information in ways that would be useful to language (Schoenemann, 2005), with language then naturally making use of them (i.e., language adapting to the human brain: Christiansen and Chater, 2008). The presence of these "language" areas in nonlinguistic animals undermine models that imply the evolution of completely new kinds of circuits (e.g., Bickerton, 1990; Pinker, 1995). Some intriguing findings suggest that these areas do function in primates in ways that would predispose them to human language processing. The homolog of Broca's area in monkeys has been shown to contain neurons that fire both when a monkey performs a specific action as well as when it hears a sound related to that same action ("mirror neurons"; Kohler et al., 2002), which may form the basis for the ability to attach meaning to sounds. Stimulation of the Broca's area homolog in macaque monkeys results in orofacial movements (Petrides et al., 2005), which are foundational to human speech. Hearing species-specific calls has been shown to activate Broca's and Wernicke's areas in monkeys (Gil-da-Costa et al., 2006). In chimpanzees, communicative signaling (begging) has activated the homolog of Broca's area (Taglialatela et al., 2008). Further exploration of the function of these areas in nonhumans will allow a better idea of how and why they became co-opted for human language.

Detailed quantitative data on the size of these areas have been reported only for humans and chimpanzees so far. For the two areas that comprise Broca's area, one study reported that Brodmann area 44 in the left hemisphere is 6.6 times larger and in the right 4.1 times larger in humans as compared to chimpanzees, while Brodmann area 45 was 6.0 times larger on the left and 5.0 times larger on the right (Schenker et al., 2009). For comparison, overall brain size was 3.6 times larger for this sample, thus suggesting that there have been disproportionate increases in Broca's area—particularly, in the left hemisphere—during human evolution. Quantitative comparisons of Wernicke's area have not been reported, though it does appear that it is significantly bigger in both absolute and relative terms in humans as compared to macaque monkeys (Petrides and Pandya, 2002; Striedter, 2005).

Given that Broca's and Wernicke's areas play different but complementary roles in language processing, they must be connected in some way. A tract of nerve fibers known as the arcuate fasciculus (Fig. 3d) directly connects these areas (Geschwind, 1974). It tends to be larger on the left side than the right in humans, consistent with the lateralization of expressive language processing to the left hemisphere for most people (Nucifora et al., 2005). In addition, it appears to have been elaborated in human evolution. The homolog of Wernicke's area in macaque monkeys projects to prefrontal regions that are close to the homolog of Broca's area, but apparently not directly to it (Aboitiz and Garcia, 1997). Instead, projections directly to their homolog of Broca's area originate from a region just adjacent to their homolog of Wernicke's area (Aboitiz and Garcia, 1997). This would suggest that there has been an elaboration and extension of projections to more closely 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 tracts *in vivo*) suggests 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 clear in chimpanzees and humans, and are even more extensive in humans (Rilling et al., 2007). These

Author's personal copy

changes are certainly relevant to language evolution, though knowing whether they evolved specifically *for* language, rather than to support more general cognitive operations involving conceptual understanding, is unknown.

Prefrontal cortex

Areas in the prefrontal cortex (in addition to Broca's area; Fig. 3c) appear to be involved in a variety of linguistic tasks, including various semantic aspects of language (Gabrieli et al., 1998; Kerns et al., 2004; Luke et al., 2002; Maguire and Frith, 2004; Noppeney and Price, 2004; Thompson-Schill et al., 1998), syntax (Indefrey et al., 2004; Novoa and Ardila, 1987), and higher level linguistic processing, such as understanding the reasoning underlying a conversation (Caplan and 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 for the entire prefrontal cortex over what would be predicted for a primate brain as large as ours (Brodmann, 1909; Deacon, 1997). MRI studies generally support these conclusions though some debate remains (reviewed in Schoenemann, 2006; see also Smaers et al., 2011). Using a proxy for prefrontal cortex, we found that connective tracts (white matter areas composed mostly of axons) seem to account for a greater portion of the increase (Schoenemann et al., 2005). This makes sense given that prefrontal areas generally have an oversight role, modifying activity in other posterior areas of the brain.

Because prefrontal areas mediate a number of important behaviors besides language, language evolution may not be the primary driving force behind these changes. A variety of higher-order behavioral abilities that were likely crucial for human evolution are known to be mediated there, including planning, maintaining behavioral goals, processing social information, temporary storage/manipulation of information (working memory), memory for serial order and temporal information, and attention (references in Schoenemann, 2006). Teasing apart the relative contributions of these various behavioral abilities to the evolution of prefrontal areas will likely be very difficult.

The prefrontal cortex itself has many components, not all of which have changed to the same extent. Broca's area has increased disproportionately, particularly on the left side, as discussed above (Schenker et al., 2009). Brodmann area 13, located in the posterior orbitofrontal cortex (posteroinferior frontal cortex, above the eyes), seems to have lagged behind the increase in overall brain size, being only ~1.5 times larger than the average ape (Semendeferi et al., 1998). This area is involved in assessing emotional aspects of social interactions. Given the increasing importance of the social context during human evolution, its increase might seem relatively small (though not trivial). However, its specific relevance to language is unclear, except insofar as it presumably contributes to conceptual understanding of social relationships, which form the basis for caring about communication in the first place (see discussion below about conceptual understanding and language evolution).

Brodmann area 10, by contrast, is ~6.6 times larger than the corresponding areas in pongids (Semendeferi et al., 2001; Chapter 9). This increase is actually close to what one would expect given the peculiar way in which area seems to scale with overall brain size in primates (Holloway, 2002). Nevertheless, because this area is specifically active in linguistic tasks that require selection of appropriate words given a specific semantic context (Gabrieli et al., 1998; Luke et al., 2002), it seems likely its increase is relevant to language evolution.

Concepts and semantic processing

As discussed above, language depends critically on a foundation of conceptual understanding of the world, which in turn appears to depend on a

Author's personal copy

wide network of many different areas of the brain. Humans 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 (Figs. 2a and 3b), where it becomes available to conscious awareness (Bear et al., 2007). From here, visual information is 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 (e.g., shape, color, etc.; Bear et al., 2007). The dorsal stream can therefore be thought of as the "where" pathway, and the ventral stream as the "what" pathway (Bear et al., 2007). These two pathways consequently correspond at least broadly to the networks involved in conceptualizing objects (which get mapped as nouns) versus actions/orientations/directions (which are central to concepts generally mapped as verbs) (cf., Hurford, 2003b).

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 and Damasio, 1992). In a comparative perspective, the human temporal lobe as a whole is 23% larger than predicted given our brain size, or about four times larger in absolute terms (though this is similar to overall brain size difference in this sample; data from Rilling and Seligman, 2002). The human disproportion in the temporal lobe appears to be greatest with respect to white matter axonal tracts, which represent long distance connections with other parts of the brain. This suggests a significant increase in the dense network of interconnectivity underlying conceptual understanding.

Areas involved in auditory processing—the primary auditory cortex of the temporal lobe (Brodmann areas 41 and 42) and immediately adjacent auditory association areas—appear to be slightly larger than predicted based on overall brain size (primary auditory by ~6%, auditory association by ~17%; Deacon, 1997). In absolute terms, these areas would still be more than approximately three to four times larger than the equivalent area in apes, suggesting the increases reflect enhancements with respect to auditory processing.

In addition to areas involved in auditory processing, and conceptual and semantic processing, the temporal lobe also contains the hippocampus (which plays a key role in memory formation) and the amygdala (which is central to marking the emotional valence of events). Both of these structures lie on the medial surface of the temporal lobes (hidden from lateral view). In absolute volume, the hippocampus is about 2.7 times larger in humans compared to chimpanzees (N=1 for each species, however; Stephan et al., 1981). In Stephan et al.'s (1987) data, the human amygdala was 3.7 times larger than their chimpanzee's (also N=1), which may indicate that marking the emotional content and/or importance of events was particularly important.

The planum temporale, located just posterior to the primary auditory cortex, has been well studied comparatively. The planum temporale is larger on the left side in humans (Geschwind and Levitsky, 1968; Sommer et al., 2008), which was assumed to reflect a functional anatomical correlate of language evolution. However, apes show a similar asymmetry in this region (Gannon et al., 1998), suggesting that the lateralized size differences are not language specific. Details of neuronal cell spatial organization have been shown to be asymmetric in the planum temporale of humans but not other primates, however, with the left hemisphere displaying wider minicolumns than the right (Buxhoeveden et al., 2001). The functional significance of this cytoarchitectural asymmetry is unknown, though presumably it

Author's personal copy

has some behavioral relevance. It may be that the planum temporale has a role in auditory information for communication generally (not just for language). If so, it would be yet another example of language co-opting preexisting language-friendly circuits.

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 neuroanatomical studies of the parietal lobe have not been reported, however. The semantic generation of verbs (the actual words themselves) seems to also involve Broca's area (Damasio and Damasio, 1992; Posner and Raichle, 1994) which also appears to have evolved disproportionately (see above).

Right hemisphere

Although the cortical language areas discussed so far are localized to the left hemisphere in most people, the right hemisphere also appears to be involved in language. The right hemisphere understands short words (Gazzaniga, 1970) and also entertains alternative possible meanings for particular words (Beeman and Chiarello, 1998), suggesting it is involved in interpreting multiple intended meanings of a given linguistic communication. The right hemisphere also plays a greater role in spatial processing in most people (Tzeng and Wang, 1984; Vallar, 2007), thus presumably grounding the semantics of spatial terms. The right frontal lobe mediates aspects of prosody (Alexander et al., 1989), which is critically important to understanding intended meaning.

As discussed above, the planum temporale has been shown to be asymmetric in both apes and humans (Gannon et al., 1998), but only humans seem to show differences in neuronal spatial organization, favoring the left (Buxhoeveden et al., 2001). Humans also show asymmetries in Broca's area, again favoring the left (Gannon et al., 1998; Schenker et al., 2009). The left prefrontal overall has been shown to be particularly large relative to the right, in humans compared to other primates (Smaers et al., 2011). Although this appears to be largely predicted by primate scaling trends for these regions, it nevertheless likely has behavioral implications. Curiously, in humans, the whole right hemisphere is actually very slightly *larger* overall than the left ($\leq$1%; Allen et al., 2002). The author is not aware of studies comparing the volumes of entire hemispheres in other primates, however. Given that the right hemisphere is very close to the left in overall size in humans, it has probably increased approximately threefold along with the cortex as a whole. Also, since Broca's area (at least) is larger on the left hemisphere, by definition other areas of the right must therefore be larger than their corresponding areas on the left, given that the right hemisphere is slightly larger as a whole. Certainly, there is nothing to suggest that the right hemisphere has particularly lagged behind the left overall during human evolution, though additional detailed comparative asymmetry studies remain to be done.

Basal ganglia

Although the cortex is heavily involved in language processing, a group of interconnected nuclei deep to the cortex, collectively known as the basal ganglia, appear to play important roles also. They participate in an important circuit loop that functions in the selection and initiation of willed movements generally (Bear et al., 2007). A variety of studies have implicated these circuits not just in language production but also in language comprehension (see references in Hochstadt et al., 2006). Important symptoms of Parkinson's and Huntington's diseases, which affect the basal ganglia in particular, include problems understanding complicated syntax (e.g., center-embedded clauses), as well as processing semantic information (Hochstadt et al., 2006). Broca's aphasia

Author's personal copy

typically requires disruption to areas other than Broca's area, 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. Since humans do not appear to have significantly more sophisticated willed movements than apes (except possibly those related to vocalization and hand manipulation), it seems possible these increases indicate an important role supporting higher cortical functions including language.

Cerebellum

The cerebellum is not only involved in modulating motor signals from the cortex (Bear et al., 2007) but has also been implicated in higher cognitive functions, including goal organization and planning, aspects of memory and learning, attention, visuospatial processing, modulating emotional responses, and language (Baillieux et al., 2008). The cerebellum appears to play a role in speech production and perception, as well as both semantic and grammatical processing (Ackermann et al., 2007; Baillieux et al., 2008; De Smet et al., 2007). The cerebellum also seems to play a role in timing mechanisms generally (Ivry and Spencer, 2004). Given the importance temporal information plays in language production and perception, this may explain why the cerebellum is implicated in studies of language brain function.

The human cerebellum is slightly smaller than one would predict based on brain size (Rilling and Insel, 1998) but is ~2.9 times larger based on body size (the largest increase of all brain regions outside the neocortex). The higher cognitive functions appear to be localized to the lateral hemispheres of the cerebellum (MacLeod et al., 2003), which have undergone a significant increase in relative proportion in both apes and humans. With respect to overall body weight, human lateral cerebellar hemispheres are ~2.9 times larger than predicted (MacLeod et al., 2003) and therefore are not explained by any possible differences in muscle mass. Given its role in language processing, this increase may therefore 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 muscles of the vocal folds, responsible for changing the pitch of the primary vocal signal, are innervated by the nucleus ambiguous. The vocal signal is filtered in various ways by manipulations of the tongue, lower jaw, and lips, thereby producing the sound changes we interpret as speech (Denes and Pinson, 1963). The tongue is innervated by the hypoglossal nucleus and nucleus ambiguous, the lower jaw by the trigeminal nucleus, and the lips by the facial motor nucleus (all in the brain stem). This whole system depends on the maintenance and manipulation of air pressure in the lungs, using the muscles of the chest and abdomen, innervated by anterior horn areas of the spinal cord (Carpenter and Sutin, 1983).

Even though vocal production is clearly important to language, these brainstem nuclei do not appear to be particularly enlarged in humans. The hypoglossal nucleus in humans is large but shows substantial overlap with apes, while 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 originates in the cerebral cortex, intentional speech utilizes direct connections from cortex to the relevant

Author's personal copy

brainstem nuclei. Humans also have two indirect pathways, the first involving connections routed through the reticular formation of the brainstem (for tongue, lower jaw, and lip movement) and the nucleus retroambiguus (for muscles of respiration; Deacon, 1997; Striedter, 2005), and a second through the cingulate gyrus of the limbic system (Jürgens, 1994), which mediates involuntary vocal responses to pain or strong emotions (Deacon, 1997; Striedter, 2005).

Comparative studies show that nonhuman primates have these same indirect pathways, allowing them a variety of emotionally mediated vocalizations, but have only weak direct connections controlling the tongue and respiration muscles, and appear to completely lack direct connections to the larynx (Jurgens, 2002; Jurgens and Alipour, 2002). This suggests that at least some new direct cortical pathways to the brainstem evolved for deliberate conscious vocalization in humans.

Auditory perception

Conscious awareness of sound depends on signals from the cochlea (where sound is translated into neural signals) reaching the primary auditory cortex located in the temporal lobe through a series of intermediate nuclei in the brainstem and midbrain. Comparative data suggest that primates have somewhat smaller intermediate auditory nuclei than expected for their brain weights (though the primate sample was small; Glendenning and Masterton, 1998). Both in absolute terms and in relation to body size, human auditory nuclei appear to be reasonably large, though not dramatically so. Overall, this suggests only modest evolutionary changes in these nuclei.

Conclusion

Our current understanding of brain/language coevolution is based on comparative gross anatomical assessments of differences in parts of the brain that are relevant to language processing. 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, which provided the central usefulness for language, thereby driving its evolution. Specific brain areas relevant to language increased disproportionately: 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, and the arcuate fasciculus connecting them, were not specially evolved for language but do appear to have been elaborated. Other areas that participate in language processing, including the basal ganglia and cerebellum, are larger than predicted based on overall body weight, though they have not increased as much relative to overall brain size. Finally, the auditory processing pathways do not appear to have changed much, though pathways allowing for enhanced conscious control of speech have been either added (to the larynx) or strengthened.

These make excellent starting points for future research, which hopefully will clarify exactly how circuitry in these areas support language and may have been modified by language evolution. A better understanding of the complex interactions between areas will allow us to test some of the more interesting speculative ideas in the literature (e.g., Deacon, 1997). Because language was not the only behavioral change in human evolution, unraveling the interplay between behavioral domains will be critical. Assessing nonlanguage functions of "language" areas will also be crucial. All these findings are consistent with the view that language adapted to the brain more than the reverse (Christiansen and Chater, 2008).

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

Author's personal copy

significant increase in the complexity, subtlety, and range of conceptual understanding that was possible; and third, an increasingly complex, socially interactive existence. 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 world that these brains would then want to communicate (Savage-Rumbaugh and Rumbaugh, 1993; Schoenemann, 2009a,b). This 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.

Acknowledgments

This review has been adapted from Schoenemann (2009a), which grew out of a contribution to the IIAS International Seminar on Language, Evolution, and the Brain held in Kyoto, Japan in April 2007, organized by William Wang and Junjiro Kanamori, as well as from Schoenemann (2009b), which grew out of a workshop on language evolution at the Santa Fe Institute in March 2007, organized by John Holland. I wish to thank Michel Hofman for thoughtful comments and for pointing out errors in an earlier draft. Any errors that remain are of course my own. My thinking on language evolution has benefited from various discussions with William Wang, James Minett, Vince Sarich, Jim Hurford, and Morten Christiansen. The galago and hedgehog brains in Fig. 2a and b were adapted with permission from images at http://www.brains.rad.msu.edu, and http://brainmuseum.org, supported by the US National Science Foundation.

References

Aboitiz, F., & Garcia, V. R. (1997). The evolutionary origin of the language areas in the human brain. A neuroanatomical perspective. *Brain Research. Brain Research Reviews*, *25*(3), 381–396.

Ackermann, H., Mathiak, K., & Riecker, A. (2007). The contribution of the cerebellum to speech production and speech perception: Clinical and functional imaging data. *Cerebellum (London, England)*, *6*(3), 202–213.

Alexander, M. P., Benson, D. F., & Stuss, D. T. (1989). Frontal lobes and language. *Brain and Language*, *37*, 656–691.

Allen, J. S., Damasio, H., & Grabowski, T. J. (2002). Normal neuroanatomical variation in the human brain: An MRI-volumetric study. *American Journal of Physical Anthropology*, *118*, 341–358.

Allman, J., McLaughlin, T., & Hakeem, A. (1993). Brain weight and life-span in primate species. *Proceedings of the National Academy of Sciences of the United States of America*, *90*(1), 118–122.

Baillieux, H., De Smet, H. J., Paquier, P. F., De Deyn, P. P., & Marien, P. (2008). Cerebellar neurocognition: Insights into the bottom of the brain. *Clinical Neurology and Neurosurgery*, *110*(8), 763–773.

Barsalou, L. W. (2008). Grounded cognition. *Annual Review of Psychology*, *59*, 617–645.

Bear, M. F., Connors, B. W., & Paradiso, M. A. (2007). *Neuroscience: Exploring the brain* (3rd ed.). Baltimore; Philadelphia, PA: Lippincott Williams & Wilkins.

Beckner, C., Blythe, R., Bybee, J., Christiansen, M. H., Croft, W., Ellis, N. C., et al. (2009). Language is a complex adaptive system: Position paper. *Language Learning*, *59*(Suppl. 1), 1–26.

Beeman, M. J., & Chiarello, C. (1998). Complementary right- and left-hemisphere language comprehension. *Current Directions in Psychological Science*, *7*(1), 2–8.

Bickerton, D. (1990). *Language and species.* Chicago: University of Chicago Press.

Blinkov, S. M., & Glezer, I. I. (1968). *The human brain in figures and tables (B. Haigh, Trans.).* New York: Plenum Press.

Brodmann, K. (1909). *Vergleichende lokalisationslehre der grosshirnrinde in ihren prinzipien dargestellt auf grund des zellenbaues.* Leipzig: Johann Ambrosius Barth Verlag.

Bruner, E. (2004). Geometric morphometrics and paleoneurology: Brain shape evolution in the genus homo. *Journal of Human Evolution*, *47*, 279–303.

Buxhoeveden, D. P., Switala, A. E., Litaker, M., Roy, E., & Casanova, M. F. (2001). Lateralization of minicolumns in human planum temporale is absent in nonhuman primate cortex. *Brain, Behavior and Evolution*, *57*, 349–358.

Caplan, R., & Dapretto, M. (2001). Making sense during conversation: An fMRI study. *Neuroreport: An International*

Author's personal copy

Journal for the Rapid Communication of Research in Neuroscience, *12*(16), 3625–3632.

Carpenter, M. B., & Sutin, J. (1983). *Human neuroanatomy* (8th ed.). Baltimore, MD: Williams & Wilkins.

Changizi, M. A., & Shimojo, S. (2005). Parcellation and area-area connectivity as a function of neocortex size. *Brain, Behavior and Evolution*, *66*(2), 88–98.

Christiansen, M. H. (1994). *Infinite languages, finite minds: Connectionism, learning and linguistic structure.* Unpublished PhD dissertation, University of Edinburgh, Edinburgh, Scotland.

Christiansen, M. H., & Chater, N. (2008). Language as shaped by the brain. *The Behavioral and Brain Sciences*, *31*, 489–509.

Damasio, A. R., & Damasio, H. (1992). Brain and language. *Scientific American*, *267*(3), 89–95.

Damasio, H., Grabowski, T. J., Damasio, A., Tranel, D., Boles-Ponto, L., Watkins, G. L., et al. (1993). Visual recall with eyes closed and covered activates early visual cortices. *Society for Neuroscience Abstracts*, *19*, 1603.

Darwin, C. (1882). *The descent of man and selection in relation to sex* (2nd ed.). London: John Murray.

De Smet, H. J., Baillieux, H., De Deyn, P. P., Marien, P., & Paquier, P. (2007). The cerebellum and language: The story so far. *Folia Phoniatrica et Logopaedica*, *59*(4), 165–170.

Deacon, T. W. (1992). Brain-language coevolution. In J. A. Hawkins & M. Gell-Mann (Eds.), *The evolution of human languages* (Vol. XI, pp. 49–83). Redwood City, CA: Addison-Wesley.

Deacon, T. W. (1997). *The symbolic species: The co-evolution of language and the brain.* New York: W.W. Norton.

Deaner, R. O., Isler, K., Burkart, J., & van Schaik, C. (2007). Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates. *Brain, Behavior and Evolution*, *70*(2), 115–124.

Denes, P. B., & Pinson, E. N. (1963). *The speech chain.* Garden City, NY: Anchor Press/Doubleday.

Dronkers, N. F. (2000). The pursuit of brain-language relationships. *Brain and Language*, *71*(1), 59–61.

Dunbar, R. I. M. (1995). Neocortex size and group size in primates: A test of the hypothesis. *Journal of Human Evolution*, *28*, 287–296.

Finlay, B. L., Darlington, R. B., & Nicastro, N. (2001). Developmental structure in brain evolution. *The Behavioral and Brain Sciences*, *24*, 263–308.

Gabrieli, J. D., Poldrack, R. A., & Desmond, J. E. (1998). The role of left prefrontal cortex in language and memory. *Proceedings of the National Academy of Sciences of the United States of America*, *95*(3), 906–913.

Gannon, P. J., Holloway, R. L., Broadfield, D. C., & Braun, A. R. (1998). Asymmetry of chimpanzee planum temporale: Humanlike pattern of Wernicke's brain language area homolog. *Science*, *279*(5348), 220–222.

Gazzaniga, M. S. (1970). *The bisected brain.* New York: Appleton-Century-Crofts.

Geschwind, N. (1974). *Selected papers on language and the brain.* Boston: Reidel Publishing Co.

Geschwind, N., & Levitsky, W. (1968). Human brain: Left-right asymmetries in temporal speech region. *Science (New York, NY)*, *161*(837), 186–187.

Gibson, K. R. (2002). Evolution of human intelligence: The roles of brain size and mental construction. *Brain, Behavior and Evolution*, *59*(1–2), 10–20.

Gibson, K. R., Rumbaugh, D., & Beran, M. (2001). Bigger is better: Primate brain size in relationship to cognition. In D. Falk & K. Gibson (Eds.), *Evolutionary anatomy of the primate cerebral cortex* (pp. 79–97). Cambridge: Cambridge University Press.

Gil-da-Costa, R., Martin, A., Lopes, M. A., Munoz, M., Fritz, J. B., & Braun, A. R. (2006). Species-specific calls activate homologs of Broca's and Wernicke's areas in the macaque. *Nature Neuroscience*, *9*(8), 1064–1070.

Glendenning, K. K., & Masterton, R. B. (1998). Comparative morphometry of mammalian central auditory systems: Variation in nuclei and form of the ascending system. *Brain, Behavior and Evolution*, *51*(2), 59–89.

Harvey, P. H., & Clutton-Brock, T. H. (1985). Life history variation in primates. *Evolution*, *39*, 559–581.

Hochstadt, J., Nakano, H., Lieberman, P., & Friedman, J. (2006). The roles of sequencing and verbal working memory in sentence comprehension deficits in Parkinson's disease. *Brain and Language*, *97*(3), 243–257.

Hofman, M. A. (1983). Energy metabolism, brain size, and longevity in mammals. *The Quarterly Review of Biology*, *58*, 495–512.

Hofman, M. A. (1985). Size and shape of the cerebral cortex in mammals. I. The cortical surface. *Brain, Behavior and Evolution*, *27*, 28–40.

Hofman, M. A. (1988). Size and shape of the cerebral cortex in mammals. II. The cortical volume. *Brain, Behavior and Evolution*, *32*, 17–26.

Hofman, M. A. (1993). Encephalization and the evolution of longevity in mammals. *Journal of Evolutionary Biology*, *6*, 209–227.

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

Holloway, R. L. (2002). Brief communication: How much larger is the relative volume of area 10 of the prefrontal cortex in humans? *American Journal of Physical Anthropology*, *118*(4), 399–401.

Holmes, C. J., Hoge, R., Collins, L., Woods, R., Toga, A. W., & Evans, A. C. (1998). Enhancement of mr images using registration for signal averaging. *Journal of Computer Assisted Tomography*, *22*(2), 324–333.

Author's personal copy

Humphrey, N. (1984). The social function of intellect. In *Consciousness regained* (pp. 14–28). Oxford: Oxford University Press.

Hurford, J. R. (2003a). The language mosaic and its evolution. In M. H. Christiansen & S. Kirby (Eds.), *Language evolution* (pp. 38–57). Oxford: Oxford University Press.

Hurford, J. R. (2003b). The neural basis of predicate-argument structure. *The Behavioral and Brain Sciences*, *26*(3), 261–283 discussion 283–316.

Indefrey, P., Hellwig, F., Herzog, H., Seitz, R. J., & Hagoort, P. (2004). Neural responses to the production and comprehension of syntax in identical utterances. *Brain and Language*, *89*(2), 312–319.

Ivry, R. B., & Spencer, R. M. (2004). The neural representation of time. *Current Opinion in Neurobiology*, *14*(2), 225–232.

Jerison, H. J. (1973). *Evolution of the brain and intelligence.* New York: Academic Press.

Jurgens, U. (2002). Neural pathways underlying vocal control. *Neuroscience and Biobehavioral Reviews*, *26*(2), 235–258.

Jürgens, U. (1994). The role of the periaqueductal grey in vocal behaviour. *Behavioural Brain Research*, *62*(2), 107–117.

Jurgens, U., & Alipour, M. (2002). A comparative study on the cortico-hypoglossal connections in primates, using biotin dextranamine. *Neuroscience Letters*, *328*(3), 245–248.

Kerns, J. G., Cohen, J. D., Stenger, V. A., & Carter, C. S. (2004). Prefrontal cortex guides context-appropriate responding during language production. *Neuron*, *43*(2), 283–291.

Kohler, E., Keysers, C., Umilta, M. A., Fogassi, L., Gallese, V., & Rizzolatti, G. (2002). Hearing sounds, understanding actions: Action representation in mirror neurons. *Science*, *297*(5582), 846–848.

Kosslyn, S. M., Alpert, N. M., Thompson, W. L., Maljkovic, V., Weise, S. B., Chabris, C. F., et al. (1993). Visual mental imagery activates topographically organized visual cortex: Pet investigations. *Journal of Cognitive Neuroscience*, *5*, 263–287.

Lieberman, P. (2000). *Human language and our reptilian brain: The subcortical bases of speech, syntax, and thought.* Cambridge, MA: Harvard University Press.

Lieberman, P. (2002). On the nature and evolution of the neural bases of human language. *American Journal of Physical Anthropology*, *45*, 36–62.

Luke, K. K., Liu, H. L., Wai, Y. Y., Wan, Y. L., & Tan, L. H. (2002). Functional anatomy of syntactic and semantic processing in language comprehension. *Human Brain Mapping*, *16*(3), 133–145.

MacLeod, C. E., Zilles, K., Schleicher, A., Rilling, J. K., & Gibson, K. R. (2003). Expansion of the neocerebellum in hominoidea. *Journal of Human Evolution*, *44*(4), 401–429.

Maguire, E. A., & Frith, C. D. (2004). The brain network associated with acquiring semantic knowledge. *NeuroImage*, *22*(1), 171–178.

Martin, R. D. (1981). Relative brain size and basal metabolic rate in terrestrial vertebrates. *Nature*, *293*, 57–60.

Mueller, R.-A. (1996). Innateness, autonomy, universality? Neurobiological approaches to language. *The Behavioral and Brain Sciences*, *19*(4), 611–675.

Nieuwenhuys, R., Voogd, J., & van Huijzen, C. (2008). *The human central nervous system* (4th ed.). Berlin: Springer-Verlag.

Noppeney, U., & Price, C. J. (2004). Retrieval of abstract semantics. *NeuroImage*, *22*, 164–170.

Northcutt, R. G., & Kaas, J. H. (1995). The emergence and evolution of mammalian neocortex. *Trends in Neurosciences*, *18*(9), 373–379.

Novoa, O. P., & Ardila, A. (1987). Linguistic abilities in patients with prefrontal damage. *Brain and Language*, *30*, 206–225.

Nucifora, P. G., Verma, R., Melhem, E. R., Gur, R. E., & Gur, R. C. (2005). Leftward asymmetry in relative fiber density of the arcuate fasciculus. *Neuroreport*, *16*(8), 791–794.

Petrides, M., Cadoret, G., & Mackey, S. (2005). Orofacial somatomotor responses in the macaque monkey homologue of Broca's area. *Nature*, *435*(7046), 1235–1238.

Petrides, M., & Pandya, D. N. (2002). Comparative cytoarchitectonic analysis of the human and the macaque ventrolateral prefrontal cortex and corticocortical connection patterns in the monkey. *The European Journal of Neuroscience*, *16*(2), 291–310.

Pinker, S. (1995). Facts about human language relevant to its evolution. In J.-P. Changeux & J. Chavaillon (Eds.), *Origins of the human brain* (pp. 262–283). Oxford: Clarendon.

Poeppel, D., & Hickok, G. (2004). Towards a new functional anatomy of language. *Cognition*, *92*(1–2), 1–12.

Posner, M. I., & Raichle, M. E. (1994). *Images of mind.* New York: W.H. Freeman.

Reader, S. M., & Laland, K. N. (2002). Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences of the United States of America*, *99*(7), 4436–4441.

Rilling, J. K., Glasser, M. F., Preuss, T. M., Ma, X., Zhang, X., Zhao, T., et al. (2007). A comparative diffusion tensor imaging (DTI) study of the arcuate fasciculus language pathway in humans, chimpanzees and rhesus macaques. *American Journal of Physical Anthropology*, *132*(S44), 199–200.

Rilling, J. K., & Insel, T. R. (1998). Evolution of the cerebellum in primates: Differences in relative volume among monkeys, apes and humans. *Brain, Behavior and Evolution*, *52*(6), 308–314.

Rilling, J. K., & Seligman, R. A. (2002). A quantitative morphometric comparative analysis of the primate temporal lobe. *Journal of Human Evolution*, *42*(5), 505–533.

Author's personal copy

Ringo, J. L. (1991). Neuronal interconnection as a function of brain size. *Brain, Behavior and Evolution*, *38*, 1–6.

Savage-Rumbaugh, E. S., & Rumbaugh, D. M. (1993). The emergence of language. In K. R. Gibson & T. Ingold (Eds.), *Tools, language and cognition in human evolution* (pp. 86–108). Cambridge: Cambridge University Press.

Schenker, N. M., Hopkins, W. D., Spocter, M. A., Garrison, A. R., Stimpson, C. D., Erwin, J. M., et al. (2009). Broca's area homologue in chimpanzees (Pan troglodytes): Probabilistic mapping, asymmetry, and comparison to humans. *Cerebral Cortex*, *20*(3), 730–742.

Schoenemann, P. T. (1997). *An MRI study of the relationship between human neuroanatomy and behavioral ability.* Unpublished dissertation, University of California, Berkeley, Berkeley.

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

Schoenemann, P. T. (2005). Conceptual complexity and the brain: Understanding language origins. In W. S.-Y. Wang & J. W. Minett (Eds.), *Language acquisition, change and emergence: Essays in evolutionary linguistics* (pp. 47–94). Hong Kong: City University of Hong Kong Press.

Schoenemann, P. T. (2006). Evolution of the size and functional areas of the human brain. *Annual Review of Anthropology*, *35*, 379–406.

Schoenemann, P. T. (2009a). Brain evolution relevant to language. In J. Minett & W. S.-Y. Wang (Eds.), *Language, evolution, and the brain*. Hong Kong: City University of Hong Kong Press.

Schoenemann, P. T. (2009b). Evolution of brain and language. *Language Learning*, *59*(Suppl. 1), 162–186.

Schoenemann, P. T. (2010). The meaning of brain size: The evolution of conceptual complexity. In *Human brain evolving: Papers in honor of Ralph Holloway.* Bloomington, Indiana: Stone Age Institute Press.

Schoenemann, P. T., Sheehan, M. J., & Glotzer, L. D. (2005). Prefrontal white matter volume is disproportionately larger in humans than in other primates. *Nature Neuroscience*, *8*(2), 242–252.

Semendeferi, K., Armstrong, E., Schleicher, A., Zilles, K., & Van Hoesen, G. W. (1998). Limbic frontal cortex in hominoids: A comparative study of area 13. *American Journal of Physical Anthropology*, *106*(2), 129–155.

Semendeferi, K., Armstrong, E., Schleicher, A., Zilles, K., & Van Hoesen, G. W. (2001). Prefrontal cortex in humans and apes: A comparative study of area 10. *American Journal of Physical Anthropology*, *114*(3), 224–241.

Sherwood, C. C., Hof, P. R., Holloway, R. L., Semendeferi, K., Gannon, P. J., Frahm, H. D., et al. (2005). Evolution of the brainstem orofacial motor system in primates: A comparative study of trigeminal, facial, and hypoglossal nuclei. *Journal of Human Evolution*, *48*(1), 45–84.

Smaers, J. B., Steele, J., Case, C. R., Cowper, A., Amunts, K., & Zilles, K. (2011). Primate prefrontal cortex evolution: Human brains are the extreme of a lateralized ape trend. *Brain, Behavior and Evolution*, *77*, 67–78.

Sommer, I. E., Aleman, A., Somers, M., Boks, M. P., & Kahn, R. S. (2008). Sex differences in handedness, asymmetry of the planum temporale and functional language lateralization. *Brain Research*, *1206*, 76–88.

Stephan, H., Frahm, H., & Baron, G. (1981). New and revised data on volumes of brain structures in insectivores and primates. *Folia Primatologica*, *35*, 1–29.

Stephan, H., Frahm, H. D., & Baron, G. (1987). Comparison of brain structure volumes in insectivora and primates. VII. Amygdaloid components. *Journal für Hirnforschung*, *28*(5), 571–584.

Striedter, G. F. (2005). *Principles of brain evolution.* Sunderland, MA: Sinauer Associates.

Taglialatela, J. P., Russell, J. L., Schaeffer, J. A., & Hopkins, W. D. (2008). Communicative signaling activates 'Broca's' homolog in chimpanzees. *Current Biology*, *18*(5), 343–348.

Thompson-Schill, S. L., Swick, D., Farah, M. J., D'Esposito, M., Kan, I. P., & Knight, R. T. (1998). Verb generation in patients with focal frontal lesions: A neuropsychological test of neuroimaging findings. *Proceedings of the National Academy of Sciences of the United States of America*, *95*(26), 15855–15860.

Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. In J. H. Barkow, L. Cosmides & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 19–136). New York: Oxford University Press.

Tzeng, O. J. L., & Wang, W. S.-Y. (1984). Search for a common neurocognitive mechanism for language and movements. *American Journal of Physiology. Regulatory, Integrative and Comparative Physiology*, *246*(15), R904–R911.

Vallar, G. (2007). Spatial neglect, Balint-Homes' and Gerstmann's syndrome, and other spatial disorders. *CNS Spectrums*, *12*(7), 527–536.

White, J. G., Southgate, E., Thomson, J. N., & Brenner, S. (1986). The structure of the nervous system of the nematode Caenorhabditis elegans. *Philosophical Transactions of the Royal Society of London B, Biological Sciences*, *314*(1165), 1–340.