BRAIN EVOLUTION AND NEUROLINGUISTIC PRECONDITIONS

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Wendy K. Wilkins
Department of English
Arizona State University
Tempe, AZ 85287-0302
atwkw@asuacad.bitnet

Jennie Wakefield
Department of Speech and Hearing
Arizona State University
Tempe, AZ 85287-1908

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Abstract

This target article presents a plausible evolutionary scenario for the emergence of the neural preconditions for language in the hominid lineage. In pleistocene primate lineages there was a paired evolutionary expansion of frontal and parietal neocortex (through certain welldocumented adaptive changes associated with manipulative behaviors) resulting, in ancestral hominids, in an incipient Broca's region and in a configurationally unique junction of the parietal, occipital, and temporal lobes of the brain (the POT). On our view, the development of the POT in our ancestors resulted in the neuroanatomical substrate consistent with the ability for representations in modality-neutral association cortex and, as a result of structure-imposing interaction with Broca's area, the hierarchically structured "conceptual structure." Evidence from paleoneurology and comparative primate neuroanatomy is used to argue that Homo habilis (2.5-2 million years ago) was the first hominid to have the appropriate gross neuroanatomical

configuration to support conceptual structure. We thus suggest that the neural preconditions for language are met in H. habilis. Finally, we advocate a theory of language acquisition that uses conceptual structure as input to the learning procedures, thus bridging the gap between it and language.

1. Introduction

It is common among linguists to assume that language is a species-specific, biologically determined characteristic of humans. Most are comfortable with the claim that certain areas of the human brain are devoted to the various language-related tasks. In spite of this acceptance of the biological basis of language, it is rare for cognitive scientists to address the question of its evolutionary emergence. Given the evidence that language is a species-specific characteristic, it would seem natural to ask how that characteristic arose in the species. But for contemporary linguistics and cognitive science this would appear to be a distinctly unnatural question, at least judging =66rom the paucity of attention paid to the matter. Most researchers currently working on language have preferred to avoid the issue of its possible evolutionary origins, at least in public fora. The reasons for avoiding the issue are many, some the result of historical precedent, others because of the inherent difficulty in studying the evolutionary emergence of any cognitive capacity.

It is our purpose with this article, through the suggestion of a plausible evolutionary scenario, to spark more interest among linguists and other cognitive scientists in the question of the emergence of language in the human species. While admittedly not conclusive, what follows will suggest directions for discussion, weaving together threads provided by paleoneurology, comparative neuroanatomy, and evolutionary theory, as well as linguistic theory. The origins and evolution of language capacity can and should be discussed scientifically and, further, should become an area of serious investigation within the field of cognitive neuroscience. We have for too long considered the origin of the linguistic capacity a mystery; it is time to treat it as a problem amenable to serious intellectual inquiry.

In speculations on possible evolutionary precursors to language, the issue necessarily arises as to the nature or usefulness of a partially evolved linguistic system.

Ancestral cognitive capacities can only be inferred from physical evidence, and written evidence of language is too recent historically to be of evolutionary value. Linguists have generally assumed (at least implicitly) that either a system is a language or it is not, and have largely avoided speculation on the nature of a partially-evolved linguistic capacity.

Despite the lack of evidence for intermediate stages in linguistic evolution, the alternatives are hard to accept. If some species-specific characteristic did not evolve in

piecemeal fashion, then there would seem to be only two ways to explain its appearance. Either it was put in place by some still- undiscovered force, perhaps through divine intervention, or it was the result of some relatively abrupt change in the development of the species, perhaps some sort of spontaneous and widespread mutation. For very different reasons, either of these alternatives is hard to accept. Most linguists prefer to address language from a scientific rather than theological perspective, and would not invoke unexplainable forces to account for the emergence of language. A few might find the mutation suggestion feasible, but the fortuitous nature of such a happenstance mutation makes that explanation seem suspect. As has been pointed out (Pinker and Bloom, 1990), the chances against a mutation resulting in a system as complex and apparently so ideally suited to its task as is language are staggeringly high.

Our approach to the emergence of linguistic capacity is based on two important tenets. First, as noted above, it would seem hard to accept either that language evolved gradually or that it emerged abruptly, fully developed. On the theory being presented here, we argue that the gradualist/abruptist issue is, in fact, a non-issue; the apparent conundrum can be resolved by reference to the biological basis of language, separating the question of the evolution of the primate brain from the question of the evolution of human language. The appropriate brain structures evolved gradually, under pressures of natural

selection, by the mechanisms typically subsumed under Darwinian theory. Language was made possible, however, only at the moment that the brain achieved the appropriate internal configuration. We suggest that the most convincing evidence points to a "moment" approximately 2 million years ago at which time Homo habilis appeared in the fossil record.

Second, we take very seriously the distinction between language (as a formal grammatical system), on the one hand, and communicative abilities and devices, on the other. It is important to our argument that the ability to communicate be treated separately from the possession of a language faculty and, further, that linguistic ability be distinguished from any other (modular) cognitive capacity. We do not argue that the ability to communicate arose with Homo habilis, but rather that the basic neurolinguistic capacity for language acquisition did. Additionally, we clearly distinguish linguistic competence from speech. Other researchers who have recently turned their attention to questions of evolution do not necessarily distinguish between language and communication, and further, often take evidence of vocal speech to be the primary indicator of language (several articles in Wind et al., 1992, are typical in this regard, e.g. Wind; Braitenberg and Sch=81z; Falk; Newman; Laitman, Reidenberg, and Gannon; Lieberman). Even linguists who otherwise might embrace a formalist approach to language, when they turn to questions of evolution, motivate a history of

linguistic development largely from arguments regarding pressures for an enhanced communicative repertoire (see, for example, Lamendella, 1976; Lieberman, 1984, 1985, 1989; Brandon and Hornstein, 1986; Hurford, 1989; Pinker and Bloom, 1990). We dissociate the emergence of linguistic capacity from the evolution of communicative abilities.

Finally, we comment on the relationship between the emergence of language in the species and the acquisition of language by the individual human language-learner. We suggest that, given the appropriate neural foundations, the situations for the early Pleistocene H. habilis child and the 20th century child faced with the task of language acquisition are not wholly dissimilar; the most substantial difference is in the nature of the input to the learner. Certain illuminating parallels might be drawn in this regard, in fact, between the degraded input to the modern-day deaf child raised in an oralist environment and that available to the first generation of language-capable humans. 2. Adaptation and evolutionary reappropriation

When we think of evolution, what comes to mind most readily is some version of gradual adaptation shaped by forces of natural selection, i.e. that process whereby those individuals of a species that have certain (genetically transmittable) traits that make them better able to respond to environmental pressures survive and reproduce in greater numbers. Eventually the naturally

selected trait becomes characteristic of the species, appearing predictably in later generations. By adaptation through the mechanism of natural selection, species become more suited to their environment and prosper.

It might seem obvious, when we think of modern humans, that language is an adaptive trait, one that makes us more able to survive in our environment. It would then seem equally obvious that, ceteris paribus, survival would be enhanced by linguistic capacity (see especially Pinker and Bloom, 1990). But direct selection for an adaptive capacity is not the only evolutionary process conducive to the emergence of structural or behavioral innovation; a structure may arise through adaptively selective mechanisms and, by its conformation alone, be neutrally preadaptive (Darwin, 1871) or exploitable for some function independent of the original function. It may, in fact, produce a new capacity not already in the repertoire of the organism. This manner of exploitation converts the raw material provided by adaptation (or by the laws of growth and form) to a function which may itself prove beneficial to the organism or taxon. Darwin's term for this is preadaptation. Because this term has developed an unintended, premeditative connotation, we wish to avoid it and instead will refer to this phenomenon as evolutionary reappropriation. By the term "reappropriation", we mean specifically to highlight the means by which a structure or function in the repertoire of a species reaches an evolutionary state that is compatible with, and facilitates,

a new function. This new function may or may not be behaviorally related to the original. The secondary function via its underlying structure may itself then be operated upon, and refined, by natural selection and, additionally, may "set in motion selection for changes in other structures" (Futuyma, 1986, p. 424). It is precisely this sort of preadaptationist view that Darwin favored with respect to the origins of higher cognitive capacities in human evolution (Sober, 1984,p. 24; cf. Darwin, 1871).

The neuroanatomical structures that underlie linguistic ability, we will argue, arose in human taxa as a direct result of evolutionary reappropriation (also see Calvin, 1992). They evolved to the state at which they were available for incipient linguistic capacity to emerge by gradual, adaptive changes in brain organization that were the result, in the hominid line, of natural selection for other behaviors that require specific, highly sophisticated neural processing mechanisms. These neuroanatomical structures were not, however, adaptations originally serving communicative functions. Our investigation of the origins of language concerns itself specifically with the reappropriative basis of these structures rather than subsequent adaptive mechanisms that may have shaped language as a communicative device.

In order to argue for our interpretation of the available data relevant to neurolinguistic capacity, we must explicate exactly which aspects of brain structure were available, compatible, and, ultimately, reappropriated. We will not be suggesting that linguistic progenitors used those structures relevant to communication; language is unlikely to have evolved directly from communicationbased precursors, nor is it likely to have been based on those structures that subserve communication. A communication-based account can parsimoniously motivate neither the precise neural character nor the apparent localization of human language cortex. Rather, as we will show in detail, language came to utilize the processing strategies available from newly evolving premotor cortex paired with those aspects of neural organization that allow for amodal concept formation and yield structured abstract representations. These aspects of neural organization arose as byproducts of the evolution of the brain with respect to the regulation of repatterned motor programs dedicated to the novel manual manipulative abilities and requisite feedback circuits associated with eye-hand coordination accompanying the hominid shift to bipedal locomotion.

Lieberman (1984, 1985, 1989, 1992) also presents a reappropriationist account of language origins (although, of course, he did not use our term). He suggests that the neural tissue that was preadaptive for syntax and phonology emerged as a response to selective pressures for motor control of the articulators for speech. While we are sympathetic to such a preadaptationist position with respect to the evolutionary biology of language origins, our interpretation of the anthropological data differs

radically from Lieberman's. No aspect of our account is motivated by selective pressures for articulatory processes or improved "speech" capacity. In fact, as will become clear in the sections that follow, we place the reappropriation "incident" leading to linguistic capacity as long as 2 million years before the development of a modern vocal articulatory system. 3. Basic neuroanatomy

Before turning to the particulars of the evolution of the neuroanatomical structures that we wish to highlight, we review our basic assumptions about the neuroanatomy of language. It is now generally accepted that a portion of the posterior aspect of the third frontal convolution (Broca's area) and the region including the posterior aspect of the superior temporal gyrus (Wernicke's area) of the left cerebral hemisphere (for nearly all right-handed, and most left-handed individuals) are the two brain regions most closely associated with linguistic ability. A lateral view of the left hemisphere, with the language-relevant structures represented, is given in Figure 1a.

Insert Figure 1 about here

Of particular significance for our thesis is the region known as the parieto-occipito-temporal cortex (see Sanides, 1975). This region includes, in humans, that portion of the brain referred to as Wernicke's area. Geschwind, in his well- known 1965 paper that became an early standard for neurolinguists (Disconnexion

syndromes in animals and man), outlined the probable significance of this general area (especially the inferior parietal lobule) for language processing. This emphasis on the traditionally recognized "language areas" is not meant to underestimate the involvement of other brain regions in language. The claim is not that language relies exclusively on these areas, rather it is a more modest one: that these areas are necessarily, but not exclusively, involved in language.

Figure 2 shows the primary sensory and motor areas of the cortex. As can be seen, these primary areas tend to lie along major sulci. As a general rule, the major fissures and sulci approximate the boundaries between zones that are characterized by distinct cell size, shape, density, and laminar organization. In other words, they delineate discrete cytoarchitectonic areas or signal the boundaries between adjacent architectonic fields (see for example Sanides, 1975; Welker, 1990). The cytoarchitectonic areas thus defined tend to be functionally as well as morphologically discrete. (See Wakefield, 1993; we return to this important point below.)

Insert Figure 2 about here

As can be seen in Figure 2, there is close proximity of secondary (terminal) association areas for visual, auditory, and somatosensory information at the periphery of the parieto- occipito-temporal junction (POT). The POT itself receives elaborately processed uni- and bi-modal input

from these association cortices and maintains a high degree of internal connectivity. The POT is, in essence, an area of integration for the three neocortical sensory association areas (Pandya and Yeterian, 1985). Incoming information is extensively, locally integrated and outgoing pathways are extremely selective with respect to the parts of the brain to which they project. What we designate as the POT has been referred to as the "association area of association areas" (Geschwind's 1965 term).

Broca's area, in the posterior portion of the third frontal convolution, lies anteriorly adjacent to motor association cortex. As the ample literature on Broca's aphasia indicates, there is no consensus on the role this area plays in linguistic processing. We will present evidence in subsequent sections, however, that like the POT, neither the location nor the functional properties of Broca's area are in any sense fortuitous. Specifically, this region will be shown to have inherited its functional organization from the motor association cortex from which it evolutionarily derives. In an abstract sense (i.e., non-language-specific), the specialization of this region is temporal sequencing (Tallal and Schwartz, 1980) and the hierarchical organization of information (Greenfield, 1992). Highly structured, multi-sensory, neocortical information, uniquely integrated via a POT-generated processing format feeds directly (and reciprocally) to Broca's area via the major fiber tract (fasciculus) connecting the frontal and parietal cortices (see Figure 1b). We suggest that

once this anatomical feedback system emerges through the appropriately adaptive evolutionary mechanisms (which, we argue, have little if any relation to languagespecific selection), so too do the appropriable foundations of linguistic capacity. We elaborate this issue in our discussion of primate brain evolution. 4. Brain evolution in the primates

4.1. Historical reconstruction

With this summary material in mind, we can turn particular attention to underlying organizational changes in the brain during the course of primate evolution that resulted in the two major neural organizational patterns, pongid and hominid, that we will emphasize. As will become clear, this dichotomy will be based on distinctive positioning of major sulcal divisions.

As in the reconstruction of evolutionary trends more generally, there are two avenues of approach to the reconstruction of primate brain evolution. The first is direct and involves the examination of fossil skulls and the use of these skullcases as molds for latex models, or endocasts, of the brains they once contained.

Occasionally, natural endocasts appear in the fossil record as well, formed by geological processes.

The most basic analysis possible given such materials is one of overall size. Brain size, both absolute and relative to the size of the body, increased over the course of primate evolution, especially in the area of the cerebral cortex.

Not only has the brain changed in size during the course of evolution, it has also undergone, more importantly, changes in organization. Evidence for changes in organization comes from the examination of endocasts; the brain leaves positive impressions of major sulci on the interior surface of the skull and the sulcal pattern is reproduced on the endocasts (Radinsky, 1968). Shifts in placement of sulci throughout brain evolution reflect shifts in underlying neural organization. There is, however, an extreme paucity of appropriate material. Presently there are only some 40 to 50 endocasts of fossil hominids available for study, and most of these are incomplete (Holloway, 1983a). The matter is further complicated by the fact that there is much debate over the correct interpretation of the endocasts. We return to this matter directly.

The claim that organization can be inferred from sulcal pattern is admittedly controversial. We adopt this view, however, because the brain can be expected, in a mechanical sense, to adhere to the same principles of deformation as other solid objects under the laws of physics. In brief summary, we suggest that the enlarging brain deforms in exactly those locations where fields of distinct cytoarchitectonic structure and organization come into close proximity. The boundaries between distinct architectonic fields function as microstructural

"discontinuities" which, under conditions of mechanical stress, facilitate the initiation and govern the placement of failure, or folding, in the brain.

4.2. The mechanics of deformation

The deformational behavior of any solid, including the brain we would suggest, is determined by its mechanical attributes which, in turn, are determined in large part by the microstructural properties of the material (e.g., strength of atomic bonds, packing order of molecules and/or larger constituents). It is a general property of deformable solids that imperfections in microstructure reduce a body's resistance to deformation (Roorda, 1969; Dekkers and Heikens, 1986). Under conditions of mechanical stress, the external force applied to a structure is propagated through the material by way of interatomic force fields. In a homogeneous structure, the applied stress is uniformly distributed throughout the material. In heterogeneous materials, however, avenues of stress propagation are disrupted when microstructural imperfections or discontinuities are encountered (just as light "bends", for example, at junctions of differing optical properties in the media through which it is travelling). The net effect of propagation disruption is the concentration of stress at the site of the discontinuity (Roorda, 1969; Smith and Sidebottom, 1969; Rice, 1976; Dekkers and Heikens, 1986). The phenomenon of stress concentration is directly relevant to the phenomenon of folding, for it is at the sites of highest stress that localized deformation is

initiated (Nadia, 1950; Means, 1976; Rice, 1976; Jaroszewski, 1984; Dekkers and Heikens, 1986).

These principles, as noted, are applicable to any solid that undergoes deformation in response to conditions of stress and are therefore applicable as well to the surface of the brain as it undergoes the mechanical stresses associated with growth and development. The architectonic areas into which the neocortex is divided are identified by regional differences in the numbers, kinds, and arrangements of neurons, neuron processes (axons and dendrites), glial cells, and myelination patterns throughout the neocortical layers. As in experimental situations (e.g. Dekkers and Heikens, 1986), the neural boundaries between architectonic areas appear to function as stress concentrators as a result of the abrupt change in microstructure, therefore of mechanical properties. Deformational energy is particularly concentrated at architectonic boundaries that separate regions of highly disparate cell organization. From a mechanical perspective, the sites expected to deform most consistently across a species' brain would be those associated with the most pronounced architectonic transitions, or boundaries. The relatively uniform placement of the major, or primary, sulci within species appears to conform to this prediction (see Welker, 1990).

The pattern of such primary sulci may be used in the identification of a species. Importantly, these patterns (reconstructed in endocast form) are the only biophysical

evidence available regarding brain organization in the fossil record. Based on mechanical principles, systematic shifts in the placement of primary sulci during primate evolution may be considered evidence of systematic shifts in underlying architectonic boundary conditions.

4.3. Comparative primate neuroanatomy

The second, indirect method for studying brain evolution is through comparative primate neuroanatomy. Brains from extant primates can be examined at the macro- and microscopic levels in order to resolve questions of structural and functional relationships. In the case of evolutionary reconstruction, given known phylogenetic relationships and structural similarities between groups of living and extinct primates, the results of such studies can be used to supplement fossil evidence.

The paleoneurological evidence with which we are primarily concerned is that dated between approximately 4 million and one hundred thousand years before the present, for at some point during this period the first hominid with a brain suitable for the acquisition of language emerged. For the purposes of determining the origins of human language then, two questions become central: Which of the fossil hominid species was the first to exhibit the appropriate neural configuration? From what specific evidence might the identification of this configuration be reliably inferred? Before proceeding to a discussion of the relevant fossil documentation, we pause

here to examine these questions themselves in detail.

With respect to the first issue, we note that the brains of the extant hominoidea approximate one of two fundamental neural configurations: the pongid configuration, expressed in the brains of the great apes, or the hominid configuration, expressed in the human brain. We cannot assume that the first hominids, the australopithecines, identified as such primarily on the basis of post-cranial material (i.e., body parts inferior to the head), necessarily possessed a hominid brain morphology. It is well established that evolutionary mechanisms rarely effect all subsystems of the organism at the same rate and/or intensity. More often a mosaic pattern predominates in which a particular portion of organismal subsystems may undergo significant evolutionary modification while another portion may experience relative stasis. Certain of the early hominid morphological characteristics, for example those associated with bipedal locomotion, may have conformed to general hominid criteria prior to the time at which the brain did so. Therefore we must ask whether the transition from a pongid to a hominid neural configuration occurred simultaneously with the transition from pongid to hominid post-cranial morphology or whether the fundamental changes in brain organization occurred during a later transition between descendent species within the hominid group. The answer to this question must be sought through the lines of evidence germane to the second

issue, that of inference of form =66rom fossil evidence. In order to introduce the relevant lines of evidence, we refer again to the fundamental dichotomy in primate brain organization.

4.3.1. Posterior configuration

The pongid pattern can be illustrated by the brain of the common chimpanzee, as shown in Figure 3a. Of particular relevance in characterizing the pongid pattern is the prominent position of the lunate sulcus; in the pongid brain, the lunate provides an overt anatomical marker of the parietal/occipital boundary. This marker allows us, on gross inspection, to estimate the relative extent of posterior tissue types, or the amount (simplistically speaking) of parietal cortex relative to occipital cortex. Portions of the brain, like portions of the total organism, may undergo a mosaic pattern of evolutionary modification which serves to shift interneural component ratios; ultimately, such shifts define the fundamental organization and processing strategy characteristic of each species. For the purposes of this discussion, we take the distinct position of the lunate sulcus in the chimpanzee (and in the gorilla and orangutan) to be a primary indicator of a typically pongid posterior neural organization.

Insert Figure 3 about here

The hominid sulcal pattern, as illustrated in Figure 3b, is

distinctly different. It has been well established that throughout human evolution there has been a marked expansion of association cortices relative to other parts of the brain. The extensive parietal expansion, in particular, has induced a downward rotation of lateral cortex, effectively "pushing" the lunate sulcus to an inferiormedial position. This parietal expansion, in the absence of concurrent occipital expansion, has also shifted the lunate to a position significantly more posterior than the position in which it is found in the pongid condition (see Figure 4). As a consequence, we find that most human cerebral hemispheres do not show gross morphological evidence of a lunate sulcus on the lateral surface, the position reproducible on endocasts. In those human hemispheres that do show lateral evidence of the lunate, the relative position of the sulcus is well back of the pongid position. In general, the hominid pattern of posterior organization is characterized by the absence of an observable lunate sulcus.

Insert Figure 4 about here

With the marked expansion of parietal cortex, coupled with continued expansion of the posterior temporal lobe initiated in earlier stages of primate brain evolution, neural topography becomes consistent with the expression of a region of confluence of the parietal, occipital, and temporal association cortices in the area we have referred to as the POT. The pongid brain, lacking sufficient parietal expansion (as signalled by the prominence of a lunate

sulcus that has not migrated toward the inferior medial aspect of the cerebral hemisphere) is not topographically consistent with a posterior organization inclusive of a POT. We suggest that this difference is directly relevant to the manifestation of behavioral distinctions, particularly those associated with language, that differentiate apes and humans, an important matter to which we turn shortly.

While our focus here has been on neural organization at the gross anatomical level, any evolutionary reorganizational processes that are involved in the conversion of a basic pongid neural structure to a basic hominid neural structure must ultimately take place at the level of cell-cell interactions (see, e.g., Holloway, 1983b, p. 111). At this fundamental level of inquiry, necessarily inferential due to lack of appropriate fossilized material, we must provide principled argument. In order to do so, we must examine in finer detail certain properties of neural organization requisite to language and the neuroevolutionary mechanisms by which these properties may be established.

Geschwind (1964 and elsewhere) has suggested that a fundamental component of linguistic capacity is the ability to "name", to associate a symbol with an object or action. Importantly, the symbol need not be produced through the same perceptual system that perceives the named object (or action). For example, auditorily perceived acoustic signals represent objects identifiable by visual means. Geschwind states, therefore, that this ability to

name is dependent on the ability to form cross-modal associations between (at least) two modalities.

While the situation is neither as simple nor as straightforward as Geschwind claimed in this early work, his suggestions do lead to certain important insights. It is true that in humans, the association cortices of vision, taction, and somesthesis converge in pairs before final transfer to the POT. That is, the primary input to the POT derives from three multi- modal sources: auditory-visual convergence, auditory-somesthetic convergence, and visual-somesthetic convergence. By the time sensory information is transferred to the POT, it has already undergone higher order processing and relinquished its uni-modal character; POT representation of sensory input is therefore entirely modality-non-specific, or modality-free (see Pandya and Yeterian, 1985).

As neocortex has evolved, so too has the extent to which neocortical neurons are locally, or internally, connected. This is apparent in the patterns of cytoarchitecture revealed through the comparative study of posterior primate association cortex. In the monkey, for example, there exists a tri-modal junction at which information from all three neocortical sensory modalities converges; the information that converges there is not, however, multi-modally integrated and can, in one processing step, be traced to its modality of origin (Pandya and Yeterian, 1985). Information at this junction in the monkey brain cannot be considered modality-free because the

modality-specific signature of incoming signals has not degenerated through intermediate integration processes. Because of the similarity of posterior neocortical anatomy in monkeys and apes, we assume that the processing situation is similar for the two. This is supported by the behavioral manifestations to which we now turn.

The distinctive pattern of connectivity, which we suggest is responsible for the creation of modality-free associations (or "information"), is partly responsible, we also suggest, for a distinctive human behavioral manifestation. According to work by Humphrey et al. (1979) and Wagner et al. (1981), humans, even infants, have the ability to form amodal concepts considerably more abstract than the instantiations in the data to which they are exposed. This is discussed in the literature on what is referred to as "metaphorical mapping." Humphrey et al. (1979) demonstrated that infants as young as 3 months, when presented with a specific temporal sequence pattern simultaneously through visual and auditory channels, form a representation of the temporal pattern itself. Importantly, the representation of temporal pattern is not bound to either of the modalities of presentation. In related research, this representational ability on the part of infants has been confirmed with respect to stimulus properties including ascendancy and descendancy, continuity/discontinuity, and hardness (see Wagner et al. 1981; Sepehr et al., 1988 (includes visualtactile presentations)). Such studies validate the claim

that while information from the environment must clearly be perceived through one or more of the senses, the representation of that information is not bound to the perceiving modality. We will return to the importance of this point for language acquisition in Sections 7 and 8.

Equally important is the fact that while nonhuman primates are capable of certain cross-modal tasks (i.e., recognizing a particular object visually after tactile presentation; see Ettlinger and Wilson, 1990), they are incapable, even with intense training, of forming the type of amodal representation apparently necessary for metaphorical matching. Ettlinger (1981), in showing that chimpanzees give no evidence of this sort of ability, and in teasing apart cross-modal and metaphorical matching abilities, notes that "in the chimpanzee, physical identity seems to serve as a bridge between vision and touch whereas attributed common properties (e.g., "strength of stimulus", "local continuity/discontinuity") do not" (p. 585).

We suggest that these studies are indicative of a uniquely human ability to identify distinctive properties of presented data and then to characterize them in sufficiently abstract form as to allow them to be generalizable across situations. This ability, which we might refer to as the abstraction of properties, and which is not in any way bound to a particular perceptual modality, might well form the basis for (linguistic) lexicalization. Because of the particular cytoarchitectonic

character of the POT (especially its level of internal neuronal connectivity), it does not seem unreasonable to expect that it is the POT (present in humans, but not in monkeys or apes) that is responsible for the ability to abstract properties (in concert with Broca's area, as we will argue below).

We are led to this speculation about the fundamental importance of the abstraction of properties for linguistic lexicalization by the myriad studies of lexical relations in recent years by linguists from many different backgrounds. Almost any analysis of the nature of the lexicon resorts ultimately to some sort of lexical (semantic) decomposition, that is, the breaking down of lexical units into component parts (or features). While there is much disagreement about the nature of this decomposition and about which features are the correct ones, there seems to be little doubt that the features must be sufficiently abstract as to be generalizable not only across linguistic categories (e.g. syntactic class) but also across conceptual fields (e.g. location, possession, orientation, etc.). We return to this important issue in Section 7.

4.3.2. Anterior configuration

While we have presented this line of reasoning couched in a discussion of the evolutionary construction of the POT area, the methods and principles as specified are equally applicable to remaining portions of neocortex. Of particular interest is their application to the evolutionary construction of a functional Broca's area, for much the same comparative situation exists between pongids and hominids in this region. Neither strictly homologous cytoarchitectonic fields (vonBonin and Bailey, 1961) nor gross sulcal morphology (Sarnat and Netsky, 1981) consistent with the more highly evolved human pattern is present in the anterior regions of the non-human primate brain (see Figure 3).

It is relevant to ask what the cellular nature of Broca's area is such that it functions to support linguistic capacity. As with the discussion of the POT, careful analysis of organization and functioning at the neuronal level would be inappropriate for our purposes here. The implicit intention of our discussion of Broca's area is to suggest that it is a processing module whose inherent specialization is the hierarchical structuring of information in a format consistent with a temporally ordered linear sequence reflective of that structure. We argue (see Section 7) that this is, in fact, the underlying function of Broca's area in linguistic processing (see Greenfield, 1992, for discussion of hierarchical coding and Broca's area).

It is important to recall that there is a major tract of association fibers that connects the frontal and parietotemporal modules that we have been discussing (see Figure 1b). The existence of this major connective pathway signals the immediate availability of information processed in either of these areas to the other. This would mean that the amodal representations, resulting from sensory input to the POT, are available to Broca's area and, hence, subject to the imposition of hierarchical structure. It is our contention that the abstraction of properties is not possible in the absence of the capacity for hierarchical structuring. In order to generalize abstract features across categories one must first be cognizant of the feature composition of the perceived stimulus. To know that identifiable "wholes" are composed of distinctive "parts," or in other words that constituents can be further analyzed into smaller constituents, would seem to be the essence of hierarchically structured cognition. The abstraction of properties, like other important aspects of human cognition, requires a POT and a Broca's area working in concert. Importantly, Broca's area and the POT, as we will discuss in the following section, appear evolutionarily at the same time; because they are so intimately connected, this is not surprising (or accidental; see Wakefield, 1993). 5. Australopithecus and Homo habilis

Sometime between 10 and 4 million years ago, a separation in primate lineages took place, giving rise on one hand to the living African apes, and to humans on the other. Of the hominids, Australopithecus is the earliest and most primitive genus. At some point between 2.5 and 2 million years ago, largely contemporaneous with at least one species of Australopithecus, there appeared a second

hominid genus, believed to be descended from one of the (gracile) australopithecines. Its most primitive member, Homo habilis, is intermediate in many morphological features between the more primitive Australopithecus and later, more advanced members of its own genus (H. erectus, H. sapiens). The first appearance of stone tools (crude choppers and scrapers) is roughly coincident with the appearance of H. habilis in the fossil record, suggesting that this species produced and used these artifacts (Harris, 1983), although the later H. erectus is the first fossil primate with a substantial archeological record. By approximately 100,000 years ago, the hominids inhabiting Africa and the Middle East (and 40,000 years ago in Europe) were anatomically modern H. sapiens, similar to living populations (Fleagle, 1988).

5.1. The lunate sulcus and the POT

As mentioned, expansion of the posterior parietal cortex through time pushed the lunate sulcus from its more anterior pongid position to the inferior medial position typical of the human brain; given the presumed role the POT plays in language processing, the significance of this organizational shift is clear. Central to the task of determining when the shift to a human-like brain organization emerged is the issue of the placement of the lunate sulcus on the Taung australopithecine endocast (holotype, or "standard," for A. africanus).

Dart (1925), in his first paper on the Taung child, reported

the lunate position to be relatively posterior, this shift from the pongid configuration having resulted, he infers, from a "general bulging of the parieto-temporal-occipital association areas" (Dart, 1925, pp. 197-198). Holloway (1970, 1974, 1975), to the extent he found the endocasts interpretable at all, concurred in this interpretation of a posterior, human-like placement of the lunate sulcus impression. Falk (1980), on re- examination of the Taung, and in opposition to the original report by Dart and those by Holloway, interpreted the position of the lunate sulcus to be relatively anterior, as it appears in the pongid brain. Falk interprets the anteriorly-positioned, furrowed marking under dispute to be the lunate sulcus, whereas Dart and Holloway assume the marking to have been created by some non-sulcal feature.

Further, Falk's interpretation of the orbital surface of the frontal lobe of seven australopithecine endocasts from the same study corroborates this initial observation; the orbital surface, at least in its lateral aspect, is, like the parietal cortex, ape-like rather than human-like in its sulcal pattern. She has reasserted this claim of a pongid neural organization in subsequent assessments of this material based on the lunate sulcus position (Falk, 1983a, 1985a) as well as other morphological criteria (Falk, 1985b; see also earlier work by Holloway, 1983c, for interpretation and discussion of these materials). Falk has proposed, in addition, that with respect to the Taung, the entire sulcal pattern appears ape-like (Falk, 1983a). In

turn, Holloway (1981, 1984, 1985) has repeatedly disputed this interpretation based on his own examination of these same materials, maintaining that the Taung endocast does not reveal a pongid neural organization, but that the evidence suggests a typically hominid organization. Others (e.g., Tobias, 1987 and elsewhere) have determined the position of the Taung lunate to be "decisively indeterminate". Clearly, it is unlikely that a consensus will be reached based solely on direct examination of the "dimple" (Falk's term) that constitutes the putative lunate sulcus on the Taung endocast.

More recently, evidence bearing on the Taung interpretation has been reported that is not dependent on positive identification of the lunate, and which militates in favor of Falk's assessment of australopithecine neural organization. Jerison (1990), for example, argues that neural reorganization involving preferential expansion of parietal cortex in the australopithecines would have entailed certain unlikely morphological changes in the medial aspect of the brain related to occipital cortex. This would be so because substantial parietal expansion, under this scenario, would have needed to occur without a corresponding substantial increase in overall brain size (australopithecine brains are roughly comparable in size to chimpanzee brains). In light of the fact that the medial region in question is similar in appearance among essentially all placental mammals, it would be extremely unlikely (although possible) that Australopithecus alone

would have deviated from the mammalian norm. An interpretation of the australopithecine lunate that places it in a human-like position, would require such a deviation (Jerison, 1990).

In related research, Armstrong and her colleagues (Armstrong, Zilles, Curtis, and Schleicher, 1991) have utilized a quantitative measure of neocortical folding (the Gyrification Index, or GI), to address the question of whether cortical reorganization (i.e., preferential expansion (hence increased folding) of parietal cortex) occurred prior to the time at which substantial overall brain size increases occurred or whether it would necessarily have occurred in conjunction with such an increase. Because their gyrification analysis supports the former scenario, and because the substantial overall size increase in question during primate evolution postdates the australopithecines, the evidence presented by Armstrong et al. is consistent with Falk's interpretation of a pongid posterior neural organization for Australopithecus.

Holloway (1992) disputes the claim that GI data, collectable only on the brains of extant species, can be brought to bear on the issue of cortical organization in extinct species for which the only database is endocast material. It is true that the amount of cortex buried within the sulci of a particular brain cannot be determined from an endocast of that brain. However, it is also true that there is a significant correlation between the mean GI for a

given primate species and the sum of all sulcal lengths as measured on an endocast from that species (Zilles, Armstrong, Moser, Schleicher, and Stephan, 1989). Hence, there is a clear and consistent relationship between a measure that is only possible on a whole brain and a measure that is available =66rom a brain endocast (see discussion in Armstrong, Zilles, and Schleicher, 1993). This would suggest that the GI data should be allowable evidence in the australopithecine neural organization issue.

Given the nature (and evident acrimony) of the debate about the interpretation of the Australopithecus endocasts, there is little prospect of any imminent consensus. If Holloway is correct, then the hominid posterior brain configuration we have been considering might have emerged in specimens earlier than H. habilis. Based on the literature that we have reviewed, and because it is the more conservative hypothesis for our purposes with respect to the evolution of linguistic capacity, we suggest that the australopithecine brain is unlikely to have undergone adequate parietal expansion consistent with the development of a POT. This brings us then to the genus Homo.

The most primitive member of this genus, H. habilis, appears contemporaneously with certain of the more specialized, robust forms of Australopithecus. In the Koobi Fora region of Kenya, both genera are represented in strata of approximately 2 million years of age; endocasts

prepared from the reconstructed skulls of two individuals from this formation have been examined by Tobias (1975 in Tobias, 1981) and Falk (1983b). The australopithecine endocast (dated between 1.26 and 1.8 MY), as revealed by the fronto-orbital sulcus and overall basic shape, is argued to be of pongid-like organization (Falk, 1983b). In contrast, the habiline endocast (older than 1.8 MY) reveals fundamentally distinctive frontal, parietal and overall shape features which clearly differentiate the brain of Homo habilis from that of Australopithecus. With respect to posterior organization, the degree of development of the inferior parietal lobule of Homo habilis appears to exceed that of the australopithecine; sulcal evidence of the presence of well-developed supramarginal and angular gyri is apparent in this specimen (similar evidence for parietal expansion is also demonstrated on three habiline endocasts from Olduvai Gorge, Tanzania (Tobias, 1987)). With the emergence of a substantial inferior parietal lobule (and the decided lack, subsequently, of an observable lunate sulcus), H. habilis appears to have been the first species in which researchers might agree that there is human posterior neural organization. She may therefore be considered the first potential possessor of uniquely human modality-free sensory representation.

5.2. The frontal lobe and Broca's area

The search for evidence of Broca's area in early hominid forms has generated rather less controversy in the paleoneurological literature. The fronto-orbital sulcus, like the lunate, is a characteristic gross morphological marker of the pongid brain, but is absent in the human. Using 3-dimensional computer technology to reconstruct the Taung sulcal pattern, Falk and colleagues (Falk, Hildeboldt and Vannier, 1989) demonstrated that with respect to indications of a fronto-orbital sulcus, this specimen expresses a pongid-like morphology. As noted, Falk also found the australopithecine endocasts in her 1980 study to be pongid-like in their overall frontal lobe morphology, and the Koobi Fora specimen (Falk, 1983b) to be so in overall shape as well as by fronto-orbital criteria.

In contrast, the fronto-orbital sulcus is absent in the Koobi Fora H. habilis brain. Further, the sulci that have been identified as the horizontal and ascending branches of the Sylvian sulcus on the Koobi Fora habiline endocast represent, in extant humans, the anterior and posterior boundaries of the pars triangularis (part of the inferior frontal gyrus) (Falk, 1983b). An impression of the pars opercularis (the remaining portion of the inferior frontal gyrus) is preserved on an H. habilis specimen from Olduvai Gorge (Tobias, 1987); on two additional habiline specimens from this site, human-like frontal lobe morphology has been verified (Holloway, 1978; Tobias, 1987). These data suggest that language-relevant frontal cortex (pars opercularis and pars triangularis) is, insofar as can be determined from gross morphological inspection, present in the habiline brain (as a consequence of preferential expansion of the inferior

frontal gyrus).

Given the fossil evidence as presented, and the (more or less) converging interpretations of the same, we suggest that the two primary language-relevant cortices, inferior frontal and inferior parieto-temporal, appear simultaneously with the emergence of Homo habilis. The evolutionary shift from a pongid to a hominid neural organization, then, insofar as can be determined based on available evidence, probably occurred closer to the present than did the transition from ape to hominid postcranial morphology. This is an example of the mosaic pattern of evolution previously referred to. With a relatively large, but still organizationally pongid-like brain, Australopithecus may have been more behaviorally capable than her predecessors, but probably did not have the neural organization apparently necessary for language.

5.3. Lateralization

Before leaving our discussion of potential incipient language capacity in early hominids, we note that there is supporting evidence in the fossil record bearing on the phenomena of cerebral lateralization and handedness, two characteristically human traits highly correlated with language. Tobias (1987) reports that of the three Olduvai Gorge habiline endocasts on which the superior parietal lobule is bilaterally represented, the impression of the left superior parietal lobule is more strongly developed than

that of the right. Cytoarchitectonically-defined as well as gross anatomically- defined parieto-temporal regions in the brains of modern humans are typically larger in the left hemisphere than are their counterparts in the right (Eidelberg and Galaburda, 1984; Galaburda, Sanides, and Geschwind, 1978; Geschwind and Levitsky, 1968). Such left hemisphere-biased asymmetries generally correspond to preferential right-handedness and lateralization of language to the left hemisphere.

The parietal asymmetry in the brain of H. habilis allows the introduction of archeological evidence corroborating asymmetric specialization in these early humans from a behavioral rather than a morphological perspective. As has been well established, the phenomenon of handedness is not one attributable to the hand itself, but is an expression of cerebral hemispheric specialization. This phenomenon should manifest itself in the refuse of any population in which preferential handedness is characteristic and in which the material culture is sufficiently developed. It is significant then that in the Koobi Fora sediments in which both A. boisei and H. habilis biological remains have been recovered, so too have the first archaeological artifacts representative of crude lithic technology. H. habilis rather than A. boisei is generally implicated in the production and use of these early stone tools (Harris, 1983; Pilbeam, 1984; Toth, 1987). Toth (1985), based on a long-term experimental research program of manufacturing and using such stone

tools, and comparing observations from these experiments with the archaeological evidence, has determined that the manufacturers of the Koobi Fora artifacts under consideration produced these tools with blows from a hammerstone held preferentially in the right hand. Thus the habiline parietal asymmetry is mirrored by a behavioral manifestation indicative of preferential left hemisphere specialization that would be consistent with the lateralization of function that accompanies language.

We have concluded that there are significant differences, evident in the fossil record, that distinguish H. habilis from the australopithecines with respect to neurolinguistic preconditions. These include a demarcated Broca's area, an identifiable POT (indicative of Wernicke's area), and asymmetrical development of the cerebral hemispheres indicative of handedness. It is relevant now to ask how, and even why, such changes in structure took place in this evolutionary line. 6. Adaptations affecting the language areas

The adaptations that resulted in an identifiable Broca's area and POT, we will argue, involve the evolution of motor programs dedicated to manual manipulation and throwing behavior, each of which were crucial to the survival of early hominids (see Calvin, 1982, 1983a,b, 1992). The motor system modifications relevant to use of the hand and thumb had important interactive relationships with forelimb development, brain organization, lateralization, and handedness, all of which have strong correlations

with linguistic capacity in modern humans. Holloway (1983b), in his work on the paleontological evidence relevant to language, stresses the importance of "the increased competence in visuospatial integration and manual dexterity associated with hunting behavior, and in particular, complex throwing behavior and tool making" (p. 112).

As already mentioned, primate brain evolution is characterized by a progressive increase in brain size relative to body size. Lashley (1949) and others following his lead (e.g. Jerison, 1973, 1976) were among the first cognitive neuroscientists to suggest that the foundations of cognition (and intelligence) can be traced to those neural structures that have developed in excess of the neuronal quantity necessary to maintain the anatomical substance of the organism. Even though the basis for cognition cannot be so simplistically localized, much of this type of excess neuronal material makes up the neocortex, particularly the frontal and parieto-temporal association cortices. In other words, the neuronal material not directly associated with particular anatomical functions is that which is evolutionarily more recent. This evolutionary development is, of course, correlated with cognitive development.

6.1. Manual manipulation and somatosensory feedback

As can be seen in Figure 2, the primary motor area of the frontal lobe and the primary somatosensory area of the

parietal lobe lie along opposite sides of the central sulcus. These two primary areas work in concert for the many motor behaviors that require sensory regulation (Phillips, 1969; Bossom, 1974; Fromm and Evarts, 1977; Evarts and Fromm, 1978). For example, the simple gesture involved in reaching out, grasping, and lifting a glass requires not only motor manipulation but also somatosensory feedback to regulate the amount of pressure applied to the grasp. Too strong a grasp will result in broken glass; insufficient pressure will preclude execution of the lift. Many manual (as well as other motor) behaviors require extensive sensory feedback. This is directly relevant to certain evolutionary changes affecting the primate line, including tool use.

The complexity of tool-using behavior correlates with other important evolutionary developments. Central to our argument is the fact that this involves developments of the hand and thumb directly related to fine motor control and increased manual dexterity.

Archaeological evidence for the emergence of such behaviors and fossilized evidence of the morphological modifications with which they are associated are relatively abundant and well established in the record of human evolution. We have previously remarked upon, with respect to the evidence of handedness, the remains of lithic tools manufactured by H. habilis. Marzke (1971, 1983, 1991; Marzke and Shackley, 1986) has been instrumental in delineating and elucidating the

morphological characteristics and evolutionary modifications of the hominid hand with respect to the grips, movements, and resistance to external forces associated with both the manufacture (flaking) and use of such hand-held tools. These same modifications, she notes (Marzke, 1983), are crucial to the process of stonethrowing, another aspect of the tool-related repertoire of behaviors associated with H. habilis remains. Isaac (1987) has examined the presence of large numbers of unmodified stones, of a type unsuitable for flaked tools but associated nevertheless with the archaeological sites containing early modified stone artifacts; she concludes that from the perspective of simple defense and hunting, the investment of energy in transporting the stones from the source for use as ballistic weapons would have been well justified. Calvin (1982, 1983a,b, 1992) has repeatedly stressed the potential for enhanced fitness brought about by the capacity for accurate and dependable action-at-adistance predation. For example, one cannot generally get close enough to a wild game animal, such as a rabbit, to capture it before it runs away; a well-aimed, one-arm throw of reasonable force, however, can overcome this obstacle in the procurement of food (two-handed throwing disallows sufficient range). Morphological variation within a population that improves an individual's capacity to perform such acts becomes a prime candidate for selectional attention.

Morphological modifications of the hominid hand

facilitating such motoric behaviors are, in themselves, insufficient as a basis for fine, visuo-spatially sophisticated manipulative capacity. Equally motivated by selectional pressures for such capacity, particularly with respect to the manufacture and/or use of stone tools (including throwing), are corresponding increases in dedication of motor and sensory cortices to the musculature and receptors of the hand (for relevant discussion see Washburn, 1959, 1960; Isaac, 1981; Isaac, 1987; Calvin, 1982, 1983a,b, 1992; Marzke and Shackley, 1986; Marzke, 1991).

Manipulatory and throwing behaviors require not only motor control, but, as discussed above, somatosensory feedback. This portends the need for extensive integration of information from the motor and somatosensory cortices. Evolutionarily this has meant that the expansion of primary motor cortex has necessitated a concomitant expansion of primary somatosensory cortex, resulting in a complex feedback loop involving the two areas.

The functional interdependence of motor and somatosensory dynamics in primates, especially as concerns our claims with respect to a feedback loop, is best appreciated by reference to the evolution of the sensorimotor system in mammals more generally. In extremely primitive mammals, such as the marsupial, there is no distinction between "motor" cortex and "somatosensory" cortex; the lateral aspect of the brain is

characterized by completely overlapping functional fields, a "sensorimotor amalgam," that subserves both functions simultaneously (Lende, 1969). In this configuration, somatic information required by any particular motor neuron may be supplied by the adjacent sensory neurons. As the mammalian sensorimotor system evolved, particularly in those lineages in which manipulatory behaviors play an important role in survival (e.g., squirrels, raccoons), differentiation of the two components led to motor localization in the anterior aspect of the cortex and somatosensory localization in the posterior aspect (Woolsey, 1958; Lende, 1969). Maintenance of the required mutual feedback system was facilitated by the parallel evolution of a myelinated bundle of motor and sensory axons that could feed relevant information from each subsystem directly to the other.

In the anthropoid primates, the cytoarchitectonic differentiation of motor and somatosensory cortices has progressed to the extent that the central sulcus, which separates the two, has become an identifying characteristic of the order. Further, the arcuate and superior longitudinal fasciculi, portions of which interconnect the two components, have become principle myelinated axon tracts.

In light of this anatomico-functional relationship, we note that certain aspects of cortical expansion through evolution of one or the other of the sensorimotor subsystems would have to be constrained by, and have consequences for, evolution and expansion of the other. For example, as the morphology of the bones and muscles of the primate hand underwent evolutionary changes in response to selective pressures toward manipulatory behavior, so too did the motor cortex evolve in order to keep pace with such (peripheral) changes. The inherent organization of the sensorimotor system of the primates then requires that somatosensory cortex evolve in order to keep pace with (central) changes in motor cortex. Ultimately, it is the system as a whole that must be functionally balanced. In light of what is known about the evolution of the hand and concomitant changes in both motor and sensory cortices, the prediction is that if motor cortex (or motor association cortex) expands through evolutionary mechanisms, an associated expansion of somatosensory cortex (or somatosensory association cortex) must also take place. Further, some portion of the axons from these expanded regions must be incorporated as part of the interconnecting fasciculus. As noted by Pandya and Yeterian (1985), this appears to be precisely the case: each architectonic subdivision of the sensory association cortex is directly and reciprocally connected to a subdivision of motor association cortex with which it shares an equivalent state of evolutionary differentiation.

The differential cytoarchitectonics of these evolutionary "appendages" to motor and sensory association cortices reflect underlying differences in the exact pattern of neuronal connections within each unit. In general, the

further away a sensorimotor cytoarchitectonic region is located from the central sulcus, the more recently it has evolved, the further removed it is from direct connections to the peripheral organs of the body, and the more module-internal are the majority of its synaptic connections (for discussion of the developmental mechanisms responsible for this arrangement, see Katz and Lasek, 1978; Aboitiz, 1988). The increasing departure from direct association with the body and the increasing degree of internal or intrinsic connectivity associated with evolutionarily more recent cytoarchitectonic regions is generally taken to generate as a byproduct, as noted, the foundations of cognition (as per Jerison, 1973).

6.2. Incipient linguistic capacity

With respect to the evolutionary emergence of cytoarchitectonic regions compatible with linguistically formatted cognition, we suggest the following scenario. During the neocortical expansion associated with selection for the hand and manipulatory capacities, frontal and parietal cortices evolved in a manner consistent with the principles outlined in the preceding subsection. At some point between the time of the australopithecines and H. habilis, the frontal motor association cortex expansion that resulted in the pars triangularis and pars opercularis of the inferior frontal convolution was coupled with the parietal sensory association cortex expansion that resulted in the enhancement of the angular and supramarginal gyri and the shift of the lunate sulcus to its

inferior medial, nonpongid position. These simultaneously evolving cortices, Broca's area and the POT, are reciprocally connected by a major axon tract, remote from connection to the body, and highly intrinsically connected, as would be expected of neocortical areas subserving cognitive functions.

We suggest that the configuration of the association cortex, derived from primary motor and sensory cortices and motivated via selection for neural control of the evolving hand, provided a foothold for the operations involved in linguistic processing. This does not imply that the respective roles of the POT or of Broca's area in language were in any sense predetermined. Rather, functional changes in parietal and frontal structures proceeded even as did changes in the structures themselves (for general discussion of relevant principles, see Bock, 1959; Futuyma, 1986, p. 424). It is our contention that, as a consequence of the configurational compatibility, these parietal and frontal substrates were subsequently reappropriated for language and, ultimately, for linguistically formatted communication. The shift in placement of the lunate sulcus as a result of the motorsensory expansion was illustrated schematically in Figure 4.

Recall that at the same time that the manual behaviors under selection were developing and becoming more complex, so too was brain function becoming lateralized (as indicated by the development of right-handedness

among the habilines). This phenomenon derives from the nature of the behaviors for which we are claiming selective advantage. As noted, in throwing, a two- handed release allows neither sufficient force nor acceleration for an advantageous weapon trajectory. In flaking stones, one hand is used to steady the target (or core) stone while the skilled movement is executed by the other. With selection operating for behaviors associated with unilateral performance, the stage may be set for preferential handedness and cerebral lateralization. 7. Conceptual Structure

If our account proves valid, by the time of H. habilis the marked sulcal division between the parietal and occipital lobes had "disappeared." In addition, there were other significant evolutionary changes affecting the hominid brain. These include the expansion of visual cortex and of the temporal lobe. The close proximity and resultant junction of the three posterior lobes culminated in a situation in which information was readily available for processing in an overlap of the three related association areas and which could result in amodal representation.

It is important to note at this point that, in light of the size of axon tracts between neural structures, geographical proximity is not necessary for processing connections. It is the case, however, that proximal location and organization is often the rule for related functions. This can be exemplified by a consideration of the organization of motor and somatosensory functions on either side of

the central sulcus. In the POT area, close proximity of the association areas for sight, audition, and the tactile sense results in the facilitated integration of sensory information.

The POT allows for a particular way of organizing perceptual information that we believe to be necessary for the typically human amodal representation of abstract features. Recall that humans, but apparently neither monkeys nor apes, can abstract distinctive properties from sensory input and apply those properties in the processing of sensory information from various modalities or, in other words, accomplish what was called metaphorical matching (see Section 4.3.1). We suggest that this is the substance associated with the process Jerison (1976) refers to as the uniquely human "construction of reality."

This human manner of building reality, utilizing the integration of information from the various modalities is derived directly from the facts of neurology. It would not seem unreasonable, then, to expect a theory of cognition (a higher level of abstraction) to be responsible to similar considerations. Cognition must, of course, ultimately be instantiated in the brain. The proposed cognitive construct (relevant to language) most apparently compatible with this view of neurology is Jackendoff's Conceptual Structure (1983, 1987, 1990, and elsewhere).

Conceptual Structure (henceforth CS) is the central concept in a theory of semantics that integrates meaning

as relevant to language with meaning as relevant to other cognitive domains. CS is explicitly developed in order to serve not only the concerns of linguistic theory but also those of theories of vision, music, motor systems, etc. It is to be seen, in fact, as the level of structure relevant to all cognitive domains. Jackendoff (1983, p. 17) says:

There is a single level of mental representation,
conceptual structure, at which linguistic, sensory, and
motor information are compatible.

CS, as conceived of here, and based on Jackendoff, is made up of basic ontological categories and constituents put together according to CS-specific rules of combination. The basic categories generalize across semantic fields and across conceptual modalities. The rules of combination construct higher-level constituents, such as STATES and EVENTS, out of the basic categories, such as THINGS and PATHS. For example, a sentence involving the verb throw (e.g. Ben threw the ball to the dog) would include a representation of an EVENT in which a THING (a ball) goes along a PATH from THING (Ben) to a different THING (the dog). Because this is a causal EVENT, one THING (Ben) CAUSEs the ACT in which the THING (ball) is acted upon. (This is discussed in more formal terms in Section 8.1.)

Importantly, CS is not part of the linguistic system per se. Rather, the linguistic system is related to CS through a set of correspondence rules. The theory of CS is a theory of mental representation, and to the extent to which CS can be shown to provide for a successful linguistic semantics, semantics will not be part of the strictly linguistic domain. From this point of view, the theory of grammar deals with syntax and phonology; semantics falls under the theory of CS.

To relate the discussion of CS more directly to what we have said regarding neuroanatomical structure, we suggest that CS is the cognitive construct that is produced by the POT through its interaction with Broca's area. By virtue of the POT, human sensory input is highly processed in association cortex and loses its modalityspecific character; by virtue of Broca's area's influence on the POT, the amodal representations are subject to hierarchical structuring. Structured modality-neutral representation, we suggest, is the essence of CS. (Further, amodality and hierarchical structure are necessary for feature abstraction, to which we return shortly.) The biological configuration of the POT imparts the modality-neutrality of the "semantic" representation. In parallel fashion, the biological configuration of Broca's area (and the connecting fasciculi) imparts a hierarchical structuring to the representations. Recall that Broca's area is derived from motor cortex. Motor cortex deals specifically with the innervation of muscle units, the firing sequences of which must be coordinated by higher levels of neural control organized in hierarchical fashion.

Because of the anatomical and physiological requirements associated with the higher level organization of an ultimate motor output, behaviors initiated by motor association cortex must be functionally hierarchical. Therefore, any behavior (or cognition) associated with Broca's area will show evidence of hierarchical structuring (see Greenfield, 1992).

Taking this line of argumentation yet further, we suggest that it is CS and its underlying biological basis that gives language its referential character. One of the most basic characteristics of human language is its ability to refer, and a basic characteristic of reference is the sense we all share that there is a connection of some sort between words, on the one hand, and things and/or events in the perceived world, on the other. Importantly, words and their denotations (however these are ultimately to be characterized) are not limited to connections involving only a single sense modality. The features necessary for even the simplest sort of naming and referring would seem rarely to be drawn from a single modality. This would appear to be a natural consequence of a neurological and cognitive arrangement wherein the integration of sense modality information was not only natural but inevitable. This capacity for reference, one of the defining characteristics of human language, is apparently not in the natural cognitive repertoire of even the most sophisticated of the nonhuman primates (see Terrace, 1985). Whether or not apes can be taught to

refer with symbols, reference is not obviously an important characteristic of nonhuman primate vocal communication systems. Nor, evidently, is there much evidence that apes comprehend the possible referential functions of non-vocal (e.g. gestural) behaviors (Savage-Rumbaugh, 1986).

There is another aspect of the reference issue that should here be mentioned. Reference in human language is not limited to the "here and now." Language readily deals with past (or possible future) events and objects not available to the perceptual systems at the moment of the speech act. F. Aboitiz (personal communication) points out that keeping in mind, or recalling, an object or event when it is not present evidently involves working memory in the prefrontal lobe (Goldman-Rakic, 1984). Prefrontal cortex is very well developed in humans and Aboitiz suggests that its main role in human evolution may well have been related to this sort of reference task.

A third aspect of referential capacity is of particular relevance here because it is arguably traceable to the important neurobiological connection between Broca's area and the POT. We consider important the fact that, according to Savage-Rumbaugh (1986), apes have great difficulty with what might be called "referential specificity." The vocabulary items that chimps can learn correspond to:

very global requests, such as for contact, play, food,

or change of location. However, as the human experimenters then attempt to teach symbols which denote more specific attributes of each of these situations (who is eating, what they are eating, the differences between eating and drinking, the act of transferring food from one individual to another, the pace of the transfer, etc.), the ape has difficulty in comprehending both the referents of such symbols and why their use results in anything more than the symbols he has already been taught to use when making requests. (p. 26, emphasis in the original)

We would suggest that the ability to achieve referential specificity is dependent upon the ability to analyze constituents into their component parts, that is, to recognize that constituents have distinctive sub-parts. This, in turn, requires the ability to abstract features, or generalize recognizable properties, across non-identical instances (what we discussed above in Section 4.3.1. in relation to metaphorical mapping). Referential specificity, like so much else in natural language, requires the ability to hierarchically structure abstract units. For human

infants, referential specificity is trivial; for the chimp it is not obviously even achievable. As far as the chimp Nim is concerned, "Nim milk, give milk, Laura give Nim milk, more milk" (Savage-Rumbaugh, 1986, p. 26) always result in Nim getting more milk. There is no evidence that the chimp, in responding to such phrases, understands the specific referents of any single symbol. The chimp will string together any combination of symbols that will result in a desired outcome, e.g. getting milk. Chimps, at least Pan troglodytes, apparently do not have the natural capacity to break abstract symbols, in this case the phrases, down into their component parts. This is due, we would claim, to the fact that the chimp lacks a POT connected to a Broca's area.

More recent work with chimps paints a somewhat different picture, especially for Pan paniscus. Bonobos have shown a considerable facility with language comprehension (as to some extent have common chimps; see Savage-Rumbaugh, Brakke, and Hutchins, 1992) and, more relevant to our concerns, certain language learning abilities often thought to lie beyond the capacities of apes. As Savage-Rumbaugh, Murphy, Sevcik, Brakke, Williams, and Rumbaugh (1993) amply documents, bonobos (and probably even common chimps) have demonstrated the ability not only to understand many (novel) sentences of spoken English, but also to acquire words (represented by lexigrams) and word use through "observational learning" (i.e. in the absence of overt tutoring). The ape who has

most amply demonstrated this learning capacity was raised in a naturalistic, culturally-enriched environment in which he was exposed to spoken English and lexigrams simultaneously (Savage-Rumbaugh, et al., 1993, p. 25). While the apparent language learning abilities of this bonobo are striking, his accomplishments do not directly serve to test the evolutionary hypotheses put forth in the present account of the emergence of language.

For reasons related to the chimps' vocal inadequacies (for linguistic phonetic expression), there was a need to expose the research subject (and other subjects similarly raised) to visually presented, manipulable symbols (the lexigrams) while he was in the spoken English environment. This mode of language presentation has (at least) two important, relevant effects. First, in such a linguistic environment there is a graphic representation of the fact that the phonetic input (the acoustic signal) could be decomposed into, and matched with, discrete units. Less obviously, this use of lexigrams also signaled that the conceptual environment that was paired with the acoustic signal could be represented in discrete, bounded, symbolic "words." This would seem to greatly simplify the acquisition problem in exactly the way that an ape would require, namely, by overtly and tangibly demonstrating that utterances are to be broken down into their component parts. (Note that neither the acoustic signal nor the visual signal for deaf children contains any reliable decompositional markers.) Second, the presentation of

spoken sentences plus lexigrams amounts to multi-modal symbolic input for the subject; the signal is presented via auditory and visual channels simultaneously. (Perhaps there was also some tactile input if the bonobo was permitted to touch the lexigrams.) This would surely facilitate a multi-modal cognitive representation. Recall that humans arrive at amodal representation even if stimuli are perceived uni-modally.

On our view, the bonobo reported on by Savage-Rumbaugh and her colleagues has demonstrated considerably advanced abilities. This was made possible by the unique linguistic environment in which the primary data were encountered. We might suggest that, in fact, this study (and others in which chimps have been exposed to naturalistic data in this bi-modal situation) can be interpreted as support for our claims about the central importance of the abstraction of properties (or distinctive features) and amodal cognitive representation. When these prerequisites for linguistic ability (and language acquisition) are facilitated for the apes, their incipient language-like abilities flourish. Naturally, however, no such facilitating environment was available for our hominid ancestors. Instead, they had the neuroanatomical advantage of connected POT and Broca's areas.

As we have already mentioned, H. habilis, by virtue of having no identifiable lunate sulcus, had a POT. Recall that there is evidence in the fossil record that she also had a Broca's area. Recall, too, that on our view Broca's area

does not directly subserve linguistic capacity. Instead, it is involved in the hierarchical organization of cognitive events. As such, it is crucial to the phonological, morphological, and syntactic aspects of grammar, and might well be responsible for the structure dependent aspect of all grammatical levels and modules. At each level, linguistic units are comprised of smaller "building blocks" (at least above the level of phonetic distinctive features). For instance, phonological units are made up of phonetic segments, phrases are built from syntactic-level words, and words are the result of the combination of roots and affixes. CS, too, is made up of component ontological categories organized into larger units like STATES and PATHS (as exemplified in Section 8.1.).

Further, and again by virtue of derivation from motor cortex, Broca's area would be responsible for temporal sequencing in the grammatical modules (as well as other aspects of cognition). A disruption to the functioning of Broca's area, therefore, would have ramifications in many identifiable aspects of linguistic competence and performance. Temporal and hierarchical structure are recognizably basic to both phonology and syntax. Clearly, temporal and hierarchical ordering mechanisms are not, in and of themselves, language. Neither, as we have discussed, is CS. Linguistic ability is possible only in a neurological environment in which the physical modules underlying these domains (i.e., temporal ordering, hierarchical structure, CS) are reciprocally interactive.

A conclusive analysis of Broca's area as the regulator of the temporal and hierarchical structural aspects of language would require extensive examination of the relevant aphasia data. If the underlying competence of Broca's area is, in fact, the superimposition of hierarchical and temporal structure on representations to which it has access, we would not expect to be able to define the behavioral characteristics of damage to this region solely in terms of one or another of the theoretically autonomous grammatical modules. Indeed, the recent structural accounts of Broca's aphasia derived from phonological, morphological, and/or syntactic theories (e.g., Zurif and Caramazza, 1976; Kean, 1977, 1980; Berndt and Caramazza, 1980; Linebarger, Schwartz and Saffran, 1983; LaPointe, 1983, 1985; Grodzinsky, 1984, 1986) leads us to assume some underlying commonality. This assumption is further supported by the recent work of Greenfield, 1992. An hypothesized disruption in the structural encoding of information across levels would indeed appear to account for reported deficits, linguistic and otherwise, in Broca's aphasia (further investigation of this matter is clearly indicated, but beyond the scope of this paper).

For the theory presented here, the POT is taken to underlie amodal representation, and Broca's area, temporal and hierarchical structure. The interaction of these components yields CS and is prerequisite to, but unlikely to be sufficient for, language. It should also be

mentioned that nothing here precludes the development, evolutionarily, of a close association between Broca's area and aspects of vocal tract control. There is undoubtedly a connection between the detailed and precise fine motor control necessary for speech articulation and the sophisticated programs of the motor association cortex adjacent to Broca's area. The evolution of a modern vocal tract, however, cannot account for the appearance in the fossil record of demarcated Broca's area and the POT (contra Lieberman, 1984, 1985, 1989); the anthropological literature suggests that these areas significantly predate extensive evolutionary changes in vocal tract morphology (see Arensburg, Schepartz, Tillier, Vandermeersch and Rak, 1990).

We reiterate here that our account of the emergence of the POT and Broca's area does not depend on selectional pressures for strictly linguistic ability in the earliest hominids. Selectional pressures for improved eye-hand coordination and manipulatory capacities are clearly established in the fossil and archaeological records. Our account relies on the reappropriation of the expanded, or appended, neural modules associated with these abilities. The cognitive products that were enabled by the aforementioned reappropriation of these structures, once established, may themselves have been highly adaptive and available for selection. It is important to remember that all known evolutionary forces, whether direct or indirect, operate on biological systems. Accounts of

selectional pressures for language subsequent to the reappropriation must be thusly constrained. 8. The learning theory

Thus far we have argued that it is not unreasonable to suggest that Homo habilis had CS. But having CS is not the same as having language. In fact, if the theory of grammar that we are assuming is correct, CS is not itself even a part of the grammar. What must be shown is that having CS permits language: in other words, that it provides a basis for the acquisition of language. This is exactly what we propose.

8.1. Conceptual Structure and acquisition

We assume the theory of language acquisition proposed in Wilkins (1994). The primary aspect of this theory that is relevant for our purposes here is that the input to the learner involves, crucially, a representation of meaning in the form of CS. An advantage of assuming that CS forms part of the input to the learner is that it is not part of grammar and therefore need not be learned in the course of language acquisition. In the assumed acquisition model, input to the language learner includes CS, but not CS alone. In each datum for the learner, the CS is paired with a syntactic structure.

Another important aspect of the assumed learning theory is that it requires no tutor and no correction from external sources. This has consequences for the course of

acquisition in terms of the unavailability of so-called negative evidence. With respect to the genesis of language, this is an important point because, of course, there would be no possible tutor or other external error-correction mechanism.

The learning model was originally developed to explain how human first-language learners acquire vocabulary items, verbs in particular. It is couched in terms of the learning of linguistic properties of predicates and how they are syntactically represented. For the learning theory, as well as for our purposes here, we assume the formalism for CS worked out largely by Jackendoff. Nothing turns, however, on our adoption of this particular formalism. What is important is that CS be made up of a limited set of primitives (ontological categories) that are modality-neutral and hierarchically structured (as necessitated by human neurology, as already discussed). Jackendoff's notion of CS is specifically intended to be a representation that is compatible with a number of cognitive modalities but is itself modality-neutral.

The lexical entry for put exemplifies a typical (partial) CS:

put

(i)
$$[-N, +V]$$

(iii) [EVENT GO ([THING =A3]j, [FROM ([PLACE]i)])]

(iv) [EVENT CAUSE ([THING =A4]i, [EVENT ACT ([THING]=A4, [THIN= G]=A3)])] The first line of the CS (line iii of the lexical entry) indicates that put involves the movement of some entity along a path from one place to another; the second line (iv) indicates that putting is a causal event in which one entity (purposefully) acts on another. The motivation for the two different "tiers" (Jackendoff's term) follows Culicover and Wilkins (1984, 1986) in relating the thematic tier to the theory of perception and the action tier to the theory of events. Perception and event theory are assumed to be independent from (but, of course, related to) language. (For in-depth discussion of the nature of CS, see Jackendoff, especially 1983, 1990; Culicover and Wilkins, 1984, 1986; and Wilkins, 1994.)

The nature of perception and event structure account for the particulars of the two tiers of CS. And CS corresponds, in ways that are only partially understood thus far, to aspects of linguistic structure, such as the subcategorization and argument structure for particular predicates. It is this relationship that must be learned. But language acquisition does not involve the learning of CS; for the purposes of the language learner, CS is given (i.e., innate).

The task for the modern human language learner, according to our acquisition model, involves determining which parts of CS in a presented datum correspond to

which parts of the syntactic structure in that datum. For example, if presented with a datum including a meaning representation (CS) and a syntactic structure (SS) such as

CS: [EVENT GO ([BALL], FROM ([PLACE ([BEN])]))]

PATH TO ([PLACE ([CALI])])

[EVENT CAUSE ([BEN], [EVENT ACT ([BEN], [BALL])])]

SS: [S [NPBen] [VP [V'[Vthrew] [NPCali]] [NPthe ball]]] the learner must discover that it is [CAUSE to GO along a PATH =46ROM PLACE TO PLACE] in the CS that corresponds to throw, which is part of the syntactic structure. In order to even begin to do this, the learner must be able to analyze both the CS and the SS into subparts. She must recognize that the input datum is made up of distinctive parts. The acquisition task, the learning of lexicalization patterns, involves associating a constituent of the CS with a particular syntactic constituent. Then, of course, the resulting lexical item must be stored in sufficiently abstract form (e.g. with variables rather than names) so that it can be used in novel instances.

On this view of the acquisition of lexical items, no learning could take place in the absence of the ability to recognize distinctive parts or to generalize abstract representations of these parts across situations, even those related to different sensory modalities. The same basic CS representation involving GO along a PATH, evident here in

the verbs put and throw, is relevant, for example, for the verb cool, meaning GO FROM a higher TO a lower temperature. The pervasiveness of such abstract categories as GO, FROM, and TO across semantic fields in the representation of lexical items has been amply demonstrated by many linguists (see, especially, Gruber, 1965, 1967; Jackendoff, 1972, 1990; Talmy, 1975, 1976, 1980). Lexicalization for human language requires the recognition of such abstract, distinctive, sub-parts of input data. And lexicalization would seem to be an undeniable, basic component of language acquisition.

8.2. The primary linguistic data for H. habilis

We turn now to the possible acquisition situation for Homo habilis. By virtue of having a brain with a POT and a Broca's area, H. habilis would have possessed structured modality-neutral representation, hence, CS. As we have stressed, this in and of itself does not mean that she had language. However, the first step in language acquisition for H. habilis might not have been so radically different from that for the modern human child.

Even the modern child presumably is not aware a priori that there is a task to accomplish. The child simply brings human cognitive capacities to an environmental context. As a consequence of the nature of human cognition, environmental context is converted, in the mind of the learner, to usable data. In other words, on our view (and this is an admittedly controversial issue), language

acquisition is accomplishable by the human child because she can "recruit" the necessary input, the appropriate triggering data, from the vastly overly rich surrounding environment. The data does not come "prepackaged" for the learner. For example, the acoustic signal does not come to the child broken down into, or labelled with, the linguistically relevant phonological or syntactic units. Neither does the environmental context in any simple way reduce down to the cognitively relevant units of CS. The usable input data for the language learner is available in the environment because it is perceived by a learner with human cognitive capacities.

Admittedly, however, for the modern human child, the complex environment contains language. In order to speculate about the acquisition situation for our habiline ancestors, we must turn attention to situations in which individuals have matured in contexts devoid of language.

In order to investigate the extent to which language capacity is innate, or whether there is a critical period for language acquisition, numerous researchers have investigated so- called feral children (for a recent review of this literature, see Candland, 1993) and children who have been purposefully deprived of linguistic stimuli (see, e.g. Curtis 1977). The consensus on most such studies is that children deprived of language data do not acquire language, or in other words, that language acquisition cannot take place in the absence of a linguistic community. This cannot be the whole story, however,

because some generation of human children, at some point in our ancestral history, must have been the first to have language.

We suggest that the failure of modern-day linguistically deprived children to show evidence of language acquisition is due not simply to the absence of language in the environment, but also to the severe psychological and social deprivation that such children must endure. The situation might be markedly different in a context in which a child were linguistically isolated but raised in an otherwise normal social environment (see overview in Hewes (1992) of attempts at different points in history to set up such naturalistic experiments). To draw a parallel with the habiline child we would need to investigate a psychologically healthy infant in a linguistically deprived but otherwise normal psycho-social situation. Something very like this was reported on by Feldman, et al. (1977) for deaf children raised in linguistic isolation because their parents and other care givers thought it best not to provide them access to a manual language. These deaf linguistic isolates underwent an acquisition process with striking parallels to what might have been plausible for the first generation of language acquirers.

According to Feldman et al., the children they studied created manual language; in the absence of language data they developed symbolic gestures. Furthermore, they developed gesture-order rules similar to the word-order rules devised by hearing children in the early

acquisition stages. Of particular relevance to our earlier discussion of representation and structure, these deaf children demonstrated naturally-occurring segmenting behavior. The knew that gestural acts could be broken down into smaller units that for them became signs. Further, and importantly for our proposed evolutionary scenario, they naturally demonstrated the ability to abstract general features across gestural situations. For instance, the twisting movement of the hand (observed in the opening of a jar) came to symbolize the lexical element jar. The abstract notion red was expressed by the pointing out of many red objects. Both of these examples illustrate the ability these children had to make referential use of language via the abstract representation of distinctive properties of perceptual units. We suggest that this is the same ability demonstrated by infants in the metaphorical mapping experiments, the identification and abstraction of features.

The children studied by Feldman and her colleagues developed referential signs based on naturally-occurring gestures in their environment. Stylized pantomimes became iconic symbols, and these symbols were subject to ordering rules. Feldman and her coauthors point out the similarity between the linguistic systems developed by these deaf children and novice language use among hearing individuals (e.g. children and foreigners) including hierarchically arranged linguistic levels.

In later work, Goldin-Meadow and Mylander (1990) report

on the continuing development of structured language in these deaf children, including many further examples of the generalization of abstract features (e.g. the use of handshapes to represent not only the handgrip around objects but also for the objects themselves, and then, in combination with motion signs, to mean the opening or closing of the object). These children have even gone so far as to develop a (rudimentary) morphological system, shown in an ability to "analyze...gestures into component morphemes" (p. 313). This development of increasing complexity in the linguistic system of these children leads us to wonder how such a linguistic situation might develop were a next generation of offspring exposed exclusively to the system developed by these linguistic isolates (see relevant discussion of the creolization process in Bickerton, 1990).

In their discussion of the deaf children, these researchers make repeated reference to the motivational need on the part of the children to develop a communication system. Nothing in our discussion thus far has suggested that our habiline ancestors lacked a communication system, so we would not argue that they were pushed to create language for strictly communicative needs. We suggest instead that in the brain/mind of a psychologically healthy individual with the necessary neuroanatomical structures, and hence, necessary cognitive capacities, language will be acquired. The nature of the linguistic system that develops in the mind of the individual will, of course, be

shaped by the nature of the environment in which the individual exists. In an environment in which some natural language is used, that language (e.g. English) will be learned. In the absence of linguistic primary data, a natural, probably pidgin-like system will develop.

Returning more specifically to the case of H. habilis, we must speculate on the situation of linguistic isolates who are not deaf. Such individuals would not have been restricted to recruiting their first symbolic units from the gestural repertoire. They had access, too, to a wide range of auditory "gestures," both of their own making and existing in the external environment. As is well known, primates are noisy animals. They tend to vocalize as they execute certain behaviors and, further, certain external stimuli typically evoke particular vocalizations. It is not unreasonable to assume that H. habilis too was a noisy animal, that she had a systematic repertoire of calls. It seems not unreasonable also to think that a habiline child might have recruited from this call repertoire to create a linguistic sign (just as the deaf children recruited from the gesture repertoire to create gestural signs). These acoustic signals, simply part of the primate call system for the adult vocalizer, might have taken the form of linguistic signs in the mind of the child. This is not meant to indicate that the vocal call system became language, rather that the calls might have served as the primary data from which signs were recruited by the first language acquirers. The situation was the same for the deaf children. Their

mothers' natural gestures did not become language; they simply provided the input from which signs could be recruited.

A vocal call could serve as input for learning only in the environment of a brain capable of supporting CS. In other words, the status, or usefulness of the call for the purposes of language acquisition would depend on the cognitive capacity of the perceiver of the vocalization. On this view, in the environment of the appropriate cognitive structure (that is, supported by a brain with a POT and Broca's area), a vocalization could be recruited as an input datum for language acquisition. Then something like the Wilkins (1994) learnability model might have served for the building of lexical entries consisting of sounds paired with CS representations.

To recapitulate, we suggest that learning in some fashion can take place even with highly impoverished input and, in fact, that primitive language-capable learners could have begun to construct a lexicon, in a fashion not dissimilar from that outlined for modern human learners, especially those deprived of normal linguistic input data, on the basis of CS and environmental acoustic signals. It falls outside the scope of the lexical learning theory to predict how the learner moves from the acquisition of lexical entries to aspects of the syntactic component. It also falls outside the scope of this article to speculate on how language evolved once the emergent capacity and CS came into existence. We think, however, that it is

suggestive that the evidence for hierarchical structure is so pervasive, as is the importance of distinctive features, both in adult linguistic systems and in the early stages of acquisition, both for children in normal circumstances and for the deaf linguistic isolates. Given the natural impetus to hierarchical and temporal ordering that results from Broca's area, syntactic structure might be inevitable once there are lexical units capable of being ordered.

We make no substantive claim here, however, about how modern syntax and phonology, might have evolved (however, of course, the hierarchical ordering, necessary to these components, would have been available). Our specific claim is that the emergent ability, driven by the evolutionary appearance of CS, was the capacity to acquire meaningful, symbolic, abstract, units -- lexical items. Once this first step is realized, researchers might well speculate on how aspects of grammar could have evolved (see Hurford, 1989; Pinker and Bloom, 1990; Newmeyer, 1991). In any discussion of evolution, however, we would take the basic biological components to be of primary importance; evolution, after all, functions ultimately at the genetic level, only subsequently being expressed at the morphological level and later yet at the level of cognition. And even though we have argued against strict adaptation as normally understood as the appropriate evolutionary mechanism for this all-important first step, it would be appropriate to expect adaptationbased explanations to come into play at later stages, once language came to be used preferentially as the human communicative system. 9. Conclusion

As we indicated in the Introduction, it was our intention in this article to propose a plausible evolutionary account of the emergence of neurolinguistic preconditions in humans. In order to do this, we built upon, and brought together, research from a number of different disciplines. Through our attempts here, we hope to encourage other cognitive scientists to join the discussion of language origins and, by extension, the evolution of cognitive capacities. In order for this discussion to reach an adequate level of sophistication, the linguist's voice must be heard. Only through a true appreciation of the linguistic capacity can strides be made in explorations of human cognition. As linguists are all too well aware, even the best and most sophisticated researchers in allied disciplines underestimate the difficulties and complexities of language. Nowhere is this more evident than in questions of evolution. We cannot leave the discussion of language origins to those researchers who have yet to understand the concerns of modern linguistics.

Throughout our presentation here we have been careful to separate linguistic capacity from communicative abilities. This has been important in our argument because we do not claim that human language developed from communication-system precursors. The capacity for language is not equivalent to the ability to communicate, which does not deny the fact that language is used as the

primary communicative tool for modern humans. But neither for modern humans nor for the emergent language-user were language and communication isomorphic.

The arguments for and against the distinction between language and communication have been rehearsed at length in the linguistics literature. Our reasons for the distinction are based on what we take to be the most convincing of the theoretical linguistic arguments, but, for us, these arguments are further bolstered by the distinct neuroanatomical bases for these two systems. Vocalizations in non-human primates, while complex and surprisingly sophisticated (see Cheney and Seyfarth, 1990), maintain close connection to limbic drives and are only rarely under strictly volitional control. Human language, while requiring some minimal limbic contribution, is largely neocortically derived and volitionally controlled (Kuypers, 1958; Robinson, 1972, 1976; J=81rgens, 1976; Ploog, 1988).

Because we distinguish language from communication, we do not find it remarkable that no convincing linguistic precursors have been discovered in the communication systems of non-human primates such as the great apes. We would expect to find such precursors only if linguistic preconditions predated the genealogical separation of hominids from the other primates, or in other words, if language capability emerged in an ancestor common to both the pongids and hominids. Our claim that the

neurolinguistic preconditions were met in H. habilis means that pongids, no matter how communicatively able, do not possess even rudimentary language. A failure to make this language- communication distinction, and/or a failure to appreciate phylogenetic relationships, has led researchers to look for linguistic precursors in the extant non-human primates (as mentioned in Pinker, 1992). Implicit in the many studies of "language" in the great apes (Gardner and Gardner, 1971; Premack, 1976; Rumbaugh, 1977; Patterson, 1978; Terrace, 1979; Shapiro, 1982) seems to have been a view of evolution based on assumptions with which we have herein pointedly taken issue.

The scenario we have developed here suggests an evolutionary explanation in terms of reappropriative mechanisms with specification of the preadaptive status of the neural substrate(s) used in complex manual manipulation. The selective pressures for the manual abilities that we have discussed were most likely operative as early as the appearance of the pseudo- opposable thumb, that is, in ancestors of the modern primates. While we predict a "gap," an apparent qualitative distinction, between the neocortical capabilities of the extant great apes and those of humans with respect to language, we would not expect such a gap in those capabilities related to use of the hand. Further, we would expect to find a gradational distribution of cognitive capabilities in the associative integrations of perceptual information. In other words, we would expect increasingly complex and more

human-like cognition in those species most closely related to humans. And further, we would predict that more language-like behavior would be demonstrable in species whose neural organization more closely resembles the hominid pattern. Hence, we would not be surprised to find that the bonobo neuroanatomical configuration more closely approximates the hominid condition than does the pongid configuration of the common chimp that we have discussed here.

Regardless of the eventual outcome (if one can ever be determined) of the debate about the adaptive status of early language (see Pinker and Bloom, 1990, and commentary thereon), the reappropriation account as formulated has explanatory force. Neither unknown pressures for linguistically formatted communication, nor unspecified adaptive responses specific to the same, need be invoked in order to account for the evolution of language-consistent neural structures; such structures are derivable from known pressures and adaptive responses already evident in the established fossil record.

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