

Language, tools and brain: The ontogeny and phylogeny of hierarchically organized sequential behavior

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Abstract: During the first two years of human life a common neural substrate (roughly Broca's area) underlies the hierarchical organization of elements in the development of speech as well as the capacity to combine objects manually, including tool use. Subsequent cortical differentiation, beginning at age two, creates distinct, relatively modularized capacities for linguistic grammar and more complex combination of objects. An evolutionary homologue of the neural substrate for language production and manual action is hypothesized to have provided a foundation for the evolution of language before the divergence of the hominids and the great apes. Support comes from the discovery of a Broca's area homologue and related neural circuits in contemporary primates. In addition, chimpanzees have an identical constraint on hierarchical complexity in both tool use and symbol combination. Their performance matches that of the two-year-old child who has not yet developed the neural circuits for complex grammar and complex manual combination of objects.

Keywords: brain; chimpanzee; construction; cortex; development; evolution; language; language development; neural development; ontogeny; phylogeny; primate; tool use

This target article has two goals: The first is to relate the ontogeny of hierarchical organization in speech and in combining objects with the hands (henceforth "manual object combination") to brain development and brain function. The construction and use of tools are particular instances of object combination. The second goal is to explore the evolutionary roots of language, tool use, and their neural substrates by examining evidence from contemporary primates.

In manual object combination, the hands are used to put two or more objects together, as in tool use or construction activity. The following examples indicate how (1) tool use and (2) construction activity involve manual object combination: (1) The hand holds a hammer, which strikes a nail held by the other hand, and (2) two pieces of pipe are manually screwed together to make a longer piece of pipe.

In hierarchical organization, lower-level units are combined or integrated to form higher-level ones. As an example of hierarchical organization applied to construction activity, suppose the above-mentioned pipe is part of the process of building a house. The two pieces of pipe are lower-order units relative to the longer pipe. The longer pipe is then joined with other elements to construct the higher-order unit, a shower. The shower is combined with other units at the same level (e.g., a toilet, itself composed of lower-order units) to make the still higher-order unit, a bathroom, and so on.

Human language is also hierarchical in structure.

Phonemes, the sound units of language, are combined to form morphemes or words, the meaning units; these in turn are combined to form sentences, the propositional units; finally, sentences can be combined to form the discourse level of human language (Hockett 1960). An important fact for present purposes is that each level grows in hierarchical complexity as ontogenetic development unfolds.

The relationship between language and object combination, including tool use, has important implications for "cognitive modularity." According to Fodor's (1983; see also multiple book review of Fodor: *The Modularity of Mind*, *BBS* 8(1) 1985) basic notion of modularity, language and object combination would be separate cognitive modules if each were (1) genetically determined, (2) associated with distinct neural structures, and (3) computationally autonomous.¹ The emphasis in this article is on the second criterion. I therefore ask how distinct the neural mechanisms responsible for language are from those that are responsible for tool use and other forms of object combination. The question is approached both ontogenetically and phylogenetically.

The existence of a common neural substrate for language and object combination would be evidence against the hypothesis that these capacities draw on two independent modules, whereas the existence of two distinct neural substrates would be positive evidence for the modularity of these two functions. Developmental data should be particularly useful for understanding the rela-

tion between language and object combination because any search for neural substrates must take into account the fact that the human brain is not static after birth; it undergoes a great deal of postnatal development.

1. Hierarchy in language and object combination

The next two sections show that both object combination and language attain increasing hierarchical complexity as ontogenetic development proceeds.

1.1. The development of hierarchical organization in manual object combination

Lashley (1951) was the first psychologist to notice that complex serial behavior could not be explained in terms of associations between contiguous acts; order must be generated by some higher-level organization. Manual object combination tasks have formed the basis for a research program on the development of hierarchical organization in children (Beagles-Roos & Greenfield 1979; Goodson & Greenfield 1975; Greenfield 1976; 1977; 1978; Greenfield & Schneider 1977; Greenfield et al. 1972; Reifel & Greenfield 1981). Systematic development toward increasingly complex hierarchical organization has been repeatedly observed for object combination in every medium: nesting cups (Greenfield et al. 1972), nuts and bolts (Goodson & Greenfield 1975), construction straws (Greenfield & Schneider 1977), blocks (Greenfield 1976; 1977; 1978; Greenfield & Hubner n.d.; Reifel & Greenfield 1981), and two-dimensional pictures (Beagles-Roos & Greenfield 1979).

As an example, let us take the strategies for combining nesting cups shown in Figure 1. The first manipulative strategy for combining the cups, pairing, involves an asymmetric relationship in which a single active object acts on a single static one. In the second strategy, called the "pot," multiple active objects act on a single static one. In the third strategy, the subassembly, two objects are combined into a pair, which is then manipulated as a single unit in the next combination (Step 2). The strategies develop in this sequential order beginning at 11 months of age (Greenfield et al. 1972). With respect to hierarchical organization, Strategies 1 and 2 involve only one level of combination: Two or more cups are combined in a chain-like sequence to make the final structure. In Strategy 3, the subassembly method, there is an additional level of hierarchy: Two cups are combined to form a higher-order unit, which is in turn combined with a third cup to make the final structure.

Given that the subassembly strategy develops last, the developmental progression is toward increasing hierarchical complexity. As suggested by the developmental theory of Heinz Werner (1957), hierarchical complexity in construction activity can be taken as an index of "manual intelligence."

That the patterns of development of hierarchical organization may be universal is suggested by the fact that they were also exhibited by the Zinacantecos, a Maya Indian group in Southern Mexico, in two kinds of object combination tasks, nesting cups where the sequence has just been described (Greenfield et al. 1989; Greenfield & Childs 1991; Greenfield et al. 1972) and the constructing

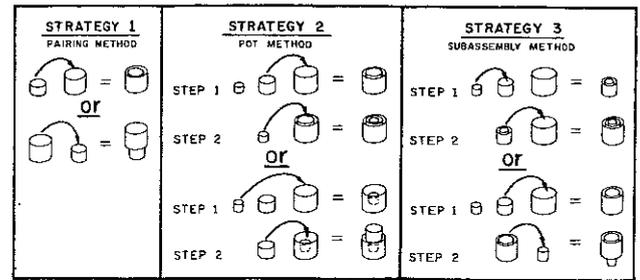


Figure 1. The development of strategies for combining nesting cups. Strategy 1 precedes strategy 2, which in turn precedes strategy 3. The age range of children tested was from 11 to 36 months of age (Greenfield et al. 1972).

of striped patterns with wooden sticks (Greenfield & Childs 1977).

The construction of striped patterns by placing wooden sticks in a frame showed a similar developmental sequence toward increasing hierarchical complexity. For example, whereas younger children could accurately reproduce patterns in which a pattern unit was created by combining sticks of two colors, only older children could reproduce patterns in which two different units, each composed of a different combination of two colors, had to be combined to form a higher-order pattern unit (Greenfield & Childs 1977).

The hypothesis of an innate developmental basis for the nature and sequencing of object-combination strategies becomes even more compelling when one considers that Zinacanteco babies and children had no toys and very few object-manipulation materials in their natural environment. The development of increasing hierarchical complexity of the combinatorial strategies therefore occurred despite the introduction of unfamiliar materials and tasks by the foreign experimenters.

1.2. An example of increasing hierarchical complexity in grammatical development

As it develops, grammar becomes increasingly complex in hierarchical structure, as illustrated by the earliest stages in Figure 2. The child starts with one-word utterances (e.g., Figure 2a). In the next developmental step, two words are combined to form a higher order grammatical relation; for example, the relation of attribution is shown in Figure 2b. The next level of grammatical complexity finds adjectives and nouns combining to form a superordinate noun phrase, which, in turn, enters into a still higher order combination with a verb (Brown 1973). The latter can be exemplified by the utterance from Brown's (1973) corpus, *want more grapejuice*, which is diagrammed as a tree structure in Figure 2c. Comparing Figures 2a, 2b, and 2c makes the growth in hierarchical complexity clear.

Modern linguistic accounts of grammar also emphasize hierarchical structure in mature human language. Although Chomsky's original accounts (1957; 1965) of tree structure as a representation of both the underlying grammatical structure of a sentence and its surface manifestation are no longer popular, more recent analyses have not abandoned the centrality of hierarchical organization (e.g., Hyams 1986). There is widespread agree-

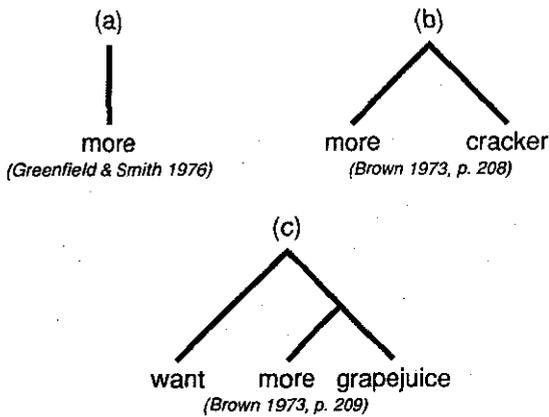


Figure 2. The development of increasing hierarchical complexity in early syntax. Nodes are not labeled in order to avoid a commitment to a particular theoretical description. The important point about (c) (which would not be disputed by any theory) is that *more* plus grapejuice forms a single complex unit, which, in turn, relates to *want*.

ment with Chomsky's (1959) argument that language cannot be analyzed as a sequential or Markovian chain of stimuli, but must be considered in terms of its hierarchical organization.

1.3. An example of parallel structural development in the domains of grammar and object combination

The earlier writings of Greenfield and colleagues emphasized the parallels between the development of object combinations and word combinations (grammar). Whereas Figure 1 presented the developmental sequence of manipulative strategies for combining nesting cups, Figure 3 depicts parallels between the same sequence and the development of children's sentence types, as formulated by Greenfield et al. (1972). Note that the grammatical analogies portrayed in Figure 3 involve quite complex structures. On the other hand, it would also be possible to say that *more cracker* (Figure 2b) involves a pairing strategy on the level of word combination, whereas *want more grapejuice* (Figure 2c) involves a subassembly. Although many analogies are possible, the problem of finding one based on the more interesting cognitive property of homology is of central importance in the sections that follow.

On the level of manual action, each combinatorial strategy constitutes a way of ordering sequential action by using a hierarchical organization of greater or lesser complexity to construct relations among objects. Grammar does the same for words. Each stage of object combination in Figure 1 appears to result from a developmental constraint on hierarchical complexity, lifted at the subsequent stage. For example, the child at the pairing stage (left side of Figure 1) seemed no more capable of creating a "pot" structure, the next level of hierarchical complexity (middle of Figure 1), than would a child at the one-word stage be capable of producing a two-word sentence. This impression of constraint comes from the fact that each child in Greenfield et al.'s (1972) nesting cup study was shown the most hierarchically complex strategy (the subassembly in Figure 1) as a model to

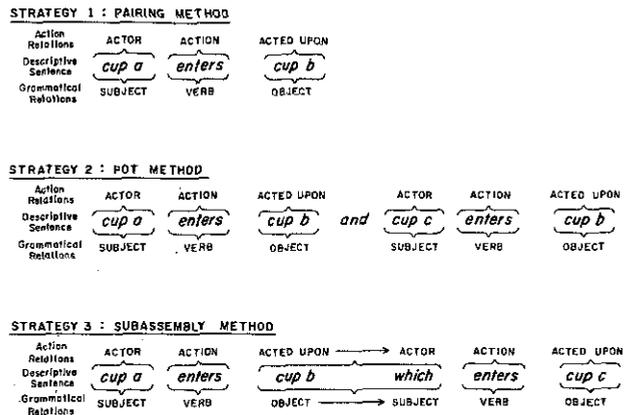


Figure 3. Structural analogy between object combination strategies and sentence types. Each sentence both describes a corresponding object combination strategy and parallels it in structure. In ontogenesis, the three sentence types develop in the same order as the three object combination strategies (Greenfield et al. 1972).

imitate. The actual strategies used in response to this uniform model, however, showed varying degrees of simplification that were inversely related to age, with no 11-month-old child ever achieving the subassembly strategy over eight trials with the cups.

2. Analogy or homology?

In evolutionary theory an analogy is based on a structural or functional parallel without any common origins, whereas a homology involves not only parallel structure but parallel origins in the phylogenetic history of the species. In developmental psychology homology refers to common structural origins in the ontogeny of individual members of the species (Bates 1979). Whereas phylogenetic homology is defined as descent from a common antecedent structure within an ancestral species, ontogenetic homology can be defined as descent from a common antecedent structure within the same organism.

There is a close relationship between the two usages, because the phylogeny of a species is a history of ontogenies. With respect to the parallels between language and object combination, analogy would be much weaker than homology. Analogy, implying distinct cognitive modules, is quite compatible with modularity; homology, implying a single underlying cognitive module for language and manual object combination, is not.

Greenfield and colleagues were limited in their experimental methods to demonstrating analogies between the development of linguistic grammar and of manual object combination. They speculated, however, that these analogies might be based on an underlying homology. Greenfield et al. (1972) wrote, "The importance of the action-grammar analogy lies in the possibility that the same human capacities may be responsible for both types of structure" (p. 305). Nevertheless, the question remained open.

Behaviors are considered homologous only if they are regulated by the same (neuro)anatomical structures (Hodos 1976; Lenneberg 1967; Steklis 1988), so the way

to decide between analogy and homology is to determine whether the neural basis of hierarchically organized computational structure is specific to language or is also used to support hierarchical organization in another area of development, manual object combination.

2.1. Neural evidence in favor of homology

Grossman (1980) used the double dissociation technique with patients who had brain damage in known locations to provide evidence of a common neural substrate for hierarchical organization in grammar and manual construction activity. He gave the tree structure task developed by Greenfield and Schneider (1977) to adults with different sorts of cerebral injury. One group was composed of agrammatic patients with Broca's aphasia; this group was central to Grossman's argument for a central processor for hierarchically structured material, including language. The other groups were fluent aphasics, nonaphasics with injuries lateralized to the right hemisphere, alcoholic Korsakoff patients, and normal controls.

2.1.1. A theoretical approach to Broca's area. Because Broca's area is central to the rest of the argument in this article, it is important to be specific about it. It is located in the ventral region of the left frontal lobe of the cerebral cortex, but there has always been disagreement about what its exact boundaries are. One reason is that there is a larger, more complex region involved in Broca's aphasia than the discoverer of the area realized in the nineteenth century (Deacon 1990a). A second, even more important reason is that the functions of this area are carried out, not by a single localized brain region acting in isolation (Deacon 1990a), but by various circuits, extending beyond the region itself. A major goal of this article is to provide evidence for a theory of different functions, subareas, and connections within the left ventral frontal region of the cortex without trying to identify a particular subarea as *the* Broca's area.

2.1.2. Evidence from adult aphasics. Broca's aphasia is associated with lesions in Broca's area, often involving portions of the adjacent facial motor cortex (Geschwind 1971) and prefrontal cortex (Deacon 1989). A major subgroup of Broca's aphasics is unable to produce syntactically organized speech, a major component of agrammatism.

Agrammatic Broca's aphasics lack hierarchical organization in their syntactic production. Here is an example of agrammatic speech from Goodglass and Geschwind (1976, p. 408): "And, er Wednesday . . . nine o'clock. And er Thursday, ten o'clock . . . doctors. Two doctors . . . and ah . . . teeth. Yeah . . . fine." Structurally, this speech is mainly a string of one-word utterances. There is no utterance with a syntactic tree structure even as hierarchically complex as that shown in Figure 2c. Grossman predicted that such patients would also have trouble in constructing nonlinguistic tree structures. He suggested that the parallels between language and hierarchically organized construction activity identified by Greenfield and colleagues were not mere analogy, but had a common basis in the brain itself. His hypothesis was that Broca's area functioned as a supramodal hier-

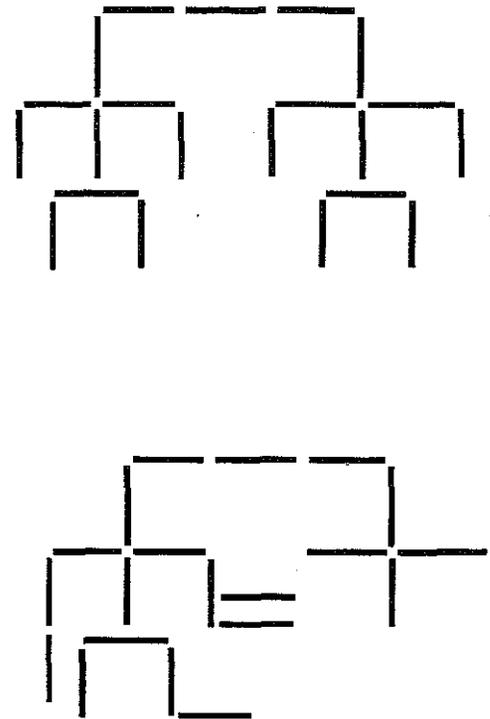


Figure 4. Hierarchical tree structures used as models in Grossman's (1980) study. The upper tree is symmetrical, whereas the lower tree is asymmetrical.

archical processor organizing grammar and manual object combination.

To test this hypothesis, each subject in Grossman's study was given two hierarchically organized tree structures to copy using tongue depressors. The one on the top of Figure 4 had been developed by Greenfield and Schneider (1977) for a developmental study of children aged 3 to 11. The one on the bottom was developed by Grossman to add the structural feature of asymmetry.

The results supported the hypothesis of a supramodal hierarchical processor. In reconstructing the model tree structures from memory (where a mental representation would be required), the Broca's aphasics did not have a general problem in construction but a specific deficit in representing the hierarchical organization of the models. (This deficit did not show up when the model was present.) A construction was counted as replicating the hierarchical structure of the model if it "exhibited two or more sub-complexes vertically subordinate to a unifying structure" (Grossman 1980, p. 301). Of all the pathological groups, the Broca's aphasics were the most successful (and closest to the normals) in matching the number of sticks used in the models. They were the *least* successful (and farthest from the normals), however, in recreating the model's hierarchical structure under a memory condition, where the model was taken away. Figure 5 shows two examples of nonhierarchical constructions created from memory by two Broca's aphasics, as well as the contrasting hierarchically organized constructions produced by fluent or Wernicke's aphasics.

The hierarchical constructions of the fluent aphasics with lesions in the left posterior area of the brain further supported the conclusion that the left frontal region of the

BROCA'S APHASICS

FLUENT APHASICS

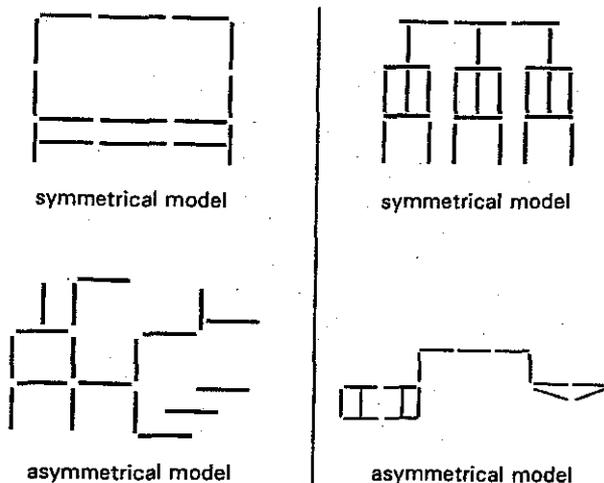


Figure 5. Reproduction of symmetric and asymmetric models by Broca's and fluent aphasics (Grossman 1980).

brain, in which Broca's area is found, processes hierarchical structure in both the grammar of language and the combination of objects. Fluent aphasics produce speech that is semantically empty but has hierarchically organized (if not always correct) syntax. Here is an example from Goodglass and Geschwind (1976, p. 410): "The things I want to say . . . ah . . . the way I say things, but I understand mostly things, most of them and what the things are." Interestingly enough, fluent aphasics also did very well at reproducing the hierarchical structure of the models, although their tree structures, like their sentences, were not always correct (compare Figure 4 and the right side of Figure 5).

In summary, data from the fluent aphasics with their intact left frontal area of the cortex further supported the relationship between this region and hierarchical organization in both language and construction activity.

Further evidence along the same lines was provided by an examination of the strategies used to construct the symmetrical model. Greenfield and Schneider (1977) had looked at the degree to which the "surface structure" of the construction process (the serial order in which pieces were added) reflected a mental representation of the tree structure. The youngest children (age six) who successfully copied the model used a nonhierarchical, chain-like

strategy in which an element would be placed adjacent to the one added just before it (see left side of Figure 6). Seven- and nine-year-olds followed the hierarchical organization of the model in their "surface structure" strategy, proceeding from superordinate (top) to subordinate (bottom) components (middle of Figure 6). Finally, many of the 11-year-olds used a top-down method in which they just skipped from one branch to another in building the structure (right side of Figure 6). This strategy was considered to indicate internalization of the hierarchical organization of the model.

Grossman (1980), using a similar measure of shifting from one part of the structure to another, found that the Broca's aphasics were most chain-like in their placement strategy. Thus, if the foregoing analysis is correct, Broca's aphasics gave the least evidence of having a mental representation of the overall hierarchical structure. The fluent aphasics, in contrast, used the hierarchical strategy *more* than the normal control group.

Note that in the foregoing Broca's speech sample the only grammatical relation to be expressed is conjunction (*and*). Conjunction is basically syntactic chaining. As such, it is an analogue to the chaining strategy used by Broca's aphasics to construct a physical tree structure in Grossman's experiment. (Although there is insufficient space to discuss the current controversies concerning the underlying nature of Broca's aphasia or agrammatism [see Bates and Thal 1989], our analysis might ultimately shed light on this theoretical problem.)

In summary, the pattern of group differences indicates a *specific deficit* in hierarchical organization associated with lesions in a specific region of the brain: Broca's area in the left hemisphere. Neural specificity is further supported by the fact that this performance was not only associated with Broca's aphasia; it was also *absent* in any other group, pathological or normal. Hence we have a double dissociation. [See multiple book review of Shallice: *From Neuropsychology to Mental Structure*, BBS 14(3) 1991.]

2.1.3. Evidence from direct study of the ventral region of the left frontal lobe through positron emission tomography. Direct observation of normal brain function through positron emission tomography (PET scan) has yielded new evidence concerning the functions of the ventral region of the left frontal lobe, what the researchers call Broca's area (Fox et al. 1988). The area functions in conjunction with the relevant area of motor cortex: the

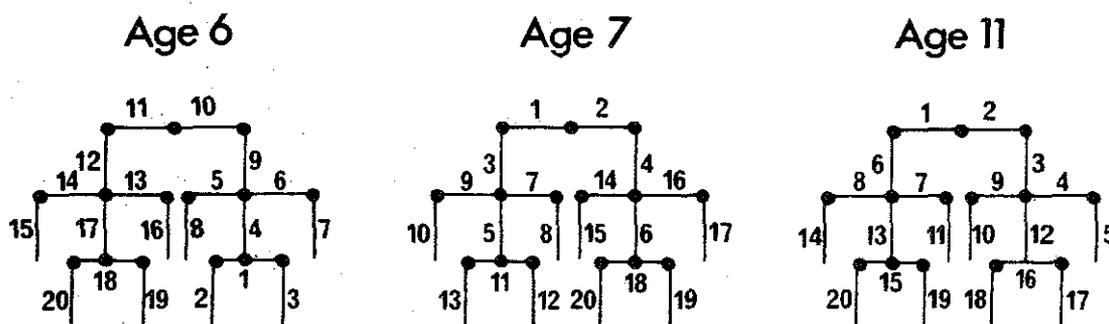


Figure 6. Typical construction strategies at different ages. Numerals indicate the serial order in which the pieces were added (Greenfield & Schneider 1977).



mouth and tongue area for imitated speech, the hand area for hand movements. Thus it is part of a number of different cortical circuits or networks involving various parts of the motor cortex. The area can also decouple from the motor cortex when movement is mentally represented but not carried out. When subjects were asked to imagine a hand movement, Broca's area "lit up" in the PET scan, but the hand area of the left motor cortex did not. These findings provide strong and direct evidence that the general region in which Broca's area is located has a directive or programming function for simple responses in a variety of modalities. Other research assessing regional cerebral blood flow during various tasks has established that Broca's region is implicated in (1) grammatical descriptive speech and (2) motor sequencing (Roland 1985).

A number of investigators have noted more generally that the left hemisphere controls sequential manual as well as linguistic production (Calvin 1990; Kimura 1979; Lieberman 1990; Steklis & Harnad 1976). Their work provides context for the more specific findings.

2.1.4. Evidence from childhood aphasia. Cromer (1983) tested a group of children with "acquired aphasia with convulsive disorder" on hierarchically organized drawing and construction tasks, based on Greenfield & Schneider's (1977) mobile (also used by Grossman [1980] and shown at the top of Figure 4). These children lacked all language and, in addition, appeared to lack such hierarchical organizing skills in other domains as the perception of rhythms. Although these aphasic children could draw and construct the modeled tree structure by using a chain-like serial method, they could not do so when required to use hierarchical planning to build up the model in terms of its subunits. Their scores reflecting the hierarchical organization of serial acts were significantly lower than those of age-matched profoundly deaf and normal children. In this study, the correlation between language and action is more global than in Grossman's (1980) study because the aphasic children (ranging in age from nine to 16 lack *all* aspects of language, not merely hierarchically organized grammar. Nevertheless, the study is of interest here because it provides converging evidence for a generalized hierarchical processor at an earlier point in development.

2.2. Neuropsychological evidence against homology

Curtiss, Yamada, and Fromkin (Curtiss & Yamada 1981; Curtiss et al. 1979; Yamada 1981) also used neuropsychological cases and several of Greenfield's grammar-of-action tasks to explore the relation between grammatical structure and action structure. Their subjects were eight mentally retarded individuals aged 6½ to 20. They found that certain members of their sample were skilled at the hierarchically organized construction tasks but weak in grammatical structure, whereas others had hierarchically complex grammatical structures but were limited to extremely simple constructions. This pattern of results indicates a *dissociation* between the neural substrate for the hierarchical organization of grammatical structure and the hierarchical organization of object-combination activity.

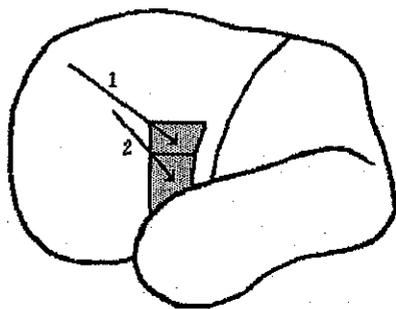
On the one hand, the results of Cromer (1983), Fox et

al. (1988), Grossman (1980), and Roland (1985) suggest there is a unified supramodal hierarchical processor and hence a homologous relationship between hierarchical organization in language and manual construction. On the other hand, Curtiss, Yamada, and Fromkin's results indicate separate neural modules for hierarchical organization in each domain; their results reduce parallel hierarchical development in language and manual object combination to mere analogy. How can these conflicting results be integrated and reconciled?

2.3. Using neural circuitry and its development to resolve the conflict between analogy and homology

The first clue to a resolution lies in the fact that Broca's area must be connected to more anterior areas of the prefrontal region of the brain, areas that specialize in programming and planning of all kinds (Fuster 1985; Luria 1966; Stuss & Benson 1986). Hierarchical organization is intrinsic to planning because, at its most basic level, a plan subordinates component elements to a superordinate goal (Bruner & Bruner 1968; Miller et al. 1960). This planned quality is also central to object combination activity and to complex sentential structure (Ochs Keenan 1977). Indeed, Petrides and Milner (1982) have demonstrated that patients with left frontal lobe excisions but intact Broca's areas are very much impaired, relative to a variety of control groups, on the strategic or planning aspect of a sequential manual task.

In fact, as mentioned earlier, many Broca's aphasics have also suffered damage to the adjacent prefrontal area (Deacon 1989). It is in this circumstance that agrammatism appears (Lieberman 1988; 1990). It may be that some Broca's aphasics show disruption in the hierarchical organization of both grammar and manual object combination activity because of damage to two different circuits emanating from the region of Broca's area (Brodmann's areas 44 and 45). The circuit for the hierarchical organization of manual sequences would include the anterior superior prefrontal cortex (Brodmann's area 9; Roland 1985). A second circuit for the hierarchical organization of grammar would include an area of the prefrontal cortex just superior and anterior to Broca's area (Ojemann 1983; Stuss & Benson 1986), probably Brodmann's area 46. (Roland's findings are based on the measurement of regional cerebral blood flow; Ojemann's are based on electrical stimulation mapping; Stuss & Benson's are based on clinical brain lesion data.) The participation in two different circuits involving the anterior prefrontal region would result in the differentiation of Broca's area itself. The hypothesized circuits are shown in Figure 7. The arrows indicate the direction of control. The lower circuit would be associated with the syndrome called Broca's aphasia. One group of Broca's aphasics has difficulty in speech production; these presumably have damage to the circuit linking Broca's area to the facial motor cortex (see right side of circuit 2, bottom of Figure 11). If only the circuit linking Broca's area to the facial motor cortex were damaged, the motor aspects of speech production (articulation), including the motor aspects of word combination, would be impaired, but there would be no real agrammatism. If the prefrontal part of the circuit were damaged, however, agrammatism would result. It might therefore be more accurate to reserve the



- 1 = manual object combination circuit
 2 = grammar circuit
 ● = region of Broca's area

Figure 7. Hypothesized neural circuits for the hierarchical organization of complex object combination and complex grammar. This is a schematic representation based on a synthesis of data from Fox et al. (1988), Ojemann (1983a; 1983b), Roland (1985), Simons and Scheibel (1989), and Thatcher (unpublished data, 1991). The anterior pole of the grammar circuit (Brodmann's area 46) is based on Ojemann (1983a; 1983b). The anterior pole of the manual object combination circuit (Brodmann's area 9) is based on Roland (1985). The role of Broca's area is based on Fox et al. (1988), Roland (1985), and Simons and Scheibel (1989).

term Broca's aphasia for the articulatory deficits arising from damage to the circuit controlled by the classical Broca's area, reserving the term agrammatism for deficits involving the anterior part of the cortical grammar circuit depicted in Figure 7, controlled by a region anterior to Broca's area itself.

The conclusion that two separate circuits are involved leads to a resolution of the conflict. Because of the topographical proximity of these two circuits, most often a lesion to the left frontal area would destroy both; occasionally, however, one of the circuits would be spared. In the former case, there would be an association between the hierarchical organization of language and manual object combination; in the latter case there would be a dissociation. Curtiss et al.'s (1979) subjects with diffuse neural damage might then happen to have had one intact circuit without the other, leading to the observed dissociations between syntactic structure and manual action structure.

Although Fox et al. (1988) call this region Broca's area and treat it as unitary, our theory would posit that it has, by adulthood, differentiated into two functionally distinct though neighboring areas, one controlling speech, the other manual action, as described earlier. Because of the imperfect resolution of the PET scan, these two subareas were probably visualized as one single region in Fox et al.'s (1988) research.

Some evidence for this hypothesis of two separable circuits comes directly from Grossman's (1980) data. Although the memory constructions of the Broca's aphasics were hierarchically organized (i.e., they exhibited two or more subcomplexes vertically subordinate to a unifying structure) significantly less often than with normal controls or fluent aphasics, an inspection of the original protocols, kindly supplied by Grossman, indicated that a minority of the agrammatic subjects was able to construct hierarchical arrangements in the tree structure tasks. The implication is that the agrammatic pa-

tients with damage to both the grammatical and the manual programming circuits (the majority) failed to represent their tree constructions hierarchically, whereas patients with damage to the grammatical circuit alone (the minority) were able to represent and build hierarchically organized constructions.

Until now the picture is one of separate circuits connecting partially contiguous brain regions so that it is possible, although not likely, to damage one circuit without the other. Specific circuits directly connecting various cortical areas, particularly distant ones, however, are not present from birth; such circuits or networks are the product of gradual postnatal differentiation (Thatcher et al. 1987). New neural connections are added in a diffuse manner through early infancy. After that, processes of "pruning" of synapses (Huttenlocher 1979) in combination with selective dendritic and axonal growth (Kolb & Whishaw 1985) lead to more specific and differentiated neural circuits between spatially separated cortical areas (Thatcher et al. 1987). Hence, Broca's area might start out, early in development, as an undifferentiated neural region, programming both manual action and language production. At this point, one would expect the functioning of this cross-modal area to be quite diffuse and immature as well. As Broca's region developed differentiated circuits or networks involving more anterior portions of the left prefrontal cortex, the structure of manual action and of language would become more divergent, autonomous and complex.

Although this position might seem at first to conflict with the rostral (frontal pole) to caudal (precentral gyrus) trend for increasing modality segregation in the frontal lobes (Deacon 1990c), the conflict is more apparent than real. It is necessary to distinguish between a neural *area* and a neural *circuit*. It is the growth of connections to the rostral area of prefrontal cortex that creates specific circuits for the complex structures in manual action and language. This does not imply that the rostral prefrontal areas in question are modality specific. Indeed, I would predict that the rostral area around Brodmann's area 46 would not only participate in the circuit required for the production of syntax, but also in the circuit for syntactic comprehension. Consequently it would, in hearing speakers, have a common abstract function across two modalities, vocalization and audition. In addition, I predict that the same rostral prefrontal area would participate in the production of sign language syntax in deaf people, thus demonstrating its use for an abstract function not specific to a particular sensory modality.

It is the presence of multiple short range connections in all directions, hypothesized to exist early in development, that makes the caudal inferior frontal area (roughly Brodmann's area 44 and 45, also known as Broca's) *cross-modal*. This is the undifferentiated state referred to above. The area is not really *amodal* or *supramodal* in the same sense as the more rostral (anterior) areas are: It does not have an abstract, modality-free function. Its cross-modal connections are in fact quite specific: They are limited to such neighboring areas as the orofacial motor area.

This could explain the shortcoming of predicting from a caudal-rostral (i.e., back to front) developmental trend in frontal cortex that relatively complex motor skills should mature before the learning of even simple skills that

require supramodal integration of many modalities. Such a view, for example, leaves unexplained the very early development of intentional thumb-sucking, a cross-modal integration of hand and mouth. (Note that the term modality has been extended from sensory modalities to the output modalities of relevance here.) The cross-modal connections of an undifferentiated Broca's area could explain this early development.

Most important, at maturity, there would be separate subregions of Broca's area for language and manual action. Hence, the state of the mature left frontal lobe of the cortex would conform to the rostral-caudal (i.e., front to back) trend for increasing modality segregation: At maturity Broca's area could be less modality specific than motor cortex, more modality specific than prefrontal cortex.

2.4. Theoretical predictions

A number of predictions flow from the theoretical model developed so far:

1. The hierarchical organization of language and manual object combination, including tool use, should be closely linked and interdependent early in development, the two domains becoming more autonomous as brain differentiation proceeds.

2. The ontogeny of left frontal lobe circuits should furnish the cortical basis for the hierarchical organization of speech and manual object combination, including tool use.

3. The schedule of cortical differentiation should correlate with the relative interdependence and autonomy of the two domains in behavior.

The first prediction is the focus of section 3, the second and third of section 4.

3. The ontogeny of relations between language, object combination, and tool use

3.1. The organization of language and manual object combination are more closely linked when language development begins

A retrospective look at the grammar of action studies carried out by Greenfield and colleagues indicated that the analogy between grammar and object combination was much stronger in the nesting cup study (see Figure 1) done with the youngest children (aged 11 to 36 months) than it was in the subsequent studies carried out with children aged three and up. Whereas in the first study (Greenfield et al. 1972) it was possible to describe precise parallels between the structure of word combination and object combination (see Figure 3), this was impossible for the more complex structures modeled for the older children (e.g., the tree structure at the top of Figure 4, used by Greenfield & Schneider 1977).

Other clues in this direction come from the close connections and parallels between language and action up to age two. For example, the child's one-word and two-word utterances, spanning the age period one to two, are placed in a sensorimotor framework supplied by the child's own perceptions, actions, and gestures (Bloom 1973; Brown 1973; Greenfield & Smith 1976). Lock (1990) points out that at 13 months, the child has a parallel

repertoire of vocal and manual gestures, to the point of equipotentiality for either spoken or sign language, depending on circumstances; Volterra (1987) has provided the empirical evidence for such a conclusion. Bates (1988) notes that meaningful relations between language and other modes of action last until approximately two years of age. With each subsequent stage of development, however, the child's linguistic productions become increasingly autonomous from sensorimotor activity (e.g., Greenfield et al. 1985; Karmiloff-Smith 1979).

If the early development of hierarchical structure in both language and manual object combination is being organized by the same undifferentiated brain region, then one would predict not only parallel sequences of structural development in the two domains, but also synchrony in developmental timing. The parallel structures depicted in Figure 3 are definitely not synchronous, however. For example, two objects (e.g., nesting cups) can be combined long before two words (Figure 2b) can be combined into a primitive sentence. The temporal gap until sentences of the complexity shown in Figure 3 can be produced is much longer still.

3.2. Sound combination and object combination develop synchronously in a structurally parallel sequence

Lieberman (e.g., 1984) emphasizes Broca's area as the seat of phonological as well as grammatical programming. He has therefore suggested (personal communication, 1988) that developmental parallels to grammars of action should be sought in *phonological rules for combining sounds*, not merely in grammatical rules for combining words. As the following analysis shows, this strategy has begun to yield very rich results.

3.2.1. A note about methodology. It should probably be mentioned at the outset that the main source for the parallels to be described lies in diary data from three children. Whereas there are many excellent studies of phonological development in various languages, none includes parallel observations of object combination. The diary observations of phonological development have nonetheless been supplemented by the findings of Smith (1973) and Macken (1979). Many other comprehensive studies of phonological development (e.g., Ferguson & Farwell 1975) have taken an analytic perspective so different that they do not provide the kind of information about the differentiation of word structure that is relevant here.

3.2.2. The evidence. The earliest meaningful words begin toward the end of the first year when children begin to combine two objects intentionally. Most interesting, the phonological and syllabic structure of these first words bears a formal resemblance to the initial way in which objects are combined. The earliest words are reduplicated consonant-vowel syllables such as *dada* or *mama* (e.g., Greenfield 1972; Greenfield, unpublished data). In data from one child, Lauren (Greenfield 1972), this occurred at 8 months, 3 weeks. In these sound combinations, a single consonant is combined repeatedly with the same vowel. Children's first intentional combinations of objects occurring around the same time have a parallel structure: One object is repeatedly touched to a second one (Piaget 1952).²

Diary data from three children – Lauren, Matthew, and Nicky (Matthew and Nicky's data are from the study described in Greenfield & Smith 1976) – indicate a second stage of word formation, following a few months later, in which a single consonant can be combined with a single vowel to form a word (e.g., Nicky's *na* for "no" at 12 months, 1 week of age; Lauren's *ma* for "milk" at 12 months, three weeks of age). This state also has a parallel stage of object combination occurring at roughly the same age: One object is combined with another, as when one cup is placed in or on a second, as in the nesting cup study (Greenfield et al. 1972). (The pairing strategy is shown at the left side in Figure 1.)

A third stage of word formation is characterized by a process called consonant harmonization (Smith 1973; Macken 1979). In consonant harmonization, the first sound, a single consonant, remains constant as it is successively combined with two different vowels. The earliest examples from my data are Nicky's *daddy* at 16 months, 2 weeks; Lauren's *baby* around 13 months; and Matthew's *cackuh* (cracker) at 12 months, 3 weeks.

On the level of object combination, there is also a parallel strategy in which the first object to be picked up remains constant as it is successively combined with two other objects in turn. In the nesting cup study, this strategy occurred when a baby would place the first cup in or on a second one and would then remove it without ever letting go of the cup, placing it in or on a third cup (Greenfield et al. 1972). Lauren was observed using this strategy for combining objects at 12 months, 1 day, when she successively placed a red circle in the red and blue holes of a form board. (Note that the timing is about one month before the first observation of her comparable word form; this timing seems quite close, considering that no systematic diary had been planned for object manipulation.)

The next development in word formation also involves harmonization, this time of the vowel. In this structure, the initial consonant varies, whereas the second sound (a vowel) with which it combines remains constant. The earliest examples in the Greenfield data are as follows: from Lauren, *tinky* (stinky) (the *n* is considered part of the vowel sound) at 15 months, 1 week; from Matthew, *kye bye* (car bye-bye) at 15 months. (Note, in Matthew's example, that the combination of two words seems to follow as a consequence of more complex syllable structure in the formation of a single word; this may provide a key to the mechanism that provides the transition from single-word utterances to combinatorial speech.) This important point will be elaborated in section 3.4.

The parallel object combination strategy was called the "pot" strategy in the Greenfield et al. (1972) nesting cup study (Figure 1); in that strategy, the initial moving cup varies while the "pot" with which each cup combines remains constant. In the nesting cup experiment, this strategy became dominant at 16 months of age. In addition to appearing at the same place in the developmental sequence as the corresponding stage of word formation, the age of appearance is within a month of the age for the corresponding word formation strategy.

The next stage of word formation involves combining already developed syllabic subassemblies into higher-order units. This can involve adding a consonant-vowel

combination to a second consonant to form a phonologically more complex word (e.g., *ball*, from Matthew at 15 months, 3 weeks) and/or making a two-word sentence out of two previously constructed sound combinations (e.g., *bye-bye tat* [cat] from Lauren at 15 months, 2 weeks).

In parallel fashion, the final stage of object combination identified in the nesting cup study was also termed the subassembly strategy. In that strategy, at least one previously constructed subassembly of cups functioned as a unit, combining with another cup or subassembly of cups (see right side of Figure 1). This strategy first appeared at age 20 months in the study by Greenfield et al. (1972).

In summary, from about 9 to 20 months of age, children pass through parallel and quite synchronous stages of hierarchical complexity in forming spoken words and combining objects. Although the quantitative evidence is preliminary, the qualitative parallels in sequencing and timing between the two domains are striking. In addition, it is clear that developments in word formation and object combination are taking place in a single chronological period that ends around two years of age.

Hence, preliminary evidence indicates that the first requirement for establishing a developmental homology – synchronous and parallel developmental sequences – can be satisfied. Although it could be argued that with such young children it is easy to find simultaneous development in several domains, it is not easy to find identical structural substages; nor is it easy to find a close correspondence in the timing of the substages (cf. Fischer & Hogan 1989). Most crucial, such sequences are not the final criterion for homology. What is being argued is that they make it worthwhile to look in this age range for evidence of the development of a common neural substrate, a topic considered in section 4.

3.3. The ontogeny of tool use

In this section, the earliest development of tool use in human infants is shown to be a special case of the development of object combination programs already described. In trying to establish the earliest tool use as a special case of the earliest stages in the development of grammars of action, I rely on a recently published study by Connolly and Dalglish (1989) on the ontogenesis of the use of a spoon, the Euro-American infant's first tool. Basic tool use can be thought of as just that type of object combination in which a single acting object serves as an instrument to act on a second object, thereby achieving a specified goal (cf. strategy 1, the pairing method, in Figure 1). Although Connolly and Dalglish (1989) did not look at the development of tool use through the lens of grammars of action, their observations have such beautiful detail that it was possible to reconstruct stages of hierarchically organized object combination.

Just as in the earliest stage of object combination already described, some of the youngest babies (11–12 months) in Connolly and Dalglish's study were observed to put a spoon repeatedly in and out of the dish. Other children of this age simply put their spoons in and out of their mouths; Gesell and Ilg (1937) had observed this behavior and placed it at 10 to 12 months of age. In both cases, the strategy consists of taking one object (the

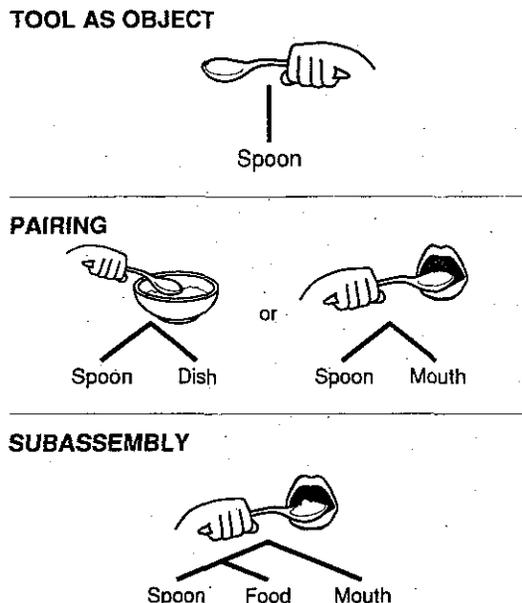


Figure 8. Developmental stages in the hierarchical organization of spoon use, based on data from Connolly and Dalgleish (1989). The first stage (top) is not referred to in the text because it is precombinatorial. The top drawing simply depicts an earlier stage at which the child is limited to grasping the spoon, like any other object.

spoon), which has the acting role, and repeatedly combining it with a second object that is acted on. As in the pairing stage of the nesting cup strategies, the child is restricted to combining two objects at a time: either spoon and dish or spoon and mouth, but not all three. (See pairing stage of spoon use, Figure 8). Thus tool use reveals the same combinatorial rule described above as

the first stage in the structural development of object combinations, with its parallel in the first stage of sound combination (see first panel of Figure 9).

The next stage of spoon use is also structurally parallel to a later way in which infants combine two objects at a time: The infant first touches the spoon (Object 1) to the food (Object 2) and then to the mouth (Object 3) (but no food arrives at the mouth). This is a variant of the pairing strategy observed in the nesting cup study in which the infant places an acting cup in or on a second cup, then removes it (without letting go) to place it in or on a third cup. This strategy parallels the strategy of word formation in which the same initial consonant successively combines with two different vowels (e.g., the *baby* example presented earlier).

The last stage of spoon use (bottom of Figure 8) is parallel to the subassembly strategy, the final nesting cup strategy (see right side of Figure 1). In this stage, the infant combines spoon with food, initially through a side-to-side scoop, and then moves the subassembly of spoon plus food to the mouth, the final object. Once again, there is a parallel stage of sound combination (the right side of Figure 9).

Although no analogue to the intermediate "pot" strategy was reported by Connolly and Dalgleish (1989), I would predict that there was one, based on theoretical considerations as well as some suggestive observations in the Connolly and Dalgleish article. I would predict an intermediate stage like the following: Baby brings spoon directly to mouth with one hand while bringing food to mouth with the other. The mouth very literally would serve as a "pot" for two objects, food and spoon. This is structurally analogous to the "pot" method shown in the middle of Figure 1. (See middle of Figure 9 for the parallel between this structure and a corresponding structure of word formation.)

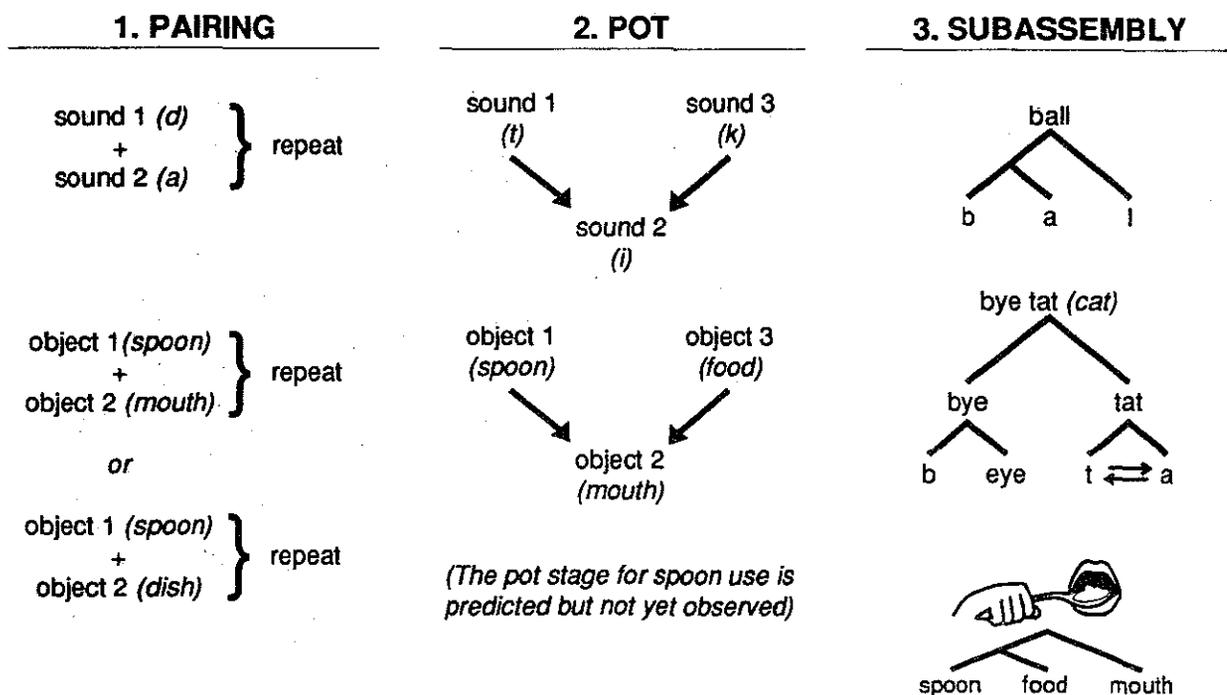
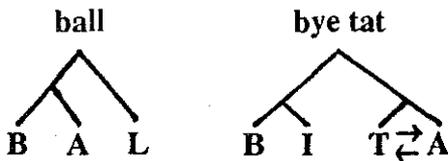
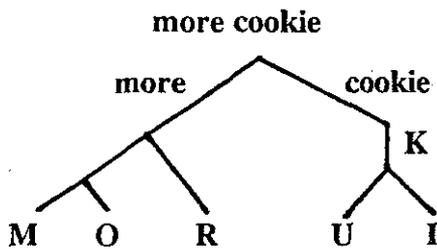


Figure 9. Parallels in the development of sound combination and object combination: The case of spoon use.

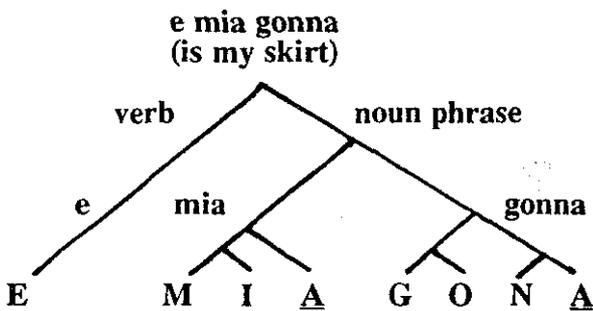
15 Months



21 Months



22 Months



23 Months

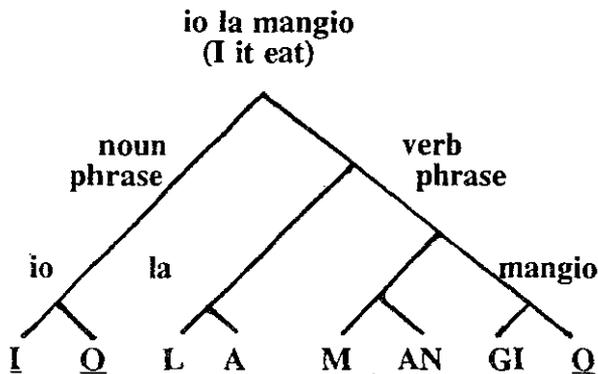


Figure 10. Hierarchical relations between word formation and sentence formation in development. (Underlined letters indicate possessive-noun agreement in "mia gonna," subject-verb agreement in "io la mangio.")

In terms of developmental timing, the sequence of structural stages of tool use covers the period from 12 to 23 months of age studied by Connolly and Dalgleish (1989), approximately the same period in which the nesting cup strategies and analogous word formation strategies were observed. The qualitative stages of spoon use observed so far indicate that the development of tool use is an instance of the hierarchical development of object combination strategies, more generally conceived.

3.4. The relation between sound combination and word combination

The developmental sequence described earlier leads to the following hypothesis: The ability to combine two words under a single intonational contour – that is, making a sentence – is an outgrowth of the ability to combine sounds into increasingly differentiated syllables. (It is the existence of one intonational contour, rather than two, that separates a two-word utterance from two successive one-word utterances.) Thus, Matthew's *kye bye* occurs at the same age as Lauren's *tinky*; the phonological construction of Matthew's two-word utterance is the same as that of Lauren's single word: (consonant 1 + vowel 1) + (consonant 2 + vowel 1). Similarly, a few weeks later, Matthew's single word *ball* has the same number of hierarchical levels as Lauren's two-word utterance *bye-bye tat* (see Figure 10).

This hypothesis fits with the notion that Broca's area is the seat of both phonological and grammatical programming. If the development of phonological combinations and early word combinations is part of a single unified process, it makes sense to put it under the programming control of a single neural area, hypothesized to be the region in which the classical Broca's area lies.

It follows from this hypothesis that the total hierarchical complexity of an utterance involves a synthesis of the phonological and morphological levels of combination, as Figure 10 shows.³

3.5. The differentiation of hierarchical organization in language and object combination

Developmental information about grammars of action and language suggests that programs for combining objects become increasingly differentiated from programs for combining words (linguistic grammars) starting around two years of age. After 20 months of age, the hierarchical organization of language continues to increase. Consider the utterance *more cookie* (Figure 10), for example. It is still a two-word combination, like *kye bye* or *bye tat*, but it has another level of hierarchical complexity: There are now three rather than two levels of branching nodes. In addition, there is now evidence of the beginnings of syntactic organization – word order: In the corpus at this time, the overwhelming majority of two-word combinations observes English word order.

The next example in Figure 10, *e mia gonna*, illustrates the subsequent stage of hierarchical complexity as well as morphological marking. *E mia gonna* ([It] is my skirt) was produced by an Italian child of 22 months (Hyams 1986, p. 138). As Hyams notes, the richer inflections of Italian relative to English make it possible to illustrate this phenomenon at this early age. Using the same method for

noting the hierarchical organization of words and their combination, Figure 10 shows that hierarchical structure has increased: There are now four levels of branching. The child's syntactic marking of hierarchical organization is indicated by gender agreement between the possessive *mia* and the noun *gonna* (denoted in the last syllable). This is a way of noting that *mia* and *gonna* compose a noun phrase "subassembly."

One can also look at the hierarchical organization in terms of the syntactic categories and relations implied by such sentences. Hyams (1986) points out that to mark subject-verb agreement requires the categories of subject and verb. Such categorical organization is manifest by the 23-month-old Italian child who said *Io la mangio* (I it eat - Hyams 1986, p. 143). In this sentence, diagrammed at the bottom of Figure 10, the child has discriminated between the subject pronoun *Io*, which requires agreement, and the object pronoun *la*, which does not. (Agreement is indicated by the *-io* suffix in *mangio*.) This level of hierarchical organization is indicated in Figure 10 by the labels "verb phrase" and "noun phrase." As a comparison of the number of levels and number of branches in the diagrams for *e mia gonna* and *io la mangio* in Figure 10 indicates, the two utterances are conceived as having the same degree of hierarchical complexity. That this complexity of syntactic organization is typical of children in this age group has been found by a number of investigators in recent years (e.g., Bloom 1990; Levy 1983; Valian 1986).

3.6. Discussion

Thus far, the behavioral evidence is very much in accord with the hypothesis that, during the earliest stages of language acquisition, there is a single neural substrate for the hierarchical organization of language and manual object combination, a substrate that subsequently undergoes a process of developmental differentiation.

Although the evidence is sufficient to suggest the theory, one must remember that it was not designed to test the theory. At this point, it would be desirable to design a study expressly for this purpose. A more rigorous test would be to look at both object combination, including tool use, and word formation with age held constant or factored out. This way, one could use variability in developmental rates to test for the ontogenetic yoking of the two skills (Bates 1988). If a positive correlation between performance in the two domains were obtained, the ontogenetic relationship would be more likely to be based on a homology rather than merely an analogy arising from two sets of skills independently developing over roughly the same age span.

In addition, because the claims that are being made imply universality, it would be desirable in future studies to collect evidence from a variety of language groups. Finally, one could also look for the predicted "pot" stage of spoon use that is missing from the report of Connolly and Dalgleish (1989).

Behavioral evidence alone, however, no matter how good, is not sufficient for attributing equivalent hierarchical status and common ontogenetic origins (developmental homology) to structures in disparate domains. This calls for evidence from neural development, to which we next turn.

4. The development of a neural substrate for combinatorial organization: Language and objects

New kinds of neuroanatomical and neurophysiological data enable us to trace the development of brain connections that provide the foundation for structural development in both language and action. I draw on Robert Thatcher's large cross-sectional data set on the development of EEG coherence (indexing neural connectivity) between pairs of locations on the cerebral cortex (Dr. Thatcher has kindly carried out special analyses for use in the present paper; his techniques are described in Thatcher et al. 1987). From the neuroanatomical perspective, I draw on a recently published study of the postnatal development of the motor speech area by Simonds and Scheibel (1989). Whereas Thatcher's EEG data span 19 neural locations over the two hemispheres (see Homan, 1988, for precise placements), Simonds and Scheibel have analyzed brain tissue from four locations, Broca's area (Brodmann areas 44 and 45) and the orofacial area, on the left hemisphere, along with analogous locations on the right hemisphere.

The focus of Simonds and Scheibel (1989) is on the analysis of dendritic branching. Because the dendrite is the cell's input mechanism, dendritic branching provides various measures of a neuron's receptive connectivity with more distant regions of the brain. As long-distance connections develop, connections with neighboring cells and areas decrease. This is part of the process of "pruning" neural connections as development proceeds (Huttenlocher 1979). Hence, the neurophysiological and neuroanatomical data converge in providing information about developing neural networks.

The two kinds of data have complementary patterns of strengths and weaknesses. EEG data are not so localized as neuroanatomical data. They provide direct information on particular neural circuits or networks, however. The neuroanatomical data are precisely localized but provide no information on exactly where the other termini of the circuits or networks are located. The direction of information flow cannot be ascertained from EEG coherence data, but the neuroanatomical study of dendrites isolates input connections to the regions of interest. The two sources of data are complementary in another way as well: Simonds and Scheibel's data stem from a relatively deep layer of the cortex (Layer 5) and therefore reflect relatively greater subcortical and local connections than Thatcher's EEG coherence data, which are based on electrical activity at the surface of the cortex.

We shall first examine neuroanatomical evidence up to 15 months of age from Simonds and Scheibel (1989), with data points at 3 months, 5-6 months, and 12-15 months of age. Using the earlier two developmental periods as a baseline, we see that dendritic branching is greater in the right hemisphere than in the left through six months of age. This emphasis on right hemisphere development occurs *before* the development of combinatorial activity in either speech or object manipulation (which were hypothesized, on the basis of the neuropsychological evidence described earlier, to be left hemisphere functions).

By 12-15 months, the beginning stages of both word formation and object combination (including tool use),

the neuroanatomical picture changes. The orofacial motor zone on the *left* side, used for speech movements, has developed enough dendritic growth to catch up with its counterpart on the right side. At this point in development, dendritic growth in the left orofacial area has developed significantly more than in the contiguous Broca's area. (It is important to note that the term dendritic growth, here and elsewhere in this article, refers to length and branching complexity of dendrites, not to their quantity.)

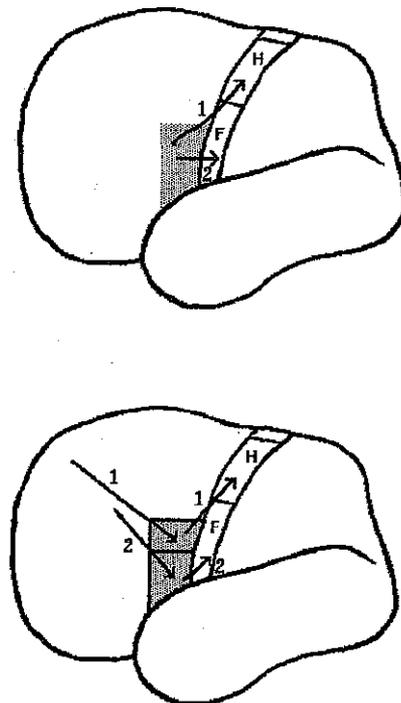
On theoretical grounds, it is hypothesized that the developing input structures in the left orofacial motor area receive input from the neighboring Broca's region, which could provide the motor program for phonological production. At this point then, input connections from Broca's area to the orofacial motor cortex should be relatively rich. The hypothesized connection is shown as Circuit 2 at the top of Figure 11. The empirical reality of Broca's area as the output source of the hypothesized connections can now be empirically tested. Most important for the present argument, if empirically confirmed, this state of affairs would provide neural support for the processes of word formation taking place during this period.

Extrapolating from Simonds and Scheibel's (1989) data on the orofacial area, I predicted a growth spurt of connectivity between the left manual motor cortex and Broca's area at around the same age. Inspection of Thatcher's cross-sectional data set indicates that this circuit has significant connectivity in this age range, reaching a modest first peak of coherence around 16 months of age. This hypothesized connection is shown as Circuit 1 at the top of Figure 11.

Before the development of the circuits connecting the left orofacial and manual motor areas of the cortex to the more anterior region where the classical Broca's area lies, it is hypothesized that vocal and manipulative functions would be poorly differentiated in the infant brain because of a large number of short-range connections between the neighboring orofacial and manual areas. This lack of differentiation in the brain would then be reflected in a lack of behavioral differentiation, including conjoint non-dissociable movements of hands and mouth (Ploog 1988). With the development of more specific connections (e.g., through dendritic growth, hypothesized to link up motor cortex with Broca's area), the diffuse connections within the motor cortex would be eliminated in a "pruning" process.

At the next neuroanatomical data point, 24–36 months of age, dendritic growth in Broca's area has caught up with and exceeded dendritic growth of the left orofacial motor area (Simonds & Scheibel 1989). What we know from these findings is that Broca's area is now receiving more distant inputs from some area of the brain; they do not tell us where. Thatcher's analysis of electrophysiological connectivity in the cortex provides important clues, however.

At this point, I predicted a spurt starting at age two in the neural connectivity between the left anterior prefrontal area and the more posterior region in which Broca's area is located. To test my prediction, Thatcher analyzed his cross-sectional data and found such a spurt of increased connectivity between approximately two and four years of age. During this period the corresponding



- 1 = manual object combination circuit
- 2 = grammar circuit
- = region of Broca's area
- H = manual motor area
- F = orofacial motor area

Figure 11. Hypothesized development of neural circuits for the production of hierarchically organized manual sequences and grammar. In the top drawing, the absence of borders and divisions for Broca's area, as well as the position of the arrows, represents its undifferentiated character at this early stage of development. The circuits in the top drawing are hypothesized to undergo development in the approximate age range of 12 to 16 months. The left-hand portions of the circuits in the bottom drawing are hypothesized to undergo development in the approximate age range of two to four years. These are schematic representations based on a synthesis and extrapolation of data from Fox et al. (1988), Ojemann (1983a; 1983b), Roland (1985), Simonds and Scheibel (1989), and Thatcher (unpublished data, 1991). The anterior pole of the grammar circuit is based on Ojemann (1983a; 1983b). The anterior pole of the manual object combination circuit is based on Roland (1985). The role of Broca's area is based on Fox et al. (1988), Roland (1985), and Simonds and Scheibel (1989). The posterior pole of the circuits (in motor cortex) is based on Geschwind (1979), Roland (1985), Simonds and Scheibel (1989), and Thatcher (unpublished data, 1991).

right hemisphere circuit showed no growth in connectivity at all. The fact that this finding was a prediction from the theory, rather than an *ex post facto* explanation of known data, strengthens the validity of the proposed theory of neural circuit development.

Putting these two pieces together, we can then hypothesize that, functionally and developmentally, Broca's area is starting at age two to receive input from the anterior prefrontal area. Given the incomplete nature of the evidence, this key proposition has the status of a theoretical prediction, ripe for direct empirical test.

The putative circuits are exactly those hypothesized to be operating in agrammatism: Production of complex grammatical speech would involve input from the left intermediate prefrontal cortex (perhaps Brodmann's area 46) (Ojemann 1983a; 1983b) to the inferior part of the left posterior inferior frontal area (probably Brodmann's areas 44 and 45, also known as Broca's area); organization of hierarchically complex programs of object combination would involve input from the anterior superior prefrontal cortex (perhaps Brodmann's area 9) (Roland 1985) to the superior part of the left posterior inferior frontal area. The hypothesized circuits are shown at the bottom of Figure 11. They are identical to those shown in Figure 7; for the sake of exposition, the neural links from Broca's area to motor cortex were omitted from Figure 7.

Because linguistic grammar and action sequences are analyzed in separate areas of the anterior prefrontal cortex (Ojemann 1983a; 1983b; Roland 1985), the hypothesized growth of long-distance connections between Broca's area and the more anterior prefrontal region should provide the neural basis for a differentiation of manual object combination programs from linguistic grammar programs. Given the anterior prefrontal area's function in planning complex, hierarchically organized sequences, the connections between the anterior prefrontal region and Broca's area also bespeak the beginning of much more complex structures.

It is known that cortical differentiation in the frontal lobes proceeds from posterior (or caudal) to anterior (or rostral) (Deacon 1990b). Hence, the hypothesized two-stage development of circuits shown in Figure 11 is in line with this known pattern of development.

The qualitative nature and timing of this development fits perfectly with the behavioral evidence: It is in this period between two and four years of age in which morphologically complex grammar emerges in language (e.g., Brown 1973; Hyams 1986; Valian 1986), generating structures that have no analogue in grammars of action. On the one hand, there is around two years of age an increase in the hierarchical complexity of linguistic productions on the syntactic level, as shown in Figure 10. On the other hand, there is also at this point the introduction of syntactic marking, a qualitatively new development. The increase in hierarchical complexity, with its syntactic marking, is hypothesized to stem from the addition of the anterior prefrontal area to the language production circuit (left part of Circuit 2, bottom of Figure 11) between approximately two and four years of age. (There is no implication here that age four is the end of either syntactic or neural development. It is simply the temporary endpoint dictated by current limitations in our knowledge of neural development.)

Also emerging for the first time in this period are complex grammars of object combination that have no analogues in linguistic grammar (e.g., Beagles-Roos & Greenfield 1979; Goodson & Greenfield 1975; Greenfield 1976; 1977; 1978; Greenfield & Hubner, n.d.; Greenfield & Schneider 1977; Reifel & Greenfield 1981). The tree structure at the top of Figure 4 is one such example.⁴

Similarly, it is hypothesized that the expansion of the hierarchical complexity possible in object combination activity stems from the addition of the superior anterior prefrontal area to the object combination circuit (left part of Circuit 1, bottom of Figure 11). The involvement of this

cortical area in the development of manual skills with sequential steps with objects has been demonstrated by A. Diamond (1991), who explored the sensorimotor consequences of earlier maturational stages of the same cortical areas in monkeys and human children.

The conclusion is that neural differentiation of higher order programs for language and object combination occurs in just that period when behavioral differentiation is taking place. According to this view, the syntax of language and the hierarchical organization of object combination are homologous in their "embryological" origins, but they are modular in the neuroanatomy of their mature functioning.⁵

4.1. The nature of the neural model

In neurology, the two major positions have been locationism and equipotentiality. The neural explanation of language has also been subject to these two opposing viewpoints. Yet neither has proven satisfactory (Kolb & Whishaw 1985). Nonetheless, because of the nature of the available data and methods, most neuropsychologists have tended to try to correlate specific linguistic (or other psychological) functions with specific areas of the brain. In recent years, neural network models have become popular. This, in essence, is a new form of equipotentiality, with a strong emphasis on learning.

The style of neural theorizing here, however, is neither locationist nor equipotentialist. It proposes to think instead in terms of neural circuits and their development. This is an extension of Geschwind's (1972) approach to the neurology of language and owes much to Deacon's (1989; in press) research and theory concerning the anatomy of neural circuits in monkeys. Whereas focusing on brain areas implies a one-to-one correlation between location and function, the circuit approach does not. One would predict that interrupting a given circuit at any point would interrupt the function, thus explaining the failure of strict locationist approaches. This prediction is quite in line with the results of Ojemann's (1983) brain stimulation studies. At a very basic level, the emphasis on circuits also agrees with what is known about the importance of neural connectivity and the transmission of impulses from one neuron to another in brain function.

It has so far been shown that thinking in terms of neural circuits and their development resolves a number of seeming contradictions in the field of aphasiology, such as (1) the existence of articulatory disorders both with and without agrammatism in Broca's aphasia and (2) agrammatism both with and without deficits in building hierarchical object constructions.

In child language development, the importance of understanding the role of the neural differentiation process in which multiple short-range connections are "pruned" to fewer, more specific, and longer-range connections cannot be overestimated. This is the process by which differentiated circuits are created. It is this developmental model that allows us to understand why early speech is so closely intertwined with other sorts of action, whereas later grammar is both more independent from action and more abstract. Such new techniques as brain imaging and computerized EEG have allowed us to begin to create models of developing circuits on an empirical basis.

4.2. The role of the environment

The description of the growth of neural circuitry in no way lessens the importance of interaction with the environment. Although maturational patterns are epigenetic in nature (i.e., canalized to follow certain paths), both neural and linguistic development require active experience to be actualized (e.g., Curtiss 1977; M. Diamond 1988) Fischer et al. (1990), for example, have incorporated both brain development and environmental interaction into a theory of cognitive development.

5. Phylogenetic implications and evidence

As a way of approaching the issues of evolutionary origins and phylogenetic homology, one can ask (1) what is the behavioral evidence concerning the structural development of object combination and symbol combination in primates? and (2) what is the neural evidence? The first question is addressed in sections 5.2, 5.3, and 5.4, the second in section 5.5.

5.1. The logic of an evolutionary argument

Because there is no fossil record of behavior, evolutionary reconstruction in behavioral domains is always a matter of inferring the most plausible scenarios based largely on contemporaneous evidence. The logic of a comparative approach to the evolution of behavior is as follows: If we find common capacities in two related descendent species of a common ancestor, it is possible that both species inherited the capacity in some form from the common ancestral species. If the same behavioral capacity is found in not just two, but *all* the species stemming from a common ancestor, the basis for the behavioral trait in the common ancestor becomes quite certain (Parker 1990). Within this framework, the comparison of language and tool use in chimpanzees, sibling species to *Homo sapiens* with whom we share 99% of our genes (King & Wilson 1975), takes on particular importance in the evolutionary investigation of the language-tool homology.

5.2. Structural development in primate object combination: Tool use and tool construction

There are clear examples of tool use in a number of species of primates that structurally parallel Stage 1 in the grammar of action (pairing strategy, left side of Figure 1): One object (the tool) acts on another (see Visalberghi 1990). McGrew (1990) observes, however, that only chimpanzees can use the same tool on different objects, a variant of pairwise combinations also noted above for children.

In addition, McGrew (1990) notes that chimpanzees are unique in having tool sets in which two tools are used sequentially on a single object (top of Figure 12). The use of a tool set is structurally analogous to children's "pot" strategy, the next stage in the development of grammars of action (middle of Figure 1). Using a stone to strike a nut placed on an anvil (Sugiyama & Koman 1979) is another example of the "pot" strategy in wild chimpanzee tool use: Two active, moving objects (nut and stone) are combined in succession with a single passive object (anvil).

Gardner and Gardner (1988) have shown that captive chimpanzees can use the "pot" strategy in a number of different construction and tool use tasks. For example, in threading beads, the chimpanzee adds a series of objects to one constant object (the string), serving as the common object.

Goodall's (1986) observations of chimpanzee object manipulation seem to confirm that chimpanzee grammars of action are limited in the wild to the "pot" strategy and do not reach the level of subassemblies, the final stage depicted in Figure 1.

But McGrew (personal communication, 1990) reports a kind of borderline subassembly in the wild. When chimpanzees "fish" for ants, they move a stick to attract them; when the ants attack the stick, the chimpanzee treats ants plus stick as a subassembly, moving it to the mouth as object. The leaf sponges used for drinking (Goodall 1986) may also be examples of the same degree of hierarchical complexity.

Indeed, in captivity, both species of chimpanzee, *Pan paniscus* and *Pan troglodytes*, have learned to use a spoon (Gardner & Gardner 1988; Savage-Rumbaugh, personal communication, 1990), thus showing the capacity for hierarchical organization at the level of a simple subassembly (bottom of Figure 8). In addition, Visalberghi (personal communication, 1990) reports that the ontogeny of nutcracking in *Cebus* monkeys is similar to the development of spoon use in human children.

That level may be the nonhuman primate limit, however. For example, both Gibson (1990) and McGrew (1990) have concluded that apes do not use "additive construction" in tool manufacture; in grammar-of-action terms, they do not combine two objects into a tool subassembly that can then act on a third object outside the chimpanzee's own body. Indeed, McGrew concludes from his comparison of chimpanzee and Tasmanian human tool construction that additive construction is a major feature distinguishing human tool construction from that of chimpanzees.

A change in object roles is a correlate of the subassembly strategy, as shown on the bottom of Figure 3: The recipient of the action in the first object combination becomes the acting element in the second. If we apply role change to the toolmaking context, an object that is the recipient of action in the construction of a tool changes into the acting element when that tool acts on another object during the tool use phase. Lacking subassemblies intrinsic to additive tool construction, chimpanzees would also lack the ability to change the role of the same object from active to passive or vice versa, a competence that, on the syntactic level, is pertinent to relative clause construction (see bottom of Figure 3).

As we would predict from our analysis of grammar of action, humans are also unique in using tools to make tools (McGrew 1990). This would involve still another level of hierarchical complexity and role change: Two or more objects would be combined to make the first tool, which would act on one or more objects (creating the second tool), which would in turn act on still another object; we now have a three-level tree structure with multiple role changes.

The captivity experiments of Koehler concerning chimpanzee tool use and tool construction (1925) confirm this analysis of abilities and limitations inherent in chim-

panzee object combination. Applying the schema for assessing hierarchical complexity to Koehler's evidence, we find that the most hierarchically complex manual construction is a rather borderline example of subassembly: One of Koehler's chimpanzees (named Tschego) bent a bundle of straw in half to construct a stronger stick, then combined this stick with an object to bring it closer to her. More frequent examples of relatively complex object combinations in Koehler's data are limited to structural analogs of the "pot" strategy: Chimpanzees pile boxes in a stack (to climb on them). Matsuzawa (1986b) reports stacking of blocks by a four-year-old captive chimpanzee. As Reynolds (1983) points out, this type of stack cannot be rotated in space as a unit. It therefore lacks the essential quality of a subassembly.

5.3. Parallel structures in chimpanzee symbol combination

If language and tool use evolved together phylogenetically and develop together ontogenetically, then the symbolic combinations of chimpanzees exposed to a human symbol system should be limited to the hierarchical complexity of a simple subassembly on the language level, as it is on the level of tool use.⁶

If chimpanzee symbolic capacity is homologous with the early symbolic skills of young children, one would predict the same structural sequence. Pairwise symbolic combinations should accordingly precede conjoined symbolic structures analogous to the "pot" strategy in grammars of action, which should, in turn, precede subassembly constructions.

Our data come from a program of research on bonobo chimpanzees (*Pan paniscus*) directed by Sue Savage-Rumbaugh (see Savage-Rumbaugh et al., 1990, for a recent summary). Although, as both Pinker and Bloom (1990) and Piatelli-Palmerini (1989) point out, the evolution of human language does not *logically require* evidence from ape language for its hypothetical reconstruction, this is one important avenue of research, one that can provide empirical clues about the capacities of a common ancestor.

Although the structural development of sound combinations was considered a homologue of manual object combination in the human case, symbol combination is considered in the chimpanzee case because the chimpanzees use a system of visual symbols (geometric lexigrams plus a few gestures) that are unitary entities in themselves. Hence, there is no level of word formation; the only possible level of combination is between individual symbols.

In a study of symbol combination in a bonobo named Kanzi, Greenfield and Savage-Rumbaugh (1990; 1991) found ordering rules for two-symbol combinations, as well as the beginnings of an ordering rule for a three-element combination. Before symbol combinations, Kanzi, like children, also had a stage of single symbol utterances. It is of theoretical interest to note also that Kanzi's symbolic combinations were extremely closely linked with the sensorimotor activity in which he was involved. He usually used his combinations to communicate about actions that he was planning or objects he wanted.

Ordering rules for two-element combinations were clearly established at the time his first three-element rule

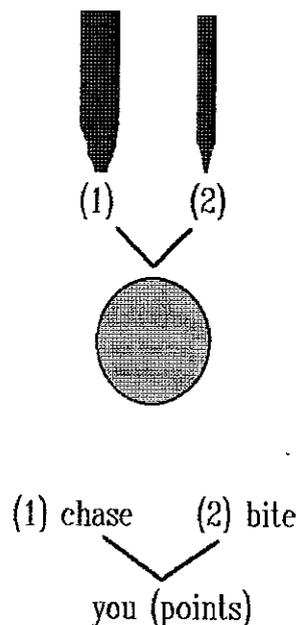


Figure 12. Parallel structure in a chimpanzee "tool set" and a chimpanzee symbol combination. Kanzi would touch or point to geometric lexigram symbols to communicate "chase" or "bite."

appeared, indicating the developmental precedence of a pairing strategy, as one would predict from the preceding theoretical considerations and data. As Figure 2 shows, a three-word combination can have a two-level, branching subassembly structure. Hence it is particularly noteworthy that Kanzi's three-element rule did *not* have such a structure; it had a conjoined structure (analogous to the "pot" structure in grammars of action) instead of the more complex branching structure. His rule-governed three-symbol utterances consisted of two ordered actions and one agent (e.g., CHASE HIDE you (gesture) (see Greenfield & Savage-Rumbaugh, 1991, for a complete corpus). From a structural point of view, two actions combine in a specified sequence with a single agent; this is structurally analogous to placing two tools in a particular sequence to act on a single object (see Figure 12). The combination of consistent symbol order, along with other criteria elaborated by Greenfield and Savage-Rumbaugh (1990; 1991), led to the conclusion that Kanzi had mastered and (in the case of two rules) invented a protosyntax.

At the next level of hierarchical complexity, Kanzi occasionally produced symbol combinations that were at the simple subassembly level shown in Figure 2c for child language. For example, he produced the lexigram utterance BALLOON WATER HIDE the day after he and his caregivers had been hiding balloons filled with Koolaid. Here WATER modifies BALLOON, forming a subassembly that serves as the object of HIDE. The syntactic organization looks similar to that of *want more grapejuice*, shown at the bottom of Figure 2. Hence, the chimpanzee's most advanced combination on the symbolic level matches the structural stage of the chimpanzee's most advanced combination on the tool level.

The rate of development in the two species is very different: Children require approximately one year to go from first word to telegraphic speech; Kanzi had been producing lexigrams for three and a half years when these data were collected. A different rate of development -

heterochrony – is common in phylogenetically related species (Gould 1977), however.

5.4. Discussion and summary

Ontogenetic parallels between action and language in people extend to phylogenetically related species: Indeed, Gibson (1988; 1990) has also hypothesized that human tool use and language differ from that of the apes primarily in degree of hierarchical organization. Using a slightly different terminology, Gibson (1983; 1988) and Reynolds (1983) likewise developed a nearly identical hypothesis. There are no developmental data for chimpanzee tool use. It would be useful to collect such data in the future to test whether the three strategies – pairing, “pot,” and subassembly – occur in the same developmental order in chimpanzees. In the absence of developmental data on tool use, however, the existence of (1) object combination strategies that parallel developmentally sequenced symbol combination strategies in chimpanzees and (2) parallel constraints on hierarchical complexity of chimpanzee activity in the two domains is theoretically relevant evidence.

Thus far, the behavioral evidence from primates is consistent with the idea that the capacities for tools and language evolved together. Is there evidence for a homologous neural substrate? This must be the ultimate criterion.

5.5. Homologous prefrontal circuits in macaque monkeys

The ideal neural evidence would be from chimpanzees but it is available only from macaque monkeys and other more distantly related primate species. The evolutionary logic remains the same, however: To the extent that we find common circuits in macaques and humans, these are likely to have existed in our common ancestor, who, much more ancient, would also be a common ancestor to the chimpanzees; the common neural circuits would therefore be likely to be homologous.

Broca's area homologues have been found in the brains of macaque monkeys (Deacon 1989; in press).⁷ Indeed, a homologue of the human grammatical circuit shown at the bottom of Figure 11 has been identified by Deacon (1990a), using axonal tracer methods. Like the human brain depicted at the bottom of Figure 11, the macaque brain also shows a more dorsally located circuit for manual action in the frontal lobe (Brooks 1986; Martino & Strick 1987), including prefrontal inputs (Muakkassa & Strick 1979). There is also evidence that, similar to the child around one year of age, the Broca's area homologue of the macaque lacks differentiation in that it activates both hand and mouth movement (Rizzolatti 1987).

These homologues occur in the context of a species that has shown distinct left hemispheric dominance for processing species-specific vocalizations (Falk 1990). MacNeilage (1988) has indirect evidence of left hemisphere dominance in nonhuman primates because of their right-handed preference in making precise manual gestures. [See also MacNeilage et al.: “Primate Handedness Reconsidered” *BBS* 10(2) 1987.]

5.6. Speculations about neural evolution from nonhuman primates to humans

Because there has been so much expansion of the prefrontal cortex in the course of evolution from nonhuman primates to humans (Deacon 1990a), one would expect neural structures in apes to be able to support very simple grammars of manual construction and manual gesture (and even simpler levels of sound construction), whereas complex structures would call for the much greater connectivity in the human brain described by Gibson (1990), particularly in the prefrontal areas.

One result of a larger brain with more connectivity is greater separation and differentiation of function (Deacon, personal communication, 1991). The Broca's area homologue in the macaque resembles the one inferred to exist in the very young child, in that it activates both hand and mouth. The evolution of a larger brain with more connectivity may well have brought with it the separation of manual and oral control theorized for Broca's area in adult humans (bottom of Figure 11).

5.7. Ontogeny and phylogeny

One reason to consider developmental evidence in an evolutionary reconstruction lies in von Baer's law that in phylogenetically related species early stages of ontogenetic development are generally more similar than later ones. This principle implies “terminal addition”: Evolutionary change focuses on later stages of the maturational process. There is a tendency in this direction because of the conservative nature of evolution: It builds on what is already there. The tendency is far from absolute, however (Studdert-Kennedy 1991). In addition, reasons other than homologous evolutionary origins are possible for the cross-species resemblance of immature stages (Deacon 1990a).

One major problem in relying on von Baer's law in the present case is that the relevant nonhuman primate data come primarily from mature animals whereas the relevant human data come primarily from early development. The argument therefore runs the risk of veering into crude recapitulationism: the idea that stages in child development recapitulate mature stages in our evolutionary ancestors.

It is accordingly important to point out a more basic reason for using developmental evidence in an evolutionary reconstruction. Homologous origins of capacities across species imply homologous ontogenetic histories. Indeed, common embryology is often taken to be the criterion for cross-species homology. Language and manual capacities involve the development of a brain and behavioral capacities that are still immature at birth – they are figuratively, if not literally, embryonic (cf. Lamendella 1976).

In the present case, it is known that the back-to-front sequence of frontal lobe development described in section 4 is common to all mammals (Deacon 1990b). That the most rostral or forward prefrontal areas of the cortex are both the last to develop ontogenetically and more highly developed in humans than in other mammals, including nonhuman primates, is a fact. It is important to note that this fact and its evolutionary significance in no way depends on the validity of either von Baer's law or recapitulationism.

6. Modularity reconsidered

Chomsky (1980) spoke of the language faculty as a "mental organ," analogous to the heart or the visceral system. Fodor (1983) systematized this view while replacing the term "organ" with the word "module." According to Fodor (1983, p. 37), a module (1) is domain-specific, (2) has an innately specified structure, (3) is not assembled by combining more elementary subprocesses, (4) is associated with specific, localized and elaborately structured neural systems, and (5) is computationally autonomous. How does the picture drawn of the ontogeny of linguistic and object combination square with these criteria? Do skills in these two domains qualify as modules? [See also multiple book reviews of Fodor: *The Modularity of Mind*, *BBS* 8(1) 1985.]

Let us start with the early stage of cortical development described earlier (top of Figure 11). At that point in development, the organization of manual object combination and sound combination fail to conform to the modularity criteria in some critical respects: (1) Having a portion of their neural substrate (the left frontal region associated with Broca's area) in common, they lack domain specificity, and (2) sharing the resources of Broca's area, they are not computationally autonomous. On the other hand, they conform to Fodor's description of modules in other respects: (1) The two behavioral domains are associated with a specific neural system and, therefore, (2) the source of structure is innate.

After approximately two years of age, the differentiated expansion of the two neural circuits into the anterior prefrontal region (bottom of Figure 11) makes each circuit increasingly domain specific and relatively autonomous. It would seem, therefore, that, with development, a basically nonmodular but innate system has become modularized. The nature of the more mature system, however, is such that it now violates another of Fodor's (1983) criteria: The early circuits constitute subprocesses of the more mature circuits (note the relationship between the earlier and later developing circuits shown in Figure 11). If we are to claim that modularity has come into existence with the later developing circuits, we must reject Fodor's criterion concerning the absence of component subprocesses as incompatible with the nature of neural development. In essence, we must modify the definition of a module.

Fodor (1983, p. 42) views the motor production of speech as involving a module that is separate from that used to process speech comprehension. Because the relevant circuits would not be expected to be the same for the processing of linguistic input (although there could be overlapping components), we basically agree on this point. Evidence concerning the relative precocity of syntactic development in language comprehension (Hirsh-Pasek & Golinkoff, in press) has accordingly been considered neither relevant to the argument nor damaging to the chronology of structural development of speech production outlined earlier.

One possible reason for the precocity of syntactic comprehension relative to production found by Hirsh-Pasek and Golinkoff (in press) might be that the connections between the auditory comprehension area, Broca's region, and/or the anterior prefrontal syntax area mature earlier than connections between oral-facial motor cor-

tex, the speech programming center in the region of Broca's area, and the anterior prefrontal syntax area. Indeed, evidence from the tracer study of macaque brains indicates that there is a vertical division of the traditional Broca's area in which one part connects to auditory processing areas while another connects to a facial area (Deacon, in press). If this division holds in humans, connections with the two parts could well mature at different rates, leading, for example, to the development of syntactic comprehension before production. (Because no data concerning such a division yet exist in humans, it was not taken into account in drawing the brain circuits portrayed in Figures 7 and 11.)

Similarly, although agrammatism does indeed involve deficits in syntactic comprehension as well as production (e.g., Bates et al. 1987; Zurif & Caramazza 1976), it is hypothesized that these involve a distinct neural circuit with common components – possibly the left part of the grammar circuit shown at the bottom of Figure 11. Because deficits in the comprehension of syntax should, according to the theory being advanced, involve their own cortical circuitry, this aspect of agrammatism has been considered to be beyond the scope of the present article.

7. Phylogeny, ontogeny and homology reconsidered

An argument for a double homology – ontogenetic and phylogenetic – has been presented: a homologous neural substrate for the early ontogeny of the hierarchical organization shared by two domains – language and manual object combination – and a homologous neural substrate and behavioral organization shared by human and non-human primates in phylogeny.

According to evolutionary theory, a cross-species similarity in behavioral organization can arise because of homologous origins in a common ancestor. It can also arise because of convergent evolution – as a common adaptive response to a similar set of environmental conditions – based on different (analogous) underlying structures. Convergent evolution between chimpanzees and humans is unlikely because the environmental niches of the species have been increasingly differentiated since the species diverged four to six million years ago. This state of affairs increases the probability that similarities in behavioral organization in chimpanzees and humans have homologous origins.

A sure criterion for the reconstruction of phylogenetic origins, however, is anatomical structure. In language, the focus of anatomical interest, since Lenneberg (1967), has been the brain. If we can connect behavioral organization in two related species to a common anatomical structure, we can definitely establish phylogenetic homology, thus excluding the possibility of analogy and convergent evolution. Although the empirical evidence is much sketchier in primates than in humans, this is the form of the argument that has been presented.

7.1. Possible evolutionary scenarios

One possible evolutionary implication of this argument is that a common ancestor of humans and present-day primates had the left frontal lobe circuitry to support the

ontogeny of both primitive object combination and primitive language functions.

Another possible evolutionary scenario is that a common ancestor of human beings and present-day primates had the left frontal lobe circuitry to support the ontogeny of primitive object combination, but not protolanguage. At a later point in evolutionary history, perhaps after divergence of hominids and the great apes, this circuitry was recruited in the service of linguistic organization. In this scenario, neural organization of combinatorial manual activity serves as a preadaptation (or exaptation) for the combinatorial aspect of language, which subsequently develops by natural selection. This general scenario has been proposed by Reynolds (1976), Kimura (1979), and Lieberman (1990).

A third logical possibility is that a neural substrate for protolinguistic combination served as a preadaptation for manual object combination, which developed later. No theorist has espoused this view, probably because it is assumed that language is the more recent phylogenetic development. In addition, counterevidence exists: There is evidence for tool use in species that diverged from the hominid line millions of years before the separation of hominids and apes (Visalberghi 1990) and in whom no evidence of protolinguistic combination has been found.

7.2. Incompatible evolutionary scenarios

A number of evolutionary scenarios are eliminated by the argument and evidence. First, the existence of cross-species neural homology manifest in corresponding behavioral organization eliminates the evolutionary saltationism of Chomsky (1972; 1980a) and Piattelli-Palmerini (1989), as well as the discontinuity between human language and the capacities of ancestral species espoused by Lenneberg (1967).

The ontogenic and phylogenetic gradualism advocated here is ultimately incompatible with Bickerton's (1990) view of the evolution of language, although there are also important areas of agreement. [See also Bickerton: "The Language Bioprogram Hypothesis" *BBS* 7(2) 1984.] Both Bickerton and I see the early stages of ontogeny and phylogeny as evidence of a common protolanguage. The discovery of simple chimpanzee syntax (Greenfield & Savage-Rumbaugh 1990; 1991) and the development and componential nature of the neural circuitry discussed here contradict Bickerton's claim of total discontinuity between "protolanguage" and "language" (examples of what Bickerton means by "protolanguage" are pidgin dialects, the communication of chimpanzees, and the language of children under 2 years of age). The fact that the differentiated circuits developing after age 2 are built on the earlier more global circuits (see Figure 11) would imply an underlying continuity between the two stages, "protolanguage" and "language."

Continuity in neural development is phenotypically realized in continuity in the development of linguistic organization (Figure 10). Hence, the combining of two subassemblies of sounds creates the first combinations of two words, combinations that may subsequently receive syntactic marking by inflections or word order. Thus there is an interesting ontogenetic continuity between two computational aspects of language: phonological processes of word formation and primitive syntax.

7.3. Selection of the most probable evolutionary scenario

The choice between the two possible scenarios compatible with the evidence and the analysis presented here depends to a great extent on whether or not one thinks that ape language capacities stimulated in captivity have a communicative function in the wild. Although it is commonly supposed that they do not, this may well turn out to be incorrect. Plooj (1978) reports gestural combinations among wild chimpanzees that are quite similar in function to the two-element combinations studied in a captive bonobo by Greenfield and Savage-Rumbaugh (1990).⁸ Most interesting is the fact that this type of gestural communication has been observed in the wild uniquely in the context of mother-child interaction (Boesch & Boesch 1990; Plooj 1978). Furthermore, the examples of gestural communication reported by Boesch and Boesch (videotape, 1990) all occur as chimp mothers apprentice their young in tool use. These researchers find that the only behavior so far observed in wild chimpanzees that requires a long apprenticeship is the use of tools for cracking nuts. This fact suggests that the first evolutionary scenario is most compatible with the evidence. I would posit an evolutionary reconstruction in which tool use and manual protolanguage evolved together, both supported by the programming function of the left frontal region associated with Broca's area. In line with the theoretical position of Lieberman (1984; 1991) and Pinker and Bloom (1990), the evolutionary process I would posit would be natural selection.

The adaptive value of nutcracking as a subsistence technique would be expanded by protolanguage: Enhanced communication would streamline the apprenticeship period for nutcracking tools, thus increasing the survival value of tool use. As tool use became increasingly adaptive, the adaptive power of protolinguistic communication would in turn, be enhanced. In this way, language and tool use, programmed by an overlapping neural substrate, would evolve together through mutually reinforced natural selection. Through a process of language-brain coevolution, the adaptiveness of primitive language and tool use would serve to draw further brain evolution, in particular, expansion of the prefrontal cortical region (Deacon 1990a).

An advantage of this evolutionary scenario, with its reliance on natural selection, is the fact that selection can operate most directly on reproductive efficiency, the ultimate criterion of fitness. According to such a scenario, selection is, by definition, direct because a mother's successful tool pedagogy enhances the survival chances of her offspring. Although reproductive efficiency is the ultimate test of fitness and successful adaptation, evolutionary explanations rarely focus on reproduction and socialization of the next generation, the most vulnerable sites for the rapid operation of natural selection (Konner 1977). Note, finally, that this scenario relies crucially on the Boesch's (1990) new observations of explicit chimpanzee pedagogy, contradicting Premack's (1985) claim that explicit pedagogy is a characteristic unique to the human species.

The theory being advanced here, however, does not depend on the truth of a specific evolutionary scenario. To the extent that the theory is correct, it simply places

constraints on the selection of a compatible evolutionary reconstruction.

7.4. Implications for language development

7.4.1. Continuity in grammatical development. Whether grammatical development is continuous or discontinuous has sparked a lively debate in developmental psycholinguistics (e.g., Borer & Wexler 1987; Gleitman 1981; Hyams 1986; Lock 1990). The model of neural development presented here implies both continuity and discontinuity. For Borer and Wexler (1987), the notion of maturation in itself implies discontinuity; they assume that the maturation of each new grammatical component, beginning with the first one, is independent of earlier linguistic (and, by implication, neural) developments.

Maturation cannot be equated with discontinuity, however. There is continuity with the earlier period in that there is a steady increase in the number of hierarchical levels, from the earliest developments shown in Figure 2 to the later ones shown in Figure 10. The continuity with the earlier structure is hypothesized to stem from the fact that the earlier developing circuit from Broca's area to the orofacial motor cortex (Circuit 2, top of Figure 11) is a component of the later developing circuit (Circuit 2, bottom of Figure 11). The qualitatively discontinuous development of syntax is hypothesized to stem from the addition of the anterior prefrontal area to the language production circuit (left part of Circuit 2, bottom of Figure 11).

Based on an examination of brain damaged and other clinical cases, Benson and Stuss (1989) point out that each functional brain system under the executive control of prefrontal areas can also operate without this control. The absence of such control leads to action without thought, a state highly typical of the child between one and two years of age, who, according to the model being proposed, would lack anterior prefrontal control. Hence, based on both the breakdown and maturational buildup of neural circuits, this model implies both continuous and discontinuous development of language forms.

7.4.2. Providing a "reason" for grammatical development. Brown (1976), after outlining the development of grammatical structures in young children, tried to find a "motor" for their development in the absence of selective social pressures for more complex syntax. He found that more advanced grammar did not improve the child's communicative effectiveness. Moreover, parents neither rewarded good grammar nor punished syntactic errors. Although much more is currently known about the role of interaction in language development (e.g., Snow et al. 1988), the existence of sensitive periods for syntactic development (Newport 1988) indicates that environmental conditions cannot be completely effective if the organism is not at an optimal developmental period. The gradual development of a cortical neural pathway from the left anterior prefrontal area to the region of the classical Broca's area, and thence to the left orofacial motor area may provide the cortical motor of grammatical development for the age period from two to four.

It remains for future research to test this hypothesis, fill in the details (including subcortical connections), and

explore expansions of the circuit to accommodate later syntactic development. Whereas the idea that brain development drives language development goes back at least to Lenneberg (1967) and has been recently espoused by Borer and Wexler (1987), the description of a precise circuit governing grammatical speech, with specification of precise developmental stages, is new.

8. Conclusion

Evidence from neural development has been presented to show that the similarities between the ontogenetic development of combinatorial organization in language and manual object combination (including tool use) are homologous rather than analogous. More specifically, evidence points to the linked ontogeny of object combination and sound combination programs in early development, based on the neural substrate of an undifferentiated Broca's area. After about two years of age, Broca's area differentiates by creating two separate networks with more anterior parts of the prefrontal cortex. From that point, language and object combination begin to develop more autonomously, each ultimately generating its own special forms of structural complexity. Each domain has an innate basis in neural circuitry, just as much so in the early unitary stage as in the later modularized one.

If this theory is confirmed by further research, then language is not modular at birth or even at the beginning of language development; it becomes increasingly modular with age and neural differentiation. The theory begins to specify more explicitly the cortical circuitry underlying an innate⁹ grammatical module, the "elaborately structured neural system" required by Fodor's definition of a cognitive module. In the model being advanced here, however, the circuitry does develop by adding more elementary cortical subprocesses with maturation. In this respect, it fails to conform to one of Fodor's (1983) criteria of modularity. If the present account is correct, it follows that, from a developmental perspective, linguistic grammar never completely attains the status of a cognitive module, as defined by Fodor.

Evidence from present-day primates shows that a parallelism between combinatorial action structures and combinatorial symbol structures is also present. Research with monkeys indicates that this parallelism could also be developmentally homologous, based on a relatively undifferentiated Broca-like region. It is hypothesized that, in comparison with humans, the development of hierarchical organization in primate behavior involves less complexity and less differentiation between the domain of action and the domain of language, because of the more limited connectivity in primate brains.

More specifically, the lesser development of a cortical circuit for syntax linking the region containing Broca's area in the left prefrontal cortex with a more anterior area (see bottom of Figure 11) in macaque monkeys may be a major language-relevant difference between humans and nonhuman primates. As the expansion and differentiation of the prefrontal area progressed during hominid evolution, the syntax of language would have developed the hierarchical complexity characteristic of human language, with its embedded relative clauses, and so on. During the same process of prefrontal expansion, a resulting increase in the hierarchical complexity of manual

object combination would have been a critical factor in the emergence of the tool use, tool construction, and general constructional skills required for modern human technology. It is the linking of the behavioral commonalities between species to a homologous neural substrate that removes this scenario from the realm of recapitulationist fantasy and makes it an evolutionary hypothesis worthy of further investigation.

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"Language, tools and brain" is dedicated to the memory of Richard Cromer, classmate and pioneer in the study of language-cognition relations, their development, and their neural foundations.

NOTES

1. A more complete presentation of Fodor's modularity concept will be undertaken in section 6.

2. Unintentional combinations intentionally repeated and transitory combinations occur earlier in both object manipulation (Langer 1980; Piaget 1952) and linguistic babbling, but these are not relevant to present purposes.

3. For this reason, in section 5.3 unitary visual symbols in ape language will be considered to be structurally equivalent to a single phoneme.

4. Using manual problem-solving tasks, Bullock (1990) reports that the ability to represent the goal in a superordinate position relative to the means develops between age two and three. This growth in hierarchical complexity seems likely to relate to the increase in hierarchical complexity occurring in manual object combination in this same period of development.

5. Also involved in the developing language circuits of the frontal lobe of the left hemisphere are subcortical connections (Janowsky & Nass 1987; Lieberman 1990). These are not discussed further here because they are not known, not because they are unimportant.

6. This prediction assumes that *capacities* that lead to symbol learning and use in captivity are present in the wild, although they would not have been actualized in the same way. See later section for a discussion of how communicative capacities may be actualized in the wild.

7. As in our discussion of the human data, we emphasize

functional circuits involving the left ventral frontal region of the cortex, without trying to define one subarea as *the* Broca's homologue.

8. Boehm (1988) reports meaningful combinations of calls in wild chimpanzees observed at Jane Goodall's field site. They are not emphasized in this account, however, because the meaning relations of chimpanzee call combinations appear much farther from human language than the gesture combinations. The fact that bonobo chimpanzees can comprehend human speech (Savage-Rumbaugh et al. 1990), however, may make call comprehension and its associated neural circuitry most relevant to the evolution of language comprehension.

9. Innate has the dictionary meaning of "inborn." "Inborn" does not literally have to mean phenotypically present at birth, however. It can also mean genotypically present at birth; that is, a genetic program is present at birth that guides later development, in this case, cortical development.

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Making the best use of primate tool use?

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Constructing her arguments for a common neural substrate underlying the hierarchical nature of early language and object manipulation strategies, Greenfield shows commendable ingenuity in selecting, sorting, and tying together diverse strands of evidence. Given that the integrative exercise takes in data from many fields, including developmental psycholinguistics and psychology, neuropsychology, neurobiology, comparative psychology, and private behavioral ecology, it would be surprising if some aspects of this particular "combinatorial activity" were not less well-organized than others. My focus is on the author's use of the behavioral evidence in nonhuman primates, to point out what I see to be some problematic interpretations and some overlooked but potentially relevant information.

One source of dissatisfaction with the target article is the way the array of complex behaviors collectively referred to as tool use is treated merely as a certain type of object combination. (Indeed, tool use is never defined in the target article.) There appears to be at least two important differences, however, between primates' use of tools and children's early object manipulation as exemplified by the nesting cups paradigm. First, tool use is highly goal-oriented. Second, and more important in the present context, there is usually only one way to achieve the desired result with a given tool. For example, a chimpanzee using a termite-fishing tool can *only* insert it into the termite mound to obtain the prey. In other words, the chimpanzee is limited by the very nature of the task, rather than by the level of cognitive organization, to using only one strategy. In contrast, human infants combining nesting cups have a greater degree of freedom in terms of possible strategies and possible final constructions, although these are assigned the same value in terms of hypothesized complexity (see Figure 1, target article). For Greenfield, the chimpanzee's behavior during termite fishing, recalls the simple pairing strategy of the

manual organization in cases where a supporting hand (frame) holds an object that is manipulated by the preferred hand, which, metaphorically, provides content elements (MacNeilage 1987). This important evolutionary development accompanied the evolution of hand-internal control in higher primates. As I pointed out earlier, the hierarchically organized acts that Greenfield considered under the manual heading are not necessarily closely linked to specific manual movements as such. Consequently, the postulation of a frame/content mode of manual organization, cited here to argue for evolutionary similarities between manual and vocal systems, has no direct implications for the cognitive bases of the manual tasks considered by Greenfield. It seems here that the task should be to explore the cognitive *but not the motor* relations between the tasks Greenfield considers and grammar. Surely, in both evolutionary and developmental terms, such cognitive concepts as subordination or coordination or temporal sequence have common implications for actions either in grammar or in operations on objects in the external world. This commonality will not be found in motor homology, however, as is revealed by the fact that grammatical morphemes are signaled differently in manual sign language (typically by movements superimposed on a concurrent sign for an open class morpheme) and in vocal language (typically by temporally discrete movement complexes). Action, in motor terms, was probably a very important factor in the evolution of cognition, but cognition is not necessarily closely constrained by action today.

Frame/content modes of organization are not confined to manual and vocal systems operating alone. Other frame/content modes are the coordination of both hands with the mouth (as in squirrels) and the coordination of one hand with the mouth, which became possible with the evolution of the prehensile hand in early primates (MacNeilage 1991). These modes of interaction between the hand and the mouth highlight a further problem with Greenfield's position. Her evolutionary view is one of the development of homologous manual and vocal organizational states from a hitherto undifferentiated substrate. Thus, she interprets Rizzolatti's finding of neurons in lateral frontal cortex that discharge only when the hand touches the mouth as evidence of a lack of differentiation in nonhuman primate cortex. I believe she underestimates these animals. It is more likely that these neurons help to mediate the very elegant frame/content operations of hand-mouth interaction in feeding that have probably been important throughout primate evolution.

The view that organizational similarities between manual and vocal systems are to some degree a matter of convergent evolution of frame/content modes of organization does not necessarily imply that there is no homologous substrate for the two domains. Elsewhere, my colleagues and I have argued that there is a fundamental homology linking the two domains in the form of a left hemisphere postural control specialization, from which both manual (right hand) and communicative specializations may have evolved (MacNeilage 1991; MacNeilage et al. 1987; 1988).

Nesting cups and metatools in chimpanzees

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Greenfield's target article was very stimulating. Having studied the cognitive behavior of chimpanzees in captivity and in the wild, I would like to present two related findings about chimpanzees for further discussion from the viewpoint of a primatologist or a cognitive psychology. One is "the subassembly strategy to nest the seriated cups by captive chimpanzees" and the other is a metatool use in wild chimpanzee nut-cracking behavior using stone hammer and anvil.

I made systematic observations on nine chimpanzees from ages 2 to 26 playing with seriated nesting cups (Matsuzawa 1986a, Table 1). The procedures are the same as those of Greenfield et al. (1972). Seven chimpanzees aged 4 and younger failed to make the seriated structure of five cups and always used the "pot" strategy of putting cups into a "pot" cup. It was also interesting that the chimps were not satisfied with the nonseriated structure and spontaneously put back the cups, trying again and again to make the structure follow the pot strategy. Two adult chimpanzees who had intensive experience in language-like skills, however, behaved just as human children of more than three years old do.

A chimpanzee named Sarah made a five-cup seriated structure in the first trial. She was given five cups, A < B < C < D < E from small to large. Her performance was as follows: In the first step, she put B into C. In the second, she put D into E. Third, she put the subassembly of BC into DE. Finally, she put A into BCDE. Sarah used the most advanced "subassembly" strategy

Table 1 (Matsuzawa). Summary data for the manipulation of seriated cups by chimpanzees.

Name	Sex	Age	Test place	Number of cups given	Trials	Seriated?	Strategy
Pan	f	2	Japan	3	24	Yes/no	Pot
Reo	m	4	Japan	3	24	Yes/no	Pot
Popo	f	4	Japan	3	24	Yes/no	Pot
Whiskey	m	4	U.S.A.	5	10	No	Pot
Opal	f	4	U.S.A.	5	10	No	Pot
Liza	f	4	U.S.A.	5	10	No	Pot
Frieda	f	4	U.S.A.	5	10	No	Pot
Ai	f	13	Japan	5	10	Yes	Subassembly
				6	5	Yes	Subassembly
				9	1	Yes	Subassembly
				10	1	Yes	Subassembly
Sarah	f	26	U.S.A.	5	4	Yes/no	Subassembly
				6	1	Yes	Subassembly

Ai and Sarah are language-trained chimpanzees. Whiskey and Opal have some experience with plastic-sign language. Popo, Reo, and Pan have intensive experience on match-to-sample.

Source: Modified from Matsuzawa 1986.



Figure 1 (Matsuzawa). A wild chimpanzee of Bossou, Guinea, is cracking an oil-palm nut using a pair of stones as hammer and anvil in the "outdoor laboratory." This adult female chimpanzee is named "Jire." She is using her left hand to hold the hammer and her right hand to manipulate the nuts. The coordinated behavior of both hands is necessary in cracking nuts with the stone-tool. The chimpanzees showed perfect handedness at the individual level but no left/right bias at the population level. [See MacNeilage et al. "Primate Handedness Reconsidered" *BBS* 10(2) 1987.]

and made the seriated structure in the minimum necessary steps. She succeeded in making the seriated structure in two of the four test trials and used the subassembly strategy in all cases.

Another chimpanzee (named Ai) behaved just like Sarah. Ai never failed to make the seriated structure of five cups from the beginning. Without any training, in the first trial she succeeded in making a 10-cup seriated structure by nesting the cups following the strategy hypothesized to be the most advanced, the "subassembly" strategy. Eventually, Ai would put one subassembly into another and the resultant large subassembly into the other subassembly in the course of making 9- or 10-cup seriated structures.

It must be noted that Ai had intensive experience of visual symbols called "lexigrams" and "graphemes" used for a language-like system (Matsuzawa 1985a; 1985b; 1989; 1990a). She could combine "words (lexigrams)" into a "phrase" like "red/pencils/five" in her favorite word order (Matsuzawa 1985a)

and construct a "word" from the elements called graphemes (Matsuzawa 1989). Her cognitive skill in memorizing a complex geometrical figure presented for a brief duration and in reproducing the copy from its elemental figures is comparable to that of human adults (Fujita & Matsuzawa 1990). In these tasks, Ai showed the ability of constructing a whole image from scratch. Sarah had shown a similar ability in "putting a face together" (Premack 1975). In conclusion, the chimpanzees can construct copies of existing or imaginary figures by means such as assembling pieces of existing materials.

One can raise the question of whether Ai and Sarah are especially gifted chimpanzees. Did the intensive training induce something different from what happens with the ordinary chimpanzee? My answer is "no." They are not superchimpanzees. I think all chimpanzees are super. I have been in Africa three times to study the cognitive behavior in wild chimpanzees since 1986. I recently observed an interesting metatool use in a wild chimpanzee.

The chimpanzees at Bossou, Guinea, use a pair of natural stones as hammer and anvil to open oil-palm nut seeds (Figure 1). I constructed an "outdoor laboratory" in the chimp ranging area to analyze the nut-cracking behavior experimentally (Sakura & Matsuzawa 1991). Each of about 50 stones was marked and the stone use was observed and recorded. Nuts were also gathered and provided by the experimenter. On January 16, 1991, an old female named Kai appeared with the other seven members in the laboratory and began cracking nuts. Kai took a pair of stones for a hammer and anvil and spontaneously took the third stone to keep the surface of the anvil flat. Kai left the three-level tool there, a hammer on an anvil on an anvil-as-anvil. Such use of a tool for another tool must be described as "metatool" use.

The experimental analysis of stone tool use in wild chimpanzees revealed that they mastered the skill at the age of about four; the skill of a seven-year-old, however, was far from the refined level of adult chimpanzees. I did the same experiment with human children from 2 to 11 years old at Bossou and found that the children under three could not use a pair of stones for nut-cracking. They could manipulate stones but failed to find the three-term relationships: nut-hammer-anvil. Young chimpanzees and humans had a tendency to miss a part: striking a nut with a hammer without an anvil; striking a nut on an anvil by hand rather than by hammer; putting nuts again and again on an anvil, and so on. I observed an 11-year-old boy put a stone under an anvil to keep the surface flat as just as Kai the chimpanzee did.

What I would like to point out is the depth of cognitive hierarchical structure shown in the skills of chimpanzees in captivity and in the wild. The cognitive ability of chimpanzees is still underestimated. The genetic difference between *Pan troglodytes* and *Homo sapiens* is estimated to be 1.7 in a comparison of DNA sequences (Koop et al. 1986). I directly compared the cognitive development of chimpanzees with that of human children in a series of diagnostic tests of stacking blocks (Matsuzawa 1987), sorting objects into plates (Matsuzawa 1990b), manipulating seriated cups (Matsuzawa 1986a), and so on.

In my opinion, the developmental course of the two species is the same. On many occasions, chimpanzees showed the rudimentary form of the most advanced stage of cognitive development in each diagnostic test. The critical difference between the two species might be the depth of the hierarchical self-embedded structures in cognitive functions. So far as is known, no "language" trained chimpanzees have mastered such metalanguage as "noun" and "adjective." Although the chimpanzees in the wild have a long list of tool use - such as sticks for termite-fishing, leaf sponges for drinking water, and stone tools for nut cracking - there are few examples of metatool use and no reports of the meta-metatool use, such as a tool for a tool for a tool. Greenfield's approach to the analysis of the depth of cognitive hierarchical structures is stimulating and exciting.

systems; each may well have its own neural underpinnings. One would expect the circuits shown in Figure 11 of the target article to develop similarly in deaf signers as in hearing speakers. Indeed, the theoretical postulation of these circuits could even explain why facial expression is used syntactically in sign language: because the connections from Broca's area to the orofacial motor cortex shown in Figure 11 could be epigenetically adapted to facial expression rather than to speech. In other words, speech would use the "oral" aspect of the orofacial area, whereas sign would use the "facial" aspect.

In addition, the manual motor cortex is next door to the orofacial motor cortex, which would facilitate connections from Broca's to this area for the manual aspects of sign language. The prediction would be that, in deaf signers, the functional area of the manual cortex expands to take over some of the space of the orofacial area in hearing people and that this appropriated space is used for the manual aspects of sign language. The development of inputs from contrasting areas of prefrontal cortex would lead to the same differentiation of Broca's area. What remains an open question is whether the two parts of Broca's area resulting from its differentiation send their input to a single homogenous, albeit larger, manual motor cortex or to a manual motor cortex that, in deaf signers only, has functionally differentiated into two areas, one for sign, the other for object manipulation. In this connection, it would be interesting to know whether the same part of the manual motor cortex is used for gesture and object manipulation in hearing people. The answer to this question might well provide the answer to the question about the differentiation of the manual motor cortex in deaf people.

Clearly, the above theory of cortical circuits in deaf sign would conflict with Deacon's suggestion that the question of neural differentiation of symbolic language and manual object combination is irrelevant to the bonobo case.

R4. Conclusion

In light of the commentaries it is exciting to see how much and how diverse a set of additional data is predicted or explained by the theoretical model presented in the target article. These data come from domains as diverse as human sign language development, Williams syndrome, the ontogeny of human spoon use, nesting cup behavior in captive chimpanzees, and tool use in wild chimpanzees.

On the other hand, the commentaries also present challenges to the theory, data-based challenges being especially significant (as compared to theoretical or logical ones). The most serious empirical challenges posed by the commentary concern (1) the possibility of significant asynchrony between the emergence of the subassembly stage of word formation and the subassembly stage of object combination (Tomasello) and (2) the simultaneous emergence of many sound combination patterns in early babbling before the corresponding object combination skills (MacNeilage).

Both these challenges should now be resolved by further research. The first requires more fine-grained neurophysiological methods that can determine if in fact language circuits develop a bit earlier than the corre-

sponding manual circuits. New EEG techniques with many more cortical leads may be extremely useful in answering this type of question. The second challenge requires neurophysiological techniques to determine whether Broca's area adds an additional level or type of neural control to the supplementary motor area just at that point where babbling begins to turn into words. More generally, it will be important to investigate other neural circuits that may be implicated in the language and object skills that have been discussed. The proposed circuits should not be construed as the only ones that are operative in either grammatical speech or manual object combination.

Together, the theory and the commentary on it suggest additional research in many directions: I am particularly looking forward to collaborating with neuroscientists to fill in missing pieces in the model of neural development and trying eventually to establish direct empirical links between neural development and the behavioral development of language and tools. I also hope that other investigators will be able to use my approach to neural development and its behavioral consequences to explore other areas of behavior, language comprehension *inter alia*.

In investigating the neural foundations of the development of language and tools, however, one must remember that language and tools are not merely biological phenomena. As the very foundations of human culture, language and tools are part of both the human environment and the human biological endowment. Each stage of neural development sets the stage for certain interactions with the sociocultural and physical environment, which, in turn, leave their marks on both brain and behavior in an epigenetic process. This must be as true for phylogeny as it is for ontogeny. Understanding the reciprocal influences of environment and neural development is an important goal for the next stage of theory and research.

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Letters "a" and "r" appearing before authors' initials refer to target article and response, respectively.

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