Embodied Meaning:

An Evolutionary-Developmental Analysis of Adaptive Semantics

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Abstract. The human brain has evolved the capacity for language not only through specific mechanisms of routinized articulation of speech patterns, but through general mechanisms of adaptive memory organization. As shown by amnesic syndromes in humans and animals, the consolidation of memory requires neural traffic between localized neocortical networks, specialized for sensory or motor articulation, and the more diffuse, densely-interconnected limbic networks at the core of the brain. The connectivity of limbic networks allows not only the integration of widespread cortical regions, but the recruitment of subcortical motivational systems. A cognitive representation, such as supports the understanding of a word, is thus multileveled, with four or five discrete network levels in the pathway linking limbic (visceral) with neocortical (sensorimotor articulation) representations. Through their influences on subcortical arousal systems, the limbic networks provide motivational control over the consolidation process. Through reentrant corticolimbic traffic, language appears to be articulated in neocortical networks through a microdevelopmental process that begins in the prelinguistic, syncretic, postural-affective matrix of felt emotional significance represented at the limbic core of the brain. In its fundamental architecture, meaning is thus embodied. On the other hand, conscious realization of meaning may require the differentiation of specific form out of the syncretic paralimbic matrix, and this realization may be uniquely achieved in language. The phyletic architecture may be essential to understand because it is integral to the morphogenesis of each brain. Because neocortical networks become fixed by myelination early in child development, the articulatory structures of speech perception and expression become rigidly specified, so that a new language is difficult to hear or speak correctly. In contrast, because the paralimbic networks retain their neotenic plasticity throughout life, the general, affective base of semantic representation remains plastic, and the meaning of the words of a new language can be learned even by adults.

Overview

Language evolved to transcend evolution. With this structured communication, the complexity of behavior can now be achieved through cultural transmission, rather than through the slow selection for genetic mutations that bring change to instinctual behavior. Modern neuroscience research is providing new insights into the mechanisms of human neural plasticity that allow each child to self-organize, to respond to patterns of environmental information with adaptive changes in patterns of neural representation. The mammalian cortex, which has expanded considerably in the big apes and hominids, begins life with exuberant synaptogenesis, such that there is a massive connectivity across cortical regions. The specification of patterns in the cortex is then achieved through experience-dependent subtractive elimination (Innocenti, 1983). Unused connections are lost. The differentiated brain then reflects the information content of adaptive exchange with the environment (D. M. Tucker, 1992).

In humans, this sculpting of cortical anatomy by experience occurs not just for a few months or years as in most mammals, but over a decade or more. If there is a single biological fact that allowed language to evolve from prelinguistic cognition, it was probably not a unique gyrus of the brain, nor a particular segment of the vocal tract. Rather, it was the radical neoteny that allows culture rather than the genome to specify the connectional anatomy of the human brain. Neoteny, the retardation of ontogenesis to allow embryonic forms to extend into the juvenile period, is a common strategy in vertebrate evolution (Gould, 1977). A simple mutation of a homeotic gene could shift the rate of maturation, allowing embryonic plasticity to continue to allow use-dependent specification of the morphogenetic process. If there was a pivotal development in prelinguistic hominid evolution, it may have been the co-evolution of neoteny with the parenting skills that allowed such immature juveniles to survive. The ones that survived maintained essentially embryonic mechanisms of neural plasticity over two decades of maturation. Given effective hominid family groups to allow this extended morphogenesis, given the inherent need for managing the behavior of incompetent juveniles, and given the emotional and attentional controls to allow the requisite communication of intentionality, language may have been the inevitable outcome.

Although this outcome has transcended the biological constraints of evolution in important ways, and probably ways we have yet to realize, it was nonetheless achieved within a framework of vertebrate neural evolution. In this framework, the neocortex is the last, specialized component added on to the the residuals of thousands of millennia of continuously adaptive, slowly evolving, nerve nets. Routine observations in clinical neurology show that the capacities of the human cortex depend on the successful operation of the entire evolved neural hierarchy, including memory control from limbic circuits, motor patterning from striatal-thalamic circuits, and arousal control from brainstem circuits. In this paper, I will outline the connectional architecture of the human brain that is emerging from modern anatomical studies, an architecture that is firmly rooted in the vertebrate plan. I will then propose that we can reason directly from the pattern of corticolimbic connectivity to interpret the structure of cognition. In this structure, both memory and motivation regulate the processes of corticolimbic consolidation to form the adaptive, embodied prelinguistic substrate that then allows the artifacts of language, words and their grammatical forms, to organize meaning.

Neural Representation of Language

Classical evidence from studies of aphasia suggested that language is represented primarily in the left hemisphere, with expressive capacities in the posterior inferior frontal lobe (Broca's area), and receptive capacities in the temporoparietal area (Wernicke's area) (Hecaen & Albert, 1978; Lezak, 1976). Both hemodynamic (PET; fMRI) and electrophysiological findings are largely consistent with this classical model, although right hemisphere contributions are often observed, such as in second languages or in sign language (Bavelier et al., 1998; Dehaene et al., 1997), or in interpreting emotional meaning of language (Borod, 2000). The evolutionary origin of cerebral lateralization is an enduring problem that must hold answers for understanding the evolution of language (MacNeilage, 1986).

Differentiation of expressive capacities to frontal, motor lobe, and receptive capacities to posterior, sensory, cortex has seemed unsurprising, given motor and perceptual requirements for language. However, this evidence does emphasize that the cognition of language is embodied (Johnson & Lakoff, 1999). The representation of language is achieved not in some abstract cognitive space, but in the neural systems that evolved initial to support more elementary functions of perception and action (Givon, 1998). This understanding of higher cognition as emergent from sensory and motor processes appears to be a consistent theme in recent PET and fMRI studies of cognition. Imagery, for example, is not a product of a disembodied mind. Sensory imagery is instantiated in visual and auditory networks, and motor imagery is instantiated in premotor and motor cortices (Kosslyn, DiGirolamo, Thompson, & Alpert, 1998).

In addition to taking on the sensory and motor forms of speech, language must achieve meaning. Two components of meaning can be emphasized. The first is memory. Meaning must be abstracted from experience and represented in a way that can be contacted by words. A second component is emotional evaluation. Although the objectification of meaning may be a critical function of language, psychological studies have shown that, underlying the denotative, conventional level, verbal semantics rests on a foundation of affective evaluation (Osgood, Suci, & Tannenbaum, 1957).

There is a common neural substrate for both memory and emotional evaluation: the limbic networks at the core of the cortex. Corticolimbic connections are essential for consolidating memory, and memory is in turn essential for language comprehension or expression. What seems to be overlooked in modern cognitive neuroscience research is that the control of memory is achieved by the same limbic circuits that are integral to emotional and motivational control. Since Broca first identified the “limbic lobe” forming the limbus or border of the medial core of the brain (Figure 1), it has been clear that the primitive limbic cortices are closely connected with subcortical structures. Since Papez’s tracing of limbic circuits by introducing seizures (Papez, 1937), it has been clear that these circuits are integral to hypothalamic regulation of emotional behavior. Modern neuropsychological researchers have rediscovered the limbic networks, but in relation to memory rather than cognition. It remains to be understood how cognitive representations are consolidated in memory in relation to motivational controls.

Memory control processes are essential to understanding both the evolution, and the current operation, of human language. When we look to the mechanisms of consolidation of memory in the cortex, we find that the limbic roots of these mechanisms evolved as visceromotor and viscerosensory control systems. Like other cognition, language is thus embodied within a context of adaptive, visceral, controls. To appreciate how language offers the capacity for objectivity, we might first appreciate its motivational basis.

The motivational controls on corticolimbic processes cannot be understood, in either an evolutionary or a developmental analysis, without a careful study of subcortical mechanisms. The human cortex represents an elaboration and extension of multiple levels of behavioral mechanisms that have appeared in vertebrate neural evolution. Considered in any detail, the prelinguistic roots of language run deep, to the fundamental self-regulatory strategies of vertebrate neural evolution that gave rise to the mammalian cortex.

Once the phylogenetic framework is appreciated, the classical biological analysis leads us to consider the ontogenetic mechanisms through which human language is self-organized within the extended plasticity of corticolimbic networks. The key issues from the phylogenetic analysis, the differential functions of the neocortical shell of the cortex and the limbic core, take on new forms in the ontogenetic analysis. Rather than the expected recapitulation of the phyletic order, with maturation of the limbic networks preceeding that of the neocortex, the ontogenesis of the human cortex inverts the developmental order, with early maturation of the neocortical shell of language (articulating the sensory and motor patterns of speech) and protracted neoteny and immaturity (and therefore plasticity) of the paralimbic core.

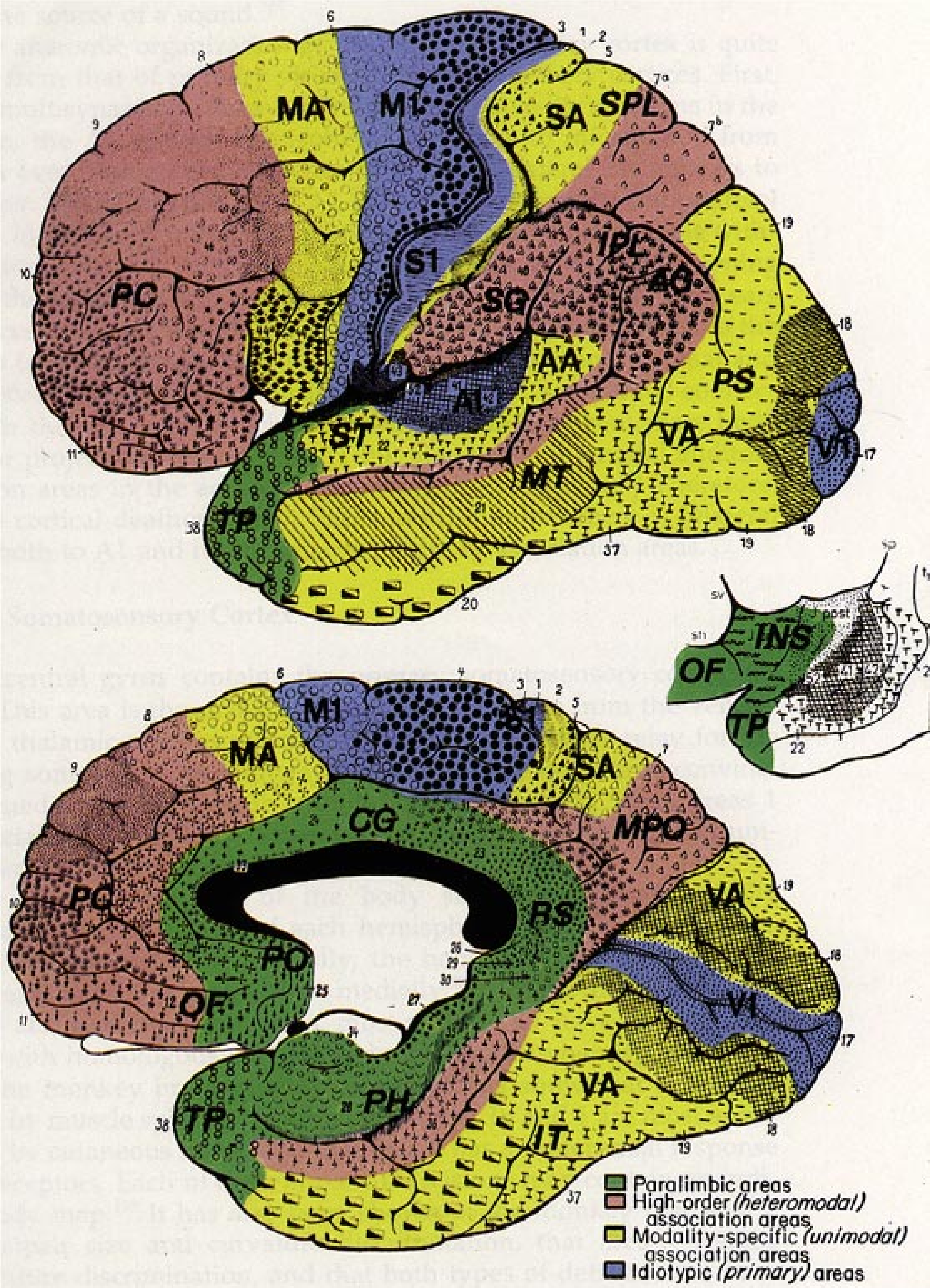

Figure 1. From (Mesulam, 1985). Reinterpretation of Brodmann's cytoarchitectonic parcellation of the human brain on the basis of modern studies of cortical connectivity in the monkey by Pandya and associates. Brocca's limbic lobe forms the limbus or border of the subcortical structures at the core of the brain (TP, temporalpolar cortex; PH, parahippocampal gyrus; RS, retrospenial cortex; CG, cingulate gyrus; PO, periolfactory cortex; OF, orbital frontal cortex). From this primordial cortex, the next wave of

differentiation appears to have formed the heteromodal association areas, then the modality-specific association areas, and finally the idiotypic or primary sensory and motor cortices.

Vertical Integration in Vertebrate Evolution

Evolution of the brain has been a process of progressive reorganization through multiple extensions of primitive strategies of neural self-regulation. The early evolutionary principle was the "Law of Terminal Additions," in which more recent forms could be added only to the terminal stage of embryogeneis. Modern biologists have rejected this principle, because mutations can and do change the morphogenetic process at earlier stages (Gould, 1977). However, this classical principle may continue to offer insight to an evolutionary-developmental analysis. Mutations of earlier stages of development are almost invariably fatal, so that the major variations for evolutionary selection are indeed the terminal forms. Figure 2 shows the embryological differentiation of the hindbrain, midbrain, then forebrain at the end of the neural tube, recapitulating the appearance of these divisions of the neuraxis in vertebrate evolution.

This realization of the evolutionary history in the morphogenesis of each individual brain means that behavior, including language, must be achieved through vertical integration of all levels of the evolved neuraxis (Luu & Tucker, 1998). The most complex functions of the frontal lobe (telencephalon), for example, require the recruitment of attentional regulatory influences from the thalamus, motivational influences from the hypothalamus (both in the diencephalon), and elementary arousal controls from brainstem reticular (mesencephalic) arousal systems.

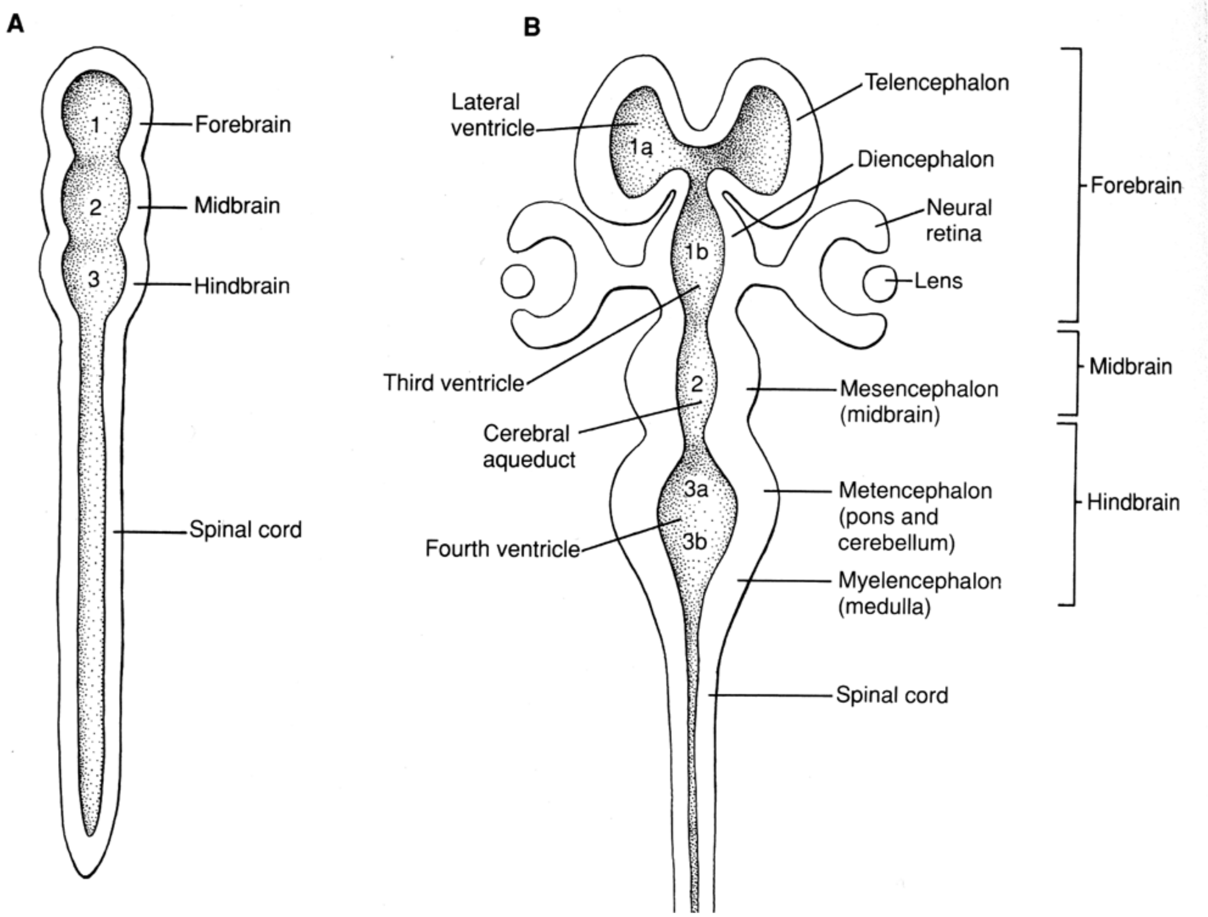

Figure 2. A. Differentiation of brain structures in embryogenesis (From Martin (Martin)). The neural tube of early vertebrates was open to sample seawater. As it closed, cerebral spinal fluid filled the spinal cord

and the ventricles of the brain, and the periventricular sensory receptors took on internal, homeostatic functions of hormonal regulation. B. Continued specification of major divisions of the vertebrate brain in embryogenesis, with the ventricles separating the myelencephalic and metencephalic from the mesencephalic from the diencephalic and finally the (now laterally-differentiated) telencephalic structures. Functional contributions from all levels are required for human language (Luu & Tucker, 1998).

Evolution of the Telencephalon

Consistent with the Law of Terminal Additions, there is remarkable evolutionary conservativism of the lower brainstem, mesencephalic, and diencephalic structures in vertebrates, including humans (Sarnat & Netsky, 1974). The most species variation in mammals is seen in the telencephalic structures, and even here, the species variations are subtle. In humans, the traditional theorizing on language has pointed to the differentiation and regional specialization of the massive cortex. A fundamental evolutionary question is then how the telencephalic structures, the striatum (or basal ganglia) and the limbic circuits (including amygdala and hippocampus) gave rise to the cortex.

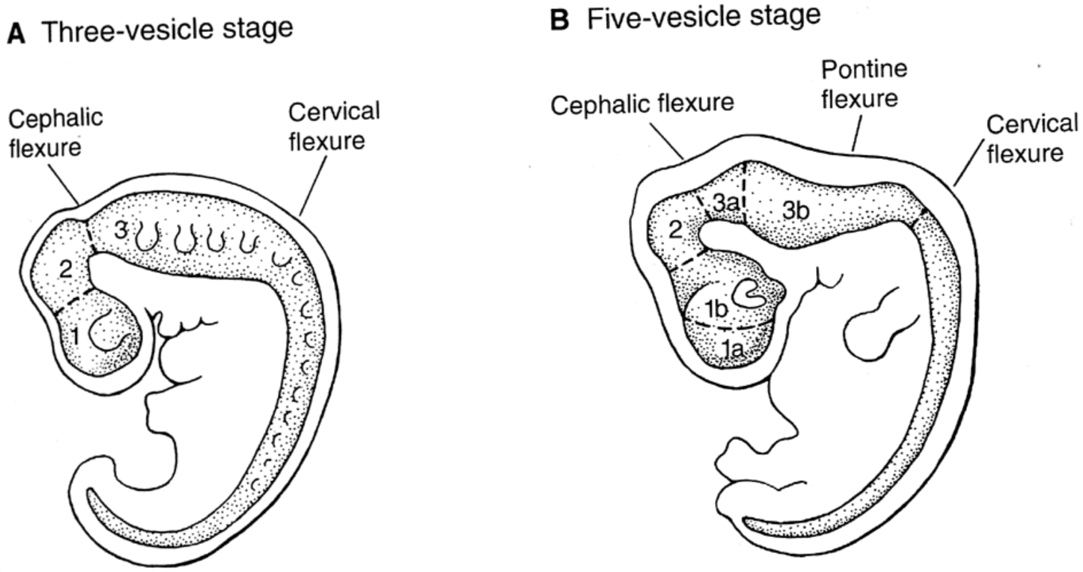

Figure 3. Differentiation of the major divisions of the neuraxis from Figure 2 as seen in the body of the embryo at early gestational stages.

Although most neuropsychological accounts of language emphasize the functions of the cortex, an important observation from clinical studies of aphasia is that the classical neocortical syndromes of expressive (Broca’s) and receptive (Wernicke’s) aphasia are limited to motor or sensory deficits when the lesions are limited to neocortex (Brown, 1979). When semantic capacities are seriously impaired, the lesions typically encroach on limbic cortex (Brown, 1988). It is therefore critical to understand not only the limbic base of the cortex, but the subcortical structures from which the limbic networks evolved.

If the evolutionary precursors of human language were the routinized and stereotyped communication of social animals, then these certainly pre-dated the evolution of the cortex. In avians, and probably in dinosaurs, neoteny set the stage for an extended plasticity of the developing brain. The requisite co-evolution was parenting behavior, coupled with the essential mechanisms of imprinting and attachment. These developments necessitated social communication. Thus the most important preadaptations for human language -- controlling neoteny, attachment, and communication -- are almost certainly precortical. They can be seen to be well-developed in species with minimal cortical development, as well as in the mammals that went on to elaborate these themes into massive cortices and developmental products (cultures) that escaped the confines of the single evolutionary medium, the genome.

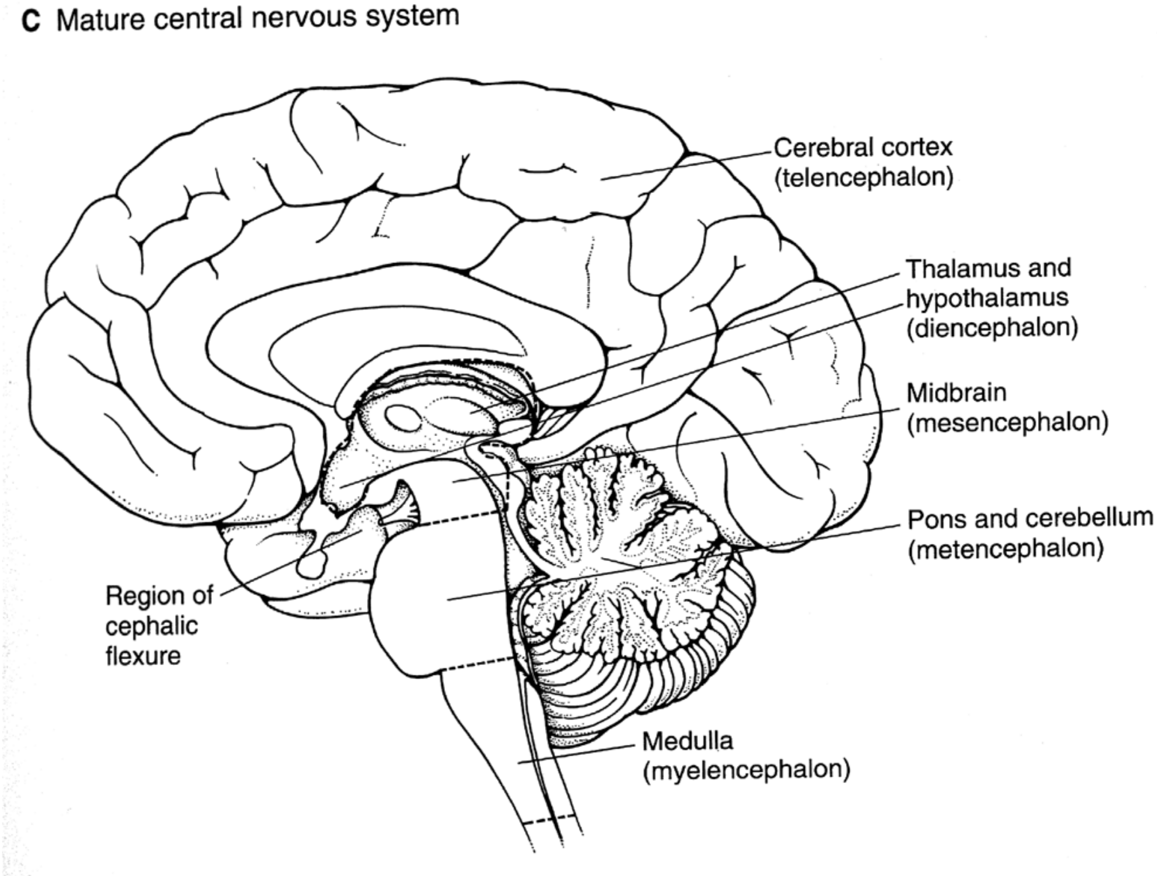

Figure 4. Major divisions of the neuraxis from Figure 2 as seen in the adult human brain.

Reptilian Limbic-Striatal Circuits Give Rise to Mammalian Cortex

We can approach the phylogenesis of the cortex with classical evolutionary-developmental reasoning. As he studied the neuroembryology of the early biologists' favorite neotenic (and thus generic root vertebrate) species, the salamander, Herrick (Herrick, 1948) proposed that the functional circuits of the telencephalon could be seen by tracing their roots in the diencephalon. There are unique projections from the major divisions of the diencephalon (thalamus and hypothalamus) to cortex, and these provide an interesting perspective on the functional organization of the mammalian cortex (Tucker, 2001). The thalamus appears specialized for the environment interface, with specific exteroceptive sensory nuclei (vision, audition, somatosensory) and specific motor nuclei. In contrast, the hypothalamus appears specialized for internal regulation, with representation both of interoceptive, viscerosensory processes and of visceromotor controls (Derryberry & Tucker, 1990; Tucker, Derryberry, & Luu, 2000).

In reptiles and avians, the specific sensorimotor circuits of the thalamus extend the representational function to a structure called the external striatum (Nauta & Karten, 1970). In contrast, the hypothalamic controls appear to be elaborated preferentially within the limbic circuits. This general functional specialization within the telencephalon must have been critical to the key preadaptive communicative specialization of dinosaurs and avians, and it is retained in mammals. The striatal (basal ganglia) circuits form functional circuits with the thalamus to organize motor responses into routinized, hierarchic patterns (Alexander, Delong, & Strick, 1986), achieved through the intrinsic plasticity of these circuits for modification through practice (Gabriel et al., 1996).

Telencephalic Confluence at the Neocortical Shell

With the development of the mammalian cortex, the thalamic representational (somatosensory-somatomotor) circuits project to the neocortex, rather than external striatum, and the external striatum disappears (Nauta & Karten, 1970). Where did this critical structure go? Without it, the basal ganglia of mammals are subordinated to the neocortex, and both sensory and motor projections from the specific thalamic nuclei are now taken up by the neocortex. Nauta and Karten (1970) speculated that the mammalian cortex absorbed the external striatum, and its embryological-evolutionary functional role. With this development, the specific somatosensory and somatomotor neocortices now become the external contact surface -- the interface shell -- for cortical evolution, communicating the brain to the environmental context.

Visceral Base of the Limbic Core

As shown by Papez's studies (Papez, 1937), the limbic circuits link the hippocampus and amygdala with hypothalamic circuits. Modern neuropsychological studies of amnesia have shown that the diencephalic extent of the limbic circuits is as important to memory consolidation as are the amygdala, hippocampus, and their adjacent (paralimbic) cortices (Zola-Morgan & Squire, 1993). Modern anatomical tracer studies confirm that hypothalmic projections to cortex are confined to the limbic cortices at the core of the brain (Risold, Thompson, & Swanson, 1997) (Figure 1). Other crtical subcortical projections are to the arousal controls from brainstem (Mishkin, 1990), and from the forebrain nucleus basalis (Mesulam, Mufson, Levey, & Wainer, 1983). Through control over these arousal and regulatory systems, the limbic circuits appear to respond to events to provide an initial screening for novely and familiarity, thus coding the the current context as to whether it is appropriate for learning (Donchin & Coles, 1988; Gabriel et al., 1996; Mesulam, 1981). These limbic attentional controls thus appear to be closely linked to the hypothalamus's visceromotor control of the internal millieux.

Self-Organization on the Vertebrate Plan

Why is this evolutionary structure of the brain important for understanding language? Because it is the plan within which human children must self-organize their intellectual capacity. Because of radical human neoteny, a long childhood extends the mammalian neuroembryonic process of massive synaptogenesis and then activity-dependent (i.e., experientially-sculpted) pruning (D.M. Tucker, 1992). This plasticity may be fundamental to the human self-organization that creates the complex and flexible neural networks of language (Deacon, 2000). To understand the essential self-regulatory mechanisms for activity-dependent pruning, we must look to the brain's systems for regulating arousal (Singer, 1987). The mechanisms that regulate emotional arousal in the developing child are the same mechanisms that regulate the activity-dependent pruning of cortical networks in embryogenesis to achieve the coherent order of sensory and motor systems (Trevarthen, 1984). Because of radical human neoteny, neural development may best be understood as self-organizing embryogenesis extended into the juvenile period.

In 1885 Pryer observed that the chick embryo shows spontaneous motor activity by the fifth day. Yet it will not show a response to sensation for many days after that (Hamburger, 1977). The reason seems to be the vertebrate plan for acivity-dependent self-organizing neuroembryogenesis. In order for sensory systems to organize a coherent pattern of connectivity, they must be exercised through input. In the developing vertebrate embryo, the primary source of sensation comes from the spontaneous motor activity that provides the simultaneous input to the Hebbian synapses of sensory systems, thereby guiding the process of subtractive elimination and thus neuroanatomical specification (Hamburger, Balaban, Oppenheim, & Wenger, 1965; Singer, 1987; von de Malsburg & Singer, 1988).

Activity-dependent neural plasticity is determined not only by coherent sensory input, but by the arousal systems that set the tone of neural activation (Singer, 1993; D. M. Tucker, 1992). Radical neoteny has produced human infants that are so immature as to be unable to self-regulate their neural arousal systems effectively. The arousal control processes therefore become entrained not only to brain growth and differentiation, but to the social communication through which parents help the infant stabilize immature and labile arousal controls (Trevarthen, 1984). The internalized basis for self-control is therefore the child's experience as it is moderated by the assistance of the parental neural auxillaries. The communication is primarily nonverbal and emotional in the first year. This is the prelinguistic adaptive substrate of object relations upon which language is constructed in the second (Trevarthen, 1984). The patterns of shared attention and social referencing formed by early emotional communication may form an essential basis for the child's learning of word meanings (Baldwin, 1993).

As the child's brain responds to the communication process, the self-regulation of neural plasticity recruits adaptive mechanisms not just in the corticolimbic networks, but throughout the neuraxis (D.M. Tucker, 1992). Language requires as much regulatory support from brainstem, diencephalic, and limbic circuits as it does from specialized neocortical modules (Brown, 1979; Luu & Tucker, 1998). To understand the vertical integration of language, across the evolved neural hierarchy, we can look to the neural mechanisms regulating primate vocalization (Luu & Tucker, 1998).

Hierarchic Anatomy of Primate Vocalization

Jurgens and Ploog have traced the control of vocalization in monkeys by combining lesion and electrical stimulation methods (Ploog, 1981; Ploog, 1992). The results illustrate the progressive elaboration of the vocalization process in each level of evolved circuitry, and, conversely, the dependence of higher systems on more elementary capacities of lower systems.

At the level of the lower brainstem (pons and medulla) are specific actions, such as control of respiration, that form the elements of vocalizations. At the midbrain level (periaqueductal gray and tegmentum) are representations of species-specific action patterns that organize the brainstem centers.

At the limbic level, Jurgens and Ploog observed that the limbic input allows vocalizations to be integrated with the animal's general emotional responses, rather than being stereotyped and isolated patterns. At the level of the cingulate gyrus (archicortex), the monkey is able to integrate the vocal pattern with general attention and goal-setting patterns, in what Jurgens and Ploog term "voluntary call initiation."

Finally, with the incorporation of neocortical (prefrontal) networks, the monkey appears able to carry out "voluntary call formation," in which vocalization is not limited to initiating the stereotyped vocalization patterns, but can be crafted into unique sequences from discrete vocal elements (Ploog, 1992).

Volition and Articulation

Consistent with the specialized neocortical networks for language articulation in humans shown by the aphasia evidence, Ploog (1992) proposes that human language evolved from increased specialization of the neocortical areas that allow monkeys the capacity for voluntary call formation, the articulation of specific vocal acts rather than holistic call patterns. In addition, however, Ploog points to the increased development of human limbic circuits, including projections through anterior thalamic nuclei to both dorsal (ACC, SMA) and ventral (orbital frontal lobe) limbic areas. These may be important to the complex motivational influences on human language. Although the Law of Terminal Additions emphasizes that viable mutations are most likely supported by the late stages of embryonic differentiation, i.e., the neocortical articulatory networks, human language is an integral component of a cognitive and behavioral system that must draw on effective operation of the entire neuraxis (Luu & Tucker, 1998).

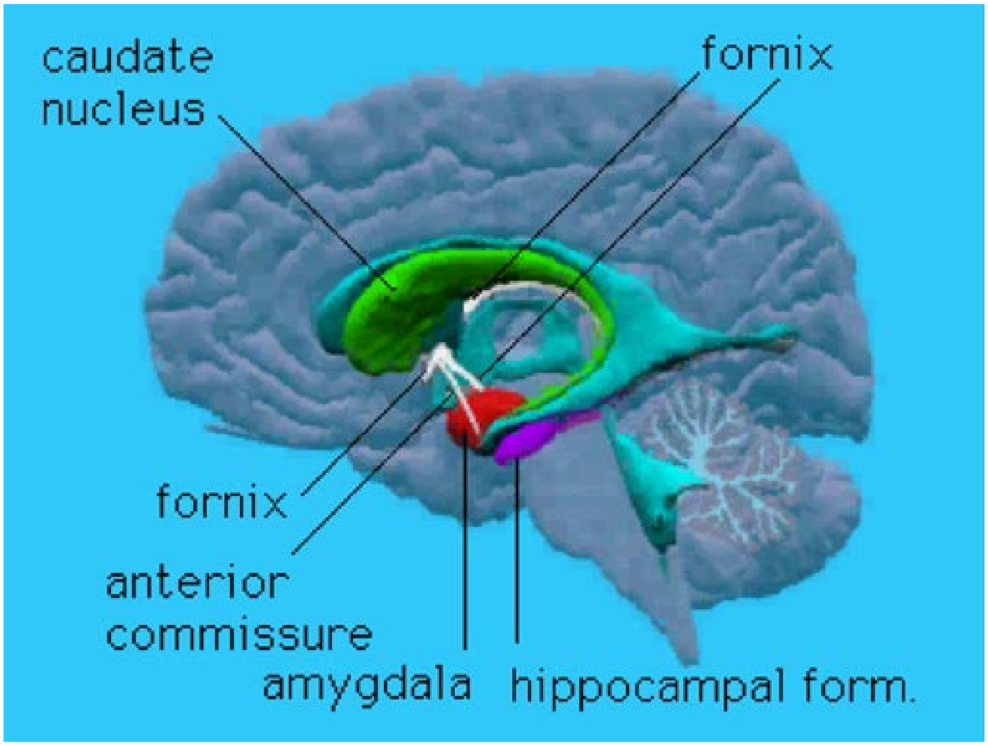

Figure 5. As the cortex evolved in mammals (and became massive in big primates), the temporal lobe was pushed from the front of the brain (at the end of the neural tube) up, back and to the sides. As this progression is retraced in embryogenesis, the amygdala, hippocampus (and the ventricles shown here in blue that remain close to these corebrain structures) are stretched around to the temporal lobes, extending the long fiber tracts (stria terminalis and fornix) that connect them with striatal, diencephalic, and other corebrain circuits.

Corticolimbic Architecture

Tracing the roots of higher cognition thus leads us to search out the primordial themes of regulation and representation that were reworked at each evolutionary level. In studying telencephalic circuitry in mammals, we can see that the functional divisions of the diencephalon seem to have given major direction to this circuitry, i.e., to the neostriatum and the limbic system. Similarly, the elementary diencephalic divisions, the interoceptive, visceral regulatory controls of the hypothalamus and the exteroceptive, somatic interface with the environment in the thalamus, seem to have continued to provide organizational influences during the continued evolution of the mammalian cortex. As we follow Herrick’s (1948) advice and trace the diencephalic roots, we find them anchoring the internal and external poles of the architecture of the corticolimbic networks, the scaffolding upon which each memory, and thus each linguistic structure, must be constructed.

Cortical Connectional Anatomy

Modern studies of the cytoarchitectonics and the connectivity of the primate cortex have offered new insights into cortical evolution (Barbas & Pandya, 1989; Pandya, 1982; Pandya & Yeterian, 1984). The cellular differentiation of the cortical layers is limited for the paralimbic cortices (Figure 1), with two or three layers and a poorly defined granular layer, consistent with the assumption that these are more primitive regions of the brain. In contrast, the greatest laminar differentiation, typically with six or seven distinct layers, is found for the primary sensory and motor cortices (Pandya, 1982). Although it was assumed for many years that the primary sensory and motor areas were the first to evolve, and the more integrative “association areas” appeared in higher mammals, the view from the studies of cytoarchitectonics by Pandya and associates is that the paralimbic cortex was the first to evolve, followed by the heteromodal “association” cortex, followed by the unimodal association cortex, and finally by the primary sensory and motor areas (Mesulam, 1985; Pandya & Yeterian, 1985). Although the term “neocortex” was used for many years to distinguish the large expanses of laminar cortex in higher mammals from the primitive paralimbic cortices, it now appears that there were several major waves (or “growth rings”) of cortical differentiation, with the first being the paralimbic cortices (archicortex and paleocortex), and the latest, and most laminar, neocortical regions being the primary sensory (visual, auditory, and somatosensory) and motor cortices.

The patterns of connectivity of these networks provide a complementary perspective to the levels of cytoarchitectonic differentiation. The following description, is taken from the studies of Pandya and associates (and is summarized in outline form in Tucker, 1992). In each sensory modality, the general pattern is for most connections to be directed to the adjacent cytoarchitectonic region. Thus, in the ventral (object) visual pathway, the “forward” connections go from the primary visual area, to the visual association area, to the inferotemporal multimodal association cortex, to the temporal pole and paralimbic cortex (paleocortex). These network-to-network connections thus appear to reverse the phyletic order, given that the primary visual input from the thalamus targets the neocortical sensory area, and the processing (through memory consolidation) is directed toward the paralimbic cortex. Each area-to-area “forward” connection is reciprocated with “backprojections,” which go from inferior cortical lamina of the relatively paralimbic network to the more superior cortical lamina of the relatively neocortical network.

The inter-regional connections provide another key piece of evidence to the global architecture. Networks of a given level of cytoarchitectonic differentiation tend to send projections to each other. The unimodal association areas, for example, send more projections to unimodal association areas of other modalities than to heteromodal association areas.

In addition, the general density of interregional connectivity decreases with neocortical differentiation. Paralimbic cortices are densely interconnected with each other, creating an integrated distributed network at the core of the cortex. The density of interconnectivity decreases with each cytoarchitectonic level, until the primary sensory and motor cortices are islands, isolated from the rest of the cortex except through connections to the immediately adjacent sensory or motor association areas.

If we interpret the connectivity directly, then the greatest integration of cortical function must occur in paralimbic regions, which are the most densely interconnected. It is of course relevant that these paralimbic regions interact closely with the hypothalamic interoceptive regulatory processes (Risold, Canteras, & Swanson, 1994). In contrast, the primary sensory and motor neocortices are specialized modules, interfaced with the thalamic input and output channels. Although it may be tempting to focus on one network within this architecture, such as for lexical access, grammatical construction, or verbal comprehension, if it involves memory, then language in the human cortex must achieve some coherence across the multileveled corticolimbic architecture.

Figure 6. Left: Visual information appears to retrace the stages of phyletic differentiation in reverse, with the major visual projections from thalamic thalamic pathways targeting primary visual cortex (V1). In the ventral trend, for example, V1 then projects to the adjacent visual association cortex (VA), which projects to inferior temporal cortex (IT), and on to temporal pole (TP) and the medial temporal lobe. **Right:** Motor control appears to recapitulate the phyletic stages directly. In the dorsal trend, for example, the initial motivational impetus and global organization of the action-in-context appears to begin in the anterior cingulate gyrus (CG), which projects to the prefrontal cortex (PC), to the premotor association area (MA), and finally to primary motor cortex (M1).

Dorsal and Ventral Roots of Corticolimbic Networks

The mammalian corticolimbic architecture appears to have evolved from two points of origin, the paleocortex at the ventral base of the brain (TP, INS, PO, and OF in Figure 1) and the archicortex at the dorsal surface of the brain (PH, RS, and CG in Figure 1). The cytoarchitectonics vary fundamentally for these two cortical moieties. Whereas the paleocortical regions include a well-developed granular layer, the archicortical regions include a well-developed pyramidal cell layer. The functional differentiation of the paleocortical and archicortical networks can be understood at the limbic level from examining the subcortical connections, and at the neocortical level from examining the differing specializations for cognitive, sensory, and motor representations (Tucker et al., 2000).

From studying the connectivity of the limbic cortices not only with the hypothalamus but with autonomic centers of the brainstem, Neafsy and associates have suggested that there is a cortical representation of the visceral functions that parallels the cortical representation of motor activities and the sensory modalities. This representation includes cardiovascular, gastrointestinal, thermoregulatory, reproductive, adrenal and immune systems (Neafsey, 1990; Neafsey, Terreberry, Hurley, Ruit, & Frysztak, 1993). Importantly, there is a functional specialization of the archicortical and paleocortical regions for traffic with the internal milliuex. The archicortical networks, centered on the infralimbic layer of the cingulate gyrus on the medial wall of the hemisphere (anterior and subcallosal regions of the cingulate gyrus, CG, in Figure 1), appear to control visceromotor processes. In contrast, the paleocortical networks, centered on the insular cortex between the temporal pole and orbital frontal cortex (Figure 1), appear to control viscerosensory processes (Neafsey, 1990; Neafsey et al., 1993).

There is thus an input-output function of the cortical regulation of interoceptive processes that may be equally important to the organization of the cortex as the familiar input-output division of somatic networks (motor output in the anterior brain and sensory input in the posterior brain). The significance of the visceral regulatory functions is not widely appreciated, but the specialization of dorsal and ventral pathways has been recognized for both perceptual and motor functions, and to some extent the memory processes that integrate them.

Dorsal Sensory, Motor, and Cognitive Functions

In vision, the dorsal (archicortical) pathway (Figure 6, left; upper arrow) has been recognized to support spatial attention and memory (Haxby et al., 1991; Ungerleider & Mishkin, 1982). Because this pathway connects the occipital and parietal neocortices to the cingulate and hippocampus, the studies of the dorsal pathway in monkeys and humans are consistent with the extensive evidence of hippocampal representation of spatial memory in rats (Nadel, 1991). The anatomical evidence shows that the dorsal pathway extends the cingulate gyrus (archicortex), which evolved from hippocampal formation, to both posterior and anterior cortices.

Although there is no obvious connection between spatial cognition and the visceromotor function of the archicortex, the studies of contextual learning may provide a clue. Perhaps the dorsal pathway is representing not just the spatial context for memory, but context more generally. Gabriel and associates have observed that hippocampal input into posterior cingulate cortex appears to inhibit or gate the learning of new responses when the context is not appropriate (Gabriel, Sparenborg, & Stolar, 1986).

The motor extension of archicortex is to anterior cingulate gyrus, medial frontal cortex, dorsolateral frontal cortex as well as supplementary motor area, and then primary motor cortex (Figure 6, right; upper arrow). Analysis of the unique contribution of this pathway in motor control has suggested that it contributes to a holistic, projectional influence on action, in which the action is launched in a vectoral direction, without discrete, ongoing feedback by sensory control (Goldberg, 1985). This is an impulsive mode of control. Goldberg speculates that this dorsal motor pathway from anterior cingulate to supplementary motor area may be responsive to immediate affective outflow. This would be consistent with direction from the visceromotor functions of limbic archicortex. One interpretation may be that the projectional, impulsive control of action in the dorsal pathway is suited to the capacity of posterior archicortical networks to maintain an updated model of the context for action. The limbic contribution to action in the dorsal pathway may be projectional and impulsive because this is the operational mode of the visceromotor functions of the cingulate gyrus. An important question is whether this mode of control, seen by Goldberg in motor processes, may also be reflected in the dorsal limbic contribution to cognition.

Ventral Sensory, Motor, and Cognitive Functions

Similarly, both the sensory and motor operations of the ventral visual pathway (Figure 6, left; lower arrow) should provide clues to how these neocortical regions extend the regulatory controls of the ventral anchor of the limbic networks, the viscerosensory functions of the insula and paleocortex. In contrast to the contextual representation of the dorsal visual pathway, the ventral visual pathway appears to be specialized for object perception and memory (Haxby et al., 1991; Ungerleider & Mishkin, 1982). How this cognitive specialization relates to viscerosensory controls is not immediately obvious. Perhaps there is a tighter constraint when viscerosensory signals direct memory consolidation than when visceromotor signals do.

In motor control, the translation of limbic regulation to neocortical representation seems easier to understand. The orbital and ventrolateral motor pathway from limbic to motor cortex (Figure 6, right;

lower arrow) appears to guide the development of actions with a discrete, immediate guidance from ongoing sensory feedback (Goldberg, 1985). This control may be well suited to direct regulation by viscerosensory signals. If so, then perhaps the tight motivational regulation of actions within the ventral trend (Tucker & Derryberry, 1992) reflects the more general psychological operation of the viscerosensory functions that will be seen in more general patterns of self-control.

Constraints on the Memory of Language

It is thus possible to argue that a complete theoretical model of corticolimbic architecture must include not only the anterior and posterior divisions of the neocortex, defined in their input/output functions by their specific thalamic projections, but also by the dorsal and ventral divisions of the limbic cortex, defined in their input/output functions by their unique hypothalamic projections. The two major diencephalic strutures, thalamic and hypothalamic, seem to have served as the anchors for the evolution of the cortex (Herrick, 1948). In the developing salamander, the thalamic projections are taken up by the lateral wall of the primtive hemisphere, and the hypothalamic projections are taken up by the medial wall. Given that the limbic cortex remains on the medial wall of the hemisphere in humans, and the neocortices are differentiated within the lateral convexities (Figure 1), Herrick's embryological-evolutionary observations on the salamander telencephalon remain quite relevant for the human brain.

Engines of Neocortical Evolution

Although the story of the evolution of the neocortex is controversial (Deacon, 1990; Kaas, 1989; Pandya & Yeterian, 1984), and it is of course not easily resolved with observational evidence, we can draw on the studies of connectivity by Pandya and associates to apply a classical evolutionary-developmental analysis to guess at the process of evolutionary differentiation (D. M. Tucker, 1992) . An important clue is the laminar projections from sensory neocortex to the adjacent, relatively more paralimbic, cortical network. This limbipetal pathway can be traced for the ventral visual pathway, for example, as V1 => VA => IT => TP in Figure 1. In this direction, the projections are from layer III in the more neocortical network (e.g., V1) to layer IV of the more limbic network (e.g., VA) (Pandya & Yeterian, 1985). Because the thalamic projections to sensory cortex terminate in layer IV, this organization appears as if the more neocortical network has interposed itself between the earlier, more limbic, network and the thalamic input (D. M. Tucker, 1992). In this way, each new module of neocortex seems to have modeled the thalamic input in a more complex way before it was projected to layer IV of the existing sensory network.

If we consider the undifferentiated, primitive general cortex of reptiles, then neocortical differentiation appears to have occurred through four or five major waves of differentiation. In each wave, a network specialized for the sensory input of a given modality (e.g., vision), and took up the thalamic projections to the cortex. Of course, in mammals these projections were formerly the external striatal projections of reptiles, so it becomes necessary to theorize that the cortex is now encephalizing the striatal as well as thalamic circuits for sensory motor representations. After each wave, the center of that now specialized network appeared to re-differentiate further, at which point it took up the thalamic input, and the relayed this input to its predecessor, through projections from layer III to layer IV (the former recipient of thalamic input).

In this network hierarchy, neocortical differentiation is driven by progressive modeling and remodeling of the specific sensory and motor input and output representations of thalamic and striatal circuits, with sensory networks in the back of the brain and motor networks in the front. At the same time, all projections must not only reach the corebrain limbic networks, but they must be reciprocated by "back-projections," i.e., in the limbifugal direction, originating in the deeper layers (V and VI) of the more limbic network and terminating in the superficial layer (I) of the more neocortical network. In the ventral visual pathway, for example, this limbifgual progression is TP => IT => VA => V1. Memory cannot be instantiated unless bidirectional corticolimbic traffic links the evolved network hierarchy in a process of recursive, reentrant consolidation.

In this process, whereas we can look to the neocortical networks for the differentiation and articulation of the conceptual product, we must recognize that the limbic networks are the motivating engines. When a seizure begins anywhere in neocortex, it is the limbic cortices and circuits that become excited, and that lead to propagation of the seizure globally (Isaacson, 1982; Papez, 1937). When electrical stimulation is applied to the cortex of animals, there is a recruitment of discharge responses, such that smaller subsequent stimulations can lead to increasing discharge responses, and finally spontaneous seizures (Isaacson, 1982). The recruitment, apparently mediated by long-term potentiation, tends to be focalized in limbic structures and adjacent paralimbic cortex (Racine & McIntyre, 1986; Teyler, 1986). These signs of electrophysiological excitement may be the best clues to the mechanisms of consolidation that synchronize the synaptic plasticity of the multiple adjacent maps in the corticolimbic hierarchy.

Given their connectivity with hypothalamic and brainstem regulatory systems, and given their excitability within the corticolimbic architecture, the limbic cortices must have provided integral formative constraints on the evolution of cortical differentiation, organizing each new wave of sensorimotor and cognitive representational capacity in relation to continuing, primordial adaptive needs.

Language Bounded at the Neocortical Shell: Sensorimotor Articulation of the Environmental Interface

Although the evolution of the cortex is likely to remain a controversial topic, a theory of the evolution of language should be informed about the major dimensions of cortical connectivity, regardless of their evolutionary precedence. In addition to the essential representational capacities of the posterior neocortex implicated by Wernicke’s aphasia, and those of the anterior neocortex implicated by in Broca’s aphasia, it may be important to consider the adaptive controls on memory from the visceromotor and viscerosensory networks of the limbic system. With their hypothalamic connections, the limbic networks form the visceral core of the brain. With their specific thalamic connections, the neocortical networks form the interface shell with the external environment (Tucker, 2001). At the surface shell, language is articulated within the speech apparatus that becomes capable of language-specific utterances. And it is perceived through specialized sensory modules that become capable of language-specific auditory discriminations. But anatomy teaches that these cognitive capacities are not isolated “modules” in some psycholinguistic space, but rather linked networks in a bounded corticolimbic hierarchy.

One bound of this hierarchy is formed by the differentiated sensory and motor cortices. Although it is often proposed that the capacity to articulate speech was important in human language evolution, it is less often emphasized that the perception of speech sounds was a causative factor (because perception skills are less obvious to a superficial analysis of language mechanisms than vocalization mechanics). Yet we can easily observe that an adult’s difficulty in learning of a new language extend to perceptual as well as motor skills.

More generally, it is typically assumed that the sensory and motor mechanisms of speech, while important, are not immediately relevant to the mental capacities of language, which are of a different, psychological or linguistic form. Given the increasing evidence from cognitive neuroscience that mental operations are carried out within the sensory and motor cortices, and their allied association cortices, we have the opportunity to recognize that the organization of each linguistic construction is linked to its articulation in sensory and motor neocortices. We may come to recognize Hughlings Jackson’s insight that the mind is “a great sensorimotor machine” (Jackson, 1931).

Thus, Broca’s area is motor association cortex of the ventrolateral, paleocortical corticolimbic pathway. The routinized access to the lexicon, and the automatized sequencing of the predictable forms of grammar (Givon, 1989; Yang & Givon, 1997) may take on their unique properties because of their place in the linked networks of the motor articulatory pathway. Indeed, as shown by the impairment of the articulatory process with disease of the basal ganglia, motor articulation is not just a cortical process, but may rely on the timing and sequencing capacities of subcortical circuits including the basal ganglia, brainstem, and cerebellum. The common evolutionary context of the mammalian brain may be important to explaining the flexible pattern generation apparatus that becomes so remarkable in human language. In reptiles, the striatum provided the ordered pattern generation that allowed more complex sensorimotor routines. In mammals, the evolution of the neocortex appears to have incorporated the external striatum (Deacon, 1990; Nauta & Karten, 1970) in what appears to be a radical encephalization of the striatal pattern generation capacity. With this encephalization, pattern generation was now extended by the extensive representation and memory capacities of the new cortical networks, allowing more abstract generation of the pattern systems of language.

If we consider the language centers of the anterior and posterior association cortex as connectionist networks, with functional capacities determined by their connections with other functional units, then, at the neocortical bound, articulation may be the essential function. Broca's area is just anterior to the motor areas for the face and mouth. It seems to have evolved its role in speech production, organizing the speaker's intended meaning into the acts of speech, because it is adjacent to and supportive of the speech articulatory networks. The process of differentiating the speech acts from the semantic intention is immediately precedent to the motor apparatus, and it takes its mechanistic form from the articulatory process itself. Language is embodied at the neocortical shell, as it is instantiated in sensorimotor form. Yet language articulation can be meaningful because it is also directed by networks with more global semantic capacities.

Language Bounded at the Limbic Core: The Visceral Basis of Meaning

The other bound of the corticolimbic hierarchy may be the visceral-limbic core networks. These exist at a level of "deep structure" in language that may be deeper than linguists typically consider, even for functional or pragmatic models. In a structuralist, e.g., Chompskian, analysis, the notion of deep structure refers to a generic frame of language that is more generalized than the "surface structure" of the specific utterance. Within the linked networks of the frontal lobe, this level might be more appropriately located to "middle structure," such as Broca's area. In a neural systems analysis, we can recognize that the deep structure must be in the paralimbic networks that provide semantics with an adaptive base, the constraints of motivational significance that ground concepts in personal meaning.

Psychological theorists have often proposed a level of cognition that is more holistic and primitive than the specified lexicon and grammar of language. Freud described primary-process cognition as fantasy, mental activity in which representational ability is immediately constrained by motivation (Freud, 1953). Werner proposed that the cognition of the young child is syncretic, with feelings, perceptions, and actions represented in holistic, undifferentiated fashion in the "postural-affective matrix" (Werner, 1957). From this primitive basis, linguistic representations are not entirely arbitrary, but retain their embeddedness in the holophrastic frame (Werner & Kaplan, 1963).

If we interpret the anatomy directly, then a word achieves meaning through links across all levels of the corticolimbic hierarchy. A complex utterance takes form through the motor-linguistic sequencing apparatus which is continually constrained by the linked, nested semantic representations, from visceral to articulatory. Although we may not be able to apprehend the fact in experience, the neural architecture teaches that the meaning of language is multileveled, from the gut level that is inherently subjective to the surface articulation that is communicable within the articulatory conventions of the culture.

Conceptual Arousal: The Encephalization of the Regulatory Functions

As the corebrain limbic networks interface the massive cortices of the cerebral hemispheres with subcortical regulatory systems, they not only translate the demands of the cortical networks into commands for the hypothalamic and mesencephalic regulatory processes. They must also represent the arousal and regulatory functions to the cortex. In this process, both archicortical and paleocortical regions may have evolved to achieve an encephalization of regulatory control processes. The self-control mechanisms that were reflexive and automatic in simpler organisms may become represented in short-term memory with the extensive elaboration of the paralimbic as well as neocortical networks in recent hominid evolution.

One clue that human cognition has depended upon evolutionary changes in paralimbic networks is the elaboration of the spindle cell of the anterior cingulate gyrus (Nimchinsky et al., 1999). This is a type of neuron that is rare in the cingulate gyrus in monkeys, present in larger quantities in chimpanzees, present in more quantitiy and in clusters in Bonobos (pigmy chimpanzees), and present in dense clusters in humans. Thus, the 3-layered archicortex, long considered by neurologists to be a vestige of the ancestral brain, now appears to contain features that point to human uniqueness.

In recent times, the ubiquity of the cingulate gyrus in neurimaging results has brought it to center stage even before the discovery of its unique anatomy. Recognizing that the anterior cingulate becomes active in PET studies whenever cognitive tasks demand attentional control, Posner and Petersen proposed that the anterior cingulate gyrus forms the basis of the anterior attentional system (Posner & Petersen, 1990). Observing anterior cingulate activity in fMRI studies when conflicting task demands must be resolved, Carter and associates emphasized the importance of this region of cortex to conflict monitoring (Carter et al., 1998). Documenting the linear increase in anterior cingulate activity in PET studies that demand increased effort, Paus and associates emphasized the importance of this region of limbic cortex in regulating arousal in response to cognitive demands (Paus, 2000).

Through linking attentional control, and very likely memory consolidation, to arousal and bodily regulation, the cingulate gyrus may provide a bridge to bring the visceromotor function as a regulatory force into the cognitive domain. The importance of arousal regulation to higher cognitive processes has been apparent to theorists for many years (Luria & Homskaya, 1970; Pribram & MacLean, 1953; Tucker & Williamson, 1984). Damasio (1999) has recently proposed that the neural mechanisms controlling bodily arousal are intimate components of conscious experience. Psychological theorists such as Thayer (Thayer, 1970, 1989) have emphasized the importance of the experience of one's own arousal mechanisms. For example, for the "energy-vigor" dimension of arousal found in Thayer's factor-analytic studies, Thayer proposes that the experience of this form of arousal gives the person the feeling of being able to succeed with challenging tasks. In this way, the cingulate representation of the visceromotor function is not a reflex operating on homeostatic circuits, but a conceptual process, providing the networks of the cortex with information on the state of visceromotor operations. This information is immediately available to conscious experience, consistent with Damasio's (1999) emphasis on the importance of arousal control processes to the sense of self that is implicit within human awareness.

In most human experience, the subcortical arousal and visceral control functions are probably implicit, unconscious. But with the increasing evolution of the hominid cortex, the elaboration of necortical networks may have been accompanied by corresponding elaboration of the corebrain visceroregulatory networks. The increasing responsibility of limbic networks was not simply to translate sensorimotor traffic into demands for hypothalamic and reticular activating adjustments, but to bring visceroregulatory operations to bear on the process of consolidating and integrating the cognitive operations of the cortex itself. There was thus an increasing need for memory representation of the regulatory processes, such that an arousal change, or a visceral adjustment, has the quality not just of an immediate adaptive reflex, but of a concept. This form of bodily concept may be integral to each episode of consciousness, as in "the feeling of what happens" (Damasio, 1999). The experience of energy-vigor may be an essential signal in personal decision-making, just as the experience of emotional depression may be a signal to decreasing coping efforts and recognizing the likelihood of failure in the current life context (Tucker, 2001). The encephalization of the visceroregulatory functions may lead to a form of “adaptive semantics,” in which meaning is evaluated, and experienced, through the implications that resonate at the gut level.

Visceromotor and Viscerosensory Contributions to Self-Control

The archicortical visceromotor and paleocortical viscerosensory networks may contribute to adaptive semantics in different ways. Keeping in mind the projectional, impulsive versus sensory feedback guidance of motor control formulated by Goldberg (1985) for the dorsal and ventral motor pathways, respectively, it may be possible to look to clinical observations for impairment of motivated cognition with lesions of the limbic base of these pathways.

With mediodorsal (anterior cingulate and dorsal pathway) lesions, patients often show the “pseudodepression” syndrome, in which there is loss of behavioral initiative even in the presence of intact motor, and at least superficially cognitive, function (Blumer & Benson, 1975). These patients may appear to have language deficits, because they fail to speak. More severe mediodorsal frontal lesions lead to “akinetic mutism.” When confronted, the patients are able to speak adequately, but left alone they remain mute. Interestingly, patients with lesions of the cingulate gyrus and associated meidal frontal cortex show a lack of concern about their problems, or even about pain they may eperience (Blumer & Benson, 1975; Tow & Whitty, 1953). Impressed by these observations, psychiatrists and neurosurgeons went on to lesion the cingulate gyrus in psychiatric and pain patients; the consistent effect was a lack of concern over previously distressing situations (Flor-Henry, 1977; Laitinen, 1972; Valenstein, 1990).

Thus the visceromotor functions of the dorsal limbic networks may contribute to cognition and experience with the same feedforward, projectional, impulsive mode of control that they manifest in motor control. We can speculate that this is a mode of control that is also important to language, providing initiative, direction, and effort to communicate a motivational intention or significant experience.

With lesions of ventral limbic areas, including anterior temporal, insular, and particularly the orbital frontal cortices, patients are more likely to reflect a “disinhibition syndrome.” Impulses are not appropriately constrained, and the result is manifested in the clinical interview by crude jokes and sexual advances (Blumer & Benson, 1975; Tow & Whitty, 1953). These patients appear to be impaired in the self-control of hedonic action in the same way that anxious and obsessive patients appear to be overly constricted (Tucker & Derryberry, 1992). This unique component of self-control may reflect the adaptive function of the ventral pathway, in which the sensory feedback guidance of action (Goldberg, 1985) has become elaborated from the viscerosensory function of the ventral limbic networks.

The lesions of the ventral pathway that produce personality deficits are typically more medial, inferior and caudal in the orbital frontal lobe (i.e., more paralimbic) than the lesions of Broca’s area that cause expressive aphasia. Yet if there is an ordered hierarchy of function from limbic to neocortical networks, then it may be useful to consider the self-regulatory characteristics of the ventral limbic networks as they relate to the lexical and grammatical operations of the left frontotemporal cortices. The ventral cortex has evolved to organize perception into objects and features in the posterior brain, and to organize actions under sensory guidance in the anterior brain. Do these cognitive skills suggest memory consolidation that evolved from the viscerosensory function?

Core-Shell Dialectics

It may be possible to study language at its functional roots as well as its structural realization. Human speech may be formed by general adaptive semantics at the limbic core of the brain as it is then articulated within specific sensory and motor routines at the neocortical shell. This argument can be made on anatomical grounds, interpreting function through the density of connections. It can also be made on physiological grounds, interpreting the excitability of limbic-cortical connections as reflective of the process of memory consolidation. Putting the mechanism of consolidation together with the anatomy, we arrive at a functional interpretation such as that proposed by Pandya and associates (Pandya, Seltzer, & Barbas, 1988; Pandya & Yeterian, 1984). In the sensory pathways, cognition cannot be understood simply by one-directional processing, in which sensory data is processed through stages progressively from neocortex toward limbic cortex. Rather, consolidation must be balaned by traffic in the opposite direction, the so-called "back-projections," from limbic toward neocortical networks.

To the extent that we can interpret the limbifugal (from limbic) traffic as determined by memory, and the limbipetal (to limbic) traffic as determined by sensation, then the bidirectional nature of consolidation has been anticipated by at least one cognitive theorist (Shepard, 1984). Shepard emphasized that perception must occur within the framework of memory, the framework of experience with the sensory information. Each act of perception is one of expectancy on the basis of both history and motivation. According to Shepard, perception could be described as hallucination constrained by the sensory data (Shepard, 1984).

Evidence that we can interpret the relative contributions of limbic and neocortical networks in Shepard's terms has come from recent single unit studies in monkey temporal lobe (Naya, Yoshida, & Miyashita, 2001). The monkey's task contrasted a perceptual signal with a signal to recall a perceptual event. Recordings were made simultaneously in paralimbic (perirhinal) cortex and neocortex (area TE of the lateral temporal lobe), and the timing of recorded activity was examined. When the perceptual signal was given, the neocortical area responded first, consistent with the direction of travel in the "forward" (limbipetal) direction. However, when the memory retrieval signal was given, the paralimbic area responded first, implying a "back-projection" or limbifugal progression. Interestingly, after the initial activity in the paralimbic network, the lateral temporal neocortex did respond, as if the perceptual network were gradually recruited in the process of reinstantiating the remembered event (Naya et al., 2001).

The integral role of adaptive control in paralimbic representations has been seen in studies of responses to food in orbital frontal cortex (Rolls, Critchley, Browning, Hernadi, & Lenard, 1999). Neurons in sensory neocortex respond in an invariant fashion to sensory qualities such as smell, taste, or the feel of fat in the mouth (Rolls et al., 1999). In contrast, neurons in paralimbic areas of orbital cortex may respond to the sensory stimulus only when the animal is hungry. At the limbic base of the linked networks of the cortex, the perceptual representation appears to be adaptive, dynamic, and syncretic, a confluence of the exteroceptive data from the shell and the interoceptive representation of the encephalized corebrain regulatory function.

Objectivity and the Emotional Disorders

In order for the conceptual process to be coherent, the neocortical articulation of representational form may need to be congruent with the paralimbic conceptualization of the internal millieu and motivational context. However, it may also be that the specification of cognition in neocortical networks provides objective, structured control over the inherently labile and subjective limbic processes (Tucker, 1981; Tucker & Liotti, 1989). In PET studies of normal subjects reflecting on sad experiences, blood flow increases were observed in subgenual (paralimbic) anterior cingulate cortex, together with decreases in right dorsolateral neocortex (Mayberg et al., 1999). The opposite pattern was observed in depressed patients who had recovered from depression: blood flow increased in right dorsolateral areas and decreased in the ventral cingulate (Mayberg et al., 1999). Mayberg and associates proposed that the reciprocal relations between frontal neocortical and limbic cortices may be important to cognitive and affective imbalance in the emotional disorders.

Similar questions of corticolimbic balance have come up in other neuroimaging studies of self-control in psychopathology. When anxious subjects were asked to think of what made them anxious while in the cerebral blood flow scanner, flow increases were observed in the left inferior frontal area (Johanson, Risberg, Silfverskiold, & Smith, 1986). These findings appear consistent with the tendency of anxious subjects to approach situations with the analytic, focused cognition of the left hemisphere (Tyler & Tucker, 1982). Given the proximity of the flow increases observed by Johanson et al to Brocca's area, additional experiments were conducted to contrast the anxiety ruminations with non-affective verbal thought. Increased blood flow was still observed in the left orbital frontal region during the anxiety condition. Importantly, the anxiety-related flow increases were seen in the posterior, more paralimbic regions of the left orbital frontal lobe (Johanson, Smith, Risberg, Silfverskiold, & Tucker, 1992). These studies provide an interesting perspective on the adjacent networks of the left inferior frontal lobe. Brocca's area is linked at the neocortical level to the motor control areas of the face and mouth, and at the limbic level to the affective, motivational functions of the posterior orbital cortex, which are in turn closely linked to the viscerosensory functions of the insular cortex and ventral limbic system (Tucker & Derryberry, 1992).

As suggested by the importance of the right dorsolateral area in the findings of Mayberg et al (1999), the frontal control of limbic responsivity may be important in the right hemisphere as well as the left. When Johansson and associates asked spider phobics to view videos of active spiders while in the blood flow scanner, the patients who reported being in control of their phobic response showed blood flow increases in the right dorsolateral frontal cortex (Johansson et al., 1998). Those patients who experienced panic showed decreases in the right dorsolateral area. Although the Xenon-inhalation measures of regional cerebral blood flow are superficial, and thus did not allow measures of limbic cortex activity in this research, the direct relation between frontal neocortical activity and the cognitive self-control of emotional response seems consistent with the interpretations of Mayberg et al (1999) that neocortical regions of the frontal lobe are able to provide inhibitory control over the affective responses of limbic regions. Although the asymmetries are clearly important (Liotti & Tucker, 1994; Tucker, 1981), a similar process of corticolimbic balance appears to occur for the nonverbal concepts in the right hemisphere and the verbal concepts of the left hemisphere.

On both sides of the brain, there may be an ongoing, microdevelopmental process which tends toward the differentiation and specification of discrete conceptual forms, such as occurs in the articulation of ideas in language. This process of articulation appears to emerge from a more primitive, holistic level of representation, in which motivational and emotional influences are fused with the semantic content. Judging from the evidence on emotional states and disorders, the allocation of cognition from one bounded constraint to the other is an important determinant of whether cognition is objective and rational or subjective and emotional. The dialectics of corticolimbic differentiation may be important not only to differing psychological states, but to enduring individual differences in cognitive and personality style (Shapiro, 1965).

Retarded Embryogenesis

Classical evolutionary-developmental analysis looks to the ontogenetic recapitulation of the phyletic history to understand the relations among the evolved parts. Reasoning in this tradition, Piaget proposed in his *Genetic Epistemology* that the best way to understand the evolution of human knowledge may be to examine the emergence of intelligence in children. Although this approach continues to be informative, the notion of recapitulation cannot be applied in a simple way to explain mammalian cortical maturation. Primate and particularly human neoteny has involved early maturation of the recently evolved neocortices, while maintaining extended immaturity of the paralimbic regions.

Maturational Gradients

In the human brain, the maturational process leads to myelination and functional fixity of the neocortical networks (primary sensory and motor cortices) early in development (Yakovlev, 1962). This early maturation led early researchers in the 20th Century to believe that the sensory and motor cortices were evolutionarily primitive, wereas the “association areas,” because they were late to mature, must have been more recently evolved. However, as described above, the study of both cytoarchitectonics and interregional connectivity suggests otherwise (Pandya, 1987).

The early myelination of primary sensory and motor cortices is consistent with a loss of neural plasticity in these networks, compared with association and limbic cortices. Barbas (Barbas, 1995), in fact, has observed a number of parallels between the plasticity of the infant brain and the characteristics of paralimbic cortex that are retained in the adult brain.

The effects of this maturational gradient may be seen behaviorally, in the difficulty of learning to speak a new language without an accent. Similarly, adults, but not young children, have difficulty discriminating the unfamiliar sounds of a new language. In contrast, the retention of juvenile plasticity in limbic cortices may be integral to the flexibility of adult human cognition, allowing adults to learn the meaning of the words in a new language, even though, to native speakers, they remain only marginally competent with the sensorimotor articulation of those words.

It is certainly possible that these effects are evolutionary accidents, the functional detritus of arbitrary selection. It is also possible, however, that the early myelination of the neocortical, articulatory shell may be essential to allow language to emerge. Fixation of the differentiated building blocks, the phonemes and graphemes, may be necessary to allow the complexity of the quasi-arbitrary representational forms to be assembled and reordered in ways that suit the organized patterns of meaning in linguistic intelligence.

Similarly, the remarkable feat of human language is not that we can make distinct speech sounds, nor even that we can order these in the motor sequence habits of grammar, but that we have anything interesting to say. The paralimbic retention of embryonic plasticity may be essential for the capacity for novel memory operations, for innovative conceptual constructions, which are continually evaluated and motivated by the prelinguistic mechanisms of adaptive semantics.

The enduring plasticity of the paralimbic core may thus be essential to flexible human cognition, but it is not without consequences. Furthermore, behavioral and experiential flexibility may become increasingly difficult for the older brain simply as a result of paralimbic plasticity (Tucker & Desmond, 1998). Fully-interconnected networks, such as found at the limbic core, are subject to the stability-plasticity dilemma (Grossberg, 1984), a limitation of distributed representation in which the accomodation of new input (plasticity) causes a disruption of prevous representations (McClelland, McNaughton, & O'Reilly, 1995). When translated to the adaptive semantics forming the core of personality, the result of the stability-plasticity dilemma may be that any new experience becomes increasingly difficult to incorporate within the old self (Tucker & Desmond, 1998). Although the corebrain networks retain their embryonic plasticity, they are also functionally active in representing a lifetime of deep structure. By early myelination, the neocortical networks may avoid the stability-plasticity dilemma in favor of stability and resistance to disruption by new information.

Through different mechanisms, then, cognitive representation gains a kind of developmental entropy at both the core and shell bounds. When constrained either to the visceral sensorimotor core, or to the somatic sensorimotor shell, cognition must remain concrete. Reframed in multiple levels through reentrant consolidation, however, cognition, and experience, may gain the capacity for abstraction. Perhaps it is in this stratification of conceptual form, linked across the nested corticolimbic networks, that we have the opportunity, however fleeting, for abstract knowledge.

Evolutionary Strata and the Structure of Experience

In his evolutionary-developmental study of cognition, Werner proposed that the differentiation of specific cognitive form out of holistic and syncretic precursors is characteristic not just of the child’s development, but the development, or microgenesis, of each idea (Werner, 1957). As he considered the microgenetic process within the context of neuroanatomy, Brown recognized that the progression must be, at least in broad outline, phylogenetic. The development of an action, and a concept, must begin in the arousal and motivational centers in the upper brainstem, must recruit some adaptive resonance within diencephalic and limbic circuits, to be unfolded across paralimbic (e.g., cingulate) association (e.g., supplementary motor) and finally premotor cortices, before being instantiated in the motor cortex (Brown, 1987).

As he considered the organization of motility in the vertebrate brain, Yakovlev emphasized that the internal core reflects the “sphere of visceration,” patterned on respiration and homeostasis. At the next level of the exteriorization of movement are the axial movements of the body, reflecting the gross coordination of posture and the bodily basis for action. Next are the appendicular movements, of the limbs, coordinated in balancing gravity with the axial adjustments of posture. The final articulation from the visceral core is achieved by the oro-digital articulations of the distal extremities, in which language may be the final exteriorization (Yakovlev, 1948).

We can extend this classical evolutionary-developmental reasoning to the modern evidence of neural plasticity within corticolimbic anatomy and physiology. If human cognition is indeed a kind of neuroembryogenesis extended unnaturally, then the evolutionary substrate of prelinguistic cognition may be of more than historical interest. It may be possible to recognize the recruitment of each level of the evolved neuraxis in the process of differentiating each linguistic construction.

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