

A Radical Reversal in Cortical Information Flow as the Mechanism for Human Cognitive Abilities: The Frontal Feedback Model

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The paper argues that the rich cognitive abilities of humans are the result of a unique functional system in the human brain which is absent in the nonhuman brain. This "frontal feedback system" is suggested to have evolved in the transition from the great apes to humans and is a product of a reversal in the preferred direction of information flow in the human cortex due to the phylogenetic enlargement of the human frontal lobe. The frontal feedback system forms an autonomous functional unit in the cortex whereby action-schemes in frontal cortices continually create fictitious sensory scenarios in posterior sensory cortices by manipulating the release of sensory representations there. These internal scenarios are created free of environmental constraints and reflect the human's internal cognitive and language processes. Nonhumans do not have a frontal feedback system and their internal cognitive processes are stimulus-bound. Evidence in support of the proposal is presented and some implications of the frontal feedback model for human experience are discussed.

Humans are, undeniably, the only animal species that writes novels, builds computers, and organizes expeditions to the moon. Thus, the cognitive abilities of humans appear to be qualitatively distinct from those of all other animals. It would seem, therefore, that there should be qualitative differences in the structure of the human brain which would account for these cognitive differences. The surprising fact, however, is that there are no qualitative dif-

I would like to thank Joaquin Fuster, David Galin, and Mortimer Mishkin for helpful discussion and correspondence. My appreciation also goes to the Hans and Clara Zimmerman Foundation Scholarship Fund for much-needed financial support. Special thanks goes to Danielle H. Emick and Sue T. Parker for helpful comments throughout the preparation of the manuscript. My deepest gratitude goes out to Elaine M. Chase, whose constant support, encouragement, and detailed editorial comments were of invaluable assistance. Requests for reprints should be sent to Raymond A. Noack, c/o Sue T. Parker, Department of Anthropology, Sonoma State University, Rohnert Park, California 94928.

ferences, only quantitative differences. That is, differences between human and nonhuman mammalian brains are marked merely by differences in the relative sizes of certain brain regions, not in the presence or absence of any structures or pathways (Akert, 1964; Fuster, 1989; Gibson, 1990). In fact, the human brain is remarkably similar in structure to that of all other mammalian brains and contains no unique structures or pathways (Gibson, 1990). Attempts to account for this disparity in cognitive abilities between the anatomically similar brains of humans and animals have taken the form of the continuity versus discontinuity debate.

Continuity theorists account for the disparity by simply denying that there is one (Gibson, 1990, 1991; Greenfield and Savage-Rumbaugh, 1990; Jerison, 1973). Instead, they argue that human and animal cognition is really quite similar, as the anatomical evidence would suggest. Cognitive capacities, they maintain, are directly related to brain size and humans merely lie on a continuum with other animals in terms of these abilities. In short, the differences between human and animal cognition are ones of degree rather than of kind. Continuity theories fit nicely with the anatomical data, and it is certainly true that humans and higher mammals share many aspects of behavior. These theories run into trouble, however, when attempting to demonstrate a direct relation between cognitive capacities and brain size: even the smallest-brained humans have a virtually unlimited ability to create and comprehend complex concepts such as grammatical structures and mathematics (Holloway, 1966); the largest-brained nonhumans, on the other hand, are severely limited at best in these abilities if they even have them at all (Holloway, 1966; Macphail, 1987).

In light of this evidence, discontinuity theorists maintain that human cognitive abilities are qualitatively distinct from those of all other animals (Chomsky, 1980; Crain, 1991; Fodor, 1983; Macphail, 1987). Differences between human and animal cognition are ones of kind rather than degree and cannot be related to brain size alone. Instead, these theorists postulate that unique neural devices, or "modules," were added to the human brain during evolution which are specialized for such abilities as language and mathematics. Discontinuity theories fit nicely with the behavioral evidence and account for the inherent problems of continuity theories. Discontinuity theories, however, are often criticized on their inability to identify these proposed modules in the human brain or to explain how they work (Gibson, 1990; Greenfield, 1991). The structural similarities between human and animal brains imply that there are no added modules. Thus, the debate continues.

Perhaps the debate continues because both continuity and discontinuity theories fail to address the real problem: how qualitatively distinct human abilities could have arisen in a brain separated only by quantitative differences. In order to make their models work, continuity theories tend to

ignore the behavioral evidence while discontinuity theories tend to ignore the anatomical evidence. What is clearly needed, then, is an alternative model which actually does address the problem and accounts for both the anatomical and behavioral evidence. The frontal feedback model offers such a model and argues that, although structurally similar, the human brain processes information in a fundamentally different fashion than the nonhuman brain. It is this difference which is responsible for the distinct cognitive abilities of humans.

According to the model, information flows in the nonhuman cortex from posterior sensory regions to frontal motor regions with the implication that sensory representations manipulate the release of action representations. In the human cortex, on the other hand, the situation is the reverse. That is, the great phylogenetic enlargement of the human frontal lobe reversed the preferred direction of information flow in the human cortex to a frontal-to-posterior direction. Thus, information flows in the human cortex from frontal motor areas to posterior sensory areas with the implication that action representations manipulate the release of sensory representations. In a phylogenetic sense, this reversal can be viewed as "frontal feedback," whereby intrinsically generated activity in the human frontal lobe began to feed back on and manipulate activity in posterior areas. This frontal feedback, then, is suggested to have separated an autonomously functioning "frontal feedback system" from environmental constraints in the human cortex thus allowing for distinct cognitive abilities (e.g., language and mathematics) in a manner described by Piaget (1954, 1971; Piaget and Inhelder, 1969). Nonhumans, who lack a frontal feedback system, do not have these cognitive abilities.

As are all models of higher brain function, the frontal feedback model is necessarily speculative in nature and many concepts are presented here in a simplified fashion in order to keep the discussion easy to follow. The intent of this paper, however, is not to rigorously defend the details of the model, but rather to merely outline its central concepts and to introduce it as an alternative to existing models.

Models of Mammalian Brain Function

In order to outline the proposed frontal feedback system and to discuss how it may have evolved in the human brain, it is first necessary to discuss how the nonhuman brain functions. This first section reviews the traditional stimulus-response model of nonhuman cortical function and makes explicit some of the implicit assumptions in the more widely accepted theories.

Some Relevant Background

If an animal is to survive in its environment by finding food, gaining shelter, avoiding predators, and so forth, it must be able to produce successful behaviors in the presence of significant stimuli. One way the animal is able to do this is by "learning" which behaviors bring reward in a given situation and which do not. Learning is achieved when certain stimuli become conditioned to certain behaviors which in the animal's past were helpful to its survival.

Consider, for instance, a monkey exploring a banana and a stick. If at one point the monkey happens to bring the banana to its mouth and attempts to consume it, the monkey will receive food reward and thus the sight of the banana will become conditioned to the behavior of eating it. Future encounters with a banana may then serve to trigger the associated consummatory behavior immediately. If the monkey attempts to eat the stick, on the other hand, no food reward will be had and thus no association will be made. Through time, such learned associations greatly facilitate the monkey's survival by providing it with a rich and ready store of successful behaviors in the presence of various stimuli.

Attempts to uncover mechanisms in the mammalian brain to account for the formation of such learned associations have found the cerebral cortex to play a major role. In a general sense, the cortex can be divided into two main functional areas, a posterior area involved in the representation of sensory stimuli and a frontal area involved in the representation of hierarchically organized, sequential motor behaviors, or "action-schemes" (Greenfield, 1991; Kolb and Wishaw, 1985; Mishkin, 1990). Associations between stimuli and behavior are made through widespread reciprocal connections between these two divisions of cortex (Jones and Powell, 1970).

According to current theory, a given sensory stimulus excites a corresponding representative pattern, or "ensemble," of neurons in posterior cortices. Under conditions of reinforcement (reward), this neuronal ensemble becomes stored as a Hebbian (1949) cell-assembly, which connects the neurons involved in the stimuli's representation into an enduring lattice-like network (Mishkin, 1993). The cell-assembly serves as the stored, central representation of the stimulus and can be reactivated, or "triggered," by the presentation of the same stimulus or a similar stimulus at some later time (presumably, the presentation of a stimulus closely related to the one represented by the cell-assembly will serve to excite some of the assembly's neurons which, in turn, will cause excitation to spread throughout the entire assembly, effectively triggering the assembly [Mishkin, 1993; Skarda and Freeman, 1987]). In the same way that the representation of a sensory stimulus is stored as a cell-assembly in posterior cortices, the representation of an action-scheme is stored as a cell-assembly in frontal cortices, and it is simi-

larly triggered. Again, with proper reinforcement, a given sensory assembly can become conditioned to a motor assembly through long-distance cortico-cortical connections provided both assemblies are active in the cortex at the same time. Reinforcement is thought to stimulate, via subcortical structures, the release of certain critical neurotransmitters into the cortex which serve to consolidate these cell-assemblies and the associations among them (Mishkin, 1990, 1993; Skarda and Freeman, 1987). Thus, on some future occasion, the triggering of a sensory cell-assembly would, in turn, trigger an associated action-scheme which in previous experience led to reward.

Importantly, individual cell-assemblies can be chained together to represent more complex sensory events or behaviors (Hebb [1949] referred to such chaining as the phase-sequence). For instance, specific sensory assemblies can be successively chained together giving rise to the storage of a temporal sequence of events, a sensory "scenario." Similarly, simple action-schemes can be chained together giving rise to the formation of more complex, hierarchically organized action-schemes (Fuster, 1989; Greenfield, 1991). Again, the reinforcement that accompanies this chaining governs whether and how strongly the chained assemblies are stored.¹

Information Flow in the Nonhuman Cortex

Building on these concepts, the now-traditional stimulus-response model of cortical function emerged that views information flow in the cortex as proceeding from posterior sensory areas to frontal motor areas in a unidirectional, "feed-forward" fashion (cf. Damasio, 1989b; Fuster, 1989; Geschwind, 1979; Kolb and Wishaw, 1985; Pandya and Seltzer, 1982). That is, incoming sensory stimuli trigger a chain of sensory assemblies in posterior cortices which, in turn, trigger an associated chain of action-schemes in the frontal cortices. Previously reinforced stimulus-response combinations, then, are greatly facilitated, and a given behavior is guided through to completion by feedback from the external environment at each step in the chain. This "perception-action cycle" is best described by Fuster (1989):

In all forms of behavior, from the simplest and most automatic to the most elaborate and deliberate, motor action is not only initiated or triggered by sensory signals, but also regulated in the course of time by sensory feedback generated by changes that action itself induces on the environment. Thus, a semblance of a circular pattern of influences is at work in motor behavior: from the environment upon the organism through sensory receptors, from the organism upon the environment through motor effectors, from the environment back upon the organism again through sensory recep-

¹To avoid complicating the discussion, only reinforcement (reward) will be discussed in this paper. It should be noted, however, that punishment also serves to consolidate associations, storing representations of stimuli and behaviors to be avoided (Stein, 1964) [see footnote 12].

tors, and so on. This pattern of interactions between the organism and the world around it . . . establishes the principle of the indissoluble union of perception and movement. (pp. 175–176)

In the example of the monkey, then, the sight of a banana would immediately set into sequence the previously reinforced chain of action-schemes involved in reaching out, grabbing, peeling, and consuming the banana. This action sequence would be maintained through constant feedback to the sensory areas from the environment. Such a feed-forward mechanism whereby posterior sensory areas continuously control frontal motor areas is important to the animal's survival because it allows constant interaction between the animal's sensory environment and its responses to it.²

Indeed, the structure of the nonhuman brain would support such a feed-forward mechanism. That is, the posterior sensory region of the nonhuman cortex is generally much larger than the frontal motor region (Kaas, 1987), and recent models of global cortical function imply that activity in a larger cortical region can continually manipulate activity in a smaller region (Bressler, 1987a, 1987b; Freeman, 1991; Skarda and Freeman, 1987).³ The implication is that the larger posterior sensory areas in the nonhuman cortex manipulate, or control, the release of action-schemes in the smaller frontal areas.

Evidence for Frontal Feedback in the Human Brain

While posterior cortical areas are significantly larger than frontal cortical areas in the nonhuman (Kaas, 1987), the same is not true for the human. In fact, the hallmark of the human brain is the large size of its frontal lobe (Damasio, 1991; Fuster, 1989; Khokhryokova, 1979; Luria, 1966/1980). It

²This traditional model should not be confused with a reflexive model of behavior since the traditional model allows for much greater behavioral plasticity. For example, in the traditional model, some stimuli can be ignored if they are not significant. Furthermore, "spontaneous," or self-organized, activity in posterior cortices can trigger action-schemes in frontal cortices even in the absence of significant stimuli, giving rise to so-called operant behaviors.

³Although not the only determinant of one cortical area's influence over another cortical area, the absolute size of a given area can serve as one marker. That is, studies of the collective behavior of large groups of cortical neurons (neural mass action) suggest that the excitation of a given cell-assembly causes the activity of its constituent neuronal ensemble to behave in a cooperative, or "synchronous," fashion (Freeman, 1975, 1991; Freeman and Skarda, 1990; Skarda and Freeman, 1987). Synchrony allows the collective activity of the ensemble to sum together, generating a carrier wave in that cortical region with greater amplitude than other cortical regions where the activity is not synchronous (Bressler, 1987b; Freeman, 1991). The greater number of neurons and interconnections, or cortical area, involved in the excited ensemble, the greater the collective signal since excitatory signals summate. Thus, given a competition between two regions where each region's activity is synchronous, a large cortical area would generate a stronger carrier wave which can manipulate activity in a smaller cortical region possessing a weaker carrier wave.

might be expected, then, that if a larger posterior region manipulates a smaller frontal region, as was suggested to be the case in nonhumans, then a larger frontal region should manipulate a smaller posterior region in the human. Indeed, evidence is presented below which suggests that the great phylogenetic expansion of the human frontal lobe "tilted the scale," so to speak, and reversed the preferred direction of information flow in the human brain to a frontal-to-posterior direction (see Figure 1). Thus, the feed-forward system in nonhumans was replaced by a "feedback" system in humans. (It is important to note that the simplified distinction between human and nonhuman cortical function is made here largely for illustrative purposes, which is why the phrase "*preferred* direction of information flow" is used. Actual cortical dynamics allow for the bidirectional flow of information between frontal and posterior areas in both humans and nonhumans [Damasio, 1989a, 1989b; Goldman-Rakic, 1988]. The important consideration, though, is that given a competition for influence in the cortex, the posterior areas will win in nonhumans and the frontal areas will win in humans. Thus, any frontal influences on posterior areas in nonhumans is transient whereas in the human it is sustained.)

Cognitive and Behavioral Evidence

As stated above, there is no clear consensus as to what the differences are between human and animal cognitive abilities. First of all, whereas introspective reports can be used to study human cognition, the study of animal cognition is based solely on observing the animal's behavior, which is not a reliable indicator of internal cognitive processes (Libet, 1992; Macphail, 1987). Second, there is little consensus even as to what the term "cognition" means or includes (Parker and Baars, 1990; Stuss and Benson, 1986), which makes it more difficult still to identify differences. Even so, any discussion of cognitive differences between humans and animals must take into account the manner in which sensori-motor representations are chained together, or "constructed," in each. This constructional process ultimately determines the plasticity of knowledge or "insight" an organism can generate and bring to bear on a given problem and, thus, is considered a direct marker of cognitive ability (Gibson, 1990; Parker and Gibson, 1979).

Indeed, humans and animals appear to construct sensori-motor representations in fundamentally different ways. For example, the classical observations of reflexive and operant behavior in nonhumans which led to the formation of the traditional feed-forward model suggest that the construction of sensori-motor representations in nonhumans is driven by sensory stimuli. That is, representations are constructed through the animal's interactions with the environment which chain together successful behaviors and the reinforcing

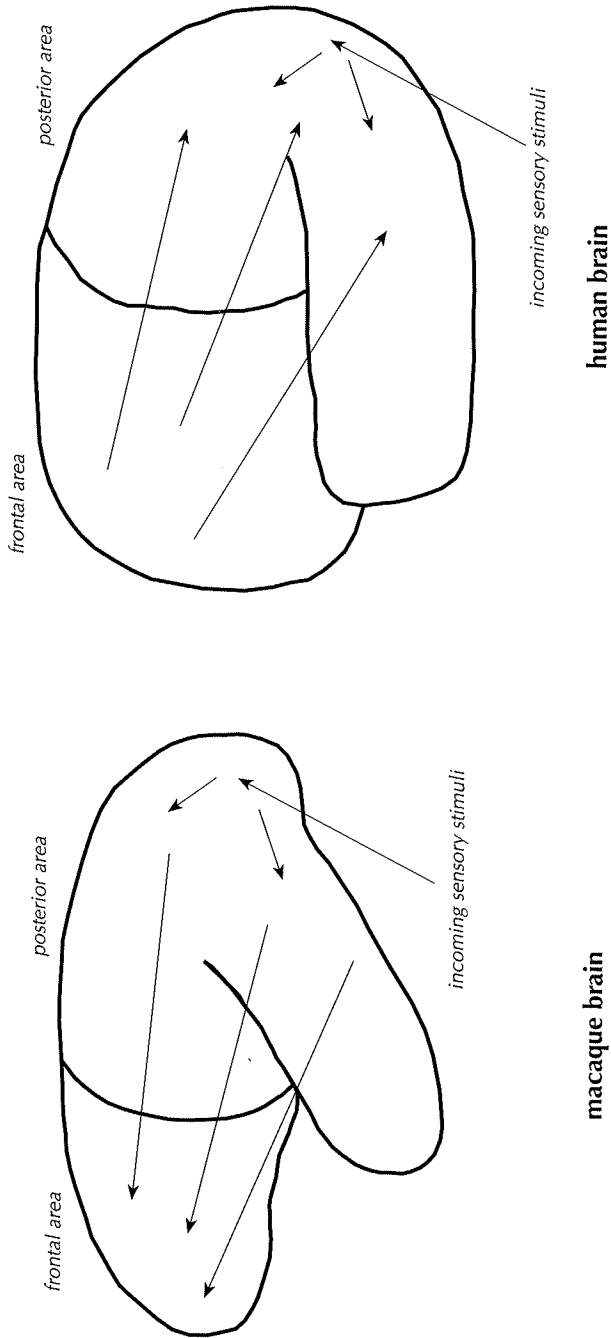


Figure 1. Highly schematic diagram illustrating the proposed direction of information flow in the nonhuman macaque brain (left) and the human brain (right).

stimuli which are associated with these behaviors. Thus, the nonhuman's sensori-motor constructions, or cognitive processes, reflect only what has actually occurred in the external environment and therefore are "stimulus-bound." No truly significant "internal," or novel, construction is possible in a feed-forward system since the construction of all sensori-motor representations are driven by "external" influences.

Accordingly, attempts to demonstrate internal construction in nonhumans have ultimately failed. Using language as a criterion for internal construction, certain investigators have claimed that some nonhuman species can internally combine "word-symbols" into a sort of primitive grammar (Gardner and Gardner, 1975; Premack, 1976). These claims, however, have usually limited the extent of internal construction in nonhumans to only two or three word-symbols. Furthermore, these claims do not conclusively demonstrate that nonhumans possess even these limited abilities of internal construction; it is just as likely that these simple constructions reflect "trained" associations brought about through external reinforcement (Macphail, 1987; Terrace, Petitto, Sanders, and Bever, 1979). Thus, the evidence for internal construction in nonhumans is inconclusive at best, and it is more likely that nonhumans do not have the capacity for any significant internal construction.

Humans, on the other hand, definitely *do* construct internal sensori-motor representations. These constructed representations can be virtually unlimited in their complexity, and, importantly, appear to be driven by the human's stored action-schemes. For instance, Greenfield (1991) has outlined a strong correlation between the organization of manual action-schemes and the organization of grammar in human language, while Piagetian models (Case, 1985; Parker and Gibson, 1979; Piaget 1954, 1971; Piaget and Inhelder, 1969) of human cognition outline a correlation between the organization of manual action-schemes and the organization of all of human cognitive processes in general. Piaget and Inhelder (1969) state:

As regards the development of the cognitive functions in the child, . . . the sensori-motor structures constitute the source of the later operations of thought. This means that intelligence proceeds from action as a whole, in that it transforms objects and reality, and that knowledge, whose formation can be traced in the child, is essentially an active and operatory assimilation. (p. 28)

Parker and Gibson (1979) state:

Intellectual development occurs through the differentiation and coordination of actions (and interiorized mental representations of actions) on objects: Intelligence arises from action rather than from perception. These coordinations create classes of objects (classification) and relations between objects (seriation), revealing properties (quantity) that did not exist before; they also reveal the nature of physical causality (gravity, inertia, equal and opposite forces, transmission of forces, etc.). (p. 367)

In short, Piaget's studies imply that the human constructs its internal cognitive processes through internalized actions, or operations, performed on objects. These constructions give rise to mental schemes (concepts) which can be combined with other schemes to form more complex mental schemes, and so on. Over time, then, scheme constructions become more and more complex and refined, guiding the cognitive development of the human (Case, 1985; Piaget and Inhelder, 1969). Importantly, these cognitive constructions in humans proceed unbounded, or "decentered," from environmental constraints and, thus, are not stimulus-bound (Piaget and Inhelder, 1969).

According to the present model, such internal construction in the human is achieved by means of a "frontal feedback system" whereby self-generated action-schemes in frontal cortices continually manipulate sensory representations in posterior cortices. It is important to make clear that the action-schemes themselves do not constitute thoughts, but rather only organize, or "become," thought processes as they invade posterior sensory cortices. Here, the action-schemes serve to recombine existing sensory representations into novel, creative representations which, as we will see later, reflect the human's internal cognitive processes. The frontal feedback system functions as an autonomous unit "free" from environmental constraints and, thus, is not stimulus-bound.

Anatomical Evidence

The comparatively large size of the human frontal cortex is the primary anatomical evidence for frontal feedback in the human brain. While absolute ratios are difficult to determine (Passingham, 1973), humans, as a rule, have a significantly larger ratio of frontal cortex to total cortex than do nonhumans (Brodmann, 1912; Fuster, 1989; Khokhryokova, 1979). The proposal here, therefore, is that while posterior areas manipulate frontal areas in nonhumans, frontal areas manipulate posterior areas in humans. At this point, it will be helpful to speculate briefly on what selection pressures may have contributed to the phylogenetic differences between human and nonhuman cortex.

One plausible scenario is that, in the majority of mammals, selection pressures favored the expansion of posterior cortical areas which were involved in the processing and detailed representation of environmental stimuli (Kaas, 1987). The ability to construct a detailed sensory map of the environment had an obvious survival benefit in that it enabled the organism to distinguish between a large variety of stimuli such as food, mates, predators, and so on (Jerison, 1973, 1976; Sarnat and Netsky, 1981). The emphasis on the development of motor abilities was not nearly as great. Accordingly, the frontal association, or prefrontal, areas of the cat and dog, both lower mammals, account for only 3.5% and 7%, respectively, of the total amount of their cerebral cortices, the rest belonging primarily

to posterior sensory regions (Fuster, 1989). In short, posterior sensory regions in nonhumans grew much larger than frontal motor regions, which led to the feed-forward processing of information in the nonhuman cortex.

In the primates, however, the evolution of the brain took a different path. As the primates took to the trees, selection pressures favored the development of motor abilities that would enable the organism to negotiate an arboreal habitat, pick fruit, clear leaves, clean foods, and so forth (Gibson, 1990; Parker and Gibson, 1979). Thus, the prefrontal areas expanded in order to facilitate the construction of more and more complex, hierarchically organized action-schemes, such as those involved in manual object manipulation (Gibson, 1990; Greenfield, 1991). This trend is reflected in the comparative anatomy of the primate cortex. For example, the prefrontal cortex of the lemur, a lower primate, accounts for only 8.5% of the total amount of its cerebral cortex. As we ascend the primate phylogenetic ladder, however, this figure increases to 11.5% in the gibbon and macaque, and 16.9% in the chimpanzee. The culmination of this trend is seen in the human brain, where the figure jumps to 29% (Brodmann, 1912; Fuster, 1989).

Most models of frontal lobe function assume that the enlargement of the frontal lobe in humans simply reflects the greater elaboration of frontal lobe functions present in all other primates (Damasio, 1989a, 1989b; Fuster, 1989; Gibson, 1990; Greenfield, 1991; Goldman-Rakic, 1988; Goldman-Rakic and Friedman, 1991). The frontal feedback model, on the other hand, suggests that somewhere in the transition from the great apes to humans the size of the frontal lobe surpassed a *threshold* whereby the preferred direction of information flow in the cortex was reversed to a frontal-to-posterior direction. Thus, an important new role for the frontal lobe arose, frontal feedback, which, as we will see later, gave the human its unique cognitive abilities.

Although the entire cortex is subject to the influence of this frontal feedback, only the more phylogenetically recent developments are suggested to be directly involved. These areas, which compose the "frontal feedback system," are the prefrontal region⁴ of the frontal lobe and the sensory-association regions of the parietal, occipital, and temporal lobes with which the prefrontal region is connected. Areas not directly connected with the prefrontal cortex, such as primary sensory areas, are only indirectly influenced by frontal feedback through feedback connections to these primary areas from sensory-association areas (see Damasio, 1989a). Therefore, these earlier primary cortices are included in the system at some time but not others.

⁴According to Fuster (1989), the human prefrontal cortex can be divided into a large dorsolateral region and a smaller orbital region. While both regions are likely to be involved in the frontal feedback system, it is the large dorsolateral aspect which is suggested to be most specifically involved. This region has undergone substantially more phylogenetic enlargement than its neighboring orbital-prefrontal region and is more specifically involved in the representation of action.

To state it in other terms, the anatomical boundaries of frontal feedback are highly dynamic and shift according to the current, relative strengths of influence between frontal and posterior areas.⁵ Thus, it is difficult to give a precise anatomical definition of the frontal feedback system considering that the anatomical boundaries are constantly shifting. However, the system can be generalized to the areas listed above for three reasons. First, as already stated, these association areas are the most phylogenetically recent anatomical developments in the human brain with the prefrontal area undergoing the greatest development (Akert, 1964; Khokhryokova, 1979; Luria, 1966/1980; Truex and Carpenter, 1969). Therefore, they are the most likely areas to have achieved frontal feedback in the transition from apes to humans. Second, the "known" functional properties of each individual area would certainly support the greater functional role of frontal feedback that is assigned to them here. Finally, damage to these association areas, especially the prefrontal cortex, impairs higher cognitive processes in humans more specifically than any other cortical region (Fuster, 1985, 1989; Luria, 1966/1980; Stuss and Benson, 1986). In fact, the prefrontal cortex is considered to be essential for such capacities.

In short, the evidence presented above suggests that the anatomy of the human cortex could support a frontal feedback system. It would be difficult to substantiate such frontal feedback in the human brain, however, merely from anatomical and behavioral evidence alone. Much more convincing evidence would come from physiological studies. Indeed, recent studies do suggest the presence of frontal feedback in the human brain and its absence in the nonhuman brain.

Physiological Evidence

Although there is a good deal of data regarding single-unit studies in the nonhuman primate cortex, comparable studies of the human cortex have obviously been harder to obtain. Recently, however, single-unit studies have been obtained from human patients undergoing surgery for intractable epilepsy (Ojemann, Creutzfeldt, Lettich, and Haglund, 1988; Ojemann, Ojemann, and Lettich, 1992). These studies reveal a marked difference between the behavior of neurons in human (posterior) temporal cortices and

⁵The boundaries of frontal feedback in humans demarcate which regions are feeding forward and which are feeding back. Thus, a significant sensory stimulus can drive up activity in posterior areas shifting the boundaries anteriorly, toward later, or abstract, sensory association cortices. Similarly, significant activity in the frontal feedback system can shift the boundaries posteriorly, toward secondary and primary sensory areas. In addition, there may be differences in the locations of these cortical boundaries in general between the left and right hemispheres (see footnote 6).

those in nonhuman temporal cortices. That is, nonhuman temporal-cortical neurons primarily respond to concurrent environmental stimuli whereas human temporal cortical activity primarily reflects internal cognitive and language processes. For instance, numerous studies have shown that neurons in the temporal cortex of monkeys respond almost exclusively to sensory stimuli, in particular to the presentation of objects in the monkey's visual field (Fuster, 1989; Mishkin, 1990, 1993). These studies have led to the labeling of the primate temporal cortex as a sensory (primarily visual) association area. Recently, however, a study of the temporal cortex in thirteen human patients found activity there to be quite different from that of monkeys (Ojemann et al., 1988). That is, temporal cortical neurons in the humans did not respond to the presentation of visual stimuli (projection slides), as they do in monkeys, but rather responded to the ongoing cognitive tasks, language tasks, and overt speech (orofacial action-schemes) tasks that the visual stimuli (slides) directed the humans to perform. Ojemann et al. (1988) state,

Thus, the identification of changes in activity related to visual perception in only 1 of 17 populations is . . . suggestive evidence of a lack of visually excitable neurons in human lateral temporal cortex. This is somewhat at variance with findings in monkeys, where the inferior temporal cortex has been generally considered a visual association area Of the sampled (human) neuronal populations, 76% had significant changes in activity during either language and/or memory. These changes, related to language and memory, were not secondary to changes related to visual perception, speech or arousal, per se Thus, the memory and language changes reported here reflect cognitive processes. (pp. 1397-1398)⁶

Ojemann et al.'s (1988) study demonstrates that activity in the human temporal cortex primarily reflects the human's ongoing cognitive/language processes, not the processing of sensory stimuli as in the nonhuman temporal cortex. Such a difference between human and nonhuman posterior cortical activity is exactly what is predicted by the frontal feedback model. Activity in nonhuman sensory association areas would represent the feed-forward pro-

⁶These studies were carried out in the temporal lobe of the left hemisphere. Later studies of right-hemispheric temporal lobe activity in humans found somewhat different activity (Ojemann et al., 1992). That is, neurons in the human right hemisphere responded preferentially to human faces and complex visual shapes and, thus, resembled more the activity in nonhuman primate cortex. There were, however, important differences in cortical activity such as some language activity and a much less dramatic response to visual stimuli in the human cortex than in the primate cortex. One interpretation of this data is that the right hemisphere lacks frontal feedback. Another interpretation, however, is that frontal feedback acts more weakly in the right hemisphere, projecting only to the highest or more abstract association areas. In this latter case, the influence of frontal feedback would project further "downstream" in the left hemisphere than in the right. In any case, both interpretations would be consistent with the known specialization of the right hemisphere for holistic, visuo-spatial abilities and the left hemisphere for hierarchically structured language and logico-mathematical abilities (Galín, 1977; Geschwind, 1979; Springer and Deutsch, 1993).

cessing of sensory stimuli, whereas activity in the human sensory association areas would represent cognitive/language processes reflective of the feedback manipulation of sensory representations by complex action-schemes.

Although certainly not conclusive, the comparative physiological data discussed above is the most telling biological evidence for frontal feedback in the human brain, and, taken as a whole, all the evidence presented at least *suggests* the possibility of a frontal feedback system in humans. In the following section, some final speculations are offered as to how such a feedback system may relate to human experience.

The Frontal Feedback System and Human Experience

So far it has been argued in the frontal feedback model that distinct human cognitive abilities are the result of a frontal feedback system which exists in the human brain but not in the nonhuman brain. The frontal feedback system forms an autonomous functional unit in the cortex whereby frontal action-schemes continually manipulate posterior sensory representations free from environmental constraints. As discussed earlier, the Piagetian model of human cognition gives some clues as to how such a system may organize the human's cognitive world: internalized actions performed on internalized representations of objects give rise to mental schemes which can be combined with other schemes to form more complex schemes, and so on. Piaget's was strictly a psychological model, though, and little indication was given as to how these schemes were organized and constructed at a neurological level. The frontal feedback model, on the other hand, yields insight into this matter through the concept of self-organization in the frontal feedback system.

Self-organization of Scheme Release in the Human Brain

The release of action-schemes in nonhumans is driven by external sensory influences. That is, external sensory stimuli trigger sensory representations in posterior cortical areas which, in turn, trigger the release of associated action-schemes in frontal cortices. The release of action-schemes in the human, on the other hand, is not driven by environmental influences since the action-schemes are, contrary to the situation in nonhumans, manipulating sensory representations through frontal feedback. This lack of an external driving force means that the release of action-schemes in the human is "self-organized," or driven by self-organization. In other words, action-schemes in human frontal cortices are not triggered by sensory cell-assemblies, as in the nonhuman, but rather are triggered by associated action-schemes whose representation immediately preceded them in the

cortex.⁷ The ongoing release of these schemes follows the "associative" rules of neural mass action (Freeman, 1975; Skarda and Freeman, 1987) whereby the triggering of a given scheme, in turn, triggers an associated scheme which, in turn, triggers yet another associated scheme, and so on.⁸ Thus, the release of these self-generated schemes follows arbitrary associative paths which, as we will see below, reflect "trains of thought."

Self-organization, Frontal Feedback, and the Creation of the Internal Environment

The importance of this self-organized release of action-schemes in the human frontal lobe lies in the influence this release has on posterior areas. That is, in addition to triggering each other, the release of action-schemes in human frontal cortices also triggers, or "retriggers," through frontal feedback, stored sensory representations (cell-assemblies) in posterior cortices with which the schemes were previously associated (the term "retrigger" is used here to denote sensory assemblies which are triggered internally by action-schemes through frontal feedback, as opposed to sensory assemblies which are "triggered" externally by environmental stimuli). Since a given action-scheme can be associated with a multitude of different sensory scenarios (see footnote 9), the release of that action-scheme at any given time can retrigger any one of those scenarios or, importantly, different portions of different scenarios both spatially and temporally during the course of the scheme's release. These retriggered portions, or "fragments," of different sensory representations can then become recombined with each other in a spatio-temporal fashion, giving rise to novel, creative sensory representations and to sequences of such representations, or "scenarios."⁹ In posterior cortices, this

⁷Since only a small representative portion of an action-scheme's cell-assembly (as little as 1%; see Skarda and Freeman, 1987) need be active in the frontal cortex in order to trigger a subsequent action-scheme, each successively triggered scheme may be closely related or disparately related (i.e., relatively unrelated) to the previous scheme which released it. This property of self-organization allows the frontal cortex to continually generate novel action-scheme sequences which, as we will see later, has several important implications for human cognition.

⁸The structure of the human frontal lobe would seem to support the self-organized activity postulated here. That is, both the large dorsolateral prefrontal cortex and its associated thalamic projection, the parvocellular portion of the mediodorsal nucleus (MDp), have undergone substantial phylogenetic enlargement in humans (Fuster, 1989; Truex and Carpenter, 1969). Interestingly, whereas thalamic nuclei neighboring the MDp have strong interconnections with limbic as well as cortical structures, the MDp has the conspicuous property of being connected to little else but the dorsolateral prefrontal cortex itself (Fuster, 1989; Nauta, 1964). Such an autonomous union between these two regions is, therefore, suggestive of self-organized activity there.

⁹A thorough discussion of how sensory assemblies become retriggered and recombined through frontal feedback would be quite lengthy and is outside the scope of this introductory paper. However, a general idea of how this recombination process might work can be outlined here.

recombination is manifested spatially as the internal creation of novel objects and environments in which those objects reside and temporally as the manipulation of those objects in those environments (the particular sequence of action-schemes active in the frontal cortex during recombination governs how the objects are manipulated). Again, in the nonhuman, the sensory scenarios played out in posterior areas reflect only the concurrent external environmental scenarios.¹⁰ In the human, on the other hand,

In the human, action-schemes retrigger sensory representations/scenarios. The sensory scenarios that are retriggered by these action-schemes are those scenarios that the schemes were associated with in previous experience. Two separate action-schemes released consecutively, then, can retrigger two different sensory scenarios in sequence, allowing these scenarios to become recombined temporally. For example, the action-scheme of my reaching out, grabbing an object, and lifting that object to my lips is associated with a sensory scenario of my lifting a cup of coffee to my lips. At any given time, the release of that action-scheme in my frontal cortices can internally retrigger that sensory scenario in my posterior cortices through frontal feedback. If the release of this "lifting" action-scheme is then succeeded by an action-scheme of my tossing an object over my left shoulder, then the "lifting" scheme/scenario would be temporally recombined with the "tossing" scheme/scenario resulting in the internal creation of a novel scenario in which I first take a sip of coffee, and then toss the cup over my left shoulder. I would experience this scenario as a "thought" even though the experience never really happened in the external environment.

In addition to temporal recombination, retriggered sensory representations can also be recombined spatially, yielding abstract, composite sensory representations and scenarios. At the cortical level, a global action-scheme is represented by various sequences of cortical activation in spatially distinct regions of the frontal cortices (Fuster, 1989; Kolb and Wishaw, 1985). The activation in a given region at a given time during the course of the scheme can be thought of as representing a particular subcomponent of the global scheme. Each of these spatially distinct frontal regions is, in turn, topologically connected to a corresponding spatially distinct region in posterior sensory cortices (Jones and Powell, 1970). Upon the activation of a given action-scheme, then, each subcomponent of the global scheme can retrigger a separate and distinct sensory representation/scenario in its spatially corresponding posterior cortical region. The particular representation retriggered in each of these spatially distinct posterior sensory regions in turn represents a "fragment" (akin to a piece in a jigsaw puzzle) of a globally defined sensory representation (akin to the complete puzzle, e.g., a visual image or impression) which occupies virtually the entire sensory cortical area (Mishkin, 1990, 1993). The end result, therefore, is the recombination of these various "local" sensory fragments into a creatively synthesized, "global" sensory scenario. For example, my "lifting" action-scheme described above is not only conditioned to the sensory scenario of my lifting a cup, it is also conditioned to experiences I have had in lifting a soda can, a slice of pizza, and a harmonica, to name just a few. Thus, the release of the lifting action-scheme in my frontal cortices can retrigger several of these scenarios simultaneously by retriggering different scenarios in different regions of posterior cortex. The triggering of several scenarios simultaneously would allow these scenarios to become recombined spatially, perhaps forming a fictitious scenario where the object I pick up is an abstract composite of many different objects. Spatial recombination may likewise allow for the creation of an abstract environment in which this object resides. To further add to the complexity of these dynamics, multiple competing action-schemes in frontal cortices can, in a fashion similar to the single scheme example above, retrigger multiple sensory fragments in posterior cortices which can also become recombined spatially. Through both spatial and temporal recombination, then, extremely elaborate and bizarre scenarios can be created.

¹⁰Again, this simplification is made for illustrative purposes. There is likely to be some "stimulus-independent," self-organized activity in nonhuman posterior areas (see Skarda and Freeman, 1987) at times which, in addition to possible transient frontal feedback influences

the self-organized release of action-schemes in frontal cortices actually *creates and organizes its own internal environment and scenarios* in posterior cortices. This point is extremely important because it means that human cognition is liberated from present environmental constraints: humans can create fictitious internal scenarios which are completely removed from the current environmental situation and which may represent a past occurrence or a possible future occurrence. Nonhuman cognition, on the other hand, is bound to the current environmental situation.

Self-organization of Scheme Construction and Human Cognition

In addition to liberating human cognition from environmental constraints, the ability of the human brain to create internal environments also allows for the construction of incredibly complex and elaborate action-schemes and cognitive processes. For example, by creating its own internal environment and scenarios, the self-organized release of action-schemes in humans continually "tests" combinations of these schemes for their reinforcing value without the need of actual, external sensory scenarios to accompany them. In the nonhuman, a given chain of action-schemes is constructed into a more complex scheme only if that combination is accompanied simultaneously by a reinforcing sensory scenario actually occurring in the external environment. Thus, the potential complexity of constructed action-schemes in the nonhuman is limited to what reinforcing events can actually happen in the external environment. The potential complexity of constructed action-schemes in humans, however, is under no such external constraint and is virtually unlimited since a given, self-organized chain of schemes actually creates its own fictitious sensory scenario to accompany it. These internally created scenarios produce reinforcement or nonreinforcement just as actual external scenarios do since both the external scenarios and the internal scenarios are played out on the same (posterior) sensory-association cortices.¹¹ These pos-

mentioned earlier, may allow for some primitive and limited form of internal construction in these posterior areas. The extent of such construction, however, is relatively negligible when compared to the highly structured and sustained internal construction provided by the frontal feedback system in humans.

¹¹The ability of internally rehearsed behavioral scenarios to generate reinforcement has been discussed conceptually by Nauta (1971), and later by Damasio (1991; Damasio, Tranel, and Damasio, 1991), with Nauta (1971) using phrases such as "the mere thought of doing such a thing makes me ill" (p. 183) to argue, on introspective grounds, for the presence of such "internal reinforcement." According to both Nauta's and Damasio's formulation, potential behavioral scenarios are somehow generated in the frontal lobe and, through fronto-limbic connections, are subsequently tested for their reinforcing value by acting directly on subcortical limbic areas involved in producing reinforcing activity. While this fronto-limbic connection is likely to play a partial, supportive role in the generation of internal reinforcement, the frontal feedback model views posterior-limbic connections as playing the more important

terior areas have strong connections with subcortical limbic structures where constructed representations in the cortex are linked to reinforcement (Mishkin, 1993). Thus, if a given combination of schemes creates a fictitious scenario which produces (or leads to) reinforcement, then that combination of schemes will become constructed into a more complicated scheme just as if the scenario had actually occurred in the external environment.

At the same time that it is constructing complex action-schemes, the frontal feedback system is simultaneously constructing complex internal sensory scenarios. As stated earlier, these created scenarios, along with the action-schemes that created them, can represent concepts, or "thought-schemes," as I call them. Through the combining of simple thought-schemes, more complex thought-schemes can be created. These newly formed schemes can then be combined with other schemes to form yet more complicated thought-schemes, and so on. For example, a simple thought-scheme involving the mathematical operation of addition may be represented by the simple action-scheme of manually combining two or more objects along with the internally created sensory scenario of combining those objects. More complex thought-schemes involved in more complicated mathematical operations may arise out of the combination of several of these simpler schemes (see Case, 1985). Linguistic structures can be constructed in a similar fashion (Greenfield, 1991). The hierarchical, sequential organization of the action-schemes is responsible for the hierarchical, sequential organization of these cognitive/language processes (Case, 1985; Gibson, 1990; Greenfield, 1991). Again, since there is virtually no limit as to how complex and abstract constructed action-schemes can become, there is also virtually no limit as to how complex and abstract these thought-schemes can become. The only requisite for the construction of creative thought-schemes is that they generate reinforcement. Provided that they do, these creations will be stored as constructed thought-schemes *no matter how "unrealistic" the creations are*. Importantly, the autonomy of the frontal feedback system insures that these constructions can proceed indefinitely and will not be interrupted by distracting sensory stimuli. Thus, the frontal feedback system allows for the construction of incredibly complex and elaborate thought-schemes and behaviors such as those involved in the writing of a novel, the building of a computer, or the planning of an expedition to the moon.

role. That is, internally created scenarios generate reinforcement in a fashion similar to that of actual external scenarios (sensory stimulation): (1) by creating scenarios in posterior regions which directly release innate reinforcing activity in subcortical regions (e.g., the image of a mate), or (2) by retriggering already pre-existing sensory scenarios in posterior areas which, in turn, retrigger their associated reinforcing activity in subcortical structures. In both instances, the excitement of critical limbic structures involved in reinforcement serve to trigger the release of consolidatory biochemicals into the cortex to store the internally created scenario as a cell-assembly (see earlier text).

To restate, the frontal feedback system is a self-organized system whereby limitless, self-generated combinations of action-schemes are continually played out and tested for their reinforcing value by creating fictitious sensory scenarios in posterior cortices. If a given combination of schemes creates a fictitious scenario which produces (or leads to) reinforcement, then that combination of schemes will become constructed into a more complex scheme. In other terms, thought-scheme constructions which produce reinforcement are formed and are strengthened while unreinforced constructions are not formed or become weakened. Successful scheme constructions survive or are selected for, whereas unsuccessful constructions do not survive. Similarly, recent, more successful constructions replace earlier, less successful ones, guiding the cognitive development of the human. In short, thought-scheme constructions in the human brain continually *evolve* in their content and complexity by this autonomous, self-organized process I call "cognitive Darwinism."

Of added interest is how the frontal feedback system can create goals and work to achieve those goals. Simply stated, a goal reflects the creation of a desired (reinforcing) scenario such as the completion of a painting or a novel. This scenario is subsequently stored as a strongly reinforced thought-scheme, or "goal-scheme." Importantly, this goal-scheme becomes frequently triggered in the frontal feedback system since its cell-assembly is strongly interconnected and thereby easily excited. Such "maintenance" of the goal-scheme in the frontal feedback system may then serve to trigger the ongoing release of schemes associated with the goal-scheme. These associated schemes, therefore, become concentrated in the frontal feedback system, and this concentration serves to facilitate the construction of supporting thought-schemes and behaviors leading to the achievement of the goal.¹²

These ongoing self-organized processes in the frontal feedback system seem to have their counterpart in our daily thought processes. That is, when presented with a situation, we usually construct several fictional scenarios or outcomes and then proceed to act on the one that will provide the most favorable outcome. Longer term, these outcomes can represent goals, and by focusing on these goals, or by "keeping them in mind," we are able to produce ideas and behaviors that lead us closer to their completion (Fritz, 1989). Indeed, damage to the prefrontal cortex or its supporting structures dramatically impairs these abilities for abstraction, creativity, and goal-directed planning in humans (Fuster, 1985, 1989; Shallice, Burgess, Schon, and Baxter, 1989; Stuss and Benson, 1986; Truex and Carpenter, 1969), possibly by impairing the process of frontal feedback in the human brain.

¹²Again, punishing constructions would also be created since their representation confers as much consolidation as reinforcing (rewarding) constructions. Such punishing constructions would represent unfavorable scenarios and behaviors to be avoided.

Human Identity and Individuality

One final, important implication of the frontal feedback model involves the separation of the frontal feedback system from environmental influences. Activity in the frontal feedback system reflects an "internal world" which can be very different from the current representation of the environment, or "external world," in primary sensory areas. It is suggested here that the human comes to identify this internal world as its "inner self," an identity which is separate and distinct from its environment and where conscious intentions, or apparent "free will,"¹³ continuously spring forth from self-organized activity in its frontal lobe. The human being comes to distinguish this internal world, or "mind," from its body and environment and, thus, gains a sense of individuality and autonomy.

While the experiential sense of autonomy arises from the physiological separation of the internal and external worlds, the phenomenon of self-awareness (self-concept, self-monitoring, metacognition, etc.; see Galin, 1992) arises entirely within the internal world. That is, the internal world functions by taking information impinging on it from neural sources external to itself (e.g., perceptions from primary cortical systems and emotional states from subcortical systems) and performing operations on this information, resulting in the internal construction of fictitious scenarios and abstract concepts built around the external information. The concepts that arise from these initial operations can then be operated on further in the internal world, yielding even more abstract concepts, and so on. Within the internal world, then, there is a dynamic interaction between the information impinging on it externally and the information it produces internally, and operations can be performed on both forms of information simultaneously. Through such operations in the internal world, a discrepancy is identified between the highly structured and reliable information coming from the external sources (environment) and the more bizarre and abstract information that is being generated internally. Included in this highly structured and reliable external information is the information coming from the movements of the individual's body, such as the visual observations of the movements of its limbs in space and the proprioceptive and tactile information regarding their positions in space. All of this information regarding the individual's body states comes

¹³Our "will" appears to be free because the will, or intention, is the product of an autonomous, self-organized process of scenario construction in the frontal feedback system, a process removed from environmental constraints. The autonomy of the frontal feedback system allows for the continuous rehearsal of many different possible scenarios and accompanying behaviors in any situation. Although we would like to believe that we "choose" our behavior in a given situation, this behavior is more likely to simply reflect the most rewarding of the scenarios built around the situation, and therefore the behavior or intention is not necessarily "free."

into the internal world from external sources and correspondingly appears to be affected by the reliable causal relations and physical laws that all other external objects appear to be governed by. Thus, and importantly, the internal world comes to regard the body that it is housed in as an external object, one object among the many that make up the universe, all of which obey the same physical and causal laws (Piaget and Inhelder, 1969). In contrast to the activity coming from its body and environment, the bizarre, abstract activity generated within the internal world does not appear to be under the constraint of these same physical laws and, thus, the internal world is regarded as a separate, nontangible entity which resides within the physical object that is its body. All of the processes that go on in the individual's internal world are regarded as belonging to this entity/body package and, through the internal world's operations and scenario constructions, these processes are continually analyzed, updated, and compiled into a concept of self. Thus, an autobiography is continually updated and assigned to this "package" as well as a set of values, beliefs, and emotional states. In short, the internal world *creates* a concept of self in the same fashion that it creates other thought-schemes. The human is aware of itself when its self as an entity/body package becomes the subject of one of its scenario constructions.

In the same way that it assigns them to itself, the internal world of the human assigns values, beliefs, and emotional states to other individuals, which are also regarded as objects. Thus, the individual develops empathy for other individuals and, therefore, a sense of morality. Relations between the self and others can be played out via scenario constructions in the individual's internal world and the human learns how to cooperate as well as compete with other individuals in society. Again, damage to prefrontal areas is known to virtually abolish the sense of autonomy, self-awareness, and social appropriateness in humans (Galin, 1992; Lhermitte, 1986). In fact, many people with frontal lobe lesions appear to become stimulus-bound (Lhermitte, 1986; Lhermitte, Pillon, and Serdaru, 1986; Shallice et al., 1989), possibly reflecting the abolition of frontal feedback in these patients. As Galin (1992) puts it, many frontal patients "seem not quite human" (p. 152).

Conclusion

The evolution of the mammalian brain followed a trend whereby posterior cortical regions involved in the representation of a detailed map of the environment continued to remain larger than frontal regions involved in the production of complex behaviors. This persisting structural feature of the mammalian brain provided the animal with a mechanism whereby quick, successful behaviors could be continually generated in response to a complex, dynamic environment. In the evolutionary transition from the great apes to

humans, however, the extreme enlargement of the frontal lobe disrupted this trend and, thus, the traditional, mammalian mechanism of cortical function. This disruption gave rise to a unique functional system in the human brain which provided the human with a distinct sense of autonomy and free will, and the cognitive ability to create and comprehend almost anything.

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