For evolutionary psychiatrists, psychologists and others interested in sociophysiological integration

ASCAP

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Too little has been written about the fact that depression is ridiculous. I can remember lying frozen in bed, crying because I was too frightened to take a shower and at the same time remembering that showers are not scary."

Andrew Solomon[1]

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The ASCAP Society represents a group of people who view forms of psychopathology in the context of evolutionary biology and who wish to mobilize the resources of various disciplines and individuals potentially involved so as to enhance the further investigation and study of the conceptual and research questions involved.

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- Elaboration of others' ideas.
- Keeping up with productions, events, and other news.
- Proposals for new initiatives, joint research endeavors, etc.

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ADDRESSED TO & FROM ...

Out Group Feelings: Experience Story

The coincidence between a friend's wonder at the mix of prejudice and tolerance expressed by a correspondent, and the new strike at General Motors caused me to recognize my prejudice against GM, and to recall its history.

I hate that company!

When I was 8 years old, my father bought a new 1935 Ford, our first new car, and pride was great (I still remember its styling). The family of an older boy, much admired by me, also had a Ford, and he told me that Fords were much better cars than Chevrolets, a kind of car owned by the family of another, much despised, boy. The company that made Chevy, General Motors, was unknown to me at the time, but I learned to recognized Chevys when I saw them and held my nose when one passed by.

Afterwards my father always bought Fords, partly because of habit and liking the cars, and partly because he was friends with the Ford dealer. Of course this was forgotten. I never owned a Ford myself, except for a used one that happened to be the only affordable car available in my early twenties.

Later, after I did know of the connection between GM and Chevrolet, I heard the remark by the CEO of GM that "What's good for GM is good for the country!" I was offended by what I took to be the arrogance of GM. Came the year, much later, that it became known that GM had put Chevrolet motors in Buicks, a much more expensive car (in which a person would naturally expect a special engine), and then wondered what the fuss was about. More GM arrogance!

The upshot of all this was that, when I heard that GM was struck the other day, while sensitized to the general topic of prejudices by my friend, I recognized a deep satisfaction in myself by the harm the strike might do GM.

What have I to do with GM? Nothing at all. How does strike affect me? If there's any effect on me at all, it will be negative, because, after all, what's bad for GM is also bad for the country. So my feeling is a pure prejudice: conclusions and behavior initiated and reinforced by inadequate and/or false information.

It amazes me that this human universal of drawing life-long inferences from tiny experiences has apparently been so little studied, that so little is known about it, that very little or no effort has been made to educate children about it. It is not that any particular prejudice maintains ignorance of a subject and is often destructive, but the syndrome itself, an example of which I have just recounted, can maintain ignorance and inculcate silly antipathies. If such a non-incident caused a lifelong emotional structure in me, can we wonder at the hatreds against science and groups of people when many children have been told horror stories about science or this or that group by the admired kid in the neighborhood or even by parents?

What was adaptive about prejudice? Did it define those others and thereby protect our territory? Or was it adaptive to act in some way, even on too little information?

Whatever its origin, it is now a mismatch. I feel that raising kids to recognize and understand the roots and nature of prejudicial assumption and its existence in everyone would benefit the sciences and people's life styles, and be more efficacious than preaching to them about specific racial prejudices.

Do scientists regularly check themselves for prejudices? Shouldn't they? We all have

them. Maybe scientists should go through a kind of psycho-analysis like psychiatrists to learn of their prejudices, not for social or political reasons, but as part of their training for science, as a service to their science. Such training might have saved Margaret Meade and her mentor from their reputation-destroying errors.

As a separate issue, I want to point out that IQism (discrimination based results of IQ tests according to broadly defined and quasi-identifiable groups of humans in conjunction with the belief that those results indicate the inferiority as human beings of some groups and the superiority of others) inevitably reinforces and tends to justify all prejudices about groups of people, whether the prejudice is of a group's inferiority or superiority.

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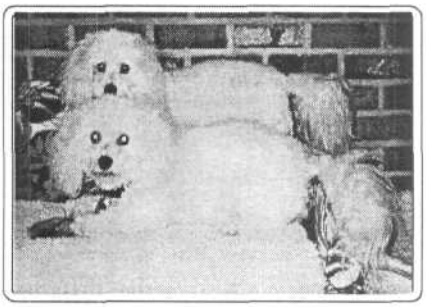

Sibling Rivalry

Nikolas Lloyd wrote:

Human siblings squabble constantly as children, and comparatively seldom as adults. Perhaps this contrast might also occur in squirrels? Might this not be something to look at?

Patricia Hausman wrote:

Seven years ago, we adopted two bichon f rise puppies. They are littermates. Much of what I know about human behavior I learned from them. Among these nuggets of wisdom, of course, is that sibling rivalry is innate.

It is impossible to give one of them anything without the other getting all uppity. The left out one will whine and dance until given a reward she considers to be of equal or better value. At night, when I try to get them to quiet down in the kitchen by giving them a rawhide to chew on, they both take pains to check out what the other one has, seemingly convinced that the other one must be better. After about three to five minutes of pretending to be innocently chewing, one will catch the other offguard and grab her chew-eez.

Supposedly these two are in middle age, in dogtime, and yet there has been no diminution of the rivalry. I suspect the seeming disappearance of sibling rivalry in human adults is due more to the relative absence of opportunity (in theory); adult siblings are generally not being supported by their parents anymore. But you know what happens as soon as the parents are gone (if not sooner); fights over the will and who got what.

Moreover, I have seen adult rivalries that revolve around issues other than resources; for example, I know several cases of female siblings who are in constant rivalry over who can be the thinnest. This is not to say that they are not extremely loyal to each other on other matters. But some competitive issue seems to be always there in a lot of sibships.

I would love to know if anyone has actual experimental data on this question. Until then, my best guess would be that sibling rivalry is forever.

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Please E-mail any contributions to ascap@utmb.edu, or mail hard copy and 3.5" HD diskette to: Russell Gardner, Jr., c/o Frank Carrel, Department of Psychiatry & Behavioral Sciences, University of Texas Medical Branch, Galveston, Texas 77555-0428, USA. WordPerfect, Microsoft Word or ASCII format preferred. Diskettes will be returned to you.

ARTICLE:

by Bruce J. Ellis

Psychosocial antecedents of pubertal maturation in girls: Parental psychopathology, stepfather presence, and family and marital stress

Abstract: In a short-term prospective study of 91 girls and their families, we tested predictions from Belsky, Steinberg, and Draper's conditional adaptation model of individual differences in pubertal timing.[1] This model suggests that contextual stressors in early childhood foster more negative and coercive (or less positive and harmonious) family relationships, which in turn provoke earlier reproductive development in adolescence.

The present study focused on the role of parental psychopathology as a distal contextual stressor. We tested the hypothesis that a history of psychopathology in parents predicts earlier pubertal development in daughters, and that this relation is mediated by negative/coercive family relationships and absence of the biological father from the home. This hypothesis was supported. In the main test of the model, we found that a history of mood disorders in mothers was associated with significantly more pubertal development by daughters in 7th grade, and that this relation was mediated by levels of stress in the mother's relationship with her mate, biological father absence, and their interaction.

In families in which the mother's mating relationship was not with the biological father, levels of stress in that mating relationship accounted for most of the variation in daughter's pubertal timing. Early age of first birth in the mother also predicted earlier pubertal development in daughters as well as more father absence and negative/coercive family relationships. Controlling for mother's age at first birth, however, did not reduce the power of any of the psychosocial predictors of pubertal development.

Stepfather presence, rather than biological father absence, best explained earlier pubertal development in girls living apart from their biological fathers (suggesting a possible pheromonal effect). The effect of biological father's psychopathology on pubertal timing was moderated by father absence and mediated by family functioning, such that in homes where the biological father was present, greater psychopathology predicted more dysfunctional family relationships, which in turn predicted earlier pubertal maturation in daughters. Belsky, et. al.'s conditional adaptation model provides a reasonable account of these data.

Editor's Note: This abstract is from the essay written by Bruce J. Ellis, Ph.D., winner of the 1998 Aaron T. Beck ASCAP Award which will be awarded in Davis, California, on July 8,1998, during the Annual Meeting of The ASCAP Society.

He is presently at: The Department of Psychology and Human Development, Vanderbilt University, Nashville, Tennessee.

Dr. Ellis is a post-doctoral fellow, having achieved his doctorate from the University of Michigan in 1995. He will receive a $1,000 check, deliver his essay in the form of a talk, and receive a plaque. *c8*

ARTICLE:

by Gerald A. Cory, Jr.

MacLean's Triune Brain Concept: In Praise and Appraisal

Abstract:

Paul D. MacLean is a trailblazer in neuroscience as well as a humanist deeply concerned with the larger questions of human life. His triune brain concept has been called the single most influential idea in neuroscience since World War II. It has been well-received in medicine, education, and with the lay public.

In some quarters of neuroscience, however, it has been criticized as outdated, erroneous, and of no impact within the discipline of neuroscience itself. Following the publication of his 1990 opus, *The Triune Brain in Evolution,* MacLean received highly critical reviews in two prominent science periodicals, *Science* and *American Scientist.* Both reviews were written by neurobiologists and both reviewers claimed that MacLean's triune brain concept has had limited acceptance or been largely ignored by professional neurobiologists.

The present paper examines the criticisms made by these reviews, with special emphasis on the influential one that appeared in *Science,* and finds them not only displaying serious deficits in scholarship, but also containing gross errors, inaccuracies, and misrepresentations of MacLean's highly documented and sophisticated work. The review in *Science* is so prejudicial and careless that, in the author's opinion, it raises a serious question of professional standards if not ethics.

Other reviewers seem to have relied uncritically on this review and parroted unreflectively the same errors, inaccuracies and misrepresentations. After reviewing and appraising the criticisms, the present paper concludes that the triune brain concept is soundly grounded in evolutionary neuroscience and, with some clarifications, is the most useful concept we have for linking neuro-science with the larger, more highly generalized concepts of the social sciences. With its focus on subjective experience it also has relevance for the emerging study of phenomenal issues of consciousness, and more importantly, for the crucial social and political issues of moral consciousness.

Introduction:

Paul D. MacLean is a pioneer, a trailblazer, a scientist, and thinker well ahead of his time. As a humanist deeply interested in the larger questions of human life, he started out studying philosophy. Unable to find satisfactory answers to questions such as the origin and meaning of life — why humans in spite of their unrivaled intelligence, often behaved in seemingly irrational ways threatening their individual as well as species survival —he turned to medicine and the study of the human brain. He anticipated that the brain, as the biological substrate of these behaviors, held the key to better understanding of these fundamental questions as well as hopefully their answers.

MacLean was, for many years, Chief of the Laboratory of Brain Evolution and Behavior of the National Institute of Mental Health. In 1952, he introduced the conceptual term limbic system into the neuroscientific literature, building on Broca's initial use of the term in 1878. In 1970, he introduced the concept of the triune brain, which became widely popularized after the publication of Carl Sagan's rather overly dramatic and simplified discussion of it in *The Dragons of Eden}* MacLean, in further developing the triune brain concept, which aroused great interest in psychiatry, education, and the lay public, produced his detailed and highly documented volume, *The Triune Brain in Evolution: Role in Paleocerebral Functions* in 1990.[2]

Criticisms of MacLean's Model:

MacLean's triune brain concept has been acknowledged the single most influential idea in neuro-science since World War II (e.g., Durant in Harrington).[3, p. 268] Nevertheless, following the publication of his 1990 opus, MacLean received highly critical reviews in two prominent science periodicals, *Science* (October 12,1990)[4] and *American Scientist* (September—October 1992).[5] Neurobiologists wrote both reviews and both claimed that MacLean's triune brain concept has had limited acceptance or been largely ignored by professional neurobiologists.

Anton Reiner, of the Department of Anatomy and Neurobiology, University of Tennessee, at that time a recent graduate, wrote the review in *Science,* which was the more extensive of the two. After initially recognizing MacLean as a trailblazer of neuroscience, whose triune brain concept has been well-received outside the field of brain research, as the centerpiece of Sagan's popular, *The Dragons of Eden,*[1] and frequently as the only discussion of brain evolution in psychiatry and psychology textbooks, Reiner makes several points in criticism of the triune brain concept.

First, he notes that since MacLean introduced the concept, neuroscientific research has tremendously grown, greatly extending our knowledge of brain function and evolution. This statement carries the general implication, which is later made explicit, that the concept is out-dated.

Secondly, in initiating criticism of MacLean's concept of the limbic system, Reiner writes: *"MacLean's presentation of the role of the hippocampus in limbic functions is not well reconciled with the current evidence that the hippocampus plays a role in memory".* [4]

Thirdly. Reiner contends that current research indicates that MacLean's reptilian complex is not a reptilian invention but seems to be present in vertebrates all the way back to jawless fishes.

Fourthly. Reiner maintains that MacLean over-reaches the evidence when he claims that the basal ganglia are the neural seat for the control of species-typical types of behaviors.

Fifthly, Reiner states that the limbic system, which widely used term MacLean authored as a pioneer neuroresearcher, is not properly represented by MacLean. Contrary to MacLean, as Reiner would have it, the limbic system did not appear first in early mammals. Amphibians, reptiles, and birds also have limbic features such as the septum, amygdala, a different-looking hippocampal complex, and maybe even a cingulate cortex.

Sixthly. Reiner asserts that MacLean assigns the functions of parental behavior, which Reiner claims that MacLean regards as uniquely mammalian, to the mammalian cingulate cortex, ignoring the fact that some reptiles (crocodiles), all birds, and possibly even some extinct reptiles (dinosaurs) also engaged in parental behavior.

Seventhly. Reiner makes a couple of other criticisms of MacLean concerning:

a. His preference for correspondence over the more evolutionary appropriate concept of homology, **and**

b. His apparently uncritical acceptance of Haeckel's idea that ontogeny recapitulates phylogeny.

Finally, although Reiner praises MacLean's motives and acknowledges the appeal of the triune brain concept for dealing with "big" behaviors that we are all interested in such as: *"How does our animal heritage affect our behavior? Why do we do the things we do? Why can we not live together more harmoniously?'*… he feels that there are some telling shortcomings as recited above, in MacLean's scholarship. He concludes that neuroscience research can shed light on these important human questions, though perhaps not in as global and simple a way as MacLean has sought.

A Critique of Reiner's Critique:

Book reviews by of their very nature are usually overly brief, and are not able to deal in depth with the points they take issue with. Reviewers, then, are often themselves guilty of the same kinds of oversimplifications and misinterpretations that they seek to expose in their reviews. When Reiner states: "... *I strongly believe the triune-brain idea to be wrong...*", he is caught up in the same oversimplifying tendency that he claims unjustifiably to find troublesome in MacLean.

The triune-brain concept may be wrong in some of its particulars, right in others, but still be very useful and valid in its more general features. After all, at this stage of our knowledge of the brain although it is quite advanced over the 1960's and 1970's, there are not a great number of things we can say with absolute confidence—very few generalizations that are without arguable interpretations of more detailed research data. And Reiner takes apart but does not offer a replacement generalization. His analysis is destructive, not constructive. This type of analysis is the easy part of the job . . . almost anybody can do it.

But in his apparent eagerness to discredit and take apart MacLean's generalization, he also fails to study his subject closely and therefore engages in careless scholarship. He makes significant omissions, outright errors, and substantial misrepresentations of MacLean's work. Let's look at the points Reiner raises one by one.

1. **Reiner blatantly misstates the facts when he claims that the triune brain concept as well as MacLean's book is outdated and lacks up-to-date documentation.**

   Reiner's first point i.e., that there has been a great growth in knowledge about the brain since MacLean first announced his triune brain concept in the 1960's and 1970's implies that MacLean has left the concept untouched and undocumented since that time and has therefore not considered any of the more recent findings. The implications of this statement are belied by the currency of research cited by MacLean and included in his discussions. In backing up his case for the alleged outdated ideas and data in the book, Reiner baldly states: *"only a handful of papers from the 1980's are cited'.* [4, p. 305] This false statement is easily contradicted by a count of bibliographic items, which contain over 180 entries (a big handful indeed!) which date from 1980 to 1988 and over 220 entries from between 1975 and 1979. This amounts to over 400 entries of rather recent documentation ... keeping in mind, of course, that the publication date of MacLean's book and Reiner's review was for both 1990.

2. **Reiner ignores or misstates the facts when he says that "MacLean's presentation of the role of the hippocampus in limbic functions is not well reconciled with the current evidence that the hippocampus plays a role in memory."**

   The phrasing of this statement indicates that MacLean is unaware of or fails to report on the extensive research indicating the role of the hippocampus in memory. Such an implication is totally unwarranted. MacLean devotes fully two chapters to reporting and discussing such research. These chapters even have memory in their titles. Chapter 26 is titled *Microelectric Study of Limbic Inputs Relevant to Ontology and Memory.* Chapter 27 is titled *Question of Limbic Mechanisms Linking a Sense of Individuality to Memory of Ongoing Experience.* These chapters deal at length with the role of the hippocampus in memory and propose an integrative role for the hippocampus in tying learning to affect or emotion (For a summary of MacLean's discussion on these matters, consult these pages 514-516. [2]

3. **By noting that the reptilian complex is not a reptilian invention, Reiner misrepresents MacLean's position.**

On the third point, Reiner contends that current research indicates that MacLean's reptilian complex seems to be present in vertebrates all the way back to jawless fishes.

This is largely a taxonomic question. At what point do we declare something to be a fish, an amphibian, an amniote, a reptile, or a mammal? And do we view mammals as branching off from the amniote tree before we have distinct reptiles in the line of descent? Or do we prefer the more likely probability that mammals descended in a line from the ancient mammal-like reptiles of the pre-dinosaur Permian-Triassic periods called therapsids, who represent a branching of the ancient reptile line (cotylosaurs). Therapsids appeared approximately 230 millions years ago, and approximately 50 million years before the emergence of the great dinosaurs of the Jurassic and Cretaceous periods.

MacLean knows these facts and clearly acknowledges them, while supporting a lineage for mammals that traces back to the therapsids, of the synapsida subclass that branched off from the diapsida line that eventually produced the great dinosaurs many years later. This is the standard position in evolutionary theory today. One might wish to compare the phylogenetic tree in MacLean[2, p. 34] with Butler and Hodos,[6,p. 72] Strickberger,[7', p. 396] and Hickman, et. al.[8, Figure 27-1], and it is the accepted position of standard zoology texts.[8a, 8b, 9] Mammals, and ultimately humans then, did not evolve from dinosaurs but from a parallel lineage that split much further back in geologic time.

If the term Reptilian Brain or Reptilian Complex causes confusion with modern reptiles, and because the reviewers haven't read MacLean's work closely, the Reptilian Complex could be thought of, and perhaps redesignated, as the ancient amniote complex or even the early vertebrate complex. And, of course, as MacLean acknowledges thoroughly, this early brain complex is not the reptilian brain of modern reptiles, but it is also not the same as that of the early vertebrates, amniotes, or therapsids. At several points in his book, MacLean makes this unequivocally clear by his reference to stem reptiles (cotylosaurs), those early reptiles from which both the diapsid and synapsid lines branched off.[2_pp._32 & 82] To assure the proper evolutionary context, MacLean also uses the term protoreptilian in his initial definition and adds the clarifying comment that he refers to the reptilian complex (or R-complex) only for brevity's sake.[2. pp_15-16, 244, & 519] This protoreptilian, or stem reptile brain, has been altered by modifications which include those produced by differentiation and elaboration of earlier structures.[2, p. 243]

These modifications, to include differentiations and elaborations, provide, in addition to their previous maintenance and behavioral functions, neural circuitry in support of the enhanced limbic structures of mammals. These enlarged mammalian limbic structures necessarily engage and enhance prior circuitry in the brain stem. And together these several had expanded limbic and brain stem circuits provide support for the greatly enhanced neocortex (or isocortex) with its eventual modifications permitting language and the development of complex technological societies.

4. Reiner misrepresents MacLean's position on the basal ganglia.

On the fourth point above, Reiner states that he knows "of no one other than MacLean who now believes the basal ganglia to be the neural seat for the control of species-typical types of behaviors."[4, p305] This statement is a misrepresentation of MacLean's position as well as an admission of ignorance on the part of Reiner. In the first place, MacLean never uses the inclusive term "neural seat." Further MacLean is not talking about all species-typical behavior but only some. He specifically excludes from this discussion such mammalian class/species typical behavior as maternal nursing and play, which are attributed primarily

to other brain parts and treated in other chapters of the book.

In part II on the Striatal Complex with Respect to Species-Typical Behavior, MacLean repeatedly emphasizes that the traditional view that the striatal complex is primarily involved in motor functions represents an oversimplification. He writes that the purpose of the present investigation is to test the hypothesis that the striatal complex plays an "essential" role in certain species-typical behaviors as well as certain basic forms of behavior common to both reptiles and mammals.[2, p. 243]

At one point after reciting the evidence, MacLean says that the results *"suggest'* that the role of the medial globus pallidus (a structure of the basal ganglia) is "a" site where neural systems converge in such species-typical mirror displays of those of gothic-type squirrel monkeys,[2, p. 189] and that *"findings indicate that in animals as diverse as lizards and monkeys, the R-complex is 'basically involved' in the organized expression of species-typical, prosematic communication of a ritualistic nature."*[2, p. 189]

Additional research, some predating some postdating Reiner's review, and of which Reiner is apparently ignorant, adds further support to MacLean's hypothesis. For example, J. Wayne Aldridge and colleagues from the University of Michigan in a research report titled "Neuronal Coding of Serial Order: Syntax of Grooming in the Neostriatum,"[10] conclude that there is *"direct evidence that the neostriatum coordinates the control of rule-governed behavioral sequences".* This study builds upon a series of earlier studies of species-typical grooming behavior of the rat.[11, 12, 13] These earlier and more recent studies certainly support MacLean's hypothesis that the striatal complex plays an essential role in some species typical behaviors of a ritualistic nature.

And of course there is the growing body of clinical evidence, going well back into the 1970's and 1980's, that neurological disorders in humans (such as Parkinson's, Huntington's, and Tourette syndromes), which involve damage to the neostriatum, produce specific deficits in the sequential order of movement, language, and cognitive function.[14. 15. 16. 17a. 17b, 18a] Such serial order patterns in behavior are phylogeneti-cally old as well as pervasive and often constitute a basis of identifying so-called species-typical behaviors.

5. Reiner misrepresents the facts when he claims that MacLean **says the limbic system first appeared in mammals.**

On the fifth point above, Reiner again misrepresents MacLean's position. MacLean does not claim that the limbic system first appeared in early mammals. He acknowledges that limbic features appear in fishes, reptiles and birds, but are rudimentary and poorly developed as compared with that of mammals.[2, pp. 247 & 287]

According to MacLean's view, then, it is not the presence or absence of limbic features themselves in ancestral amniote or reptilian vertebrates, but rather the significant and prominent development of limbic features in mammals which is appropriately of interest in understanding the evolution of characteristically and uniquely mammalian behavior. Further, care must be exercised in making comparisons across existing modern species. We can only infer that the structures and undeveloped and/or rudimentary homologues of such structures in modern species were also present in ancestral lines. Brains don't fossilize, so the point can't be made conclusively. The currently accepted inferential position in neuroscience is that there are homologues of limbic structures going well back into vertebrate history, although these homologues in modern species are often difficult to establish and sometimes downright dubious.[18b, 18c]

6. Reiner displays careless scholarship and misrepresents the facts of neuroscience, evolution, and animal behavior as well as MacLean's **position on parental behavior and the cingulate cortex.**

Reiner writes: "MacLean assigns to the cingulate cortex the functions of parental behavior, which he regards as uniquely mammalian. This ignores the fact that some reptiles, such as crocodiles, and all birds engage in parental behavior, not to mention the possibility suggested by paleontological data that some extinct reptiles, namely dinosaurs, also engaged in parental behavior."[4, p. 305]

This statement makes one wonder if Reiner felt it worth his while to even consult the book he is reporting on. Firstly, MacLean does not "assign" parental behavior to the cingulate cortex. He reports the recent (at that time) research on maternal mechanisms in the septal or medial preoptic area[2, pp.351-353] and indicates that this area may have provided the initial potentiality for full scale mammalian maternal behavior,[2, p. 354] which would include play and the development of empathy. The very title of his Chapter 21 is *Participation) of Thalamocingulate Division in Family-Related Behavior.* Participation is participation not unilateral and unequivocal assignment. And MacLean uses the systemic term thalamocingulate to indicate intra-limbic nuclei and cortical connections, not simply cingulate cortex as Reiner states. MacLean cites good evidence for thalamocingulate participation in *"nursing, conjoined with maternal* care",[2, p. 380] after all lesions in certain portions of the cingulate cortex interfere with nursing and other maternal behavior,[19, 20] not with blanket parental care as Reiner asserts.

It may be too early or simply erroneous in neuroscience to assign anything specifically and finally to any exclusive part of the limbic area. There is more likely some localization of minor function, but for most behaviors of any scale there seems to be fairly wide-ranging neural circuitry which may be interrupted by lesions at many different points. For example recent research on maternal behavior (nursing, retrieval, nest-building) in rats has focused on the medial preoptic area with its connections to other limbic structures and the brain stem.[21]

Alison Fleming and her colleagues, summarize what we know about the neural control of maternal behavior.[22] Not only the medial preoptic area with its brain stem projections, but also other limbic sites are involved as well, including the amygdala,[23, 24] hippocampus,[25, 26] septum,[27] and cingulate cortex.[19, 20] Most emotions, emotional behaviors, and emotional memories seem to be distributed and involve multiple pathways.

Specific behaviors and categories of behaviors can be interrupted by lesions at varying points in these multiple pathways.[28, 29] More recent research has again confirmed that the cingulate cortex is involved in emotion and motivation.[30] In a recent research report John Freeman and colleagues conclude that the neural circuitry formed by interconnected cingulate cortical, limbic thalamic and hippoc-ampal neurons has fundamentally similar functions in the affective behaviors of approach and avoidance.[31]

Like any good scientist with an open mind, MacLean, at the close of his chapter on participation of the thalamocingulate division in family-related behavior, calls for more research to explore the extent of this participation.[2, p. 410] It is also noteworthy that MacLean is one of the few thinkers in neuroscience who shows concern for the neural substrate of such family based behavior, characteristic of mammals, as play and the underpinning but illusive quality of empathy. Although such characteristics have been reported on behaviorally (e.g., for play, see[32, 33, 34a, 34b]), they have largely been ignored in the search for neural substrates, not because they are unimportant, but because of the extreme difficulty in defining and objectify-

ing them. But the evidence clearly points to neocortical as well as limbic cortical and subcortical representation.[35, p. 169; 36, pp. 154-155; 37, p. 98]

Reiner also indiscriminately uses the blanket term "parental behavior" coupled with attributing that same blanket usage to MacLean. In this usage, Reiner shows a remarkable deficit of scholarship, naivete, or both. MacLean is not discussing all parental behavior. He discusses those nurturing behaviors that are the most distinguishing characteristic of mammals and a fundamental part of their taxonomic classification and differentiation from birds and reptiles. These behaviors must be found in either new structures or modifications to existing structures. As Butler and Hodos point out, new structures may be added to organ systems, but modification of existing structures appears to be more common.[4, p. 86] The jury is still out on the neurophysiology of these defining mammalian behavioral features. What's more with the emphasis on cognition in neuroscience, there has been surprisingly little attention paid to the extensive work on the neural and hormonal basis of the motivational and emotional aspects of maternal care. This is openly acknowledged by leading scholars in the brain science field. [38, 39, 40]

The blanket term "parental care" as used by Reiner in his criticism of MacLean amounts to condemnation by indiscriminate generalization. Parental care has been defined by a leading authority as "any kind of parental behavior that appears likely to increase the fitness of the parent's offspring".[41, p. 8] It is a very broad and inclusive term. The term includes nest and burrow preparation. The very production of eggs itself is included. This kind of "parental care" is found in the earliest vertebrates with very primitive brains indeed. If the all-inclusive definition of parental care can be stretched to include the production of eggs and digging a hole to place them, perhaps it could conceivably be stretched to include even the sharing of cellular membranes during asexual reproduction by single-celled organisms.

But specifically ... what about parental care in modern reptiles? Contrary to Reiner's claim, MacLean reports on parental care in crocodiles [2, pp. 136-137] and also in some species of skink lizards[2, pp. 248-248] A recent review article on parental care among reptiles by Carl Gans of the Department of Biology, University of Michigan brings us up to date. He writes:

"Perhaps the most spectacular instance of reptilian parental care occurs in crocodylians, in which both members of the mating pair will respond to the call of hatchlings, although the specificity of the response needs further study. The call is recognized by both sexes and even by members of other crocodylian species. However, it is unclear whether the response sequence pertains only to their own young. The hatchlings vocalize underground while emerging from the eggs, causing the adults to dig them up and carry them to the water within the relatively enormous buccal pouch. [42] *Not only are the young then washed, but they stay in association with the adults fora relatively brief period after which their response to large crocodylians reverses. Thereafter the juveniles then spread suddenly into small adjacent channels and may even dig themselves tunnels here. In view of the fact that crocodylians may be cannibalistic, there seems to be both an inhibition of cannibalism in the parents and an inhibition of a possible adult avoidance reaction in the neonates."* [43]

This kind of short-lived parental care during which the cannibalism of parents is inhibited may be impressive in reptiles, but it is a far, far cry from the highly developed family-related behavior in mammals; behavior which is so further developed in the human species that it extends often throughout an entire lifetime and becomes the basis for a vastly extended social life. The equating of parental care in reptiles with parental care in mammals is simply

ludicrous. It is this mammalian family behavior that concerns MacLean, and the neural substrate is appropriately sought in the brain modifications that became prominent with the appearance of mammals.[44]

7. Reiner's further inaccuracies: recapitulation, homology, and correspondence, etc.

Near the end of his review, Reiner makes the following isolated statement: *"MacLean also errs in his apparent sweeping acceptance of Haeckel's idea that ontogeny recapitulates phylogeny"* Again Reiner distorts and misrepresents. From a close review of the book it is by no means altogether clear that MacLean "sweepingly" accepts Haeckel's concept.

In fact, he only refers to it once while at the same time noting the well-known exceptions.[2, p.46] Haeckel's concept has been replaced in neuroscience today by the principles of von Baerian recapitulation. The von Baerian version holds that while ontogeny does not recapitulate phylogeny in the thoroughgoing Haeckelian sense, it does recapitulate the features of an organism in terms of the organism's general to more specific classification.

In other words, the von Baerian principles state that the more general features of an organism develop before the more specific features.[6, pp. 51-52] The issue, however, is still not so clearly settled. The emergent discipline of evolutionary developmental biology is looking more closely into such questions.[45,46] For instance, evolutionary biologist Wallace Arthur, in summarizing the main themes of this emerging discipline writes:

"No single comparative embryologicalpattern is universally found or can be described as a 'law'. Von Baerian divergence, its antithesis (convergence) and a broadly Haeckelian (quasi-recapitulatory) pattern can all be found, depending on the comparison made." [47, p. 292]

On the additional point that MacLean prefers to think in terms of correspondence rather than homology probably reflects his functional-behavioral orientation. In fact, it is specifically in discussing the issue of the relationship between structure and behavior that makes this comment.[2, p.37] Later, he returns to a more standard use of homology.[2, p.228] There is, in fact, presently no sure fire way of demonstrating that homologues have the same one-to-one functions or produce the same one-to-one behaviors across species. Reiner shows what can only be considered a misplaced and sophomoric "gotcha" exuberance when he writes:

"*... in his presentation on the evolution of the R-complex, MacLean makes a comment that should leave Stephen J. Gould, not to mention all other students of evolution, aghast. Claiming that the concept of homology is confused and not clearly defined, he discards it in favor of what he regards as a much less equivocal term, namely, correspondence. This is a very critical misjudgment to make in a work on evolution.*"[4, **p. 305**]

This is truly a naive, if not preposterous statement by Reiner. Could it be that Reiner is not aware of the long history of the pervasive problems associated with the definition of homology? For example, Leigh Van Valen, of the Biology department of the University of Chicago, in the first sentence of his frequently referenced article on homology and its causes, writes that: *"Homology is the central concept of anatomy, yet it is an elusive concept.*"[48, p.305]

Further on, in view of the persistent ambiguities, Van Valen practically equates the terms homo-logue and correspondence when he writes: "In *fact, homology can be defined, in a quite general way, as correspondence caused by a continuity of information"…*," although in a footnote Van Valen admits that correspondence itself needs further definition beyond the scope of his paper.[48, p. 305: footnote 1] Although there has been some sharpening of the concept of

homology, with emphasis on phyletic continuity, the ambiguities have by no means been adequately resolved,[47, 49, 50]

And there is the haunting question that is still wide open for research and investigation … do most homologous behaviors share a homologous structural basis or can homologous behaviors be rooted in nonhomologous structures? [50, p. 29: footnote 23] A recent report by William Blessing on the lower brainstem raises the question of multiple neural representations of body parts and behavior, in that behavior originally represented and controlled in the brain stem of an earlier vertebrate may maintain its brain stem representation, but be controlled by an added representation in the frontal cortex of a more highly developed mammal. Such multiple representations at different levels as the brain became more complex would certainly confuse the issue of a straightforward homologous match of structure and function.[55, 52]

Research on very limited aspects of function are often suggestive but far from conclusive. Establishing homologues of the pref rontal cortex can be particularly vexing. A recent research article by Gagliardo and colleagues,"*Behavioural effects of ablations of the presumed 'prefrontal cortex' or the corticoid in pigeons,*"[53] indicates, not only in its discussion and conclusions, but in the very title itself, the uncertainty, ambiguity, and cautions that currently characterize such research efforts [35, pp.7-11]

Much assuming goes on in neuroscience on this issue, which simply cannot be settled at this time based on the empirical evidence. This is one of the problems and cautions that must be acknowledged when generalizing across species —say from rats to humans. In maternal behavior for example, can we say factually that the medial preoptic area plays the same part in the maternal behavior of humans that it does it the rat brain? No, we cannot. At least not yet. But neuroscientists, after first hedging themselves, and following homologous logic, seem inclined to think so.

Nevertheless, it is entirely within the realm of possibility that we may find that it does so only in part or not at all. As neuroresearcher Joseph LeDoux notes *"Some innate behavioral patterns are known to involve hierarchically organized response components".* [54, p. 120] And further on he adds: *"Species differences can involve any brain region or pathway, due to particular brain specializations required for certain species-specific adaptations or to random changes."* [54, p. 123] After all, as neurologist Richard Restak points out in the case of aggression:

"In animals, multiple areas within the limbic system increase, modify, or inhibit aggression. Moreover, the same area may enhance or diminish aggression depending on the site selected, the conditions of the experiment (electrical stimulation versus destruction of brain tissue), and the animal selected for experiment. Destruction of one limbic system component, for instance, the cingulate gyrus, increases aggression in dogs and cats, while the same operation in monkeys and humans exerts a calming action." [55, p. 149]

Or perhaps, as Blessing suggests, that there are multiple representations. Then we might have to go to correspondence rather than homology (even homoplasy might not apply, since homoplasy, or parallel evolution, would probably not apply in such closely related species) to account for the behavioral circuitry. In other words the corresponding neural circuitry — that circuitry controlling maternal behavior — may be found in the same, slightly differing, multiple, or perhaps (though highly unlikely) even totally different structural homo-loguesor modifications.

In fact if homology is correct and functionally, to include behaviorally, uniform ... that is the same structures account for the same functions and behaviors across classes, orders, and species ... this finding would support the triune brain concept as set out by MacLean, which says generally that the protoreptilian complex common to both reptiles and mammals functions largely the same in both classes. This finding would also support

MacLean's position that the expanded circuitry areas of the mammalian complex bear characteristically mammalian functions and are the circuitry for characteristically mammalian behaviors such as nursing, a defining taxonomic feature of mammals (which, in part distinguishes them from reptiles and birds).

In a final series of somewhat negatively gratuitous comments Reiner writes, among other things equally gratuitous, about some of MacLean's legitimate speculations. For example, Reiner states ". . . *and mathematical skill (he thinks the cerebellum could be involved). . .*"[4, p. 305]

And why not? See MacLean's discussion on the subject. [2, pp. 548-552] Recent research has indicated that the cerebellum is not just a motor mechanism, but is also likely involved in higher cognitive and perhaps even language function. Especially relevant is the rather well-supported hypothesis that indicates a cerebellar mechanism involved in all tasks that require precise temporal computations. This could well suggest an involvement in mathematical processes. True, the evidence is insufficient to permit firm conclusions as to the cerebellar role in higher cognitive processes, but it is a research direction which needs further refinement and is currently pursued by a number of neurobiologists.[56, 57]

Campbell's Review in the *American Scientist.*

The review by Campbell in *American Scientist* is much shorter than Reiner's. It brings up some of the same points, but is less prejudicial in its tone. Since it is less detailed it expresses primarily the preferences and value judgements of the reviewer. Campbell repeats Reiner's erroneous charge about outdatedness. He writes:"... *that except for a very few papers, most of the references were published prior to 1980.*"[5,p. 498] It has already been noted that these "few" amount to more than 180 citations. One suspects that Campbell, proceeded from his preconceptions and found what he expected to find.

Campbell ends his review with the statement: *"Unfortunately, the data presented are, to some degree, outdated, and the evolutionary reasoning is unsophisticated.*"[5, p. 498] The use of the term "unsophisticated" by the reviewer exemplifies gratuitous abuse of review. It is a sweeping value-laden term that communicates more about the reviewerthan the reviewed. For anyone who has closely read MacLean's detailed and thoughtful work, such blanket judgments are not warranted. The evolutionary reasoning is, on the contrary, quite thoughtful, well-presented and sophisticated. Such blanket judgments tell us more about the sociology of neuroscience and neuroscientists that they do about the subject matter of the discipline.

The Comments of Butler and Hodos:

In their recent comprehensive and overall admirable work on comparative vertebrate anatomy, Butler and Hodos attempt to formalize the assignment of MacLean's work to the relics of history. Their comments reflect the standard oversimplified criticisms that have become popular to repeat ever more unreflectively. For example, Butler and Hodos assign the triune brain concept inaccurately and indiscriminately to a category they called "theories of addition." And without any detailed discussion or analysis, of the very significant indisputable points of accuracy in MacLean's concept, they write:

" *The extensive body of work in comparative neuro-biology over the past three decades unequivocally contradicts this theory. First, the homologues of the limbic cortical areas that MacLean considers to have been first present in early mammals have been found in nonmammalian vertebrates. Second, homologues of isocortical structures and of dorsal thalamic nuclei also have been found in nonmammals. Third, MacLean's observations on the behavioral differences between mammals and nonmammals are oversimplified and ignore the elaborate social and parental behaviors of nonmammalian vertebrates.*"[6, p. 86]

How incredible that two such qualified authors should accept the same flagrant misrepresenta-

tions, inaccuracies, and oversimplifications of MacLean's work that have become commonplace in some sectors of neurobiology over the past decade. It is apparent that they merely parroted the errors and misrepresentations of Reiner and others rather than reading MacLean's 1990 work closely and open-mindedly. Or perhaps they simply took their understanding from Carl Sagan's overpopularized and oversimplified presentation in *The Dragons of Ederf* and didn't consider the issue worth looking into further. There is no point in repeating the responses given earlier to Reiner's review.

The same points hold for Butler and Hodos' comments. The rebuttal points are clearly made and easily accessible to verification by anyone who chooses to make the effort. The categorical statement by Butler and Hodos that the extensive body of work in comparative neurobiology over the past three decades unequivocably contradicts MacLean's theory, which they apparently have not read, constitutes on that point poor, if not irresponsible, scholarship.

The Utility and Validity of MacLean's Triune Brain Concept:

The triune brain concept may have its faults. But such faults have been patently misrepresented in some cases and grossly exaggerated in others. Whatever its faults may prove to be the triune brain concept gets at a fundamental truth. The mammalian modifications, differentiations, and elaborations, to the early vertebrate and ancestral amniote brains had the effect of introducing endothermy (warm-bloodedness), maternal nursing, enhanced mechanisms of skin contact and comfort, as well as enhanced visual, vocal, and other cues to bond parents to offspring and serve as the underpinning for the extended and complex family life of humankind. The mammalian modifications, therefore, added greatly enhanced affectional, other-interested behavior to the primarily (although not exclusively) self-preservational, self-interested behaviors of ancestral amniotes and early vertebrates (not necessarily their modern representatives).

The simplistic representation and attempted demolition of MacLean's triune brain concept is not good science. Reiner's review, where it has any validity at all, is like discovering a termite or two in the bathroom wall — and then proceeding to pronounce a full alarm that the house is full of termites, only to find that it is necessary to treat a couple of boards in the subflooring. Further In his deconstructive, analytic fervor, Reiner has not offered an alternative, higher level generalization. The review represents a dysfunction common to a lot of scientific practices, that of an analytical approach that takes apart but can't put back together.

Perhaps we should call it analytic myopia. Being not interested in the bigger questions of humanity that we so desperately need help on, and lacking an interest in therapy, these analytic myopics continue their fine-grained focus. Fine-grained focus is fine, laudable, and much needed. It becomes analytically myopic, however, when it fails to place in context what it finds and defines, when it employs sloppy scholarship, and when it attempts prejudicially to destroy or deconstruct that which it lacks the imagination and courage to put together.

On the other hand the theories of brain evolution that Butler and Hodos review favorably and the synthesis which they present at the end of their book focus on the immunohistological, hormonal, and morphological mechanics. [6, pp. 463-473] They say, in fact, almost nothing at all about behavior or the significance for behavioral evolution for the various mechanisms of evolution they identify. And they make no attempt whatsoever to confront the larger behavioral questions of humanity where we need help and guidance from neuroscience in defining the neurobiological basis of human nature in order to establish links up the scale of generalization with the social sciences. The theories they present are only of interest to the technical aspects of neuroscience. They are not, however, incompatible, but rather tend to support MacLean's concepts when these concepts are thoughtfully considered and not inaccurately reported, misrepresented, or grossly oversimplified.

The key point in comparing these theories with that of MacLean's is that they are comparable at best only in part. They ask and respond to different questions. MacLean tries to address the larger questions of human nature and behavior. The others show no interest in such questions but address the fine grained technical questions of anatomical and functional evolution. At the level where they meet they do not contradict each other but are largely compatible. At the point they diverge they primarily address different questions.

This is, I think, the root of the tension between the two. MacLean's concept facing up the scale of generalization is useful and has been appropriately well-received in the therapeutic sciences, and is also very useful for the social sciences. On the other hand, it has not been, but may yet become, more useful and better received in other quarters of neuroscience ... especially when subjective experience is eventually given its due in the study of consciousness. There are, in fact, recent signs that the importance of subjective experience, which is of great interest to MacLean, is beginning to be more fully recognized in the newer studies of consciousness.[58]

The triune brain concept may need modification, then , as the body of neuroscience grows … but certainly not outright rejection. With appropriate clarifications, it is still by far the best concept we have for linking neuroscience with the larger, more highly generalized concepts of the social sciences. This is true even if its level of generality has limited utility for some neuroscience researchers who are doing ever more fine-grained research into neural architecture and function.

The transition from early vertebrate to amniote to synapsid reptile to mammal was in behavioral effect the transition from a nearly exclusively self-preserving organism with relatively little or less complex social life to, at least in part, a nurturing, "other-maintaining", "other-supporting", or "other-interested" organism. And that makes all the difference in the world for human evolution. Our other-maintaining mechanisms combined with our self-preserving ones provide the biological glue as well as the dynamic for our remarkable behavioral evolution, our social life, and ultimately the crucial social and political factor of our moral consciousness.

The qualitative differences between the familial and social behaviors of even the most caring of reptiles (say, modern crocodiles), birds or social insects and the mammal we call human are overwhelmingly evident. Humans with their social, cognitive, and language skills, for better or for worse, dominate the planet and no other species comes close. Any neurobiologist who cannot see or appreciate the difference is suffering from analytic myopia or some form of misplaced species egalitarianism.[6, pp. 3-4]

The proper study of humans is humans and to some extent their lineal antecedents. The triune brain concept generalizes a fundamental truth out of much that is yet unknown and uncertain in neuroscience. And this generalization, when properly understood, appreciated, and applied, is the most useful bridging link, thus far articulated, between neuroscience and the larger and press-ingly critical questions of humanity's survival... as well as the hoped for transformation of humanity into a truly life-supporting, planet-preserving and enhancing custodial species.

When other neuroscience researchers reach the conceptual point in their grasp of the discipline where they feel an increasing obligation to take a more holistic view and proceed to move up the scale of generalization in order to confront the larger questions of human life, they will likely produce concepts closely resembling the triune brain. Homology and behavioral evolution will almost inevitably take them in that direction.

When that time comes, if the triune brain concept has been buried in the scrap heap of scientific history, it will be exhumed, refurbished, and honored. Frankly, despite its current lack of popularity in some quarters of neurobiology, I do not think it will be consigned to the scrap heap. I think that it will continue to be influential, and with

appropriate modifications as research progresses, provide an important underpinning for interdisciplinary communication and bridging.

Endnotes:

1. **For a highly favorable review of MacLean's 1990 book see the review by Emre Kokmen, M.D. of the Mayo Clinic, Rochester, Minne sota.** [59]

   In this article I focus instead on the reviews in *Science* and *American Scientist* because they have reached a wider audience and have become red flag reviews unjustifiably inhibiting the thoughtful application of the triune brain concept in related fields as well as in the psychological and social sciences. The author has recently presented a paper at the 1997 annual meeting of the American Political Science Association which utilizes the triune brain concept with some clarifications as the basis of a new behavioral model.[60, 61, 62]

2. **The criticisms made by Reiner are not necessarily in his exact order presented.**

3. **The use of the term "additions" is deliber ately avoided here because it has been the source of some confusion.** [6, p. 86]

   New brain structures do not spring de novo out of nowhere but rather evolve from the differentiation of previously existing structures. When differentiations become sufficiently established, they are often referred to loosely as "additions." This does not deny that seemingly new additions may possibly and occasionally arise, but the intent here is to emphasize the phyloge-netic continuity that underpins the concept of homology.

4. **The accuracy and utility of the concept and term limbic system has itself been a separate topic of some disagreement in recent years.**

Some authors state that it does not represent a truly functional system and the term should be discarded. Others defend its use. Most texts continue to find the term useful and because of its longtime usage it will probably remain in the literature. Some recent and prominent scholars illustrate the controversy well. Pierre Gloor of the Montreal Neurological Institute, McGill University in his thorough-going work, *The Temporal Lobe and Limbic System,* by the very use of the term in the title indicates his position. Further on in the text, while acknowledging the controversy he writes:

"... *In addition, in mammals the hippocampus and amygdala exhibit close mutual interconnections that do not appear to be at all prominent in nonmammalian vertebrates. Thus in all mammals the hippocampus and amygdala, together with and partially through the basal forebrain areas and the preoptico-hypothalamic continuum extending along the medial forebrain bundle down to the midbrain tegmentum, form the core of a system, the limbic system, which has some anatomical and functional unity inasmuch as it embodies mechanisms that relate 'external' reality perceived by the extero-ceptive senses to 'internal' reality embedded in memory and affect. This system in mammals exhibits an organization that is sufficiently different from that characterizing other areas of the cerebral hemisphere to merit such a designation* " [63, p.106]

And well-known neurologist, Richard Restak writes: " *Summarizing a great deal of experimental work, it's fair to say that, depending on the areas stimulated, the limbic system serves as a generator of agreeable-pleasurable or disagreeable-aversive affects.*"[55, p. 143] Further on, he notes: *"While mostneuroscientists agree that emotions are mediated by the limbic system, there is little agreement in regard to the individual contributions to emotion of the different components, and the influence that each component exerts on the others.*"[55, p. 149]

On the other hand, William Blessing, a neurologist at Flinders University, in his study of the lower brainstem, feels that emphasis on the limbic system has detracted from the study of brainstem mechanism, that it has been *"plagued by its anatomical and physiological vagueness and by the lack of precision with which the term is used,"* [5051, p. 15] and should be dropped from the literature.[51, p. 16]

A third recent author, neuroscientist Joseph LeDoux,[54, chapter 4] argues that because the limbic system is not solely dedicated to the single global function of emotion, a claim that MacLean fully recognizes in his chapters on memory,[2, chapters 26 & 27] the concept should therefore be abandoned. LeDoux apparently prefers a single functional criterion for the definition of a system, whereas MacLean seems to prefer a combination of functional and anatomical criteria.

Le Doux concludes his argument by stating: *"As a result, there may not be one emotional system in the brain but many."*[54, p. 103] Compare this with the concluding line of the definitional description by Kandel, et. al., authors of the most widely used textbook on neuroscience and behavior: *"The limbic system contains neurons that form complex circuits that play an important role in learning, memory, and emotion."*[40, p. 708]

The use and value of the conceptual term limbic system, then, seems to depend on one's research focus and how one chooses to define a system. It might be added that the definition of what constitutes a system is controversial in all disciplines, not just neuroscience.

5. See especially the articles by Stubenberg [64] and Galin [65] who writes:

"*I assert that what is most interesting about mental life for most ordinary people is not mechanism, not performance, not information processing; it is what it feels like! Subjective experience*! "[65, p. 121] *c8*

The Triune Brain -- Les Trois Cerveaux

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1983,29 minutes, 40 seconds

Abstract: This informative film illustrates American physician Dr. Paul MacLean's theory of human brain structure and evolution--the triune brain. The human brain, he theorizes, functions through the interaction of three cerebral formations: the reptilian complex, the limbic system, and the neocortex. These control instinct, emotions, and intellect, respectively. Using computer animation to explain the development of these formations, the film documents our current knowledge about this most complex of human organs.

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That if he chose this focal spot, His life would never be forgot. Alas, though we now muse on cost, All thoughts of him are long since lost.

These two tombs our futures presage,
Passing on the sombre message: When we depart this earthly sphere, Before too long, we disappear,

Mike Waller
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ABSTRACTS & EXTRACTS...

Rainer G; Asaad WF & Miller EK: Selective representation of relevant information by neurons in the primate prefrontal cortex . *Nature,* 1998;393:577-579.

Abstract: Selective representation of relevant information by neurons in the primate prefrontal cortex. The severe limitation of the capacity of working memory, the ability to store temporarily and manipulate information, necessitates mechanisms that restrict access to it.

Here the authors report tests to discover whether the activity of neurons in the prefrontal (PF) cortex, the putative neural correlate of working memory, might reflect these mechanisms and preferentially represent behaviourally relevant information. Monkeys performed a 'delayed-matching-to-sample' task with an array of three objects. Only one of the objects in the array was relevant for task performance and the monkeys needed to find that object (the target) and remember its location. For many PF neurons, activity to physically identical arrays varied with the target location; the location of the non-target objects had little or no influence on activity. Information about the target location was present in activity as early as 140ms after array onset. Also, information about which object was the target was reflected in the sustained activity of many PF neurons. These results suggest that the prefrontal cortex is involved in selecting and maintaining behaviourally relevant information.

Nowak MA & Sigmund K: Selective representation of relevant information by neurons in the primate prefrontal cortex. *Nature,* 1998;393:573-577.

Abstract: Darwinian evolution has to provide an explanation for cooperative behaviour. Theories of cooperation are based on kin selection (dependent on genetic relatedness), group selection and reciprocal altruism. The idea of reciprocal altruism usually involves direct reciprocity: repeated encounters between the same individuals allow for the return of an altruistic act by the recipient.

Here the authors present a new theoretical framework, which is based on indirect reciprocity and does not require the same two individuals ever to meet again. Individual selection can nevertheless favour cooperative strategies directed towards recipients that have helped others in the past. Cooperation pays because it confers the image of a valuable community member to the cooperating individual. The authors present computer simulations and analytic models that specify the conditions required for evolutionary stability of indirect reciprocity. They show that the probability of knowing the 'image' of the recipient must exceed the cost-to-benefit ratio of the altruistic act. They propose that the emergence of indirect reciprocity was a decisive step for the evolution of human societies.

Adolphs R; Tranel D & Damasio AR: The human amygdala in social judgment. *Nature,* 1998;393:470-474.

Abstract: Studies in animals have implicated the amygdala in emotional and social behaviours, especially those related to fear and aggression. Although lesion and functional imaging studies in humans have demonstrated the amygdala's participation in recognizing emotional facial expressions, its role in human social behaviour has remained unclear.

The authors report here their investigation into the hypothesis that the human amygdala is required for accurate social judgments of other individuals on the basis of their facial appearance. They asked three subjects with complete bilateral amygdala damage to judge faces of unfamiliar people with respect to two attributes important in real-life social

encounters: approachability and trustworthiness. All three subjects judged unfamiliar individuals to be more approachable and more trustworthy than did control subjects. The impairment was most striking for faces to which normal subjects assign the most negative ratings: unapproachable and untrustworthy looking individuals. Additional investigations revealed that the impairment does not extend to judging verbal descriptions of people. The amygdala appears to be an important component of the neural systems that help retrieve socially relevant knowledge on the basis of facial appearance.

Morris JS; Ohman A & Dolan RJ: Conscious and unconscious emotional learning in the human amygdala. *Nature,* 1998;393:467-470.

Abstract: If subjects are shown an angry face as a target visual stimulus for less than forty milliseconds and are then immediately shown an expressionless mask, these subjects report seeing the mask but not the target. However, an aversively conditioned masked target can elicit an emotional response from subjects without being consciously perceived.

Here the authors study the mechanism of this unconsciously mediated emotional learning. They measured neural activity in volunteer subjects who were presented with two angry faces, one of which, through previous classical conditioning, was associated with a burst of white noise. In half of the trials, the subjects' awareness of the angry faces was prevented by backward masking with a neutral face. A significant neural response was elicited in the right, but not left, amygdala to masked presentations of the conditioned angry face. Unmasked presentations of the same face produced enhanced neural activity in the left, but not right, amygdala. The authors results indicate that, first, the human amygdala can discriminate between stimuli solely on the basis of their acquired behavioural significance, and second, this response is lateralized according to the subjects' level of awareness of the stimuli.

Barinaga M: Owl study sheds light on how young brains learn. *Science*, 1998;279:1451-1452.

Knudsen EI: Capacity for plasticity in the adult owl auditory system expanded by juvenile experience. *Science,* 1998;279:1531-1533.

Extract: In sensitive periods, the juvenile brain seems to be ready to acquire skills and information much faster than the adult brain. Knudson at Stanford reports that young barn owls can retain a "memory trace" for a behavior and reactivate it in adulthood after a long period of disuse. He put prisms over the eyes of the young owls resulting in a shift of the visual fields and studied the owl's ability to localize sound in space in a blackout. The ability to collate visual and auditory signals from a specific site is localized in the optic tectum (superior colliculus). Within 1 -2 months, the young owl adapted to the prism shift. Feldman found that the neurons in these birds formed an additional connection as the adjustment occurred. When the prisms were removed, the birds reverted to the previous way of sound localization. When the birds became adults (over 1 year old), these same birds were tested and could again adapt to the prisms. However, they could not adjust to prisms that were different than those used in their youth. Adult birds without this early prism experience could not make the adjustment as adults.

Other examples of behavior persisting after early experience (with or without periods of disuse):

- bird songs
- bird and mammal sexual imprinting
- human language acquisition.

Extracted by: Beverly Jewel Sutton, M.D.

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