CULTURE, SYMBOLS, AND HUMAN BRAIN EVOLUTION: A SYNTHESIS

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INTRODUCTION

It was Frederich Engels' essay in 1896, "The Part Played by Labour in the Transition from Ape to Man", that situated biological–cultural–evolutionary variables in a materialistic rather than idealistic framework, although he is seldom mentioned by physical anthropologists. Engels had claimed that the hand was freed when bipedalism arose and that the labor of the hand – using and making tools – brought about other changes leading to greater perfection of the hand and the further development of the brain. Of course, our understanding of the relationship among these variables indicates that human evolution has been more complex than Engels implied and that it is insufficient to think in the strict terms of a linear (if also dialectically developing) sequence.

I shall focus here on the role of the brain in human adaptation and attempt to relate its evolution during the Plio/Pleistocene to the archaeological record that shows a concurrent increase in cultural complexity. However, this must be accomplished in such a way that the other variables in human evolution, such as bipedalism, social behaviour, tool-making, language, hunting, delayed growth and maturation, etc., can be integrated in a developmental matrix [1]. It is, therefore, necessary to avoid the kind of theorizing that had conceptualized human evolution as a series of simple, single adaptations somehow adding to each other in a neatly divisible chronology.

In the present account, the brain is considered as a continually evolving organ, that is, something that emerged directly following bipedalism, the use and making of stone tools, and the freeing of the hand for "labor", but also as an organ that changed along with these other complex transformations, and possibly before them. My contention is that the most significant evolutionary changes leading from an apelike hominoid to humankind were in the area of *social behavior* and, moreover, that the fossil record provides us with the clues about the reticulation of the totality of these changes with social behavior.

In considering the uniqueness of the human being, we need to explain carefully the process of human adaptive interaction with the environment while not violating the essentials of continuity between humans and their earlier mammalian ancestors. Motor skills involving the hand, hand–eye coordination, proprioception (sense of body position), sensory sensitivity, memory storage, facility in learning, ability to delay responses, curiosity, need for sociality and varied stimulation, etc., are all aspects of behavioral organization where continuities with nonhuman primates (and other animals) are extensive. *Homo,* of course, is unique in possessing a language based on arbitrary symbols [2].

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The significance of symbolizing goes beyond the mere manipulation of environment by communicating to or with others. Symbols must also be welded to their effects in structuring cognition, the setting or "gating" of perception (what we "select" to observe in our environment), and the actual creation of an environment [3], which, in turn, generates selection pressures that react on us.

Through *arbitrary* symbol systems the human being *imposes* structure upon his environment. Arbitrary here means non-iconic: there is no necessary relation between the symbol and the referent. An Acheulean hand axe, in all its various forms of cutting edges, axes of symmetry, etc., depends more on the thought processes and integrated motor skills of its maker than on the original form of the stone cobble from which it is made [4]. The *standards* of form are *social* and *arbitrary*, not instinctive or innate. Kinship systems need not be based only on outright biological principles although they are certainly constrained to varying degrees by the logics of biology. Rather, the human being can *impose* these constructions on his fellows and his environment at large [5].

Of course, one can argue that human beings have a built in necessity or "imperative" to produce order or structure. But this must rest upon a complex interaction of neurological, motivational, social, and perhaps ideological variables, and the interaction of these is *patterned by human society. Impose* is chosen to signify the process because of its self-constructive connotation, and to underline the sheer anthropocentrism of the human being, the ability (and perhaps need) to order experience and environment as he sees fit. How this all came about, indeed, even to find more suitable ways of talking about our uniqueness, is still a major problem within the social sciences and will not be solved in this paper.

Finally, it must be emphasized here that the attempt to correlate brain enlargement and refinement with the growth of cultural complexity and other variables *is not a causal analysis.* The growth of the brain reflects selection pressures for increased behavioral adaptability. But perceptual, cognitive, and motor aspects of stone tool-making were only an aspect of social behavioral adaptability and evolution during the Plio/Pleistocene. Rather than seeing stone tools and the makers' motor skills as the primary focus for pressures of natural selection, I regard them as *clues* to the more complex social processes that were under direct selection pressures. *In other words, it was not the tools themselves that were the key factors in successful evolutionary coping. Rather, the associated social, behavioral and cultural processes, directing such activities as tool-making, hunting and gathering, were basic.*

Since the interrelations of several variables are focused upon, a brief outline may be useful. First, to appreciate human evolution it is necessary to have some idea as to what we are and how we differ from other creatures. To do this, we must look at some of our psychological attributes – language, mediated by arbitrary symbols, is at least one attribute specific to ourselves and must rest upon a determinate brain organization. Since the appearance of stone tools made to a standard pattern precedes any really clear demonstrable change in the brain (as measured by its volume), the beginnings of human cultural behavior preceded the major enlargement of the brain, which thereafter seems to parallel the evolution of cultural complexity.

The question of brain and cultural interaction is then dealt with, using a dialectical framework, integrating this process with factors of cultural and brain complexity. Finally, in the third section, the "initial-kick" is discussed. Here the question of human evolution prior to really demonstrable brain enlargement and cultural evolution is returned to; that is, those possible kinds of changes that might have begun the process. The initial kick is

viewed as selection for social behavior based on increasingly cooperative and less aggressive behavior within social groups. It is speculated that these changes were based on endocrine–target tissue interaction that effected not only the development of cooperation and the diminishment of aggression, but also changes in growth rates affecting brain and body size, sexual dimorphism, and social behavior.

One caveat is necessary. Language is based on sequences of words and sentences, which makes it difficult to explicate a number of processes operating simultaneously. Sequential discussion of these variables should not be interpreted as a linear sequence of automatically cumulative adaptations, but as a reticulation of processes operating concurrently. That is, these processes should be understood as mutual-causal.

HUMAN UNIQUENESS

We are unique [6] because we have evolved the capacity to alter our environments to an extent unprecedented by any other creature. Symbol systems and the material and social basis of such systems – the ensemble we call "culture" – emerges as the created environment *to which we must also accommodate.* At the same time, we are prey and predator to our own species, as well as others, and more importantly, we are sometimes prey to the artificial environments we have created. Of course, these are only artificial in the sense that we have created them: their artificiality does not violate their reality. Human productions often kill us. Cars, cities, pollutants, and the manipulation of ecological variables affecting our food supply take their toll, as do natural catastrophes, and there is also the abstract, dissociated violence of modern war.

It cannot be known exactly how selection pressures have changed through cultural behavior since early human evolution, but it is fairly certain that extremes of behavioral variation not concordant with human biosocial survival were weeded out and that the intensities of such selection pressures probably varied at different times. Selection for sociality and language behavior must surely have been very strong.

Moreover, human beings are characterized by the tendency for "imposition" [1]. This implies processes of behavior that are a key to understanding ourselves, because we are the only beings that attempt to make ideational systems work, and we alone can impose our fantasies, our arbitrary (non-iconic) constructions upon the environment. These then react on us, shaping our perceptions and creating new selection pressures, encouraging different adaptations or impositions and so on, in a "positive feedback" relationship. Imposition also connotes an intense anthropocentrism, in which the universe is integrated symbolically to suit human self-centered perceptions.

Symbol systems are the means humans use to impose arbitrary form upon the environment, and define what is now to be *figure,* and now *ground.* With a language woven from the fabric of arbitrary symbols, we can expand or constrict the welter of environmental stimuli in selective and arbitrary ways. We are all aware that certain optical designs appear to alter when we look at them. An example is the Neckar cube, the face–vase, which changes profile from vases to a face and back again. Figure and ground become reversed, as it were, the vase figure and the face ground, and vice versa.

My point is that these figure–ground representations or assignments are at least partially defined through social convention and consensus. Learning is, in part, a process whereby any animal acquires facility in distinguishing among stimuli from its environment. In other words, what was once undifferentiated background in the environment can next become the figure to be attended to in perception and cognition.

Symbol systems, through the use of a non-iconic set of a very small set of minimal, but

"meaningful" units, combinable in a near exponential number of ways, enlarge that capacity to differentiate figure from ground. This not only applies to the recombinational power inherent in human language codes, but also the powers of written and oral traditions which add elements of permanency to the process. Much of human behavior is directed not only to expansion of its codes and meanings, but also to their recording.

Furthermore, and in oppositon to "animal learning" per se, the human being is *not* constrained by either previous example or social learning, to invent and impose its own set of figure/ground relationships upon the human and natural environment. Symbol systems thus organize experience into different frameworks that facilitate not only some degree of human control over environmental resources, such as tool objects, or hunting and other subsistence techniques, but also *command of the person's own social relationships.* That is, the relationships of various human beings in and between social groups can be defined outside of strictly biological premises. Behavioral prerogatives, such as social status, and thus authority, can be assigned. Who marries whom, and who assigns tasks, who performs them, need not have any relationship to biological attributes, i.e., size, strength, etc., but can be defined by role attributes. This gives the human being a vast potential for constructing cultural forms in differing ecological contexts.

It seems quite feasible to argue that stone tools made to a standard pattern presuppose symbolic language. (This is an old argument, of course, and not unique to this paper, or even without controversy) [8]. But my contention is that any theoretical model that describes language *also* describes stone toolmaking. Both processes utilize a limited number of basic units that are combined in a finite number of ways (with reference to a specific language or specific tool), and there is an overlying set of rules, or syntax (grammar), about how units combine and concatenate.

The stone tools of the archaeological record thus become our most important empirical evidence about the processes (and their evolution) of early humankind's growing perceptions, cognitive processes, and control of the environment. These are very important clues to the evolution of human social behavior. What should be stressed then, is the need to start looking at stone-tools and their manufacture more in terms of their significance to social behavior than as simply extrasomatic devices to cut up the world.

THE EVOLUTION OF THE BRAIN [9]

The human brain represents about three percent of the total weight of the body and yet utilizes, more or less continuously, over twenty percent of the total blood supply. This alone indicates the metabolic power of the brain as an instrument of adaptation and underlines its importance.

The brain is also unusual in that it is an organ having a tremendous number of cells (about ten billion in modern *Homo*), but mitotic division of its nerve cells is complete within the first year or two of postnatal life. Thereafter, the brain enlarges through growth, rather than multiplication, of the cells, with selective cell death – except for the glial cells that support the neurons metabolically. Cells tend to slowly die until old age when the brain has lost up to roughly one third of its neurons.

This should immediately suggest something very important about the nerve cells and their functions, such as remembering and making computations, comparing the past with the present and coming to a coordinated decision with the future "in mind". Cells with such functions cannot continually be in the process of duplicating themselves; they must be stable and permanent for other purposes. The growth of the brain, then, both in the ontogenetic and evolutionary senses, depends on at least two important aspects of growth: (1) multiplica-

tion of units through mitotic division (hyperplasia) and (2) growth of the units themselves (hypertrophy).

The evolution of the human brain, say from the Australopithecine hominids of about three million years ago to modern man, certainly involved changes in these two aspects of growth, as well as reorganization of the brain at large. In general, the trend must have been to prolong both periods of growth, hyperplasia and hypertrophy, thus underlining the importance of social adaptations that permitted a longer period of development for the brain.

The fossil record allows only a few morphological characteristics of the brain to be examined in evolutionary context with any certitude. They are: (1) size, or cranial capacity, that is, the number of ml or cm^3 of space filling the cranium; (2) significant asymmetry of the once underlying cerebral hemispheres; (3) detectable cortical convolutional patterns, suggesting a human rather than ape pattern. This refers to the infamous lunate sulcus or "affenspalte," which in pongids separates primary visual striate cortex from parietal "association" cortex. It is always more anteriorally located in non-human primate brains than in humans (and hominids).

The first parameter, size, tells us nothing about the reorganizational changes that must have occurred in the course of human evolution during the Pleistocene. The interconnections of many systems within the brain, such as the overlying mantle of gray matter, the cerebral cortex, and underlying nuclei systems, such as the reticular formation and thalamus (involved in attention and perception), or the hypothalamus, septum, and limbic system (associated with memory, emotions and vital functions), cannot be understood from the fossil endocasts of the interior of the cranium. Comparative neuroanatomy, or the study of other primate brains, can only give broad hints of what might have occurred, since the living forms are, so to speak, "end products" rather than actual stages in human development.

The surface features of the fossil endocasts are not reliable guides (at the present time) to the reorganization of the cerebral cortex, since in life these are covered by no less than three tissues (the meninges) and various amounts of cerebrospinal fluid [10]. Only very broad changes can be seen, and those dimly, such as the expansion of "association cortex", the reduction of visual primary cortex, etc.

The fossil record shows that with the arrival of *Homo erectus* (roughly one million years ago) and possibly with the antecedant Australopithecines, there emerged a new activity, characterized by the appearance of stone tools made to standardized patterns, and an increasingly omnivorous diet (providing greater amounts of protein-rich nourishment for a longer-growing, and thus longer-dependent animal), implying, in turn, significant changes in social behavioral patterns associated with subsistence.

From the Australopithecines to the modern period, there was almost a three-fold increase in brain size. But there is no evidence of any really significant qualitative behavioral change, in terms of cognition or social behavior, from the fossil record up to the last glaciation, ten to fifteen thousand years ago, unless we wish to include carvings and cave paintings as such. The fossil record does suggest a continuous, gradual evolution of both brain size and cultural complexity.

The question of cerebral asymmetries in hominid ancestors is a fascinating one, as is indeed the larger problem of hemispheric specialization, handedness and cognitive processes, e.g., symbol-manipulation and visuospatial integration. It would be well beyond the scope of this paper to elaborate on these issues, but it can be mentioned that the fossil hominid endocasts, from *Australopithecus* on, do show a typical *Homo* pattern of left-occipital, right-frontal petalial asymmetry, which has been strongly correlated with right-handedness in modern humans. It is the strong

combination of the two asymmetries which is striking both in modern *Homo* and in the fossil hominids. In part, asymmetries do appear in pongid examples, particularly *Gorilla gorilla*, but these are almost always confined to a left-occipital petalia, and not to greater right-frontal width, or left-occipito–parietal width.

It is no accident that these manifestations appear concurrently with the making of standardized forms of stone tools, living, camping and butchery sites (particularly in Africa and Europe), a more catholic subsistence pattern (hunting and gathering), and widespread spatial movements of hominid groups.

The trend of a correlative increase in brain size and cultural complexity in the evolutionary dynamic has often been noted. The most frequently encountered explanation for this trend is that "culture" and "biology" interacted to increase brain size and that the increase was adaptive [11]. Some have related this increase to better memories, others to language processes such as "object-naming", etc.

Obviously, the size of the brain increased because it was adaptive, and certainly many behavioral processes were involved, including memory and language. But at the expense of such platitudinous parsimony, we should try to understand how this happened and how it reticulated with other evolutionary changes, particularly those involving social behavior. Accordingly, the related variables of brain and environmental complexity need to be discussed more fully. It should become apparent that the parsimonious explanations cannot adequately grasp the human evolutionary process. They are incorrect because such explanations postulate brain evolution as a terminal phase in human mosaic evolution, following on other changes – notably, the hands, pelvis, feet and teeth.

Above all, it is necessary to realise the current lack of knowledge concerning the evolution of the brain. The brain is a tremendously complex organ, with over ten million parts, if nerve cells in the cortex alone are counted. Underneath the cortex are a very large number of groups of nerve cells, called nuclei, which have nerve fiber connections with each other as well as with the cortex. It is not possible to localize function (or behavior) to any one particular area exclusively. One can only say at the present time that certain nuclei and fiber tracks are *involved in* or *mediate* this or that behavior. The brain functions as a unit, a symphony of thousands of interdependent actions among its parts.

The differences in behavior among animals, even those closely related, must depend on the diverse interactions among neural systems in their brains. We are all familiar with the fact that Siamese cats behave somewhat differently from alley cats, or that different breeds of dogs have varying temperamental profiles. The problem is two-fold: (1) what is specifically divergent in the behavior patterns of a chimpanzee and gorilla, for example, and (2) how do these differences relate to neural organization?

It is not a question of adding new and different parts – the basic structures are the same in all primates, although there are quantitative and, perhaps, qualitative distinctions. When we speak of the brain being reorganized through evolution, we are really talking about changes of interaction among parts of the brain. The increase in quantity of the parts and their interactions transform the total output of the brain – its behavior. Furthermore, development of the brain (of any animal) is not confined to a uterine environment, but is also a function of the outside, social and material world. When and how various neural systems develop and mature through interaction and transaction with a material, social and nurturant milieu is one of the most important questions facing neurobiologists today [12].

Inspection of the fossil record shows the bony remains of animals that had nervous systems responsible for their particular behavioral patterns, but nothing precise can be

said about the internal organization of their brains. The point is, of course, that when different bony patterns are seen, varying patterns of musculoskeletal action are also seen. A different pattern of musculoskeletal elements, such as in bipedalism, or in tool-making, makes it apparent that the nervous organizations implementing these patterns differed from those of other anatomical bony configurations. Similarly, when we find evidence for behavioral action that suggests a certain cognitive structure, as in the case of stone tools made to a standard pattern, we must assume that the brains behind these actions were *different* in some way(s) from other animals, *whether their size was the same or not.* Thus, when we find that the Australopithecines had a pelvic structure more like that of *Homo* than apes, or stone tools associated with their remains, or faunal evidence related to hunting or scavenging, or pieces of hand skeleton showing advances over apes in the human direction, we can be certain that their brains were also different, whatever their size.

It is an oversimplification to claim, on the basis of brain size, that behavior comes first, then structure. Obviously, behavior is the link between structure and natural selection. An animal will be successful according to what it does and how well it does it, measuring success, of course, by the continuation of the species.

It should be equally obvious, however, that how well it does will depend on the effectiveness of the structures underlying its behavior; if there are no structural bases for its behavioral effectiveness in comparison to other members of the population, there is nothing for natural selection to act upon. The task of the physical anthropologist is to understand the linkages among behavior, bodily structure (morphology) and adaptation. To do this, the physiological and anatomical significance of the bony patterns of both present and fossil organisms must be understood within the framework of genetic and evolutionary theory. This applies particularly to the brain. It cannot be said that it evolved first or last simply on the basis of its outward size, but it is certain that it evolved concurrently with all other anatomical systems.

DIALECTICAL PROCESS

A more specific and technical term for this process in physical anthropological literature is "deviation-amplification", described by Maruyama [13] as:

> ... all processes loosely termed as "vicious cycles" and compound interests; in short, all processes of mutual-causal relationship that amplify an insignificant or accidental initial-kick, build up deviation and diverge from the initial condition.

Evolution is continual change, where the differences between ancestral and present forms have come about through natural selection. This, of course, recalls the concept of negative feedback, or homeostasis, where a system tends to maintain some property or variable in a constant state or within definite limits. The governor on a car, or the thermostat in a heating system, or the production of sweat when the body exceeds a certain temperature are all examples of homeostatic devices operating by negative feedbacks. That is, the output of one component in a system tends to cause a decrease somewhere else in the system until that component becomes sensitive to the change and implements a complementary change so that the system continues.

Positive feedback, or deviation-amplification, is the obverse of this kind of process, since there is no self-correcting device or component to limit the activity of the system. A good example might be the accumulation of money through compound interest in a bank account. Naturally, there are limits to positive feedback. There is only so much money available in spite of theory; the growth of the brain through time is restricted by metabolic require-

ments for mitosis and hypertrophy, or by the size of the pelvic canal in the mother through which the fetal head and brain must pass during birth.

There is, then, no positive feedback cycle that can go on forever, unchecked by homeostasis. Positive feedback among variables means that they are involved in interactions whereby a change in one variable produces a change in a second variable and this in turn increases the original change, and so on, back and forth until other factors constrict or terminate this interaction, and a homeostatic synthesis is reached.

It should be clear that such a relationship may be a useful model for explaining the change in the two main variables of environmental and brain complexity, and each of these will be considered in turn. First, two points should be noted: (a) because of language and its productivity – the ability to say things that have never been said before – and arbitrary symbols, human behavior is a relatively open system capable of creating new and different constructs at rates well above the replication of genetic instructions; and (b) given the human communication system, traditional transmission and material artifacts, the so-called "rapid-fading" quality of purely vocal communication is counteracted [14]. These two points are critical in understanding how human behavior and its constructions can increase environmental complexity through positive feedback.

ENVIRONMENTAL COMPLEXITY

The environment provides the stimuli among which an animal must discriminate and to which it must selectively respond. Environmental complexity may be said to increase for an animal as these stimuli configurations or sets become more numerous and complex. The archaeological record of early man provides evidence for at least three indicators of complexity: stone tool assemblages, living sites, and a plurality of animal and plant remains associated with tools and shelters. This differentiation suggests an increasing complexity of hominid perception and attendance to selective parts of the environment. These indicate, in turn, that there was an increase in the complexity and plurality of social relationships within, and perhaps among, hominid groups.

Passing from the Lower to Upper Palaeolithic, the tool assemblages contain more items, and each is a result of a more complex process of production. Of course, we have no precise knowledge of the exact uses of the various tools, but it is assumed that since increasing numbers and kinds of animal remains are associated with them, they served an expanding number of functions. Aside from noting these material factors, we must also ask how the techniques were learned, and whether they suggest an increase in social interaction and the codes for passing on such skills. We should never forget that much can be learned purely through watching and imitation.

It is assumed that the tools and the supporting apparatus of social rules and symbolic codes were, in a gross sense, adaptive, and thus the more obvious aspects of external environments that had to be perceived throughout hominid evolution must also be considered. In terms of energy alone, environments may stay constant, or nearly so; but they shrink or expand *depending on the organisms' awareness of them.* Weather, soil, rock, water sources, game spoors, animal (prey and predator) behavioral habits, seasonal variations, animal anatomy, etc. add to environmental complexity as the awareness and utilization of each contributes to positive selection for their being perceived. The increasing complexity of stone tool types, the proliferation of assemblages and the plurality of animal remains in different archaeological contexts all lead us to assume an expansion of external environmental complexity for the hominids. *Awareness* of relationships expanded; the hominids became better and better at the ecological game.

For the time being, it is convenient here to think of stone tools *as environments* in addition to the usual view of these objects as a means of coping with the environment. This point is suggested because the stone tools in a sense represent fossilized behavior: they "tell" us something about the perceptual, cognitive, and motor actions of their past makers. They suggest certain relationships and attributes that must have been important considerations to their past makers, for otherwise the makers would not have bothered to standardize their actions, and it would not be possible to recognize patterns of actions in the stone tools.

It should be obvious from the quantified studies summarized below that as hominids and their tools evolved, they spent more time at the task, were more skillful with their hands, and made tools with greater economy of design, as, for example, in the length of cutting edge per tool. Since many (but not all) of the various tools are highly standardized (as reflected in the archaeologists' recognition and naming of them), they suggest that social behavioral adaptations were of a sophisticated nature, involving symbolic communication and learning of arbitrary standards. There is thus heuristic value in regarding stone tools as environments in so far as they enable us to think about the selection pressures associated with the total range of actions (perceptual–cognitive–motor tasks, imitation, learning, cultural transmission of arbitrary form, etc.) involved in tool-making.

As the stone tools increased in complexity, so did the challenges to the hominids making them. Leroi-Gourhan [15] tried to arrive at a scheme for quantifying stone tool complexity by measuring the length of cutting edge in a kg of rock for different types of tools. An Oldowan pebble tool, for example, yielded roughly 40 cm of cutting edge. These are the tools found associated with the Australopithecines and *Homo habilis* fossils, particularly from East Africa. Chellean/Acheulean hand-axes provided about 60–100 cm of cutting edge, and the Acheulean gave about 100–120 cm. These two types are often associated with *Homo erectus* fossils. Mousterian and Levallois flakes can provide about four meters (400 cm), and blade tools like those of the Upper Palaeolithic (Aurignacian, Solutrean, etc.) yield about 10+ m of cutting edge [16].

Similarly, there is an increase in the number of tool types made on both core and flakes throughout the Pleistocene. Leroi-Gourhan suggests a progression from one type at the Australopithecine level to about twenty-five types in the Upper Palaeolithic. Of course, the number of types categorized at any particular time level depends both on excavation and the conceptions of the investigator; such numbers as given above should be accepted only as approximations. Surely, there is good evidence that the stone tool types at Olduvai and elsewhere number more than one?

Semenov [17] made a study of the work involved in making different kinds of stone tools. Oldwan pebbles suggest no more than three or four blows with a hammerstone; the Chellean hand-axes can be made with about twenty to thirty-five blows; the Acheulean with about sixty to seventy-five, involving two kinds of operation – roughing out by hammerstone and finishing with a bone or wooden baton. A Mousterian point involved more time and energy. Perhaps as many as four operations were involved in reducing the flake from a small core or large flake. The number of blows has been estimated at close to one hundred. A blade tool may have involved from one hundred to three hundred and fifty percussions.

The challenges to hominids as the stone tools increased in complexity clearly involved more than the hand. They also required perceptual actions in selecting different attributes of the tool to pay attention to, finer and finer degrees of proprioception, and increasing length of concentration and span of attention at the task.

How much of this increase in skills, which

must have involved learning and thus social skills, can be explained by simple expansion of the brain is impossible to answer, but such processes surely involved many regions of the brain (hence, the concern with hemispheric asymmetry in hominid brain endocasts [18]. Certainly, a considerable degree of skill can be gained through learning and practice without having the brain increase in size (perhaps it increases in complexity or "programming"). From Neanderthals to modern *Homo sapiens* there has been no known increase in cranial capacity or significant change in the brain, yet the complexity of the material (and consequently social) culture grew precipitously. Progressing from an Oldowan pebble tool to that of a Mousterian point involved perhaps as much as two to three million years, and the respective makers show a growth in cranial capacity amounting to about 900–1000 cm^3, which is, incidentally, the total range of variation of cranial capacity in normal modern *Homo sapiens.*

It would be a gross simplification, if not an outright mistake, to relate cranial capacity in any linear or causal sense to the advancing complexity of stone tools during the Pleistocene. After all, the hominids' brains accomplished more than simply making stone tools for the future archaeologists' digs. The tools were used in different environments, and cooperative social behavior was also basic in formulating and facing the rigors of a hunting and gathering existence. Hunting is a complex organization and sequence of acts, requiring not only perceptual and motor skills, but intelligent learning of the surrounding plants and animals, terrains, spoors, tracks, habits of prey, seasonal effects on these, anatomy, butchering techniques, and perhaps storage.

It is the total range of cultural acitivities that must relate to brain increase, and the complexity of stone tools relates only partly to that whole. To the extent that the hunting of large animals involved cooperative enterprise, selection would certainly have favored structures which facilitated the increasing symbolization of language, and this would have meant an increasing complexity of social interaction, involving cues from social and material environments along with control and inhibition of immediate responses. In short, the accelerating complexity of stone tools reflects these other variables, but we cannot make more than educated guesses about the ecological complexity involved in the selection pressures for human biosocial constructions.

COMPLEXITY OF NEURAL STRUCTURE

It is only possible to mention certain aspects of brain structure which seem to have changed during hominid evolution. The major expansion undoubtedly affected the cerebral cortex. This does not mean that other parts of the brain did not change during hominid evolution, but rather that such changes are not visible from the fossil endocasts. The major portion of expansion in the cerebral cortex has involved five main variables: (1) nerve cell size; (2) the distance between nerve cells (neuron density); (3) the amount of branching of the nerve cells (dendrites), resulting in more connections or synapses; and (4) the ratio of supporting glial cells to the neurons (the glial/neural ratio). In addition, there has been (5) an increase in the basic number of cells, but there is reason to doubt that it was as large as has been claimed. Rather, the four increments noted above probably account for the major part of brain expansion. Finally, there has also been an expansion of so-called "association" areas of the cortex, and changes in cerebral asymmetry, which have been important to the evolution of language, handedness, and skill.

Three kinds of data from brain studies are significant here: (*1*) phylogenetic; that is, comparative studies of contemporary animals, particularly primates; (*2*) ontogenetic, or how the brain changes during growth and the effects on behavior; (*3*) experimental (e.g., with rats),

where the brain structure is altered and the effects on behavior analyzed, or the environment is changed and the effects on both brain structure and behavior are examined. There is also the direct study of fossilized brains, or palaeoneurology. In studies (*1*) and (*2*), there is a concordance among the increases in the five variables mentioned above, which seems to hold for mammals in general, as well as for human beings [19].

There are two experimental sets of evidence that are commensurate with the above rat experiments which may be worth mentioning. One set manipulates the hormonal condition of the animal, the other manipulates the "psychological" environment of the animal. In the first case, removal of the thyroid gland in rats at a particular stage will cause a decrease in all the above four brain variables and a loss in the efficiency of problem-solving behavior. These effects can be reversed with the administration of thyroxin. On the other hand, if growth hormone is applied to pregnant rats, the offspring, in comparison with control cases, will show an increase in the variables as well as behavioral scores.

The second set involves enriching the environment in which rats are raised by providing them with toys, handling them, and introducing communal living arrangements, as compared to their litter-mate controls raised in isolation. A number of studies show that there is a resulting increase in the four neural variables.

If brain size during hominid evolution is considered, it can be appreciated that part of the reorganizational change has been in the direction of the spatial geometric relations discussed above. Thus, the three-to-four fold increment in brain size is not really paralleled by a four-fold increase in neural units, but by augmentations in the variables outlined. It is the growth of the units themselves that has accelerated the number of switching points, or synapses, in the cortex.

These variables should be more useful than cranial capacity for consideration, since the experimental evidence relates in a general way to differences in problem-solving ability, whereas the variations in cranial capacity for modern man, at least, do not. To discuss small changes in cranial capacity as adaptive would be meaningless, even if variability and populations were the units for statistical manipulation.

The foci for natural selection were the glandular (hormonal) and developmental processes that resulted in greater degrees of complexity-management at the level of neuron size, density, dendritic branching, glial–neural interaction, and other possible subcortical and neurochemical changes. *The outward manifestation of these changes was a 1000 ml increase in cranial capacity.* It is consistent with this that present-day biological variation in cranial capacity has no demonstrated behavioral significance. This should underline the fact that the variables discussed in this paper are pertinent in reference to long-term evolutionary change, and that the relationship between increased neural and artifactual complexity is better seen in terms of these variables than cranial capacity per se.

The interacting process by which each of these two complex sets affected the other was through deviation-amplification, as discussed above. But having made an argument for this interaction, one is still left with the task of understanding the nature of the "initial kick" [20] which might have set the process off.

THE INITIAL KICK: A BEGINNING SYNTHESIS

Of course, human evolution has not only been a matter of brain and cultural enlargement, regardless of the importance of these variables and their interaction. Thus far we have considered that early hominids advanced enough to allow a dialectical interaction to take place among a few variables. The further back in time we go, the more difficult it becomes to identify processes of interacting variables, or to find empirical support for something like

"efficiency of bipedalism", "permanent receptivity of the female", or sexual dimorphism in secondary sexual characteristics that were important for either signalling sexual status or attractiveness. Consequently, the level of speculation necessarily increases, and one must be satisfied with merely outlining some of the other variables that were probably important in human evolution and that led to the concurrent increase in brain and cultural complexity.

Probably, *social behavioral patterns* were the major focal point for natural selection during earliest hominid evolution, i.e., the "initial kick". This can be defined as a transition made to a type of social ordering based on different components of aggressive control within small groups. This type of social ordering would have included the following phenomena: sexual division of labor in the food quest, cooperative sharing between and among sexes and social nurturing of offspring; decreased sexual dimorphism in size, but increased dimorphism in so-called epigamic structure (related to sexual signalling) such as the permanently enlarged breast, fat and hair distribution*; raised threshold to aggression within primary groups; permanent sexual receptivity of the female and male; and a new way of transferring information about the environment, through language and gesture.

The basic shift was possibly related to a change in endocrine–target relationships; as aggression and sexual dimorphism were effected so were prolonged periods of gestation, growth, and offspring dependency. Furthermore, it is most probable that these changes were brought about more at the level of regulatory, rather than structural, DNA. It should not be understood that this was necessarily a sudden, overnight, quantum leap into a new realm; it could well have taken several million years to accumulate, but once it reached a critical threshold, it led to a strong positive feedback among the variables we have discussed, probably between *Ramapithecus* from twelve to fourteen million years ago and *Australopithecus,* about three to five million years ago. Let us examine these variables more carefully.

*I stress these secondary sexual characteristics as *clues*, not *fates*. Their precise function, as well as traits that could be mentioned for men, are not precisely known. The female breast as an epigamic signalling device has always struck me as a weak argument, since I prefer to regard the human female breast as an enlarged zone of warm, soft, surface area that is nurturant and comforting to young offspring. Both aspects may have played an important evolutionary role.

1. Arbitrary Symbols – Cognition and Social Authority

The use of arbitrary symbols can be seen in at least two ways: (a) They facilitate molding of the environment to suit the needs of their users by defining, and keeping salient certain important features as distinct from others. Communication about the environment, and the emotional states and intentions of social actors, were obviously of profound significance. Symbol systems were the vehicles for cognition, particularly foresight, memory, abstraction and prediction, each based on abstracting out essential properties while ignoring idiosyncratic variation, and utilizing information more efficiently. (b) Symbols signify that social *clues* are operative and can exist outside of any strictly biological framework; that is, authority and labor can be allocated.

The development of the symbolizing faculty was the basic social phenomenon engendering more cooperative social behavior by ultimately transforming aggressive tendencies. G.H. Mead's [21] "significant symbol" meant that it was possible to "take the role of other" and thus forecast the likely sanctions coming to one's self for acts destructive of the group.

Symbols, of course, can only be learned in a social context; this takes time, and also requires social facilitation between mother and offspring, and analogous pairings. The appearance of stone tools made to a standardized pattern with the Australopithecines or the

earliest cadres of *Homo* suggest that such processes were developing by that time, although the stone tools hardly prove such an assertion. The brain casts of the fossils are likewise inadequate to the problem, but are supportive. There is nothing that one can deduce from the surface details that would immediately rule out language capacity, and size alone is a particularly poor parameter to use. A better understanding of the psychological structuring involved in tool making and of what we mean by symbolization is imperative.

2. Sexual Dimorphism

Along with these developments, there was probably both reduction and increase in sexual dimorphism; that is, the anatomical, physiological, and marginal behavior differences between males and females. One imparative in this context was a changing interaction between the endocrine glands and target tissues responsive to endocrine secretions.

The reduction aspect involved mainly size differential, that is, of the body and even, possibly, of the canines. Almost all terrestrial primates except humans are noted for their considerable sexual dimorphism, including their canines. By Australopithecene times, the canines are reduced in both sexes, the difference being about six percent, in contrast with fifty percent in other terrestrial primates.

The field studies of many different primate species also give the impression that aggressive behavior is more likely to be expressed by terrestrial primates than arboreal species, but much more data is needed before this speculation can be accepted.

Of course, there are many problems attendant on interpreting the significance of sexual dimorphism in social construction. One school of thought contends its main function relates to predator pressure; so the larger male can more effectively defend the group against carnivorous predators [22]. It is also possible, (and I favor this explanation), that sexual dimorphism is more immediately related to intra-group behavior, aggressiveness, dominance, and accessibility to mating advantages.

It is certainly recognized that cohesiveness of troop or group structures is a positive advantage in an environment like the savanna, where carnivores are readily present. Estes' [23] studies on how the prey (ungulates) can effectively inhibit the advance of carnivores simply by facing them is an interesting example of the adaptiveness of group structure *without utilization of defensive anatomical equipment,* such as powerful canines. However, there is no necessary reason to view the problem in either–or terms. Both processes were of equal importance in eventually leading to genetic changes of structure and behavior. Cooperative behavior could have been a more effective way of dealing with so-called predator pressure than long canines or small pebbles of stone.

The increases in sexual dimorphism of features of the body related to signalling sexual status cannot be gleaned from the fossil record. From looking at ourselves, our hominid precursors are imagined as possibly something like a generalized hominoid, most often as something like a chimpanzee. It must be concluded that during early hominid (or even later) evolution, changes had to take place, inclusive of permanently enlarged breasts, differences in shape of the body related both to bone structure and fat deposition and differences in the patterns and distribution of hair. These are secondary sexual characteristics, and their relationship to endocrines, particularly the steroids, such as testosterone and estrogen, are unmistakable. Here there are rich possibilities for speculation, and many books have already been written about the meaning and evolution of dimorphism. They must surely have had some important function in changing the psychosocial relationships between the sexes, probably related to the formation of more permanent pairing.

Another aspect of sexual dimorphism is,

of course, the sexual receptivity of the human female. In all monkeys and apes described so far, the female will receive the male only during a fairly brief span of time. The receptivity is intricately but not totally related to hormonal events, and it is often paralleled by quite visible changes in the tissues of the anogenital region, involving swelling, reddening, the production of secretions that act as pheromones to the male's sense of smell, and also behavioral changes usually including increased aggressiveness and more active solicitation for male sexual advances.

This sexually receptive estrus period occurs in cycles varying for each species and in some cases appears to be related to external environmental conditions. There are even a number of published reports on male sexual cycles related to spermatogenesis and activity of the testicles. For the remaining time, when the female is pregnant or lactating, she is not normally receptive. This loss of estrus and development of a relatively constant receptivity in human females was a matter of endocrine reorganization, naturally involving more than hormones and (probable) psychological changes. Perhaps pair-bonding was one context in which this occurred.

Such changes would have been bound up with a shift in the nature of affective ties between the sexes that would have been important in providing more permanent social nourishment to the longer-dependent offspring – a development, incidentally, which is coherent with increased brain development in the Australopithecines as measured by both absolute and relative brain size.

3. Prolongation of Growth and Dependency

While the Australopithecines certainly had small brains, these were larger, both relatively and absolutely, than those of chimpanzees, which probably have similar body weights. From chimpanzee or gorilla to humans, there is a significant difference in maturation time and prolongation of growth. By 9–11 years, the process is complete in a chimpanzee, whereas it takes about 20–25 years for humans.

We cannot yet look at the fossil record and say when a certain fossil became fully adult and in how many years, but we must assume that growth rates and durations have changed over the course of human evolution. A large brain cannot evolve without a prolonged growth for the organ. Growth is a complex process involving interplay between genetic instructions for the locus and timing of growth, tissues and hormonal environment (growth hormone, thyroxin, and androgens), and proper nourishment, both of food and social interaction.

One of the organs most vulnerable to malnourishment is the growing brain, particularly during its period of mitotic division and enlargement of nerve cells.

As the brain increases in size in the fossil record, there are also the first intimations of the use of protein-rich foods, i.e., animal flesh. It seems inescapable that there was a close relationship between hunting and gathering and the evolution of the brain, mediated through longer periods of growth and infant dependence. The challenge, of course, is to find ways of providing it from the fossil record.

Thus, the "initial kick" was a complex reticulation of anatomical, physiological, and behavioral changes, which also related to bipedalism (securing protein-rich sources by scavenging and/or hunting), the hand, stone tools and the brain. It is, however, impossible to set down this reticulation in any linear sequence or simple concatenation of events [24].

TOWARDS A SYNTHESIS

As the stone tools became more complex, varied, and more finely fashioned, the animal associations in the living sites suggest that more reliance was placed on hunting as an economic and social activity. The processes active during the Australopithecene phase of hominid evolu-

tion continued to intermesh, the results being modern *Homo sapiens* of the Upper Pleistocene and an increase in the biosocial grounding of human life. Greater effectiveness in hunting, scavenging, travelling to new areas for water, game and plants, would have placed natural selective demands on the locomotor apparatus: legs, pelvis and feet. By the time of *Homo erectus* in Java and East Africa, these changes were essentially complete: they were certainly well-advanced in *Australopithecus,* as the Leaky footprints from Laetoli in Tanzania demonstrate.

Increased effectiveness in differentiating out from the surrounding environment those features important to survival and social construction, such as suitable rock materials for tools of different kinds and purposes, habits and tracks and spoors of game and possible predators, sites suitable for camping, water and food supplies (including vegetable sources), would have encouraged larger brains, increased communicative skills, which in turn required not only larger and better brains, but more effective and affective social nourishment for the transmission of culture in the making.

Furthermore, prolonged growth and dependency go along with larger brains and longer periods of learning. I have characterized this interplay of structures and environmental vectors as "complexity-management", suggesting that it was largely a matter of degree following the more "qualitative" changes associated with the "initial kick", and explainable by the kinds of brain evidence discussed under "Brain Complexity".

Consequently, in this framework, the stone tools are *not* regarded as the most significant aspect of hominid emergence, nor is toolmaking per se viewed as the most important focus of natural selection, resulting in larger and larger brains during the Pleistocene. The significance of stone tools is in the clues that they give concerning the *total biosocial emergence* of their makers. Another way of putting this is that tools do not "makyth" man, but symbolic communication does, and men "makyth" tools only in the context of their ever-increasing awareness of their environment, a matter dependent upon symbol systems, social organization and brains.

CONCLUSIONS AND SUMMARY

1. The brain has always played an important role in human evolution, but if brain size alone is the single neural variable considered, we cannot understand either the richness, complexity, or challenges inherent in a theory of human evolution. The brain is not simply a terminal product in mosaic human evolution.

2. Brain size is only *one* phenotypic "window", as it were, which allows the investigation of the role of the brain in human evolution. Of equal, if not more importance, are other phenotypic "windows", on the brain such as its organizational (meaning the quantitative relationships among its parts) and its hierarchical development. This latter aspect refers to the species specific time-course of developmental, maturational, and social interactional and transactional patterns that shape the brain through natural selection.

3. One aspect of brain size increase during human evolution relates to the geometric changes that took place in the central cortex. That is, *one* of the manifestations of increased cell size, decreased neuron density, increased dendritic branching, and increased glial/neural ratios, was an increase in absolute brain size. These aspects, albeit imperfectly, reflect one manifestation of neural complexity. Greater relative brain size, reorganization of cerebral tissues (e.g., the ratio of "association" cortex to primary visual cortex), hemispheric lateralization, and cognitive competence in symbolling and visuo-spatial integration, represent another set of neural evolutionary changes in *Homo.*

4. While all animals may "learn" and perhaps even have "traditions," no other being organizes its experiences in arbitrary symbol

systems *imposed* by social groups, where there are non-iconic (arbitrary) relationships between the symbol(s) and referent. The power of this "new" language, integrated with "natural" neural "languages" is enormous, and escalates the complexity of social and material environments to which the human animal attends. Environments can be created through productivity and displacement. Culture is a human domain, if any definition of culture is to have meaning relative to the unique behavioral and cognitive patternings that typify the human being. It is impossible to understand the unique evolutionary past of our species without holistically integrating behavioral (cultural) and neural complexity, and the cognitive basis for both.

5. Stone tool-making patterns from the prehistoric past should be viewed as indices or clues to the totality of complex social behavior in the past, rather than as targets for natural selection in the limited sense of tools as extrasomatic adaptations. Camping, living, manufacturing and butchering sites should be similarly viewed. The challenge is to try to understand these activities as clues to how social experience was organized and transmitted. In this framework, such activities reflect cultural and cognitive complexity and not cultural evolution per se.

6. Prolonged dependency and growth periods must be integrated with the evolutionary changes in neural and cultural complexity. It is at this level that more molecular genetic changes, i.e., regulatory RNA, can be related to the more molar anthropologically-oriented evidence of the evolutionary past. Such changes in growth and dependency were probably dependent upon the development of affectional relationships between the sexes and members of social groups, which minimally increased the duration, if not intensity, of social, cooperative, nurturant relationships. Changes in sexual dimorphism, for example, which can only be inferred, are clues to those social relationships that set brain and behavioral complexity into a mutually-causal and interdependent evolutionary schema. The changes discussed above are the "initial kick" in that schema.

NOTES

1 It should be emphasized that this is not intended to be a full list of important components in human evolution, nor is any temporal order among these being implied here. These variables are only gross descriptive labels for complex processes that are commonly discussed. Indeed, one of the major challenges facing anthropologists is to formulate variables or units more appropriate to synthesis between genetic, evolutionary and adaptational levels.

2 As a caveat, one might say that the full evidence for certain sea mammals, such as whales and porpoises, as true language bearers, is not complete. There is always room for surprise. This statement stipulates "possession" of a language based on arbitrary symbols. Despite the ingenuity of some people in teaching "symbols" to chimpanzees, it remains a fact that we have not discovered them to possess a language based on arbitrary symbols.

3 This might also be called "extropy", the opposite of that thermodynamic term "entropy", which is the tendency to return to the most probable condition, randomness. Extropy, or structuredness, is a measurement of nonrandomness, or the measureable deviation from randomness. Symbol systems permit almost any degree of structuredness imaginable to the human mind.

4 This is not to deny that raw materials had or have constraining influences on the production of form. The point is that the human creature attempts, and often succeeds, in overcoming the constraints.

5 Ants, bees, and other animals also produce structure in their environments, building elaborate tunnels, hives, etc., but this is the result of inherited mechanisms that blindly follow out their proscribed course when given the necessary environmental stimuli. However, animals such as the "social" insects cannot produce new, arbitrary structures unless their genetic or developmental patterns change. To replicate whatever new structures do occur, instructions must be passed to the next generation at the *genetic* level.

6 Needless to say, opposing viewpoints may be found throughout the literature. For example, see Mundiger, P., "Animal cultures and a general theory of cultural evolution", *Ethology and Sociobiology*, I, (1980), pp. 183–223; John T. Bonner, *The Evolution of Culture in Animals* (Princeton: Princeton University Press, 1980).

7 Earlier discussions of this framework may be found in R.L. Holloway, "Culture: a human domain", *Current Anthropology*, 4 (1969), pp. 135–168, and "Human aggression: the need for a species-specific theory framework", in *The Anthropology of Armed Conflict and Aggression*, edited by M. Fried, M. Harris, and R. Murphy (NY: National History Press, 1968), pp. 28–48. More recently, I define culture "... as that biosocial evolutionarily-derived

and socially-sustained ability, possessed only by human beings as members of societies, which organize experiences in a blend of both arbitrary and iconic symbol representations. These representations can be imposed by any level or unit of a human social structure, including the individual." Obviously, as I had pointed out in the above papers, in footnotes, not everything the human animal does is arbitrary (non-iconic) or mediated by such symbols.

8 See for example, J.H. Hill, "On the evolutionary foundations of language", *American Athropologist*, 74, (1972) pp. 308–317, who regards this a very "infelicitous" choice. Neurophysiologically, the hand and mouth areas on motor cortex are very close together, which proves nothing, but should give pause to thought.

9 More extended discussions of this topic may be found in some of my earlier papers: "The evolution of the human brain: some notes toward a synthesis between neural structure and the evolution of complex behavior", *General Systems*, 12, (1967), pp. 3–19; "Some questions on parameters of neural evolution on primates", *Annals New York Academy of Science*, 167, (1969), pp. 332–340; "The role of human social behavior in the evolution of the brain", 43rd James Arthur Lecture (1973) (New York: New York American Museum of Natural History, 1975).

10 For a fuller discussion of endocasts, see R.L. Holloway, "The relevance of endocasts for studying primate brain evolution", in C.R. Noback, editor, *Sensory Systems in Primates* (New York: Plenum Publishing Company, 1978), pp. 181–200.

11 If this sounds circular, it is. But if feedback relationships did exist between brains, behavior and adaptation, circularity may not be an incorrect summation.

12 I have attempted to offer a synthesis between size, allometry, reorganization, and hierarchy elsewhere. See R.L. Holloway, "Brain size, allometry, and reorganization: toward a synthesis", in M.E. Hahn, C. Jensen, B.C. Dudek, editors, *Development and Evolution of Brain Size: Behavioral Implications* (New York: Academic Press, 1979), pp. 59–88.

13 M. Maruyama, "The second cybernetics: deviation-amplification, mutual-causal processes", *American Scientist*, 51, (1963), pp. 164–179.

14 See, for example, C.F. Hockett and S.A. Altmann, "A note on design features", in T.A. Sebeok, editor, *Animal Communication: Techniques of Study and Results of Research*, (Bloomington: Indiana University Press, 1968).

15 Leroi-Gourhan, A., *La Geste et La Parole, I, Technique et Langage*. (Paris: Editions Albin Michael).

16 I hope it is obvious that I am talking only about certain "classical" tool types, and am perfectly aware that other types existed, and that in fact many stone tools were not made to some standardized pattern, e.g., many flakes, cores, scrapers, etc. This does not change the basic fact that some tools were made to standardized patterns, and those patterns were transmitted through time and space.

17 S.A. Semenov, *Prehistoric Technology*, (New York: Barnes and Noble.)

18 Modern right-handed *Homo sapiens* show a strong pattern of asymmetries of cerebral cortices upon gross examination: a left occipital petalia (or extension) posteriorly and laterally, and a right frontal petalia laterally. This *combination* is not seen in apes, but is common in hominid endocasts, including *Australopithecus*. The significance of this is very important both in terms of brain organization, cognition, and motor skills, and in relationship to theories of a gestural origin to language (e.g. G. Hewes, "Primate communication and the gestural origin of language", *Current Antropology*, 14 (1973), pp. 5–24). I sincerely doubt that a gestural language could have been developed with such laterality, unless *Australopithecus* was only gesturing with one hand.

19 Some of these relationships were reviewed in R.L. Holloway, "Cranial capacity, neural reorganization and hominid evolution: a search for more suitable parameters", *American Anthropologist* 68 (1966), pp. 103–121; also, "The evolution of the primate brain: some aspects of quantitative relationships", *Brain Research*, 7 (1968), pp. 121–172. See also notes [9] and [12].

20 This term was introduced by Maruyama. See note [13].

21 G.H. Mead, *Mind, Self, Society*. (Chicago: University of Chicago Press, 1934).

22 Actually, evidence for any large-scale carnivore predation against primates from published field studies is very meager, and in my opinion has always been overstated in the primate literature.

23 R.D. Estes, "Predators and scavengers", *Natural History*, 76 (1967), pp. 20–29.

24 cf. T.D. White, "Evolutionary implications of Pliocene hominid footprints", *Science*, 208 (1980), pp. 175–176; H.M. McHenry, "Fossils and the mosaic theory of human evolution", *Science*, 190 (1975), pp. 425–431. Both of these authors claim a terminal role for brain evolution according to their understanding of "mosaic human evolution", which tends to place evolutionary events in a linear single-item sequence. Again, brain size and brain structure need not be the same thing.

25 See K.P. Oakley, "Tools makyth man", *Antiquity*, 31 (1957), pp. 199–209.

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