GENERAL SYSTEMS
Volume XII, 1967

THE EVOLUTION OF THE HUMAN BRAIN: SOME NOTES TOWARD A SYNTHESIS BETWEEN NEURAL STRUCTURE AND THE EVOLUTION OF COMPLEX BEHAVIOR[1]

Ralph L. Holloway, Jr.

INTRODUCTION, SCOPE, AND LIMITATIONS

In this essay I shall discuss the evolution of brain and behavior in terms of several interrelated variables. The discussion will be limited to the problem of increasing behavioral complexity; it will not deal with the more difficult problem of the emergence of qualitatively new characteristics. The framework will incorporate the following variables: (1) individual variability; (2) positive feedback and the amplification of deviation; (3) environmental complexity; (4) complexity of neural structure; (5) redundancy in both neural and behavioral organization. These variables are viewed as mutually-causally interrelated with positive feedback from one to the other, such that orthoselection for increasing behavioral and neural complexity has taken place. Finally, I will examine early hominid evolution as a set of social adaptations which served as stimuli or structures leading to the above interacting variables. Following Maruyama's (1963) usage, this set will be referred to as the "initial kick" in the amplification of deviation.

As thus stated, this article is a synthesis of variables related to the evolution of brain and behavior during hominid evolution. The article is a continuation of the common quest in Anthropology to understand how "man makes himself," and also to offer some speculations as to how "man made himself." Considerable progress in this quest has been made by numerous students concerned with the interlocking of cultural and biological factors in the course of human evolution (Coon 1953, Tappan 1953, Spuhler 1959, Washburn 1960, Caspari 1961, Garn 1963, Hockett and Ascher 1964).

In a general sense, the five variables listed above reflect a number of variables which I feel have been somewhat neglected in previous attempts to outline human evolution. These variables are not my invention, but are being elaborated in this essay because more attention should be given to them by students of human evolution. Thus the model offered in this paper is not providing any unique framework, nor is it intended to necessarily replace others; the purpose is rather to synthesize aspects of hominid adaptation with brain structure at some level more meaningful than cranial capacity. To do this, I think it is necessary to stress positive feedback factors between behavior and structure, rather than elaborate upon the essentially homeostatic or negative feedback features which in part characterize both biological and social structures. In addition, it is necessary to more fully appreciate the significance of environments and their complexity since these have been fashioned by brains and have structured further evolution of that organ. For this purpose, I feel that some discussion of individual variability as an aspect of the environment is necessary. Dobzhansky (1962) has underlined the value of plasticity in both genetic and behavioral terms. Primate field studies (see DeVore's 1965 volume, for example) have brought to the attention of many students that adaptation depends on behavioral factors and their integration within the group. Such studies have shown that behavioral variability is great between different group members. Here I will elaborate on this aspect of environment, i.e., individual variability, as both a structure and process, and attempt to integrate this aspect with brain structure and selection pressures.

Before proceeding with the synthesis, it is essential to indicate certain limitations of this framework and outline some of the assumptions under which synthesis is being attempted. I have deliberately chosen the above title to emphasize the incomplete and selective orientation of this essay. The reader must fully appreciate that no general theory of human behavior in terms of neurological entities is being offered in this paper. Instead, I will focus on only one aspect of brain and behavior during hominid evolution: the large-scale expansion of cranial capacity which followed the Australopithecine phase up to the late Pleistocene, i.e., the late Neandertal-Sapiens recens phase.

This does not mean that I will totally ignore early hominid evolution (e.g., the hominoid-hominid

---

[1] This paper is a contraction of a version of a paper presented at the American Anthropological Association meetings, Denver, Colorado, 1965. I would like to acknowledge my gratitude to Prof. Marvin Harris, Dept. of Anthropology, Columbia University, who critically read an earlier version of this manuscript and offered many helpful suggestions. I also thank Dr. Ward Goodenough, Dept. of Anthropology, University of Pennsylvania, for his encouragement and suggestions of presentation. Naturally, I bear full responsibility for the views outlined in this essay.

transition) or problems associated with defining significant behavioral adaptations, such as symbolization, cooperative sharing and hunting, decreased sexual dimorphism, and other aspects discussed by Hallowell (1956, 1960, 1961), Etkin (1954, 1963), and Hockett and Ascher (1964). Speculations regarding Maruyama's (1963) phrase, "initial-kick," will be offered with reference to early hominid evolution, and will include a number of behavioral and biological changes which acted to structure subsequent hominid evolution. The phrase "Human Revolution" (Hockett and Ascher 1964) can be taken as essentially synonymous with Maruyama's phrase. The reasons behind this choice will become more apparent later in this paper when I discuss positive feedback and the amplification of deviation.

Two other introductory points should be made concerning the plan and purpose of this synthesis. First, the question of behavior of "degree" versus behavior of "kind," and the extent to which this dichotomy can be related to neural structures. In an earlier paper (Holloway 1966a) I have argued that we do not have an adequate knowledge of changes in brain structures based on either endocasts or extant comparative materials. I have tried to show that the human brain has been reorganized in the course of human evolution, and have given numerous examples of these changes in relation to sensorimotor structures, the cerebral cortex, and some subcortical structures which mediate emotional responses. While no new neural structures are known for man in comparison to other primates, the operations of this organ are specific and not explained by reductionistic analyses to matters of neuron number (Gerard 1959, 1960; Jerison 1963), "cerebral rubicons" (Keith 1931, Vallois 1954), sensorimotor cortical maps (Washburn 1959, 1960) frontal lobes (Clark 1961), or particular gyri associated with motor or receptive functions of speech (Count 1958, 1964; Geschwind 1964, 1965). Analysis of microcephalics (Holloway 1964, 1966a) and bird-headed dwarfs (Lennenberg 1964) makes this point clear. Instead, I have contended that whatever specificity there is in human behavior, it can only be related to a systems-type analysis[2] involving the interaction of the brain as a whole within the context of a peculiar human environment. I will not attempt any further analysis of this approach in this paper. Nor do I intend to review the very important problem of the nature of the human specificity in behavioral or cognitive terms. While my own bias is in accord with Hallowell's (1956, 1960, 1961) position that man has undergone a total "psychobiological structuralization," and with Tappen (1953) that symbolic communication is a quantum leap, I do not wish to review this problem here. To be more specific, I hold the position that stone tools made to a standard pattern represent a different kind of cognitive organization than known for any other animal, primate or not. Furthermore, I am assuming that the Oldowan tools found at Olduvai Gorge were made by Australopithecines, and that these early hominids possessed symboling abilities.[3] I believe that this ability to impose arbitrary (as against iconic) form on the environment is an example of behavior of "kind," which is finely interwoven with behaviors of "degree," i.e., those continuous with general adaptive problem-solving abilities such as "intelligence," of the other primates. I emphasize these above statements as assumptions, because I know of no convincing analysis of behavior of "kind" vs. "degree" which has settled the matter. I am in basic agreement with Geertz (1962) who has pointed to the fallacies of viewing culture as something which merely overlies or supplements a hard core of other behavior. In short, I recognize that many problems will be left unexplained in this essay, but I am convinced that these exclusions are necessary.

I will use the term "complexity-management" throughout this essay to refer to subsets of behavioral attributes which I take as continuous with other primates. By "complexity-management" I will mean those behavioral attributes related to

---

[2] Elsewhere, (Holloway 1964) I suggested three possible models for approach to the problem of behavioral emergence. These were (a) a systems approach, based on reorganization of the entire brain, and based on shifting sizes and thresholds of cortical and subcortical components and their interactions; (b) a sustained-activity hypothesis based on a symbiotic interplay between the neuron and its surrounding glial cells, in which both long- and short-term memory could serve as intervening psychological constructs to explain emergence, or acquisition of arbitrary, concatenated symbols; (c) a modulatory hypothesis based on increased interconnectivity of cortical neurons, such that arbitrary representative factors, i.e., symbols, could be acquired and maintained once some threshold in a wide expanse of neural nets was exceeded. In no case is there adequate neuroanatomical evidence to demonstrate these hypotheses. Furthermore, these models were not regarded as exclusive; that is, they are conceived as interdependent.

[3] I recognize that this assumption is not shared by all students of palaeoanthropology, and that my references to the Australopithecines glosses over a considerable number of real problems regarding the association of stone tools with these fossils in East and South Africa. The present length of this paper militates against any review of these problems, or the different views regarding the appearance of more advanced hominid types (such as Homo erectus at the Sterkfontein Extension site, or the so-called "Homo habilis" at Olduvai Gorge) outlined elsewhere by Leakey, Robinson, and Tobias is Current Anthropology, January 1966. For the purpose of my assumptions made in text, I do not accept as final any verdicts which assert that the Bed L "pre-Zinj" is truly outside the range of variation of Australopithecus africanus. Nor do I take as proven the assertion that robustus members of this Australopithecine taxon did not make stone tools. Should further fossil and archaeological evidence upset the assumptions made in text, it would not change the fact that somewhere in hominid evolution these early forms made tools to a standard pattern, and that these processes were carried out with brain capacities below that of the middle Pleistocene Pithecanthropine taxon.

efficiency and fineness of discrimination, and adaptive problem-solving ability, which includes factors such as memory storage, recall, attention-span, and delay of response. This designation, "complexity-management," is not far removed from Wallace's (1961:75) "cognitive capacity." By this term, Wallace meant the following set of functions: intelligence, educability, concept formation, self-awareness and self-evaluation, reliability of performance under stress, attention span, sensitivity in discrimination, creativity, etc. I have chosen "complexity-management" because I do not find that comparative psychology has much to offer concerning Wallace's subsets, nor do I see any way to relate these subsets empirically with human evolution. My definition of "complexity-management" thus excludes other possible behavioral attributes such as emotional involvement, Freudian constructs, or cognitive "strategies" based on the symbolic mode of organizing experience, even though these constructs may be key factors in any description of human behavior. I ignore them because I do not have a framework to handle them in evolutionary or archaeological contexts, not because I regard them as unimportant.

Secondly, the synthesis offered herein is based on the belief that the variables mentioned earlier have interacted in mutual-causal rather than linear-causal ways. It is impossible to write about these variables in any satisfactory manner which preserves the essence of mutual, multi-causality. I believe that most attempts to explain biosocial integrations in hominid evolution suffer from the accent on linear-causal relationships. For example, Hockett and Ascher (1964) describe a number of adaptations in serial fashion, e.g., tool-use, tool-making, hunting, symbolization, cooperative sharing and hunting, etc. The writings of Washburn (1959, 1960) have stressed tool-using and tool-making as causative factors in the evolution of the brain and reduction of maxillary canine size. Tappan (1965:438) has recently pointed out that a major separation in the analysis of hominid adaptations revolves about the question of whether tool-making is an outcome of a more general cognitive structuralization, or whether tool-making preceded them. I do not understand how tool-making can be explained by reduction of maxillary canine length, or how natural selection was for tool-making, per se. I agree with Hallowell (op. cit.) that tool-making represents one outcome of many that were based on a total "psychobiological structuralization." Included in these "many" would be the processes discussed by Etkin (1954, 1963), such as cooperative sharing and hunting, symbolic communication, decreased sexual dimorphism and increased intragroup cooperation, full-time receptivity of the female, the domestication of the male, the home base, etc. Some of these aspects will be discussed more fully under the later section, "Question of the Initial-Kick." The point is that we need a framework in which these aspects can be united, and natural selection linked to the "life ways" (Washburn 1960) of early hominids.

Hopefully, this long introduction explains what I regard as certain major problem areas, and why it is necessary for the present framework to be so selective in terms of orientation.

SYNTHESIS

1. The Factor of Individual Variability

Individual variability here refers to something additional to the usual sense of a ready reservoir of genetic material for natural selection to act upon. I also mean individual variability in the sense that it is a part of the environment for every member of any particular social grouping. I view individual variability as a factor in generating complexity, or increased interrelatedness, in the environment. Individual variability is a "structure" of the environment in the sense that any "actor" of a social group must take into account the nature of his surrounding environment and the individual perturbations emanating from the other members of the group. The behavior patterns of the other members are partly determinate for the actor's behavior. In the same sense, an actor's reactions to others becomes a part of the environment for the other actors. But behavior is epigenetic, i.e., an outcome of both genetic potential and the interaction of this biological datum with the on-going environment. The behavior is not only epigenetic in the sense of an outcome between interaction of structure and environment, but also in the wider sense that it varies during the actor's lifespan. Individual variability as a component of environment is thus both a "structure" and a "process" for a social grouping. The mechanisms of genetic diversity and epigenetic development guarantee individual variability both in terms of individual biological structure and individual behavior patterns. Hale (1962) has shown that the emotional attributes in most mammals are more labile in terms of genetic change than sensory or motor patterns. Scott and Fuller (1965) have documented this fact in great length for the dog, and have successfully bred dogs based on selection for emotional attributes or temperament. Rank and order in dominance interactions for many mammals is surely good indirect evidence for temperament variability (see Collias 1944 and Scott 1958 for review; for primates, see Hall 1965), with glandular (hormonal) interactions having a mediating role in terms of aggression threshold, mating receptivity, agonistic responses, placidity, etc. Primate field and laboratory studies have made it clear that variability of behavior at both the group and individual levels is considerable. Indeed, these variations are important labels identifying individual members in the wild (Schaller and Emlen 1961, Schaller 1965). Dominance rank in aggressive terrestrial primates (e.g., the macaques and baboons) depends on both biological inheritance and the structure of social relations; e.g., offspring of dominant females tend to be high in the dominance order (Kawai 1958; see also Mason 1965). Within the primate groups studied so far, it seems conclusive that the actors pay considerable attention to these variations. Inattention may include severe penalties, such as a set of fangs in the neck. Current summaries of primate behavior (Altmann 1962, Hall 1965, Hall and DeVore 1965, Marler 1965) certainly give the impression that primates are excellent at the task of discriminating between items of a large repertoire of motor responses. Status testing seems to be a constant on-going activity in any primate group, and while overt violence may be rare as claimed by DeVore and Washburn (1963), agonistic expressions are hardly uncommon.

It is logical to conclude that the actors' reactions to their environments (social and physical) would be heterogeneous. Thus each individual's interaction with information from the environment would be different in terms of how his sensory receptors process information, the efferent or motor structuring of input (selective perception), patterned output of information, and "strategies" for the storage and retrieval of information. To the extent that differential reproduction can be related to the ascendency or "superiority" of a grouping of social and physiological attributes, the social environment for the population of actors has changed, e.g., from high aggression to one of lower or higher thresholds, tolerance, agonistic interactions, etc. DeVore and Washburn (1963) and Hall and DeVore (1965) have shown that dominant males (baboons) inseminate females during the most susceptible portion of their estrus cycle. This observation provides a clear example for understanding the replication of behavioral characteristics through time, assuming of course that those males who inseminate during non-susceptible portions of the estrus cycle have behavioral attributes with a genetic basis somewhat different from the less dominant males. From Etkin's (op. cit.) discussions of early hominid adaptation, it is obvious that behavioral attributes other than sheer dominance were foci for natural selection. Surely individual variability for the species sapiens is no less than other gregarious primate groups whose basic adaptation and success depends on their social ordering. Cooperation, leadership, sexual division of labor, possible specialization in technological tasks, continuous sexual receptivity of the female, predictive and discriminative ability, memory, etc., must have been the main ingredients in social adaptation. The fossil and archaeological records do not tell us about these factors. But these records do indicate that variability in terms of hominid skeletal structure was high, and that there was also considerable variability in tool types and their increasing diversity with time. To the extent that qualities relating to differential reproduction and survival of groups depend on individual variation, this heightened aspect in primates becomes an important feature in the future selection pressures exacted on groups. Environmental changes such as faunal supplies, water, climate, etc., <u>and</u> individual variability can logically structure <u>future</u> selective pressures. The variability maintains the necessary plasticity in terms of genetic potential and environmental change, but is also deterministic in channeling differential genetic and epigenetic possibilities. One of the major tasks in any other future synthetic attempt will be to spell out, more concretely than I have here, the behavioral attributes most important in terms of adaptation and evolution, and relate these in some meaningful way with neural and glandular structures. Chance (1962) has made a beginning in this direction by analyzing cortex-amygdaloid interactions relating to rage control in different primate groups. While it is true that many of these neural structures at the subcortical and cortical levels are associated with homeostatic functions (Dempsey 1951), the fact remains that these structures have changed in evolution and behavior also. The point of this section is to emphasize that environments do change as a result of the structure and process of individual variability, in spite of the richness of homeostatic devices at both the individual structural level of the organs, and at the social level. Individual variability cannot be discussed in isolation however, and the next section, the "deviation of amplification" will try to integrate more fully individual variability and change.

2. The Factor of Deviation-Amplification

This label has been defined by Maruyama (1963:165) 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.

Maruyama considers this concept as synonymous with the more familiar terms "positive feedback," "morphogenesis" as against "morphostasis," suggesting that most cybernetic concern has been with negative feedbacks, homeostasis, or morphostasis, and that the emphasis on positive feedback factors might be called the "Second Cybernetics." Maruyama has used this framework of the amplification of deviation, or positive feedback, to analyze the accumulation of capital, the evolution of organisms, the generation of structure, interpersonal processes and the development of psychopathology. A similar framework was described by Bateson (1936) which he termed "schismogenesis."[4] Deviation amplification adds the dimension of time and direction to these considerations of the generation of structure by incorporating the necessary loop of positive feedback.

Evolution is continual change, a process in which certain differences between beginning and extant forms have increased. When these patterns of difference appear to be invariant, such as brain or body size, one speaks of orthoselection (Simpson 1949) rather than the vitalistic or finalistic notion of orthogenesis. With respect to human behavior which is based in part upon arbitrary symbols concatenated according to specific rules (Hockett 1960), there has been an orthoselection for the apparatus (biological and social) to handle ever-increasing degrees of complexity. By complexity I mean essentially an increase in configurations or relatedness between configurations. In this sense, I also mean that there has been a generation of increased degrees of improbability or information as time proceeds.

I have briefly alluded to an "initial-kick" in the Introduction when I discussed aspects of the "human revolution" (Hockett and Ascher) such as symbolization, or some of Etkin's variables dealing with the organization of affective interactions between members of early hominid groups, suggesting a basis in biological structure involving both the brain and glandular or hormonal systems. These will be discussed more fully in a later section. Here, I am concerned with the deviation-amplification process once the initial-kick has occurred. I have suggested that individual variability can remain a part of the environment through differential reproduction. Different responses or reactions to individual variations of behavior by other actors can become part of the environment for the group in general. Memory mediates these shifts in responses and environment through the ontogenetic development and life span of individual members. A small behavioral shift, with or without some advantages, can feasibly alter the environment and future selection pressures. Since reactions to these shifts can reinforce the shift, deviations from an initial to succeeding conditions can amplify. In the human case, these individual variations in behavior can become fixed in the environment through symbolic processes which can even be transmitted at rates greater than births. The human communication system has the important feature of "productivity" (Hockett, op. cit.). This means that almost any degree of improbability can be generated and become social fact, i.e., parts of the environment to which the actors must now react. The outcomes of this design feature, "productivity," (e.g., stone tools, kin categories, myths, rituals, definitions of enemies, "needs," emotional propriety, etc.) are deterministic and, where social cohesion is involved, can be significant in terms of new foci for natural selection. Determinism here means structuring future events that the actors will be exposed to; it is also meant to imply that the "productions" will structure or raise the probability that other "productions" will follow. Surely, certain systems of social structuring depend on biological duality and "arbitrary" definitions of different ways of combining gender and age in terms of relationships. This is trivial, of course; but the corollary that social structuring may logically produce other patterned relationships is not. This is the task of the social anthropologist, however, and I will leave the question here.

Returning now to the issue of invariant change in a structure through time, I submit that it is profitable to consider the expansion of cerebral cortex as a general example of orthoselection. This expansion was probably attended by other changes in the subcortical systems, but it is impossible to pinpoint any of these with reference to hominid evolution. The problem remains to explain this cortical expansion in terms of deviation-amplification, or positive feedback. For this task, the remaining variables of (3) environmental complexity and (4) neural complexity are essential. In essence, individual variability contributes to environmental complexity, setting selection pressures for adequate neural complexity to handle the increasing complexity. The increased neural complexity increases the complexity of the environment and individual variability. These variables are continuously interacting with each other in positive feedback cycles. While individual variability (1) might be more conveniently subsumed under (3) environmental complexity, as a particular instance, I have chosen to develop it separately. I have done this because I believe the process of individual variability to be an important factor in giving rise to deviation-amplification, environmental complexity, and eventually, neural complexity. Cortical expansion, however, must be explained in

[4] I am indebted to T. D. Lanagan for pointing out to me Bateson's concept of schismogenesis, and for placing the seeds in my mind of many aspects of conflict-generation and resolution. While Maruyama is responsible for the term "deviation-amplification," it is totally clear that Bateson had the essentials of this process in mind when he used the term "schismogenesis" in his 1936 work. Bateson further recognized two aspects of this process, viz., complementary and symmetrical schismogenesis. Furthermore, in the 1958 Epilogue to the second edition of Naven, Bateson explicitly points out that the concept of schismogenesis now has wider significance in view of the impact of cybernetics on the Social Sciences. As I have used "deviation-amplification" throughout this essay, I should add that both complementary and symmetrical aspects are operative. While I may be stretching these connotations somewhat, I would suggest that these ideas were appreciated by Simmel in 1908 (see Simmel 1955). The application of deviation-amplification to the evolution of species does not originate with this essay, nor any of the notions that an animal's reactions are part of the environment for other animals. This idea is openly discussed in Bateson's 1958 Epilogue.

more molecular terms than simply cranial capacity, as I have shown elsewhere (Holloway 1966a). To set the stage for that discussion I will now discuss the variable of environmental complexity.

3. The Factor of Environmental Complexity

Environmental complexity refers to the quantity of stimuli configurations or concatenations of stimuli which an animal must discriminate among, and to which it selectively responds. It is convenient to discuss environment as having two important subsets: (a) the external environment of the organism and (b) the internal environment of the animal. Subset (b) is only roughly equated to memory, or to those intrinsic codes which are the organism's stored experience. I suggest this dichotomy only for heuristic purposes; I do not suggest that there are actually two separate environments in reality.

The outside subset (a) would include physical factors such as ecological resources, climate, predators, etc., and the events of a social nature to which the animal is particularly sensitive, or "attuned." Ethologists have been particularly concerned with the critical stimuli configurations to which animals are attuned, and the relation of these to adaptation and evolution. Thorpe (1963) and Hess (1965) have given numerous examples of critical sign stimuli and stereotypical motor sequences; the example of butyric acid for the tick, and the red belly of the stickleback fish are familiar to all. Gestalten are defined as the relational characteristics between critical sign stimuli (Hess) and the totality of critical sign stimuli makes up the Umweg of the animal. Higher animals are also attuned to certain critical sign stimuli, e.g., the white patch of fur on the tails of certain deer and gazelle, and the flashing white eye-lids of the baboon. However, it is not at all certain that the ethological approach is the most useful approach with higher mammals, since stereotypism is reduced as one proceeds up the phylogenetic scale. In the case of man, the issue is far more complex because his communicational system has both "productivity" and "displacement" design features (Hockett, op. cit.). These features provide for an unlimited number of configurations for Man to respond to when he is appropriately "programmed."

The last two features mentioned bring up the matter of how humans organize their experience by symbol systems and the contribution of this kind of organization to (b), the internal environment. It is obvious that the world of man enlarges beyond any immediate perceivable limits of the external environment through this organization. Not only can many fine distinctions be drawn through symbol tags; the opposite can occur through conceptualization. Man can make his environment as complex as he pleases, and can impose this environment upon others by simply opening his mouth. I submit that "culture" is a quantum leap in terms of a capacity to generate information, or alternatively, increased degrees of improbability, mainly through "productivity" and "displacement." Associated with this process is an important biological propensity, highly developed in man and the other primates, namely, the central nervous system "demands and seeks" stimulation that is varied (Hebb 1954, 1955). Current work on sensory-deprivation (Solomon et al. 1961; also Harlow 1962, and Mason 1965) suggests that variety of input is essential to the "normal" operation of the human system, particularly the central nervous system. Play, exploration, curiosity, seem to be essential ingredients in the "biogram" (Count 1958) of primates, and that these propensities are heightened in our own case.

Another consideration of this matter of complexity is the nature of the environments during the evolution of man. The Pleistocene was a time of tremendous and wide-scaled climatic changes. Other animals also faced the continual flux of environments. Shifts in weather produced changes in water supply, flora, support of fauna, and shifts in the relations between faunal lines, e.g., carnivores and herbivores, man and mammoth. In the case on hominid evolution, the significant adaptation to changing environments was culture. Stone tool distributions covering periglacial and temperate areas of Europe, Africa, and Asia show a distribution of hominid types adapting simultaneously to different environments. There is no sound evidence suggesting a plurality of hominid species at any one time level, except perhaps in the Australopithecine phase.[5] The tools show change and expansion of types through time, and their increasing complexity and specialization is coherent with the view taken here of increasing complexity with time. This complexity can be viewed both in terms of extension of tool-kits to include more kinds of tools, and more complex techniques for the manufacturing of the tools. Certainly many more environmental attributes must be in mind when manufacturing a Levalloisian flake, or specialized blade

---

[5] This statement should not be construed as a definite implication that present morphological evidence for South and East Africa definitively demonstrates the presence of different Australopithecine species (sensustrictu) during either the late Pliocene or early Pleistocene. The statement simply means that of all the evidence from the fossil record, the strongest case can be made at this time period. I do not regard the Mauer Jaw, Steinheim, Ehringsdorf, or Swanscombe fragments as proof of different hominid species living at roughly the same time level. Similarly, the so-called "generalized" vs. "specialized" Neandertal remains, and the origin of present-day sapiens morphology is not regarded as essential to the point I am trying to make. In terms of ecological adaptations, these later problems would seem to be of a different order than at the beginning of the Pleistocene, where there are suggestions of an ecological separation and implied behavioral separation between africanus and robustus members of the Australopithecine taxon.

or burin, than in making an Oldowan chopper or Chellean handaxe. Making stone tools to a set pattern not programmed in the genes suggests a plurality of other relationships which had to be taken into account by the makers. Making stone tools was not only a technological process; it must also have been a social process. It should be apparent that such processes structure the environment of the actor. If he is to make stone tools, he must learn how in terms of motor patterns, selection of materials, their properties, and their use. What part of his environment and time consists of a different social network than before? Do increasingly technological designs suggest that social time is used differently than in cases where the production is simple and swift? What does specific selection of particular materials imply in terms of what the hominid is exposed to when selecting materials? One can phrase an endless number of such questions. This exercise in triviality suggests an important aspect that is not trivial. A shift in one behavior pattern will structure the rest of the environment acting on the animal. Pinpointing these interactions and their change through time is an impossible task. For the purpose of this paper, it should be enough to recognize this dynamic and relate it to positive-feedback processes and, hopefully, to biological structure.

It should be noted however, that responses to environmental change do not include a portion of output or feedback that causes all sectors of the environment to change. It is impossible to see any loop from stone tool-making activities to climatic changes, although this is a present-day possibility. On the other hand, the hominids' interactions with faunal and floral sectors might, depending on ecological parameters, deplete an area of resources. This would structure the situation so that movement would be necessary for survival, which in turn would call for new technological productions, hunting techniques, appreciation of relatedness, and so on.

A hunting adaptation seems, on the face of it, a more complex operation than eating grass or bamboo shoots. I find it logical to assume that many more stimuli, configurations of stimuli, must be taken into account when considering human evolution. It is difficult to appraise the necessity for an extended maturation and dependence time unless these confer some advantage to the animal in understanding his environment and making adaptive responses to it. Natural selection acted upon the ability to handle complexity in the environment. Man makes his own environment, however, and these productions set new selection pressures, or shifted the directions of previous ones. The rates of evolutionary change for the hominids after the Australopithecine phase were very rapid (see Kurten 1959), indicating that no one "solution" lasted long enough to suggest any significant homeostasis. Surely the rapidity must in part relate to the fact that man is "productive" and generates much of his own environment. Plasticity had a high adaptive value, and selection has maintained this advantage. Selection for the mediating factors of plasticity also heightened individual variability, which, in combination with the unique human code, continuously increased the complexity of the environment.

4. Complexity of Neural Structure

At the neural level, I have already discussed parameters such as neuron size, neuron density, increased dendritic branching, and possibly the glial/neural ratio as the internal manifestations of cortical expansion during primate evolution (Holloway 1966a). In this section, I shall elaborate further on these parameters in terms of complexity-management and the striking increase of cranial capacity in hominid evolution. Other aspects of neural structure involving subcortical centers are not included here. Also, other changes involving differential expansion of different cortical tissues (e.g., "association" cortex) will not be described here, as I have treated them elsewhere (Holloway, op. cit.). While the evidence is clear that such changes have occurred (Bonin 1963, Bonin and Bailey 1961), there is no evidence that these shifts radically change the basic behavioral repertoire within the primate line. Recently, however, Geschwind (1964, 1965) has suggested that expansion of the inferior parietal lobule in man can be related to "object-naming" behavior. Geschwind argues that only in man are purely non-limbic to non-limbic associations made, that is, not tied into any affective response. In the case of nonhuman primates, these form only cortical to limbic associations, i.e., tied into affective responses. In the first case there is no limit to associations possible, and symbol acquisition and manipulation are unlimited in man. Geschwind draws extensively from the clinical and comparative experimental literature to demonstrate these claims. It would be but a short step from this observation to the plunge into single factor reductionism, a step that Geschwind does not take. In other words, an animal that can make symbolic associations about his environment (name objects) and communicate them, has a great advantage, and this ability will be a focus for strong positive selection pressures to acquire an expanded inferior parietal lobule. No one harbors any doubts that the symboling ability conferred tremendous advantage to humans in the course of evolution. The question is whether this ability can be reduced to one small structure in part of the cerebral cortex. Untouched here, of course, are the problems of syntax and concatenation, arbitrary rules, the propensity of the human infant to babble, echo, and the affect-interplay between child and parents in terms of motivation and reinforcement, the latter aspects involving limbic structures as well as the cortex.

Attempts to bring more specific neural factors into the question of human evolution have depended on the student's view of which behavioral attributes are to be regarded as critical in explaining human behavior. For example, Geschwind has emphasized Brodmann's (1912) and Weidenreich's (1936) observations on expansion of the parietal lobe and speech reception in man. Emphasis on tool-making and tool-use has lead Washburn (1959, 1960) to compare cortical "maps" of man and monkey with respect to motor areas for hand, thumb, and tongue. Count (1958) has been concerned with the evolution of man's language, and has underlined the growth in the region of the third inferior frontal convolution associated with the motor aspects of vocalization. Jerison (1963) and Tobias (1965) have concentrated on neuron numbers in different primate brains, particularly those associated with "complex functioning." In fact, Tobias (1965) has used these mathematical interpolations of neuron number to argue for a particular taxonomic placement of the controversial "pre-Zinj" hominid. Gerard (1959, 1960) and Garn (1963) have emphasized that the evolution of the primate brain has mainly involved the addition of units, and that these additions account for behavioral differences between man and the other primates. On the other hand, Straus (1953), Dart (1956), and myself (1964, 1966a) have stressed reorganizational changes in the brain, implying that changes additional to the increase in units has taken place. Rensch (1954, 1959) has been concerned with correlating changes in cortical structure, such as neuron size, neuron density, ramification of nerve processes (dendritic branching), with increasing efficiency of behavior in terms of memory storage and recall. Chance (1962) has analyzed subcortical-cortical interactions, namely, the amygdaloid nuclei and control of rage in primate groups.

I do not intend to critique these various contributions. Any more general theory of the evolution of brain and behavior will incorporate aspects from each contribution. The point can be made, however, that so far no clear-cut framework exists which unites human-subhuman behavioral differences with structural differences of the brain. My purpose here is to extend one aspect of brain structure, the cortex, into molecular terms which can be integrated with increasing cranial capacity and complexity-management. In the 1966 article, I tried to show that increase in cranial capacity was related mainly to spatial parameters of the neurons rather than addition of units commensurate with the increase in brain volume. These parameters are the same discussed by Rensch and partially analyzed by Jerison by logarithmic mathematical interpolations. In general, these authors (see also Shariff 1953, Tower 1954, Bok 1959) showed that as body and brain size increases, average neuron size increases, neuron density (distance between neurons) decreases, and dendritic branching increases.

There is phylogenetic, ontogenetic, and experimental neuroanatomical evidence that increased efficiency in complexity-management is attended by the following changes in neurohistological parameters: (1) decrease in neuron density; (2) increased average size of neuron; (3) increased dendritic branching; (4) possible increase in glial/neuron ratio. All of these relate to the cerebral cortex only. Of these lines of evidence, the phylogenetic is poorest. Neuron density has been related to brain size rather than phylogenetic level per se (Tower 1954). The observed relationship within phylogenetic lines, such as the primates, between level and density (Shariff 1953, Bok 1959) is probably a function of the correlation between size and level or status. Aside from the studies of Erp Taalman Kip (1938) and Barasa (1960) on rodents and other lower mammals, there are no comparative studies on dendritic branching. There is a lack of any good comparative evidence for neural/glial ratio. Haug's study (1958) included primates, and led that author to assert that there was no relationship between phylogeny and glial/neuron ratios (see also Haug 1960). Careful examination of his 1958 work shows that zoo animals were used, a few of which were diseased, including one chimpanzee with a gliotic infection of the brain. When these are extracted from his data, the relationship is more evident (see Holloway 1964 for details). Actually, Haug's data are arranged according to nuclear volumes, and not the usual presentation of numbers of neurons as against glial cells. His data also suggest that individual variability is high. At the present time it seems best to await more positive and primary study of this parameter. This is unfortunate, since it is becoming obvious that it is the neuron and its surrounding supportive neuroglia which is the functional unit, rather than the neuron alone. The glia and neurons are interlocked in a metabolic interdependence (Hyden 1962), and the former show properties of motility and potentiation which might act to lock-in local firing patterns (Hild and Tasaki 1962). Hyden has shown that base ratios of nucleotides in both glial and neuronal RNA undergo reciprocal changes during learning.

Ontogenetic or developmental studies are more clear with regard to the parameters listed above. In general these changes have been shown for the guinea pig by Peters and Flexner (1950); for the cat by Sholl (1956, 1959), Brizzee and Jacobs (1959), and by Purpura et al. (1960) who also correlated the electrophysiological changes with the morphology; for the rabbit by Schade and Baxter (1960); for the rat by Eayrs and Goodhead (1959); for human middle frontal gyrus by Schade and Van Groeningen (1961; see also Conel, 1939-1963). In all cases, maturation is attended by decrease in neural density, hyperplasia (increased size) of neurons, increased dendritic branching, and increased efficiency in cortically-mediated adaptive behavior.

Two sets of experimental data will be mentioned here. The first are Clendinnen and Eayrs' (1961) work on the administration of growth hormone to pregnant rats. Using Sholl's (1956) method of quantifying dendritic branching, they found significant increases in branching parameters from offspring of GH-treated females. This increase was associated with decreased neural density, increased size of neurons, and an increase (small) in cortically-mediated adaptive behavior, in comparison to experimental controls. Earlier works by Eayrs (1960 for review) on the effects of removal of the thyroid gland showed the opposite configuration of results, i.e., decreased size of neuron, increased density, decreased dendritic branching, and a decrement in problem-solving ability. The second set of experimental data is that of Rosenzweig et al. (1962) on the effects of an enriched environment upon the behavior, biochemistry, and neurohistology of the rat cortex. Diamond et al. (1964) have demonstrated that shifting the environmental variables in the direction of greater complexity has positive effects on the histology of the cerebral cortex. In the visual cortex of maze-bright S_1 rats, litter mates put through the ECT (extra-environmental complexity training) milieu showed significant increases in cortical weight and depth, and decreased neural density. Using Sholl's method and Golgi-Cox staining methods, I have collected data on a total of 15 pairs of these S_1 animals. The results show that dendritic branching of certain neurons in the second cortical layer have increased in 11 out of the 15 pairs (Holloway 1966b). These data thus put all of the parameters into a tight concordance, and tie together the increase in brain weight reported by the above authors with the neurohistological, neurochemical, and behavioral changes. Note that in the ontogenetic and experimental cases, there is a tie-in between the changes in parameters and endocrine interactions. This point will be returned to later when discussing some aspects of early hominid evolution.

If cranial capacity and its increase during hominid evolution are considered, it can be appreciated that part of the organizational changes have involved reorganization of the spatial relations in the cortex. Thus the fourfold increase in brain size is not paralleled by a fourfold increase in neural units, but by decreased density, increased average neuron size, increased dendritic branching, and possibly an increase in glial/neural ratio, the latter being necessary to sustain the increase in metabolic demands effected by increased fibers. Obviously, this explanation oversimplifies matters, since there probably were also changes in subcortical centers and possible changes in neurochemical parameters. The data for the latter are not yet available. Furthermore, there have been changes in terms of areal distribution of different cortical areas and tissue (Bonin and Bailey, 1961). It should also be pointed out that the experimental evidence cited above should be accepted on a tentative basis only, since replications are needed, and experiments devised to pinpoint how the changes are mediated. With these limitations in mind, it can readily be appreciated that a comparison of cranial capacities between different species cannot be a comparison of equal units.

Moving to a more general level, I suggest that neural structures relate to behavioral adaptations in one of two ways: (a) through a high signal/noise ratio where internal and external redundancies are low; (b) through low signal/noise ratios where internal and external redundancies are high. Examples of (a) would include those animals with high or specialized sensitivity to particular critical sign stimuli (see Section 3), and which are characterized by rigid stereotypical patterns of behavior. By low external redundancy, I mean that only a few signals from the environment are significant, and these are highly specific. By low internal redundancy, I mean that very small nervous systems with many fewer components do not have as much random firing, and the channels or nerve fibers bringing in information do not tend to conflict or intermesh. In general, method (a) has been taken mainly by lower mammals, invertebrates, particularly the insects. Many of the well known motor and stimuli patterns described by ethologists (e.g., Thorpe 1963, Hess 1965) for various fish, insects, and birds, would serve as examples of (a).

Since I have emphasized positive feedback, it should be pointed out that behavioral patterns from ethological studies better fit within the framework of negative feedback. The movements of many birds, such as the "appetitive" and "aversive" behaviors discussed by Hess, maintain homeostasis in relations toward mates, predators, and ecological parameters. In this case, the loop from behavior to environment follows the negative feedback model. The biological variations "await" a shift in environmental factors, seldom if ever contributed directly by the behavior of the animal in question. In the case of man, however, the selective pressures alter as a result of what he does. The loop from behavior to environment is more in the positive sense; that is, the positive factor overrides the negative or homeostatic loop. This last qualification is necessary, since at the individual level, the nervous system, the neuroendocrine system, and remaining biological apparatus act to provide homeostasis (see Dempsey 1951, for general discussion and examples). Even at the group level, it is possible to crudely equate social processes as attempts to maintain homeostasis in terms of group welfare (Allee 1951, Wynne-Edwards 1965). As mentioned earlier, man's evolution demonstrates that the positive factors have overriden the negative processes.

In method (b), where signal/noise ratios are low and external, and internal redundancies high, higher mammals such as the primates serve as the best examples. In this method, general sensitivity to a number of sensory modalities have been selected for, with no real specialization in any one mode. Sensitivity to particular stimuli is more diffuse, and rigidified stereotypical behavior patterns replaced by an essential plasticity. Signal/noise ratios are lower because of multi-channel input which includes a plethora of stimuli configurations to be dissected, compared, and interpreted. By high redundancies, both internal and external, I mean that many more parts in the cortex spread remembered or coded engrams extensively across the cortex. I also mean that inputs from the environment are in a sense isomorphic (e.g., verbal and nonverbal behavior) and that the same interpretation can be made of signals which are quite dissimilar in terms of energy (e.g., sound vs. light waves) and channel. On the other hand, more parts in the cortex act to lower signal/noise ratios by random firing and death. More parts also provide for more increase in memory storage (see Rensch, op. cit.), providing that other structures, e.g., the hippocampus, and "strategies" (Miller et al. 1960) are available to enact storage and retrieval. Memory and symbolic constructs alter the external and internal subsets of the environment discussed above (Section 3). One matter of signal and noise is made more complex by trying to account for the coding operations which organize percepts. Brown and Lennenberg's (1954) and Luria's (1961) studies on children and color-naming provides good evidence that symbol-tags facilitate complexity-management, if problem-solving can be accepted as an example of this rubric.

In a social group with transmission of symbolic constructs by non-somatic means, there is the ever-present situation of environmental shifts. The fixity or rigidity of neural structures and behavioral interactions in lower animals and insects insures replicability of responses which have been chosen through natural selection. While the plasticity factors have been sacrificed, and a change in environment is more likely to lead to extinction of a specific group, there are balancing factors insuring success and diversity. One factor relates to large quantities of offspring and very short life cycles. The other balancing factor must relate to the ease with which specific responses and definition of critical sign stimuli are mediated through small nervous systems and change through random mutations. In a sense, natural selection works through a very large number of specific behavioral "strategies." In terms of information, it might be said that in lower animals there has been a tendency to generate a large number of improbable solutions. This statement is concordant with the fact that the proportion of biological species in the world which are insects is extremely high.

Another factor regarding neural complexity should be mentioned. The longer dependency and maturation times of primates insures an effective programming of the brain to cope with the environment and its increasing complexity. Negative as well as positive feedbacks have operated at this level. It is not possible to know whether or not the frequencies of neurological disorders, i.e., of organic rather than functional etiology, have increased during man's later evolution. Nor is it possible to show empirically that there are a wider range of neurological disorders for man than in other animals. The 1957 Report of the National Committee Against Mental Illness, indicated that in the U.S. about 10% of the population suffers from mental illness. Statistical breakdowns are difficult, but the evidence seems clear that frequencies of mental illness in urban areas are greater than in rural areas (Rose 1955; see also Hollingshead and Redlich 1958). In New York City, estimates have run as high as 25-30%. One does not receive the impression from animal studies that rates of neurological disorders are particularly high, unless strains are carefully selected in the laboratory (see McClearn 1963, for example). The point is, that culture contains the seeds of deleterious programming of the brain as well as the benefitial components of adaptation. It seems hardly arguable that the nature of societies also provides the mechanisms, partly through interpersonal relationships and institutional failures, to damage the brain and the general health of the population. Consider alcoholism, venereal disease, pollution and poisoning of natural resources, the insistence by profit-motivated structures that one is a better man or woman for burning carcinogenic substances in his mouth, or the increased frequency of heart troubles and accumulation of cholesterols in the arteries (Dobzhansky 1962:309-311). While it is possibly true that there is the potential for dealing with these problems through medicine and more rational planning, the fact remains that man has created this environment and is forced to live with it.

Returning to the neural parameters discussed earlier in this section, I have related complexity-management to changes in spatial arrangements in the cortex, which included decreased neural density, increased dendritic branching, and possibly an increase in glial/neural ratio. In addition, there was an increase in the number of neurons, although it is difficult to state exactly the increase. Jerison's calculations indicate a doubling if man is compared to the chimpanzee, but these figures are not in agreement with Shariff's empirical counts, which indicate a jump of 1.25x from chimpanzee to man. (See Holloway 1966c for critique.) The point is that the major part of the expansion of the cortex has not been addition of units, but growth of the units themselves, which has increased tremendously the number of switching points, or synapses in the cortex. These parameters are hopefully more useful than cranial capacity, since phylogenetic, ontogenetic, and experimental evidence cited above relates in a general way to differences in problem-solving ability; cranial capacity does not. To discuss small changes in cranial capacity as adaptive would be meaningless, even if variability and populations were the units for manipulation.[6] The foci for natural selection were the peculiar glandular (hormonal) and epigenetic processes which resulted in greater degrees of complexity-management, processes at the level of neuron size, neuron density, dendritic branching, glial-neural interaction, and other possible subcortical and neurochemical changes. The outward result was a thousand cubic centimeters increase in cranial capacity. It should be emphasized that with this framework, present-day biological variation of cranial capacity has no demonstrable behavioral significance. The variability of neural structures that could account for significant behavioral differences today are at some level more molecular than cranial capacity. There is no published evidence of any significant behavioral differences in man today which can be related to any of the parameters discussed above. This should underscore the fact that the parameters discussed are useful only in reference to long-term evolutionary change, and that the relationship between increased neural complexity and the increase in archaeological complexity is best seen in terms of these parameters and not cranial capacity per se.

5. Redundancy in Neural and Behavioral Organization

I have briefly introduced a discussion of redundancy in the preceding section in terms of repetition of patterned input. In this section, I will discuss this matter further and suggest parallels to redundancy in patterns of human behavior. I will admit at the outset that this latter task is tenuous. While redundancy in the brain is easier to explain, human behavior has facets of complexity that make any reductionistic attempt suspect. I purposely put this section at the end of the synthesis, since the other sections can stand alone; that is, redundancy is not a critical concept to arguments advanced throughout this essay.

It is common today for various students to regard the central nervous system as containing high levels of "noise" (Arbib 1965, Gerard 1959; also Garn 1963). Noise here means random perturbations or disturbances caused by random firing of elements and loss of nerve cells through death. Arbib has discussed the fact that while neuron loss is high, the brain successfully carries out its computations. Brody (1955) estimated that during maturation, millions of neurons (up to one-third of the total cortical neuron population) die before old age. The whole field of computers, information theory, and the brain cannot be reviewed here. It can be pointed out that almost all models of the brain used by cyberneticians include some notion of reverberation and spread of patterned impulses throughout the cortex (see Fields and Abbott 1963, Ashby 1960, and George 1962 for reviews). Memory stores or "engrams" are extensively spread throughout the cortex since local ablations or deletions of tissue do not deplete specific memories (Lashley 1950). McCulloch (1958, 1963) has discussed the utility of extensive neural networks and interconnections (anastomoses) in combating internal noise generated in the cortex. Short-term reverberations are sometimes viewed as a necessary prelude to eventual long-term biochemical changes of RNA associated with memory (Hyden 1962, Gaito 1966). The wider the extension of coded patterns, the more insurance there is against local upsets, because the associations are more widely spread, i.e., redundant.

Redundancy can also be discussed in terms of irrelevant stimuli. Barlow (1958) has pointed out that the human brain has about 3×10^6 sensory nerve fibers providing impulses at any instant of time, and that the brain is faced with a critical problem in digesting and processing this input. Barlow proposed that recoding of past sensory messages would lead to selection of current messages such that redundancy would be reduced. There is no conflict here in terms of redundancy, since Barlow is considering the amount of input, while I am discussing redundancy as essentially repetitions or amplifications in a plurality of channels. This position is similar to that taken by Brown (1958) who argued that if either initial redundancy was high, or if it was increased by further learning trials, long-term retention would be insured (assuming that traces have a tendency to decay). Both senses of redundancy apply in insuring effective behavior. Through a wide extension of synaptic interconnections in the cortex, trace patterns can be established in many places (see Hebb 1949 for extensive discussion). In the other sense, many of the neurons probably act as both inhibitors and facilitators which dampen out unnecessary portions of input. The cortex is but one structure which enters into the redundancy

---

[6] The futility of dealing with cranial capacity as a unit can be appreciated by trying to account for small shifts in time with this parameter and its correlation with behavioral advance based on our present understanding of modern variation. Take 1,000 c.c., divide it by 1,000,000 years, and multiply by a generation span of 25 years. What results, is about 0.025 c.c. increase per generation. Even thinking in population terms, or various degrees of variability, or of translating these small units into other terms such as dendritic branching, one cannot successfully integrate back to anything meaningful in individual behavioral terms.

question; included would be the hippocampus, thalamus, septum, and hypothalamus, since the cortex has intimate two-way paths with these components.

The question of redundancy at the level of behavioral organization is more difficult. Basically, I wish to suggest that cultural behavior might be viewed in the two senses of redundancy described above. Human language and symbol constructs both inhibit and facilitate parts of the sensory field. Perception is an extremely selective process. The whole process of conceptualization lumps together into categories or concepts similar attributes of different sets of sensory stimuli, whether these be events "out there," or purely mental constructs, i.e., abstract thought. This aspect seems fairly straightforward. Redundancy in the sense of repetitions, reverberations, or amplification by isomorphic phasing is somewhat more difficult to understand. At the level of individual interactions, the matter is more simple than at the group, or institutional level. Nonverbal behavior might serve as an example of this second sense of redundancy at the individual level. Humans are extremely sensitive to picking up cues concerning their own behavior from that of the person emitting nonverbal signals. Hall (1959) and Birdwhistle (1952) have demonstrated many of these nuances. These patterned expressions are built up under particular sociocultural dynamics. In purely verbal episodes, such as telephone conversation (paralanguage aside), one is deprived of a considerable portion of feedback which aids one in adjusting his behavior so that it is compatible with the situation. Ekman's (1965) study is of interest here. He demonstrated on the basis of stress interviews, that nonverbal behavior functioned in seven ways to supplement verbal messages: (1) repeating; (2) contradicting; (3) substituting; (4) reflecting the person's feeling about his verbal statement; (5) reflecting changes in the relationship; (6) accenting parts of the verbal message, and (7) maintaining the communicative flow. Obviously, not all of these seven functions can be construed as redundancy operations, e.g., (2), (3), or (7). Nonverbal communication surely has many functions beyond that of providing redundancy so that messages are unambiguous; expressing personal style (making ego statements), the discharge of affect, and discharge of nervous energy without any necessary direction. At the evolutionary level, verbal patterns of behavior have followed the nonverbal mode. While the former cannot be overemphasized in terms of the human existence and adaptation, it is arbitrary to split these two ways of transmitting information, since the capacity for such transmission was surely selected for in toto. However rich the repertoire of these expressions for nonhuman primates, it hardly seems feasible that the richness has decreased or become less meaningful for humans.

Do group processes and human institutions show parallels with this sense of redundancy in which ambiguity is reduced by reverberation, amplification, and extension? To what degree are institutions such as trade circles, men's long houses, witchcraft, secret societies, initiation ceremonies, age and class groupings, etc., a set of interconnected redundant nets to insure and reaffirm some common sentiment or solidarity? Man has affinities and antipathies toward his fellow man, and the ties that bind also generate the conflicts that split them apart.[7] Do these institutions act as devices to "enforce" interpersonal commitments, so that some minimal cohesion in social groups is insured through a kind of redundancy? In other words, I am suggesting that these institutions are each variations on the same theme, and that redundancy in this second sense might be a profitable way to approach the invariant aspects of commitments found in each of the institutions. I am suggesting that these institutions have been necessary adjuncts to the biological sector of evolution, particularly in reference to ego definition and total "psychobiological structuralization" (Hallowell, op. cit.), and have their origins within this sector and variable (1), individual variability. The diversities of the institutions in different human groups would be of far less importance compared to the almost universal occurrences of the basic patterns.

Constraints must be placed on human expression and variation if primary tasks faced by the group are to be successfully met. Rules, i.e., symbol systems, militate against untoward variation, yet provide an openness for individual expression. Perhaps the most important feature of these various institutions is the structuring of human relations in economic terms, so that (i) commitments to others are possible at a number of intersecting levels, and (ii) human time and commitments are fragmented so that these will not be bound to any one locus. That is, the institutions act to scatter commitments around and prevent overconcentration in only one locus. In other words, in this second sense redundancy is both conflict-ameliorative and conflict-generative.

The above ideas are purely speculative and are suggested on the basis that redundancy might be one entry into a future general theory. As I indicated before, they are not strictly necessary for the main body of the synthesis proposed.

THE QUESTION OF INITIAL-KICK IN HOMINID EVOLUTION

Finally, I would like to relate this general framework more closely to the fossil record.

---

[7] See footnote 4 and Simmel's works. Coser's The Functions of Social Conflict (Free Press of Glencoe, 1956) has emphasized the opposite component of this interaction, viz., the results of conflict as increasing certain aspects of cohesion and solidarity in groups.

Throughout the major part of this essay I have discussed the evolution of the brain and behavior in terms of complexity-management, or behavior of degree. The question of initial-kick, or aspects of "the human revolution" (Hockett and Ascher) mentioned in the introduction has been avoided. What follows are some tentative suggestions which I believe merit further attention.

At some time shortly before the Australopithecines, perhaps during the time of Ramapithecus (Pilbeam and Simons 1965), natural selection favored an important strategy (or deviation) for both processing and transferring information about the environment. I do not mean language only, since I view this process as an outcome of a wider set of cognitive changes. "Object-naming behavior," discussed by Geschwind, would be one aspect of this strategy. At this time a transition was made to a type of social structuring based on different components of aggression control within small groups. This type of social ordering would be based somewhat on the wolf analogy suggested by Etkin, and would have included sexual division of labor, decreased sexual dimorphism, raised threshold to aggression within primary groups, sexual receptivity of the female on a full-time basis, domestication of the male, and cooperation in food sharing and possibly hunting. I suggest that this selection favored neural developments based on changes in neuroendocrine relationships between the hypothalamus, the pituitary gland, gonads, and adrenal cortex. A basic shift in endocrine interaction (hormones plus end organs) was involved which effected simultaneously aggression thresholds and sexual dimorphism, and provided for longer maturation times and larger brains. I conceive of this process as a pleiotropic one, where the initial selection pressures for the underlying physiological mechanisms mediating lessened aggression would have produced the neural changes of the type discussed throughout this paper. Obviously, direct evidence for these changes and their precise physiological concomitants cannot be provided. I offer the following as indirect evidence for the above:

(1) The female did become continuously receptive to sex, and this had to involve some endocrine reorganization.

(2) There was a significant reduction in sexual dimorphism, particularly secondary sexual characteristics such as the maxillary canines (see Robinson 1956 for the Australopithecines, and Pilbeam and Simons 1965 for evidence that this process had begun at least by the time of Ramapithecus).

(3) Relative brain size of the Australopithecines was certainly larger than any of the apes, which indicates some change in maturation rate, mediated through hormonal means (interaction between receptor tissue and hormones).

(4) The ontogenetic and experimental neurological evidence discussed on pages 5 and 6 involved hormonal mediation. The growth hormone and thyroid removal studies seem unequivocal in this regard.

The development of bipedalism suggests that these early hominids had the ability to travel long distances, perhaps in relation to hunting, scavanging, finding water supplies, or even materials for stone tools (see, for example, Hewes 1961, Robinson 1962, and Washburn 1959, 1960). Whatever the actual relationships, these early experiments in a new social and cognitive order might have involved environments in continual flux. The appreciation of this flux and increased complexity would have meant better strategies to deal with the complexity. At the same, the complexity would have increased, encouraging selection for better neural and social structures to handle the new demands. The cooperative forms of behavior (hunting, toolmaking, rules, and symbolism) involved increasing complexity for future generations in terms of deviation-amplification and accumulation. This set the process of orthoselection for neural structures and social forms. Thus the initial-kick would have involved a new social and cognitive order based more on cooperation and lessened aggression.[8] These changes could have been mediated through a series of physiological shifts which would also have had effects on neural structures described under (4); increased neuron size, decreased neural density, and increased branching of dendrites, increased interconnections and increased efficiency in adaptive problem-solving ability, i.e., complexity-management.

In sum, I am saying that one aspect of human evolution, complexity-management, has involved these five variables in mutual-causal amplification of deviation framework. It should be appreciated that some of the discussion in Sections 1 through 5 have been artificial. Our language does not allow us an efficient way to talk about mutual-causal interactions, but rather linear cause-effect statements.

---

[8] It is necessary to add a note of caution regarding this general picture of aggressiveness and cooperation. When I discuss an increase in the cooperative aspects of behavior, I do not mean to imply necessarily that man became less aggressive than any other animal. It is the focus of aggression and the way it is mediated within human groups that has changed. I submit, on the contrary, that man has heightened aggression, at least in the sense that arbitrary symbol configurations can elicit aggressiveness. Man also has an elaborate set of rules, social and internal (cognitive) which he uses to deal with aggression. One way is to displace the aggression that builds up from the nature of primary and secondary social ties onto other groups. Another way is to exact upon himself the aggression. I am suggesting (from an unpublished manuscript on sexual dimorphism in primates) that terrestrial species have a lower threshold, generally, to aggression, than arboreal species. The early hominids underwent a remarkable reduction of sexual dimorphism, which I suggest is tied into certain aspect of their social adaptations.

Starting from the viewpoint of individual variability, it was recognized that selection for plasticity of response was also selection for individual variability. If any aspect of individual variability in a gregarious species becomes ascendant and fixed through natural selection, the course of future selection is structured. Selection for the biological apparatus which can deal effectively with the environment generates a more complex environment which acts back on the biological structure, and so on. The process is one of positive feedback; and I have suggested that this aspect of general feedback must be emphasized, since change in human evolution has been rapid and extensive despite the ingenuity of homeostatic structures at the organ level. Aspects of an initial-kick, which provided the essential basis for the on-going positive feedback and orthoselection, were placed in a pleiotropic framework cementing behavioral and structural features together, such as sexual dimorphism, aggresivity, maturation times, and expansion of cerebral cortex.

EPILOGUE

I have defined the "initial-kick" in terms of a new social order based on an interrelated set of behavioral and structural changes mediated through hormonal processes. It should be made clear that the physiological and neural correlates of these changes probably continued to change after the basic pattern became established. For example, growth patterns leading to longer maturation times, increase in absolute body size, and increase in relative brain size continued throughout the Pleistocene. With the growth of the brain, there was a diminution of cranio-facial skeletal ruggedness, elaboration of hunting technologies, and possibly an increase in size of social aggregates in economic cooperation. In terms of the archaeological record, there does not appear to be any evidence for a significant change in cognitive processes, unless these would include magico-religious practices and art. From this time in the late Pleistocene, the cultural complex becomes staggering in terms of proliferation and invention; yet these last 40,000 years are not correlated with any significant outward biological changes that appear in the skeletal system or, as far as we know, the brain. The point I am stressing is that the divorcement between biological and cultural change has grown greater with time. Aside from blood groups, malarial resistance, stature, brachycephalization, tooth morphology, etc., neural complexity can be dropped from the framework, at least in the terms discussed in this paper. To what extent functional attributes can be deleted is another matter. Brains are not closed systems, but are programmed throughout the life of their possessors. Perhaps, in functional terms that we cannot yet measure, the neural operations of modern man in mass society are different from those of his Aurignacian ancestors. Perhaps in modern mass societies different temperaments are more successful in terms of reproduction than in earlier times or in other extant societies. No structural evidence exists on this point, however. Does this negate the deviation-amplification framework, and the feedbacks between structure and environment discussed throughout this paper? Why this apparent biological homeostasis? In the first place, the problem cannot be answered adequately in a few pages. Secondly, the changes discussed in this paper took something over two-million years. Forty-thousand years is but 1/50 of such a time span. Finally, the framework provided for the changes mentioned in this paper was not presented as some sort of finalistic schema. Perhaps the picture has changed basically with the development of such high levels of environmental complexity. Perhaps the picture is best represented as one environment acting on another, where human beings are simply mediating devices in an essentially new game. Yes, the environments are changing, but is Man? Gene frequencies are changing with every birth and death in the world, but there is no way to read back from these events to the types of structures discussed here.

Returning to the early hominid phase, it should be apparent that the five variables can be discussed only in the general terms already outlined. If an attempt at microanalysis is made, any factor can serve as an "initial-kick" for the other variables. The microanalysis may essentially be impossible, precisely because the framework is one of mutual-causal relations. What, then, is the value of this framework? For one thing, it puts neural structures into terms that are more amenable to correlations with behavior and synthesis with the fossil and archaeological records. It underlines the fact that environments are what the organism does to them, and this aspect is all important for our understanding of what Man is and how he got that way. The design features of Hockett, such as productivity, displacement, arbitrariness, take on additional meaning as process statements regarding the generation of the improbable. It further underlines thrust or momentum in hominid evolution, which is directional, but not by dint of supernatural or finalistic agencies. Mutations were surely random, providing the basis for somatic and behavioral changes, but the selection pressures were not. Finally, the framework permits explanation of the curious fact that widely spread hominid populations evolved in the same directions, yet with diversity. It becomes evident that the diversities are not important in the causal sense, but are only basic variations of the same theme, complexity-generation and complexity-management. Man makes himself, but it remains to be seen how well he does it.

REFERENCES

ALLEE, W. C. (1951) Cooperation Among Animals. New York: Henry Schuman.

ALTMANN, S. (1962) A field study of the sociobiology of Rhesus monkeys, Macaca mulatta. Ann. N.Y. Acad. Sci., 102, 2, 338-435.

ARBIB, M. A. (1965) Brains, Machines, and Mathematics. New York: McGraw-Hill.

BARASA, A. (1960) Shape, size, and density of neurons of the cerebral cortex in mammals of different body size. (Italian Text). Zeitschr. Zellforsch., 53, 1, 69-89.

BARLOW, H. B. (1958) Sensory mechanisms, the reduction of redundancy and intelligence. In Nat. Phys. Lab. Symp. #10. Mechanisation of Thought Processes, Vol. 2, London: H.M.S. Office, pp. 535-574.

BATESON, G. (1936) Naven. 2nd Ed., 1958. Stanford: Stanford Univ. Press paperback.

BIRDWHISTLE, R. L. (1952) Introduction to Kinesics. Louisville: Univ. of Louisville Press.

BOK, S. T. (1959) Histonomy of the Cerebral Cortex. Amsterdam: Elsevier.

BONIN, G. von. (1963) The Evolution of the Human Brain. Chicago: Univ. of Chicago Press.

BONIN, G. von and BAILEY, P. (1961) Patterns of the Cerebral Isocortex. Primatologia, Bnd II, Teil 2, Lieferung 10.

BRIZZEE, K. R. and JACOBS, L. A. (1959) Postnatal changes in volumetric and density relationships of neurons in cerebral cortex of cat. Acta Anat., 38, 291-303.

BRODMANN, C. (1912) Neue Ergebnisse uber die vergleichende histologische Lokalisation der Grosshirnrinde mit besonderer Berucksichigung des Stirnhirns. Anat. Anzeiger, Bnd. 41 (Supplement).

BRODY, H. (1955) Organization of the cerebral cortex. III. A study of aging in the human cerebral cortex. J. Comp. Neurology, 102, 511-556.

BROWN, J. (1958) Information, redundancy, and decay of the memory trace. In Nat. Phys. Lab. Symp. #10. Mechanisation of Thought Processes, Vol. 2. London: H.M.S. Office, pp. 729-752.

BROWN, R. and LENNEBERG, E. (1954) A study in language and cognition. J. Abnorm. Soc. Psychol., 49, 454-62.

CASPARI, E. (1961) Some genetic implications of human evolution. In Social Life of Early Man, S. L. Washburn (ed.), pp. 267-77. Viking Fund Publ. in Anthrop., No. 31.

CLARK, W. E. LeGROS. (1961) The Humanity of Man. Brit. Advanc. Sci., 18, 213.

CLENDINNEN, B. G. and EAYRS, J. T. (1961) The anatomical and physiological effects of prenatally administered somatotrophin on cerebral development in rats. J. Endocrinol., 22, 183-193.

COLLIAS, N. E. (1944) Aggressive behavior among vertebrate animals. Physiol. Zool., 17, 83-123.

CONEL, J. L. (1939-1963) The Postnatal Development of the Human Cerebral Cortex. Vols. I-VIII. Cambridge, Mass.: Harvard Univ. Press.

COON, C. S. (1950) Human races in relation to environment and culture with special reference to the influence of culture upon genetic changes in human populations. In Cold Spring Harbor Symposium on Quantitative Biology, 15.

COUNT, E. W. (1958) The biological basis of human society. Amer. Anthrop., 60, 1049-85.

________. (1964) Comments on Hockett and Ascher's "The Human Revolution." Current Anthropology, 5, 156-157.

DART, R. (1956) The relation of brain size and brain pattern to human status. S. Afr. J. Med. Sci., 21, 23-45.

DEMPSEY, E. W. (1951) Homeostasis. In Handbook of Experimental Psychology, S. S. Stevens (ed.). Ch. 6, 209-35. New York: Wiley.

DeVORE, I. (ed.) (1965) Primate Behavior: Field Studies of Monkeys and Apes. New York: Holt, Rinehart and Winston.

DeVORE, I. and WASHBURN, S. L. (1963) Baboon ecology and human evolution. In African Ecology and Human Evolution, F. C. Howell and F. Bourliere (eds.), pp. 335-367. Viking Fund Publ. in Anthrop., No. 36.

DIAMOND, M. C., KRECH, D. and ROSENZWEIG, M. R. (1964) The effects of enriched environment on the histology of the rat cerebral cortex. J. Comp. Neurol., 123, 111-119.

DOBZHANSKY, T. (1962) Mankind Evolving. New Haven: Yale Univ. Press.

EAYRS, J. T. (1960) Functional correlates of modified cortical structures. In Structure and Function of the Cerebral Cortex, D. B. Tower and J. R. Schade (eds.). Amsterdam: Elsevier, pp. 43-50.

EAYRS, J. T. and GOODHEAD, B. (1959) Postnatal development of the cerebral cortex in the rat. J. Anat., 93, 385-402.

EKMAN, P. (1965) Communication through nonverbal behavior: A source of information about an interpersonal relationship. In Affect, Cognition, and Personality, S. S. Tomkins and C. E. Izard (eds.). New York: Springfield Publ. Co., pp. 390-443.

ERP TAALMAN KIP, M. J. v. (1938) Lichaamsgrotte en hersenschors. Batavia Groningen: Noordhoff.

ETKIN, W. (1954) Social behavior and the evolution of man's mental faculties. Amer. Naturalist, 88, 129-43.

________. (1963) Social behavioral factors in the emergence of man. Human Biology, 35, 299-310.

FIELDS, W. S. and ABBOTT, W. (eds.). (1963) Information Storage and Neural Control. Springfield, Ill.: C. C. Thomas.

GAITO, J. (ed.). (1966) Macromolecules and Behavior. New York: Appleton, Century, & Crofts.

GARN, S. M. (1963) Culture and the Direction of Human Evolution. Human Biology, 35, 221-236.

GEERTZ, C. (1962) The growth of culture and the evolution of mind. In Theories of the Mind, J. M. Scher (ed.). New York: Free Press of Glencoe, pp. 713-40.

GEORGE, F. H. (1962) The Brain as a Computer. Oxford: Pergamon Press.

GERARD, R. W. (1959) Brains and Behavior. In The Evolution of Man's Capacity for Culture, J. Spuhler (ed.). Detroit: Wayne State Univ. Press, pp. 40-53.

__________. (1960) Neurophysiology: an integration. In Handbook of Physiology, J. Field, H. Magoun, and V. Hall (eds.), Sect. I, Vol. 3: Neurophysiology, pp. 119-1966.

GESCHWIND, N. (1964) Development of the brain and evolution of language. Georgetown Univ. Monograph Series on Language and Linguistics, 17, 155-170.

__________. (1965) Disconnexion syndromes in animals and man. Brain, 88, 237-294; 585-644.

HALE, E. B. (1962) In The Behaviour of Domestic Animals, E. S. H. Hafez (ed.). Baltimore: Williams and Wilkins, Ch. 2.

HALL, E. T. (1959) The Silent Language. New York: Premier Books.

HALL, K. R. L. (1965) Aggression in monkey and ape societies. In J. D. Carthy and F. J. Ebling (eds.). The Natural History of Aggression. New York: Academic Press, pp. 51-64.

HALL, K. R. L. and DeVORE, I. (1965) Baboon social behavior. In DeVore (1965) Ch. 3, 53-110.

HALLOWELL, A. I. (1956) Structural and functional dimensions of a human existence. Quart. Rev. Biol., 31, 88-101.

__________. (1960) Self, society, and culture in phylogenetic perspective. In Evolution After Darwin, S. Tax (ed.), Vol. 2, 309-372.

__________. (1961) The protocultural foundations of human adaptation. In Social Life of Early Man, S. L. Washburn (ed.). Viking Fund Publ. in Anthrop., No. 31, pp. 236-255.

HARLOW, H. F. and M. K. (1962) Social Deprivation in Monkeys. Sci. Amer., 207, 137-46.

HAUG, H. (1958) Quantitative Untersuchungen An Der Sehrinde. Stuttgart: G. Thieme.

__________. (1960) Die quantitativen Zellvolumenverhaltnisse der Hirnrinde. In Structure and Function of the Cerebral Cortex, D. B. Tower and J. P. Schade (eds.). Amsterdam: Elsevier, pp. 28-35.

HEBB, D. O. (1949) The Organization of Behavior. New York: Wiley.

__________. (1955) Drives and the CNS. Psychol. Rev., 62, 243-54.

HEBB, D. O. and THOMPSON. (1954) The social significance of animal studies. In Handbook of Social Psychology, Vol. 1, G. Lindzey (ed.). Reading, Mass.: Addison-Wesley, 532-62.

HESS, E. H. (1965) Ethology: An approach toward the complete analysis of behavior. In New Directions in Psychology, Vol. 1, E. Gallanter, et al. (eds.). New York: Holt, Rinehart & Winston.

HEWES, G. W. (1961) Food transport and the origin of hominid bipedalism. Amer. Anthrop., 63, 687.

HILD, W. and TASAKI, I. (1962) Morphological and physiological properties of neurons and glial cells in tissue cultures. J. Neurophysiol., 25, 277-304.

HOCKETT, C. F. (1960) Logical considerations in the study of animal communication. In Animal Sounds and Communication, W. Lanyon and W. Tavolga (eds.). Am. Inst. Biol. Sci., Wash., D.C., pp. 393-430.

HOCKETT, C. F. and ASCHER, R. (1964) The human revolution. Current Anthrop., 5.

HOLLINGSHEAD, A. B. and REDLICH, F. C. (1958) Social Class and Mental Illness: A Community Study. New York: Wiley.

HOLLOWAY, R. L., Jr. (1964) Some Aspects of Quantitative Relations in the Primate Brain. Unpubl. Doctoral Dissertation. Univ. of California, Berkeley.

__________. (1966a) Cranial capacity, neural reorganization, and hominid evolution: a search for more suitable parameters. Amer. Anthrop., 68, 103-121.

__________. (1966b) Dendritic branching in rat visual cortex: effects of extra environmental complexity and training. Brain Research, 2, 393-396.

__________. (1966c) Cranial capacity and neuron number: critique and proposal. Amer. J. Physical Anthrop., 25, 305-314.

HYDEN, H. (1962) A molecular basis of neuronglia interaction. In Macromolecular Specificity and Biological Memory, F. O. Schmitt (ed.). Cambridge, Mass.: M.I.T. Press, pp. 55-69.

JERISON, H. (1963) Interpreting the evolution of the brain. Human Biology, 35, 263-291.

KAWAI, M. (1958) On the rank system in a natural group of Japanese monkeys. Primates, 2, 2, 111-148 (in Japanese).

LASHLEY, K. S. (1950) In search of the engram. Sympos. Soc. Exper. Biol., 4, 454-482.

LENNENBERG, E. H. (1964) A biological perspective of language. In New Directions in the Study of Language, E. H. Lennenberg (ed.). Cambridge, Mass.: M.I.T. Press, pp. 65-88.

LURIA, A. R. (1961) The Role of Speech in the Regulation of Normal and Abnormal Behavior. New York: Pergamon Press.

McCLEARN, G. E. (1963) Genotype and mouse behaviour. In *Genetics Today,* Vol. 3, 795-805. Proc. Internat. Congr. Genet. Oxford: Pergamon Press.

McCULLOCH, W. S. (1958) Agatha Tyche: of nervous nets—the lucky reasoners. In Nat. Phys. Lab. Symp. #10, *Mechanisation of Thought Processes*, Vol. 2, 611-633. London: H.M.S. Office.

_________. (1963) Anastomotic nets combating noise. In *Information Storage and Neural Control,* W. S. Fields and W. Abbott (eds.). Springfield, Ill.: C. C. Thomas, pp. 283-296.

MARUYAMA, M. (1963) The second cybernetics: deviation-amplifying mutual-causal processes. *Amer. Sci.*, 51, 164-179.

MARLER, P. (1965) Communication in monkeys and apes. In *Primate Behavior,* I. DeVore (ed.), pp. 544-584.

MASON, W. A. (1965) The social development of monkeys and apes. In *Primate Behavior,* I. DeVore (ed.), pp. 514-543.

MILLER, G. A., GALLANTER, E., and PRIBRAM, K. H. (1960) *Plans and the Structure of Behavior.* New York: Henry Holt.

NATIONAL COMMITTEE AGAINST MENTAL ILLNESS, INC. (1957) "What Are the Facts About Mental Illness?"

PETERS, V. B. and FLEXNER, L. B. (1950) Biochemical and physiological differentiation during morphogenesis. *Amer. J. Anat.*, 86, 133-61.

PILBEAM, D. R. and SIMONS, E. L. (1965) Some problems of Hominid classification. *Amer. Sci.*, 53, 237-259.

PRIBRAM, K. (1958) Comparative neurology and the evolution of behavior. In *Behavior and Evolution,* A. Roe and G. G. Simpson (eds.). New Haven: Yale Univ. Press, pp. 140-64.

PURPURA, D. P., CHARMICHAEL, M. W., and HOUSEPIAN, E. M. (1960) Physiological and anatomical studies of development of superficial axodendritic synaptic pathways in the cortex. *Exper. Neurol.*, 2, 324-47.

RENSCH, B. (1954) Relation between the evolution of central nervous functions and body size of animals. In *Evolution as a Process,* J. Huxley, H. C. Hardy, and E. B. Ford (eds.). London: Allen & Unwin, pp. 181-200.

_________. (1959) Trends toward progress of brains and sense organs. Cold Spring Harbor *Symposium on Quantitative Biology,* Vol. 24, 291.

ROBINSON, J. T. (1956) The Dentition of the Australopithecinae. Transvaal Museum Memoir, No. 9, Pretoria.

_________. (1962) The origin and adaptive radiation of the Australopithecinae. In *Evolution und Hominisation,* G. Kurth (ed.). Stuttgart: G. Fischer, pp. 120-140.

ROSE, A. (ed.) (1955) *Mental Health and Mental Disorder.* New York: W. W. Norton.

ROSENZWEIG, M. R., KRECH, D., BENNETT, E. L., and DIAMOND, M. C. (1962) Effects of environmental complexity and training on brain chemistry and anatomy: a replication and extension. *J. Comp. and Physiol. Psychol.*, 55, 429-37.

SCHADE, J. P. and BAXTER, C. F. (1960) Changes during growth in the volume and surface area of cortical neurons in the rabbit. *Exper. Neurol.*, 2, 158-78.

SCHADE, J. P. and VAN GRONINGEN, W. B. (1961) Structural organization of the cerebral cortex. *Acta Anat.*, 47, 74-111.

SCHALLER, G. B. (1965) The behavior of the mountain gorilla. In DeVore (ed.), pp. 324-67.

SCHALLER, G. B. and EMLEN, J. T. (1963) Observations on the ecology and social behavior of the mountain gorilla. In *African Ecology and Human Evolution,* F. C. Howell and F. Bourliere (eds.). Viking Fund Publ. in Anthrop. #36, pp. 368-384.

SCOTT, J. P. (1958) *Aggression.* Chicago: Univ. of Chicago Press.

SCOTT, J. P. and FULLER, J. L. (1964) *Genetics and the Social Behavior of the Dog.* Chicago: Univ. of Chicago Press.

SECKEL, H. P. G. (1960) *Birdheaded Dwarfs: Studies in Developmental Anthropology Including Human Proportions.* Springfield, Ill.: C. C. Thomas.

SHARIFF, G. A. (1953) Cell counts in the primate cerebral cortex. *J. Comp. Neurol.*, 98, 381.

SHOLL, D. A. (1956) *The Organization of the Cerebral Cortex.* London: Methuen & Co.

SIMMEL, G. (1955) *Conflict and the Web of Group Affiliations.* Trans. by K. H. Wolff and R. Bendix (from Ch. 4. of Simmel's 1908 *Soziologie*). New York: Free Press (paper).

SIMPSON, G. G. (1949) *The Meaning of Evolution.* New Haven: Yale Univ. Press.

SOLOMON, P. (ed.) (1961) *Sensory Deprivation.* Cambridge, Mass.: Harvard Univ. Press.

SPUHLER, J. N. (ed.) (1959) *The Evolution of Man's Capacity for Culture.* Detroit: Wayne State Univ. Press.

STRAUS, W. L. (1953) Comments in Chapter 15, pp. 262-265, in *Reappraisal of Anthropology Today,* S. Tax (ed.). Chicago: Univ. of Chicago Press.

TAPPEN, N. (1965) Review of "Culture and the Evolution of Man," M. F. Ashley-Montagu (ed.). *Amer. Journ. Phys. Anthrop.*, 23, 437-438.

TAPPEN, N. C. (1953) A mechanistic theory of evolution. *Amer. Anthrop.*, 55, 605-07.

THORPE, W. H. (1963) *Learning and Instinct in Animals.* London: Methuen, 2nd Ed.

TOBIAS, P. V. (1965) Early man in East Africa. *Science,* 149, 22-33.