Farland reviews this literature in the context of feeding behavior viewed as a component of the mechanism for metabolic homeostasis.

Another attack on the generality of currently accepted categorizations of learning comes from psychologists working on the phenomenon of auto-shaping. A hungry pigeon will come to peck a response key if the key is illuminated just prior to food presentation, even though food presentation is not contingent on pecking. B. R. Moore and H. M. Jenkins present their extensive experiments on this phenomenon, which blurs the distinction between Pavlovian and operant conditioning. S. J. Shettleworth and P. Sevenster present examples, using hamsters and sticklebacks, of the differential effectiveness of certain reinforcers for certain behaviors. The notion that any arbitrary response can be associated with any reinforcer is simply no longer tenable.

The final section of the book documents a variety of situations in which specialized learning mechanisms appear to operate in man. The formulations of Piaget are considered by A. S. Etienne and H. Sinclair, and Etienne indicates how one of the signposts of cognitive development in infants—the object concept—can be studied comparatively in several animal species. The analysis of developmental constraints and predispositions in human learning is also considered by S. J. Hutt and the special characteristics of language learning by J. C. Marshall and J. Ryan.

The relationship between psychology and ethology has passed through several phases, which Niko Tinbergen recently (*Psychology Today*, March 1974) characterized as follows:

At first you ignore the other approach, because it is uncomfortable to contemplate. Then you criticize. That is a good sign, because it means that you have an interest in each other. Then you begin to collaborate. In the final phase, you say "It's all so self-evident that we don't need to talk about it any more."

As the studies in this volume witness, the study of animal learning is in stage three, and represents one of the most fruitful syntheses of the approaches of psychology and behavioral biology.

The book presents a very important and useful set of insights into the factors governing the expression of learning in animals. Physiologists on safari in the interneuron jungle searching for the elusive engram would do well to consider what tasks their animal may

have evolved specialized mechanisms to learn. This strategy recently made it possible to demonstrate one-trial food aversion learning in a terrestrial mollusk whose central nervous system is amenable to detailed cellular analysis. Anyone working on the behavioral or physiological analysis of learning should consider this book—perhaps in conjunction with the treatment of the same matters in *Biological Boundaries of Learning*, edited by Seligman and Hager (Appleton, Century, Crofts, 1972)— required reading.

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On the Meaning of Brain Size

Evolution of the Brain and Intelligence. HARRY J. JERISON. Academic Press, New York, 1973. xiv, 482 pp., illus. $25.

The first step is to measure whatever can be easily measured. This is okay as far as it goes. The second step is to disregard that which can't be measured or give it an arbitrary quantitative value. This is artificial and misleading. The third step is to presume that what can't be measured easily isn't very important. This is blindness. The fourth step is to say what can't be easily measured really doesn't exist. This is suicide.—DANIEL YANKELOVICH (1)

This description of what its author calls the "McNamara fallacy" might, I believe, characterize a good bit of past and present biological research, and particularly some of the arguments presented in this interesting, but highly debatable, book by Jerison. I'm not sure the fourth step is actually taken, but a case can surely be made that the first three have been, and the beginnings of four.

This is a book about brain size more than brains per se. It deals with the evolution of brain size in almost all vertebrate taxa and its relationship to behavior ("biological intelligence") and to other variables such as body weight, neuron size and density, neuron numbers, glial/neural ratios, and dendritic branching. Those who have followed some of Jerison's earlier writings (2) will find nothing new in his philosophy here, but instead an expanded and more detailed approach to the use of brain weights and volumes to predict other, "more interesting" variables (or parameters) such as the numbers of "vital" and "extra" neurons in fossil animals.

One of the claims made on the dust

jacket is that this book "is quite possibly a landmark publication." I will agree here, for since Edinger's two marvelous publications (3) nothing has appeared in the English language which brings together so much of the paleoneurological evidence and which offers a number of theoretical positions that might be debated and tested. Whatever this reviewer's personal opinions of the merits of this book, it clearly deserves the most careful attention, thought, and additional research.

We are also told on the dust jacket (by T. Melnechuk) that the author is "stubborn about preferring his own methods of analysis and interpretation; honest about admitting his biases; generous in trying to perceive the good points in the work of friendly rivals." As a rival I would like to take special exception to the last comment, particularly as Jerison claims this book will be of particular interest to the anthropologist. Jerison has done a remarkable job of avoiding my own past criticism of his work, particularly my 1966 article (4). That he must have read it is clear from the discussions, but he does not cite it. In that article, I pointed out that the neuroanatomical evidence clearly indicated that during primate evolution there have been quantitative changes in the three major types of cortical tissue—agranular, eulaminate, and koniocortex—and that the evidence also indicated different neural densities for each of the three major regions. This would make the use of *one* density figure erroneous when applied within evolving lineages, such as the fossil hominids. In other words, I was concerned in that critique with the generation of fictional numbers. That concern has only been made stronger with the publication of this book, and

I shudder to think of current and future physical anthropologists who know nothing about the brain avidly trying to calculate for their textbooks just how many "extra" neurons were in the brains of *Homo habilis* or some other hominid species. I don't think they will have much success. Jerison has calculated numbers of "extra" neurons (N_c) for the hominids according to an equation $N_c = N - N_v$, where N_v is the number of "vital" neurons and the total number of neurons, N, is $8 \times 10^7 E^{2/3}$, E being brain weight. What is required, however, is an equation such as

$$N = (v_1)(nd_1) + (v_2)(nd_2) + (v_3)(nd_3)$$

where v_1, v_2, and v_3 refer to specific volumes of different cortex and nd_1, nd_2, and nd_3 refer to the specific neural density for each kind of cortex. I tried this in 1966 using Shariff's (5) data on different types of cortex volume in relation to Hebb's (6) A/S (association to sensory cortex) ratio and came out with figures different from Jerison's. I doubt that these results were much of an improvement, however, because Shariff combined areas 4 and 6 as sensory, and he was working on single specimens. But more to the point, there is very little agreement anywhere about densities or neuron numbers, let alone N_c, or "extras." Jerison has avoided this problem, ignoring, for example, Pakkenberg's (7) estimate of 2.6×10^9 neurons in a normal 1400-gram male brain. Jerison's derived N_c's run about 8×10^9. As I pointed out in 1966, the only empirical evidence for primates, based on actual histological counts, is Shariff's data. Jerison uses these for densities, but his neuron numbers are quite different from Shariff's. Now someone is in the fictional realm, and we have no guarantee that the order of differences between species is any truer through Jerison's mathematical derivations which do not agree with empirical data.

This question of fictional numbers deserves more discussion. For example, Jerison's main diagram which yields his basic formula for the relationship between brain and body weights, $E = 0.12\ P^{2/3}$, is based on Crile and Quiring's (8) data on 3581 vertebrate specimens representing 198 species. Jerison (pp. 42–49) explains that he chose only one pair of weights for each species, sometimes the average, but mainly one pair of values, the heaviest for the species reported, on

the assumption this would be "more representative of the full range of the phenotype than an average of trapped specimens" (p. 43). This is consistency to be sure, but does it best reflect reality? Do we lose information by this process? What about skewed distributions, which we know exist for cranial capacities?

It further turns out that Jerison's comparisons are based on eyeballing a principal axis to the convex polygons that has a slope of 2/3. Jerison claims this is more realistic and preferable to drawing axes by least-squares regression methods. He states on pp. 47–49 that he always finds that the mathematical analysis shows a slope close to 2/3. By setting all slopes to 2/3, one can then directly compare the k's, or coefficients, to arrive at encephalization estimates. Perhaps this is quibbling on my part, but what about the lost information from slopes not exactly 2/3? Why are the approximations preferable to the empirical data? If the facts differ, that is information to be analyzed.

This approach to convenience characterizes most of the book. Body weights for fossil vertebrates are calculated from a range of body-weight body-length regressions, which vary according to body habitus (pp. 52–54). This is ambitious perhaps, but it doesn't particularly help with possible fictitious numbers. When we come to consider hominid fossils, we discover that Jerison has relied almost exclusively on Tobias's (9) published brain-body weights data on the hominids. These are in the realm of guesswork and are surrounded by controversy. Using them you can reconstruct brain-body weight regressions with slopes varying between 0.2 to well over 1.0, even up to 2.4, depending on what weights you prefer. In fact, it is possible to draw regression lines of different slopes between different hominid lines, such as 0.66 between gracile australopithecines and *Homo habilis*, 1.0 from habilines to *Homo erectus*, and from there a slope of 1.9 to modern *Homo sapiens*, depending on your weight preferences. This whole question becomes more critical when we consider what these different slopes might mean in terms of selection pressures for increasing brain size. It is also of importance since Jerison claims (pp. 362, 396) that in primates, at least, there are no known correlations between brain and body weights within species. This probably is not true, as

analyses of Pakkenberg and Voigt's (10) data on Danish brains will show, as well as data for rhesus macaques, particularly when analyzed by partial correlations. The correlations are low, but significant.

More basic issues need to be examined than absolute numbers of nerve cells, however. Jerison makes a good case, I believe, for the use of brain weight and volume in looking at large-scale evolutionary comparisons, and surely added numbers of nerve cells in the cerebral cortex must have some relationship to behavioral adaptability, although I question whether behavioral adaptability can be as easily reduced to capacity to process information as Jerison seems to believe. Jerison's own bias can best be appreciated by considering this discussion (p. 81) of the concept of "reorganization of the brain," for which he cites no references:

In recent years there has been some emphasis on the reorganization of the brain in "higher forms" or in man. That emphasis is misplaced. It is likely that as we learn more about the wiring diagrams of various brains we will recognize more . . . differences. These differences should impress us no more than the behavioral differences that are much more easily observed. . . . Reorganization, on the other hand, corresponds to a notion of change associated with speciation. We should expect adaptations to various niches to be made possible by the evolution of appropriate structures and functions, and reorganizations of the brain would be no more than the neural equivalents of species-specific behavior patterns.

Of course the concept refers to species-specific adaptations at the terminal end, but these reorganizations also took place in earlier periods of lineages' evolutionary development. And the physical anthropologist, to whom this book is in part addressed, is interested in precisely this: just what is it that makes the human species what it is, and how did this come about, and when did it start? It is erroneous to attribute to me, as Jerison does (p. 388), the view that brain size or capacity is not suitable for studies of the evolution of the brain, a view that Jerison attempts to refute by distinguishing between cranial capacity as a "suitable parameter" and as a "statistic" that is used to estimate other parameters. My dissatisfaction with brain size alone refers specifically to the study of human evolution, not brain evolution in toto. Apparently Jerison does not understand my position, or the contexts in which cranial

capacity has been used. Cranial capacity has been (and still is being) used as a "parameter," rather than just a statistic, to explain human behavior in comparison to any other primate behavior. But the well-known cases of microcephalics capable of language, however impoverished, show fairly clearly that human behavior is not going to be related only to brain weight, the number of cortical neurons ("extra" or "vital"), glial/neural ratios, or dendritic branching, but to some aspects of organization of components or neural subsystems. Jerison may want to dismiss these unfortunately complex matters as mere species-specific epiphenomena, but to anthropologists, at least, they are the critical matters. Brain size is obviously an important statistic, but we will never understand human brain and behavioral evolution if we ignore species-specific organization. Indeed, how meaningful is it to say that between gorilla and chimpanzee males there is a matter of 0.24×10^9 "extra" neurons when between STS 60 and STS 5, two gracile australopithecines from Sterkfontein, South Africa, there is a difference of 0.39×10^9 "extra" neurons? Or a difference of 0.62×10^9 "extras" between male and female *Homo sapiens* (pp. 390–393)?

Here, then, is yet another problem. If there is a brain-body weight relationship between different classes, orders, or species of animals at about 0.66 exponent, and this relates to effectiveness of information processing, and there is another regular relation of these "statistics" between species (with an exponent of about 0.2 to 0.3), how is it possible to claim that there is no regular relationship *within* the species? In fact, there are relationships between brain and body weights within species. Pakkenberg and Voigt (*10*) showed this for *Homo* in a study of Danes, finding the relationship stronger between brain weight and body height than between brain weight and body weight. A partial correlational study in progress in my laboratory shows a much stronger relationship between brain and body weights when height, age, and brain/body weight ratios are controlled. If there is no regular relationship obtaining within the species between brain and body weights, and between brain weight and information-handling capacity, what are the driving forces or evolutionary dynamics that produce the lawful relationships between species or between

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higher taxa? Somewhere, there is a hiatus in explanations which claim a set of biological (functional) relationships at supraspecies taxon levels but deny such a relationship within the biological unit (the species) undergoing evolutionary change.

To return to the quotation at the beginning of this review, the fourth step, that of saying that what can't be easily measured doesn't exist, may have been taken. For example, one of the main arguments on which Jerison bases his dislike for the concept of reorganization, and his preference for the use of "biological intelligence" as a concept that can be related to brain size, is that "encephalization of function" is probably a fiction, and therefore should be dismissed from evolutionary arguments (pp. 11–12). Yet on p. 25 he uses both sensory integration and the flexibility and adjustability of behavioral response to this sensory information to talk about cortical function in cats and monkeys with respect to vision and hearing. Perhaps there is a semantic snarl here, but encephalization, or corticalization, of function cannot be so easily dismissed. The clinical and experimental work of the past 75 or more years suggests very securely that cortical lesions have more permanent and serious effects the higher the animal on the phylogenetic scale.

In this review I have tried to focus on a number of underlying assumptions and difficulties in the possible generation of fictional numbers. As we all know, much more quantitative neurohistological research needs to be done, particularly on primates. Lest the reader regard this review as only critical, I would like to emphasize that this book is a useful bringing together of sources and data and presents much substantial work and many provocative hypotheses which deserve the closest attention. Many of the middle chapters on birds, reptiles, amphibians, and primitive and advanced mammals should be of interest to both paleontologists and neuroanatomists. I believe Jerison has taken an advanced step in analyzing what is easy to measure, but I am afraid that as far as human evolution is concerned, he has also taken the wrong subsequent steps. We need much more information to get us out of the realm of fictional numbers we may be left in.

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Biomechanical Adaptations

Primate Locomotion. FARISH A. JENKINS, JR., Ed. Academic Press, New York, 1974. xii, 390 pp., illus. $34.

Locomotion figures prominently in most accounts of primate phylogeny and is integrally related to the complex social behavior and high levels of intelligence that characterize the order. Yet its analysis has been largely restricted to general observations and broad categorizations. A lack of sufficiently detailed behavioral and kinematic data has made the validity of various proposed phyletic models difficult to judge. This volume is a significant contribution toward the partial elimination of this deficiency in primate studies.

The majority of the 11 contributions are directed at the locomotion of subfossil and extant prosimians or paleogene primates. The general emphasis is thus on the role of locomotion in primate origins and early Cenozoic evolution. Sophisticated techniques (for example, cineradiography, electromyography, three-dimensional photoelastic analysis) are employed by several of the contributors. The basic approaches are largely kinematic or morphological or both. No kinetic data are presented.

The most significant dissent from prevailing general theory is to be found in the contribution by Cartmill. Here the "time-honored" generalization that primate chiridial modifications are attributable entirely to the arboreal substrate is carefully dissected and found to be an insufficient explanation of prosimian adaptation. A review of nonprimate arboreal adaptive strategies including those of marsupials and sciuroid rodents forms the basis of Cartmill's argument. Noting that a clawed manus allows an animal to subtend a