JAMES ARTHUR LECTURE ON
THE EVOLUTION OF THE HUMAN BRAIN
1955

CULTURE AND THE STRUCTURAL EVOLUTION OF THE NEURAL SYSTEM

FRED A. METTLER
Professor of Anatomy
College of Physicians and Surgeons
Columbia University

THE AMERICAN MUSEUM OF NATURAL HISTORY
NEW YORK: 1956

JAMES ARTHUR LECTURE ON
THE EVOLUTION OF THE HUMAN BRAIN

JAMES ARTHUR LECTURE ON
THE EVOLUTION OF THE HUMAN BRAIN
1955

CULTURE AND THE STRUCTURAL EVOLUTION OF THE NEURAL SYSTEM

FRED A. METTLER
Professor of Anatomy
College of Physicians and Surgeons
Columbia University

THE AMERICAN MUSEUM OF NATURAL HISTORY
NEW YORK: 1956

PREFACE

In 1931 the American Museum of Natural History received a bequest from Mr. James Arthur to establish an annual lecture on the evolution of the human brain. As a result the James Arthur Annual Lecture was established in 1932, with the late Professor Frederick Tilney as the first lecturer. No provision was made for publishing the lectures when the series was inaugurated, and none have been published since under the sponsorship of the foundation. The various lecturers were free to publish elsewhere if they wished. Some of them did, but others for one reason or another did not. Thus some of the lectures which were valuable contributions have not had the distribution they deserved. Moreover, it has been our experience after the delivery of each lecture that there is a considerable demand for published copies of it. It seemed desirable, therefore, even twenty-five years after its commencement to initiate a publication series of the lectures. I trust that the consequent lack of coincidence between the seriation of the lectures and the publications will not prove a nuisance to librarians.

I am happy, indeed, that this new venture can begin with Dr. Fred A. Mettler's stimulating lecture which he delivered in April, 1955. It is a good augury for its success.

Harry L. Shapiro

The American Museum of Natural History
New York, New York

JAMES ARTHUR LECTURES ON THE EVOLUTION OF THE HUMAN BRAIN

Frederick Tilney, *The Brain in Relation to Behavior;* March 15, 1932

C. Judson Herrick, *Brains as Instruments of Biological Values;* April 6, 1933

D. M. S. Watson, *The Story of Fossil Brains from Fish to Man;* April 24, 1934

C. U. Ariens Kappers, *Structural Principles in the Nervous System; The Development of the Forebrain in Animals and Prehistoric Human Races;* April 25, 1935

Samuel T. Orton, *The Language Area of the Human Brain and Some of its Disorders;* May 15, 1936

R. W. Gerard, *Dynamic Neural Patterns;* April 15, 1937

Franz Weidenreich, *The Phylogenetic Development of the Hominid Brain and its Connection with the Transformation of the Skull;* May 5, 1938

G. Kingsley Noble, *The Neural Basis of Social Behavior of Vertebrates;* May 11, 1939

John F. Fulton, *A Functional Approach to the Evolution of the Primate Brain;* May 2, 1940

Frank A. Beach, *Central Nervous Mechanisms Involved in the Reproductive Behavior of Vertebrates;* May 8, 1941

George Pinkley, *A History of the Human Brain;* May 14, 1942

James W. Papez, *Ancient Landmarks of the Human Brain and Their Origin;* May 27, 1943

James Howard McGregor, *The Brain of Primates;* May 11, 1944

K. S. Lashley, *Neural Correlates of Intellect;* April 30, 1945

Warren S. McCulloch, *Finality and Form in Nervous Activity;* May 2, 1946

S. R. Detwiler, *Structure-Function Correlations in the Developing Nervous System as Studied by Experimental Methods;* May 8, 1947

Tilly Edinger, *The Evolution of the Brain;* May 20, 1948

Donald O. Hebb, *Evolution of Thought and Emotion;* April 20, 1949

Ward Campbell Halstead, *Brain and Intelligence;* April 26, 1950

Harry F. Harlow, *The Brain and Learned Behavior;* May 10, 1951

Clinton N. Woolsey, *Sensory and Motor Systems of the Cerebral Cortex;* May 7, 1952

Alfred S. Romer, *Brain Evolution in the Light of Vertebrate History;* May 21, 1953

Horace W. Magoun, *Regulatory Functions of the Brain Stem,* May, 1954

CULTURE AND THE STRUCTURAL EVOLUTION OF THE NEURAL SYSTEM

Two propositions, considered more or less self-evident, have played prominent roles in the consideration of the evolutionary development of man. Indeed, it is often assumed that reference to these propositions is sufficient to decide any doubtful issue as to whether or not man's present structural condition represents an advance over the past. In the first place it has been widely asserted that the size of the brain has steadily increased in those biologic lines leading (and related) to man and that this process has continued until the present and will probably continue through the future. In the second place it is universally assumed that this is or would be a good thing, because, the argument runs, a large brain (especially one with a large frontal lobe) is positively correlated with a high order of intelligence, and the present state of man's development depends upon this alleged cerebral increase.

It will be necessary in the following pages to question the validity of these assumptions, which really are far from self-evident, for there are definite data demonstrating that the size of man's brain has not continued to increase to the present. Moreover, there is good reason to believe that useful or workable intelligence, as we employ the term in day-to-day terminology, is a general aspect of capacity for over-all neural efficiency rather than a localized brain function, and that, in view of the dependence of the individual upon learned cultural traits, the frontal lobe may not be an indispensable substrate for "intelligent" living. I hope then to present certain technical reasons which lead me to question whether *Homo sapiens* can profitably develop a significantly enlarged brain without first undergoing rather radical structural and physiologic alterations in other respects, for it is possible that the size of man's brain might prove to be a limiting factor not merely in his further structural evolution but even in his survival.

Finally I wish to emphasize the role that culture has played in protecting the individual from his natural environment on the one hand (and thus shielding him from the necessity of developing structural adaptations to it) and, on the other, of creating new environmental demands. I shall conclude with a brief inquiry into the nature of these demands and whether or not the nervous system may be expected to serve as the limiting factor in meeting them.

Has man's brain continued to increase in size and is brain size positively correlated with intelligence?

One of the basic diffiiculties in coming to a decision about the evolutionary trend of the brain is the fact that modern man's brain is far from constant in size, shape, or configuration. This situation has long been known, but people, and scientists are no exception, show a strong disinclination to pay attention to data that do not fit into a frame of reference in which the other data are more or less in concurrence (Craik, 1952).

Many years ago Vierordt (1893) brought together the brain-weight data for different geopolitical groups, which are shown here in table 1. In this table variations of well over 10 per cent in brain weight are obvious, not among markedly different races but among white Europeans. Various reasons could be advanced for such differences. They might be due to genotypic variability, having its basis in racial subvarieties and apart from other somatic variation, or they might be a general reflection of differences in corporeal size. (A variation according to sex is explicit in the table.) Again, such variation might be due to age or correlated with differences in intellectual capacity.

In a consideration of the relation of age to brain volume, which is closely related to brain weight, table 2 demonstrates that the brain, whereas it becomes larger with age, reaches its maximum gross size long before the body does and that, beginning around 50 years of age, it ultimately becomes absolutely smaller.

As a result of such an observation, one would expect that body weight would not be a very satisfactory index of brain size, and table 3 shows that beyond a certain point the relationship between these two variables may be of an inverse nature. Because weight is a poor indication of actual somatic development, stature and degree of muscular development should be correlated with

TABLE 1

Absolute Average Weights (in Grams) of Brains of Europeans Twenty to Eighty Years Old from Different European Politico-geographic Districts (from Vierordt, 1893)

Investigator	Source of Material	Male	Female
Krause	Hanover	1461	1341
F. Arnold	Grand Duchy of Baden	1431	1312
Reid	Scotland	1424	1262
Peacock	Scotland	1423	1273
Sims	England	1412	1292
Tiedemann	Grand Duchy of Baden	1412	1246
Quain	England	1400	1250
G. H. Bergmann	Hanover	1372	1272
Rud. Wagner	Mixed	1362	1242
Th. von Bischoff	Bavaria	1362	1219
Sappey	France	1358	1256
Huschke	Saxony	1358	1230
Hoffmann	Switzerland	1350	1250
Blosfeld	Russia	1346	1195
Clendinning	England	1333	1197
Dieberg	Russia	1328	1238
Boyd	England	1325	1183
Parchappe	France	1323	1210
Lelut	France	1320	—
W. Hamilton	Scotland	1309	1190
Meynert	Austria	1296	1170
Parisot	France	1287	1217
Weisbach	German-Austrian	1265	1112

TABLE 2

Relation Between Age and Volume of Brain

Age	Number of Cases		Volume of Brain (in Cc.)	
	Male	Female	Male	Female
0– 6 months	29	28	499	478
7–12 months	19	24	772	700
2 years	9	10	929	976
3 years	11	9	1123	1038
4 years	11	9	1190	1049
5– 6 years	8	11	1300	1147
7–10 years	9	12	1333	1204
11–15 years	9	10	1285	1213
16–19 years	13	10	1289	1099
20–29 years	73	43	1223	1148
30–39 years	74	59	1279	1193
40–49 years	77	60	1264	1164
50–59 years	80	57	1275	1146
60–69 years	84	65	1237	1143
70–79 years	70	55	1212	1088
80–89 years	10	23	1164	1072

TABLE 3

BRAIN WEIGHT CONSIDERED AS A PROPORTION OF TOTAL BODY WEIGHT (FROM VIERORDT, 1893, AFTER BISCHOFF)

Body Weight (in Kilograms)	Brain Weight Male	Female
20	—	4.47%
30	3.7 %	3.37%
40	2.98%	2.70%
50	2.5 %	2.29%
60	2.16%	1.99%
70	1.99%	—
80	1.59%	—

TABLE 4

WEIGHT OF THE BRAIN (ENCEPHALON) AND ITS SUBSIDIARY PARTS IN SANE PERSONS, ACCORDING TO SEX, AGE, AND STATURE (FROM DONALDSON, 1895)

(a, above average according to age; s, above average according to stature.)

	Age	Encephalon	Cerebrum	Cerebellum	Stem
MALES					
Stature 175 cm.	20–40	1409	1232	149	28
	41–70	1363	1192	144	27
and upward	71–90	1330	1167	137	26
Stature 172–	20–40	1360	1188	144	28
	41–70	1335	1164	144	27
167 cm.	71–90	1305	1135	142 s	28 a s
Stature 164 cm.	20–40	1331	1168	138	25
	41–70	1297	1123	139 a	25
and under	71–90	1251	1095	131	25
FEMALES					
Stature 163 cm.	20–40	1265	1108	134	23
	41–70	1209	1055	131	23
and upward	71–90	1166	1012	130	24 a
Stature 160–	20–40	1218	1055	137 s	26 s
	41–70	1212 s	1055	131	26 s
155 cm.	71–90	1121	969 s	128	24
Stature 152 cm.	20–40	1199	1045	130	24 s
	41–70	1205 a	1051 a	129	25 a s
and under	71–90	1122	974	123	25 a s

TABLE 5

WEIGHT OF THE BRAIN (ENCEPHALON) AND ITS SUBSIDIARY PARTS IN INSANE PERSONS, ACCORDING TO SEX, AGE, AND STATURE (FROM DONALDSON, 1895)

(a, above average according to age; s, above average according to stature.)

	Age	Encephalon	Cerebrum	Cerebellum	Stem
400 MALES					
Stature 175 cm.	20–40	1378	1192	156	30
	41–70	1354	1170	154	30
and upward	71–90	1333	1158	146	29
Stature 172–	20–40	1363	1186	149	28
	41–70	1305	1129	148	28
167 cm.	71–90	1305	1135 a	142	28
Stature 164 cm.	20–40	1299	1127	144	28
	41–70	1285	1119	139	28
and under	71–90	1216	1047	139	30 s a
325 FEMALES					
Stature 163 cm.	20–40	1220	1056	136	28
	41–70	1215	1053	134	28
and upward	71–90	1240 a	1076 a	136 a	28
Stature 160–	20–40	1189	1027	134	28
	41–70	1216 s a	1054 s a	135 s a	27
155 cm.	71–90	1171	1008	135 a	28 a
Stature 152 cm.	20–40	1141	986	128	28
	41–70	1194 a	1036 a	129 a	28 s a
and under	71–90	1135	985	123	27

variations in cerebral weight, but tables giving such information have not yet been developed. Because brain volume is obviously influenced by age, some correction for the latter factor must be introduced. Tables of this nature have long been available and show a definite positive correlation between brain weight and stature (table 4) when corrected for age (Donaldson, 1895; Dubois, 1914).

Table 4 may be compared with table 5 to see whether the size of the brain is correlated with condition of rationality. It will be observed that no significant difference is disclosed by comparison of these two sets of old figures. Although the validity of these figures has been abundantly contested in the years which have passed since they were compiled, no one has yet been able to bring for-

TABLE 6

BRAIN WEIGHTS (IN GRAMS) OF EMINENT MEN (FROM DONALDSON, 1895, TAKEN FROM MARSHALL AND MANOUVRIER)[a]

Age	Encephalic Weight	Eminent Men
39	1457	Skobeleff, Russian general
40	1238	G. Harless, physiologist
43	1294	Gambetta, statesman
45	1403	Assezat, political writer
45	1516	Chauncey Wright, mathematician
49	1468	Asseline, political writer
49	1409	J. Huber, philosopher
5[0]	1312	Seizel, sculptor
50	1378	Coudereau, physician
52	1358	Hermann, philologist
52	1499	Fuchs, pathologist
53	1644	Thackeray, novelist
54	1520	De Morny, statesman
54	1629	Goodsir, anatomist
55	1520	Derichlet, mathematician
56	1503	Schleich, writer
56	1485	Broca, anthropologist
57	1559	Spurzheim, phrenologist
57	1250	v. Lasualx, physician
59	1436	Dupuytren, surgeon
60	1533	J. Simpson, physician
60	1488	Pfeufer, physician
62	1398	Bertillon, anthropologist
62[?]	1415	Melchior Mayer, poet
63	1449	Lamarque, general
63	1332	J. Hughes Bennett, physician
63	1830	G. Cuvier, naturalist
64	1785	Abercrombie, physician
65	1498	De Morgan, mathematician
66	1512	Agassiz, naturalist
67	1502	Chalmers, preacher
70	1352	Liebig, chemist
70	1516	Daniel Webster, statesman
71	1207	Döllinger, anatomist
71	1349	Fallmerayer, historian
71	1390	Whewell, philosopher
73	1590	Hermann, economist
75	1410	Grote, historian
77	1226	Hausemann, mineralogist
78	1492	Gauss, mathematician
79	1254	Tiedemann, anatomist
79	1403	Babbage, mathematician
79	1452	Ch. H. Bischoff, physician
80	1290	Grant, anatomist
82	1516	Campbell, Lord Chancellor

[a] The entries in this table have been in part revised. Different methods have of course been employed in determining the several weights.

ward conclusive data that the brains of insane persons are customarily smaller or lighter than those of a corresponding "normal" population, although, of course, they may be so.

If we cannot explain variation in brain weight on the basis of rationality or its absence, we may ask whether weight variations not accounted for by sex, age, or body size can be explained on the basis of the possession of unusual intellectual capacities on the part of some of the population. A comparison of the values in table 6, which gives the weights of the brains of certain eminent individuals, with the weights shown in table 1 discloses a range of from 1226 to 1830 grams for eminent individuals between 39 and 82 years of age as compared with 1265 to 1461 grams for average values of samples taken from all over Europe. Moreover, the range encountered in eminence covers the average for insane persons of the same age groups (table 5).

Weidenreich (1946) gives the range of skull capacity for normal individuals in all races of modern man as being from 910 to 2100 cc. As the weight of one cubic centimeter of cerebral tissue is about unity (1.036 grams) and the brain generally occupies two-thirds of the total endocranial capacity, Weidenreich tacitly accepts a weight range of from 625 to 1450 grams as normal. With such figures it would be quite impossible to determine whether any sort of trend in cerebral size has been operative during the last half of the Pleistocene (figs. 1 and 2). Indeed, Weidenreich's range can have really very little meaning even in modern times unless we neglect entirely the influence of age which is operative over a much longer period with regard to skull size (fig. 3) than with regard to brain volume (table 2). We know, of course, that skull volume does not change appreciably between 50 and 90 years in normal individuals, but we have seen (table 2) that the brain does become atrophic. Now we observe that, although the volume of the brain does not increase notably after the first decade of life, head size does increase quite regularly through and even beyond the second decade. (The skull itself thickens in essentially the same period as skull size increases, if we accept Roche's, 1953, figures for the former dimension.) Estimates of endocranial capacity urgently require qualification, in terms of age at least, and it is impossible to be dogmatic about the age of skulls on the basis of the degree of suture closure (Cobb, 1954).

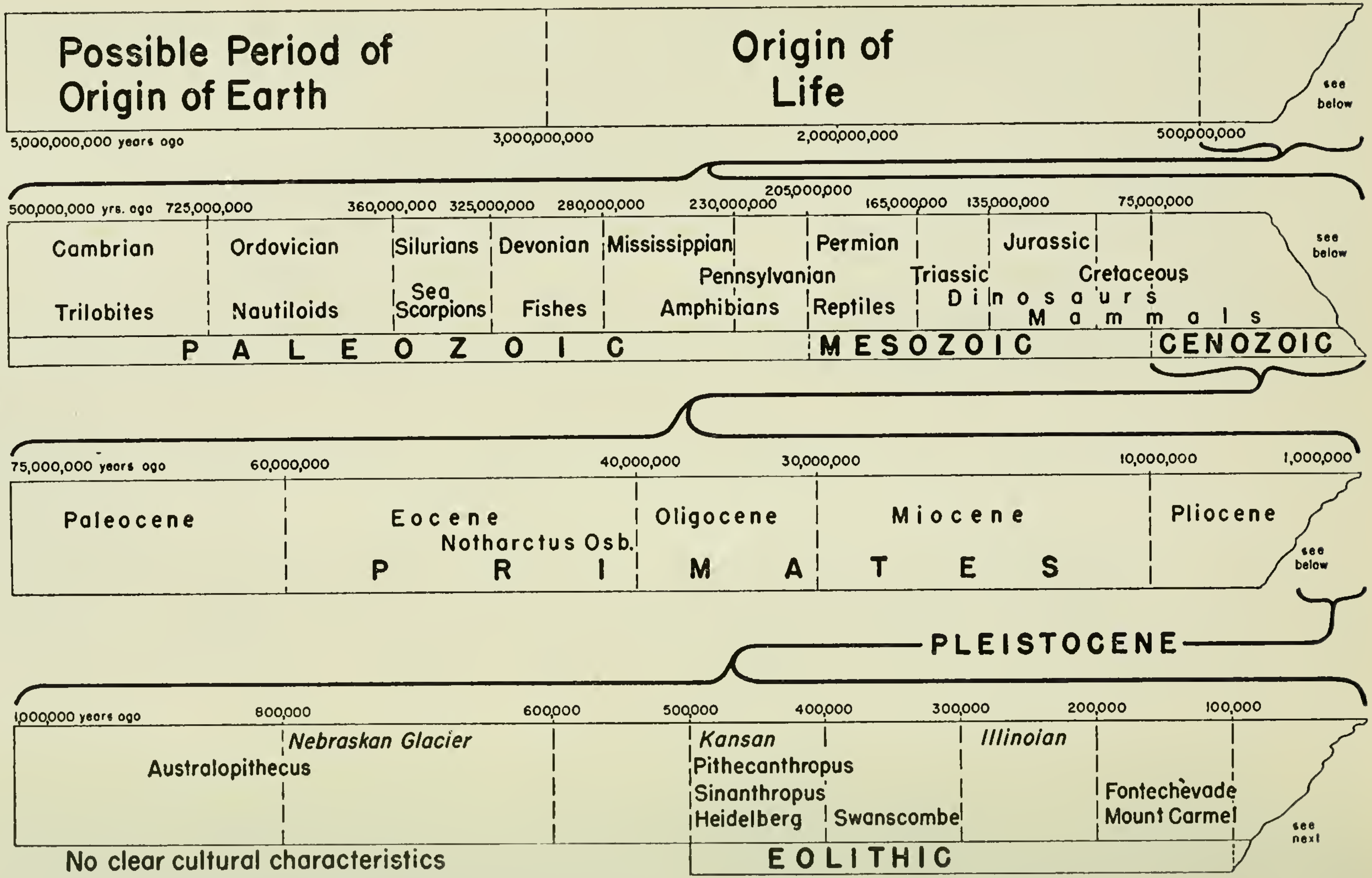

FIG. 1. Approximate time table for origin of man. In second bar graph, right terminal portion of first bar graph is enlarged, as shown by bracketed material. Terminal right portion again enlarged in third bar graph, and so on.

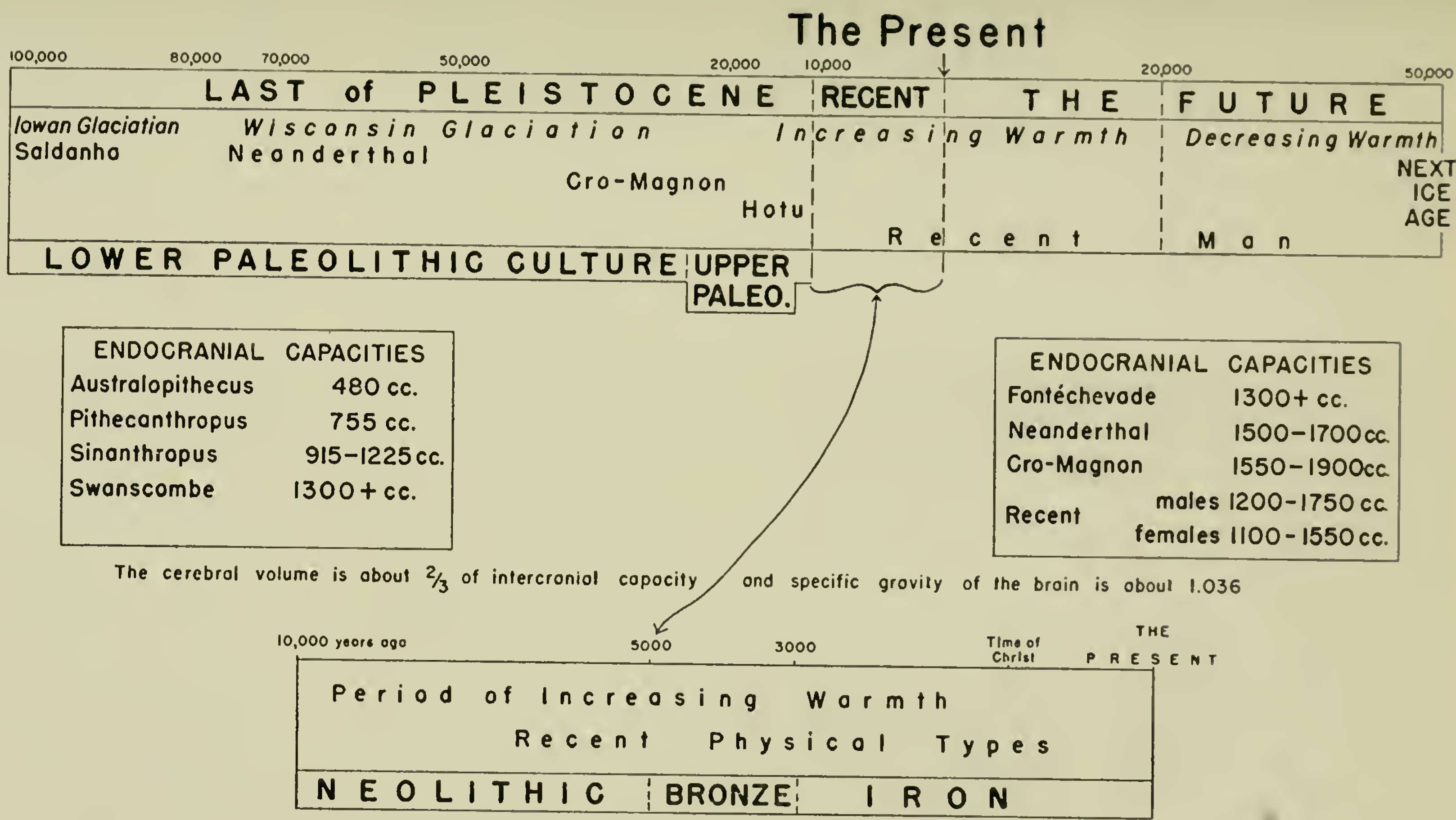

Fig. 2. Paleolithic and Recent periods, together with values of endocranial capacities of Pleistocene anthropoids and man. Terminal portion of last bar graph in figure 1 reproduced in enlarged form.

Measurements of the volume of the brain are themselves not beyond the possibility of misinterpretation. Physical anthropologists are well aware that large brains often hide dilated, water-containing ventricles. Even brain weights may suffer from artifactual error.

Table 7, the source of which shall remain unidentified by me, is an interesting example of incredible nonsense which might have been produced as the result of the operation of rather simple

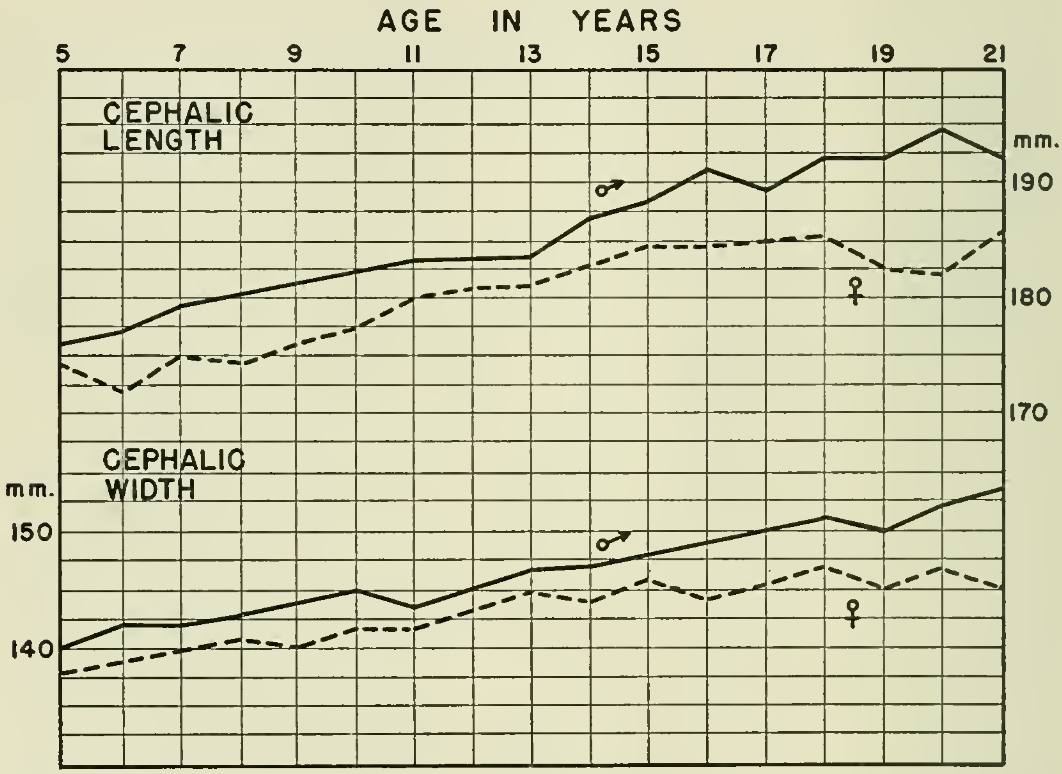

Fig. 3. Age changes in length and breadth of head (from Donaldson, 1895, after West).

artifactual principles, notably the post-mortem changes in weight and volume that brains undergo. It is surprising how easily startling results can be achieved as a consequence of artifact.

Some years ago Lewis Rowland and I set out to determine whether the brains of psychotic persons contain fewer cells per unit of cubic volume than do normal brains (Rowland and Mettler, 1949). When we compared our figures, obtained on material from living psychotics, with the values in the literature for normal brains, we came to the astonishing conclusion that the material from our psychotic individuals quite regularly exhibited not merely the same number of cells as, but *more* than, that obtained from normal humans! This curious paradox became explicable when we recalled that all the available figures for the "normal" brain were based upon post-mortem material, whereas our specimens had been obtained from living persons during psychosurgical operations. Although all tissues shrink during histological preparation, the post-mortem material had undergone an intervening swelling which occurred after death and which continued during fixation in the formalin.

Fixation-swelling gradually reverses itself, and the brain returns to and then passes below its original size and weight, depending upon how long it remains in a fixative. It is obvious that in instances in which an investigator was particularly interested in what he considered a rare or valuable brain he would study this as soon as it was adequately fixed and thus at the peak of its artifactual increase in size (von Economo, 1929). On the other hand, the brains of such ordinary folk as "laborers" would be left in a common crock to be weighed and measured at leisure—or, in other words, after they had passed the period of swelling and had begun to shrink. Further, such brains would probably have been removed by less careful assistants who may have ripped off the infundibulum and the membranes of the lateral and median cerebellar recesses so that, with shrinkage, all the contained ventricular fluid would run out to be replaced by air during the process of draining before weighing. I suspect forces of such a nature to have been operative in the development of the data shown in table 7.

TABLE 7

Example of Manner in Which Brain Weights can be Employed to Bolster an Hypothesis (see Text)

Occupation	Number of Cases	Weight	Percentage Over 1400 Grams
Day laborers	14	1410	
Laborers	34	1433	26.2
Attendants, supervisors	14	1436	
Tradespeople, craftsmen	123	1450	42.8
Minor officials	28	1469	48.5
Major officials, physicians	22	1500	57.2

Artifactual confusion due to solicitude for "rare" material can be even more profound. It is the custom, when histologic studies are contemplated, to perfuse the tissue to be removed. Until now we have had very little evidence about how such perfusion solutions influence quantitative studies of neural elements. Professor José Frontera-Reichert of the Department of Anatomy of the Medical School of Puerto Rico has recently shown me figures he has obtained from brains perfused with a variety of mixtures commonly employed for such a purpose. The results clearly indicate that we must reinterpret much "standard" data, for not only do all these fluids engender swelling, but the extent to which cytologic counts of surface elements, such as those in the cerebral cortex, are affected is variably influenced by the magnitude of the radius of the spherical substance which is the brain.

We come therefore to the necessity of concluding that brain size, whether determined by weight or volume, must, like that of other genotypically determined portions of the body, be considered in association not only with factors of handling and age and sex but also in connection with the general bodily characteristics of the individual from whence the material came. There is a direct correlation between the morphology of the brain and race, but that this correlation has any particular meaning in terms of what we call intelligence remains to be demonstrated and, as is shown below, it would be very surprising if a simple correlation could be derived. In attempting to arrive at an opinion as to whether or not modern man's brain has increased in size, we are necessarily forced to deal with endocranial capacities. From what is said above it is clear that a systematic body of data relating encephalon to endocranial capacity has not yet been developed, as this must necessarily be part of the still lacking correlation between brain and body type. Allowing for the shortcomings of the material, we can, however, see if what is available to us discloses any recognizable evolutionary trend.

Endocranial capacity shows variations with regard to sex and bodily development, and these seem to be like those influencing the size of the brain, but we have already commented that the age alterations in endocranial capacity are restricted to the first third of life and progress more slowly than does brain growth. We might expect that, because most primitive races were much smaller than modern man, they might be anticipated to have had smaller endocranial capacities, and this is true. Cro-Magnon man, who was larger than most moderns, had a larger endocranial capacity (fig. 2). In order for us to know whether or not the brains of any of our predecessors were relatively smaller, we should need to have more satisfactory estimates than we possess about the size and weight of many of these Pleistocene forms. Such estimates are only approachable in *Australopithecus, Sinanthropus,* and Cro-Magnon man. The data with regard to the so-called "giant" races of antiquity are confusing. The size of the bones and even of the teeth of the few widely scattered specimens which have given rise to the supposition that giant hominids existed are massive indeed, but the intracranial capacity, where it is determinable, is slight. Le Gros Clark (1954) has pointed out that these so-called giant forms were probably not unusually tall, and Straus (1954) has even suggested that they are merely pathological specimens. If we attempt to correct for differences in bodily magnitude, we do not emerge with very good evidence that man's brain has been increasing. Figures such as those shown in table 1 illustrate the obvious difficulties that arise in an attempt to correlate brain size with something as meaningless as nationality, for it is clear that genotypic variation is more significant than residence in a particular geopolitical locus. This same difficulty arises when we investigate endocranial capacities, for we have only fragmentary knowledge of the movements of genotypically distinct populations of the past. The recent finding, for example, of a group of fifth-century or sixth-century Finnish skulls averaging 1050 cc. for females and 1185 cc. for males of individuals only slightly over 5 feet tall (Blomquist, 1953) discloses remains quite different from others in the area and suggests that these smaller people may have been enslaved Lapps who were imported from another locus or were the remnants of an indigenous group, possibly to be identified with Procopius' Skrithiphinoi. Not all such older people were diminutives with small brain cases. Moreover, Tilly Edinger, who has delivered an earlier James Arthur Lecture, has demonstrated that if there is such a thing as evolution (increase in size and volume) of the brain, it is not related to body size. Among the only slightly taller tenth-century and eleventh-century Slavs of Bled (5½ feet as against 5 feet 2 or 3 inches for Blomquist's material) the intracranial capacity runs about 1437 cc. for males and 1310 cc. for females (Skerlj and Dolinar, 1950). We must therefore conclude that racial (genotypic) variation has long been, as it is now, the major factor in variation in intracranial capacity.

In some districts man has changed very little since the Paleolithic. Torgersen, Getz, Hafsten, and Olsen (1953) report a Bleivik paleolith that was about 5 feet 4 inches in height and quite similar to modern, mesocephalic Norwegians.

Endocranial casts therefore do not appear to support the notion that the brain of modern man has increased in size. Such casts do

TABLE 8

Relation Between Endocranial Capacity and Encephalic Volume, Absolute Encephalic Weight (in Grams), and Ratio of Weight of Encephalon to That of Body for Different Species

Form	Encephalic Volume/Skull Volume	Encephalic Weight	Encephalic Weight/Body Weight
Homo	*Ca.* 1/1.5	1100–2000	1/30–60
Pitheci			
Simia troglodytes	*Ca.* 1/1.66	209–463	1/14–213
Macacus	*Ca.* 1/2.2	56–145	1/25.8–108.6
Cebus capucinus	—	36–97	1/23–72
Hapale rosalia	*Ca.* 1/2	7.9	1/30
Prosimii, *Lemur*	*Ca.* 1/2.2	14.5–26.3	1/41
Chiroptera, *Vespertilio murinus*	*Ca.* 1/2.2	0.13–0.17	1/30–36.6
Carnivora			
Felis domesticus	*Ca.* 1/2.86	21–35	1/22–185
Meles taxus	*Ca.* 1/3	46–48	1/128–159
Canis familiaris	*Ca.* 1/2.5	54–125	1/37–358
Pinnipedia, *Phoca vitulina*	*Ca.* 1/2.5	302	1/242
Insectivora, *Erinaceus europaeus*	*Ca.* 1/3–4	0.18–3.6	1/43–390
Rodentia			
Mus rattus	*Ca.* 1/2.6–3	1.8–10.0	1/66–194
Lepus cuniculus (domesticated)	—	11.20	1/301
Ungulata			
Sus scrofa (domesticated)	*Ca.* 1/8	105–110	1/630–660
Equus caballus	*Ca.* 1/7	600	1/379–801
Elephas africanus	*Ca.* 1/8–10	2536–4000	1/125
Sirenia, *Manatus americanus*	—	*Ca.* 344	—
Cetacea			
Phocaena communis	—	468	1/38–93
Balaenoptera musculus	—	4700–6700	1/12,000–25,000
Edentata, *Dasypus setosus*	*Ca.* 1/3	18	1/141
Marsupialia, *Petaurus sciureus*	*Ca.* 1/2.2	3–66	1/40–800
Monotremata, *Echidna hystrix* and *Ornithorhynchus paradoxus*	—	16–32	1/80–130

show variations, but these variations are all explicable on the basis of age, sex, and the intermingling of genotypically different peoples. There is no evidence of a selective forward march from a smaller to larger brain. As soon as we come upon modern man, some of his representatives have as large a brain case as those of our contemporaries who we consider to be very satisfactorily equipped with regard to both quantity and quality of cerebral substance.

When it becomes apparent in science that a generally accepted hypothesis has really very little to support it, there is always a tendency to look around to discover who the culprit was who brought the suspect hypothesis into polite company. The background for the notion that man's brain has continued a process of progressive forward evolution up to the present is the same as that which lies behind all considerations of homologous structures, i.e., such structures have a lineage and have remained static, regressed, progressed, or have been diverted into quite different forms for performing essentially the same or very different functions. As man's brain is both absolutely and relatively quite large (table 8), it would seem clear that it has not merely failed to participate in the otherwise general degradation of the human form but has, in fact, undergone positive development. Such a conclusion seems sound enough with regard to the animal kingdom as a whole, but difficulty begins to develop when we draw near to man himself. It is not difficult to admit that the brain of man is superior to that found in fish, or in amphibians, or in reptiles, but even some rather lowly primates have relatively more brain than does man (table 8). The notion that there has been a continuous increase in the size of the brain from early, low primates, directly up to and through modern man is explicit in Broca's studies on intracranial volumes (Broca, 1862), but Retzius (1915) expressed, as the title of his article indicates, a distinct doubt about the validity of such an assumption. We have known for a relatively long period of time that the endocranial capacity of Neanderthal man (1500–1700+ cc.) compares very favorably with that of modern man and that Cro-Magnon man's intracranial capacity (1500–1900 cc.) surpassed present day man's, but these observations were ignored. It was emphasized that *Pithecanthropus* had a low endocranial capacity (775+ cc.) and, when *Sinanthropus* was also found to have a small brain case, the difficulties raised by the Neanderthal and Cro-Magnon forms were glossed over, although many serious writers failed to subscribe to Broca's thesis. Among these, besides Retzius, may be mentioned Keith (1925), Tilney and Riley (1928), and especially von Bonin (1934). Von Economo (1929) also expressed the opinion that intracranial capacity and intellectual ability need not parallel each other. Von Bonin expressed himself to the same effect by saying that "the conclusion that there has been a lessening of intelligence throughout the ages is hardly acceptable." (He was ridiculing an oblique statement of Martin's, 1928.) Von Economo (1929) and von Bonin both shifted the search for a correlation between intellectual capacity and structural substratum to a new area by suggesting that the active elements in the brain might increase without any increase in total cerebral dimensions. This argument had been implicit in Flechsig's (1896) and Ferrier's (1890) thesis (see below) that particular cerebral loci were of relatively greater importance than others for intellectual activity and in Parker's (1922) emphasis upon the neurocyte as the critical element.[1] It is the former point of view that has enjoyed popularity among physical anthropologists, as it is not possible to determine how many cells existed in a vanished brain but something can be said about the form of the head which contained that brain.

Does intellectual function reside in a particular aspect of cerebral configuration?

Those writers who take the position that man's neural system must necessarily have evolved structurally in a progressive fashion since Neanderthal man and who admit that no such progression can be substantiated on the basis of increase in size or weight are inclined to seek for modern "superiority" in some more subtle alteration. Weidenreich (1946), for example, sought such supe-

[1] This apparently self-evident consideration is not necessarily deictic. There is, for example, a gradual decrease with age in the number of cells per unit volume of cerebral cortex, as Conel (1939, 1951, 1947, 1951, 1955) has shown, and it seems reasonable to assume that a smaller number of strategically situated cells, provided with elaborate synapses, may be more significant than a larger number of inconsequential elements. It is even conceivable that greater metabolic efficiency on the part of a few cells would more than compensate for the potential advantage of number in a more abundant population.

riority in shape. He says, "The height of the Neanderthalian brain is, in all cases, clearly inferior to that of modern man." "Superiority," for Weidenreich, means an increase in prominence of the dorsal convexity above the locus of the junction of parietal and occipital lobes. Because this increase in dorsoventral diameter of the brain occurs in a structure the over-all size of which is not increased, it must be achieved by a reduction in the rostrocaudal diameter. Just why Weidenreich thought such a shift constituted an advance or "superiority" is far from clear. His reasoning devolves from the observation that the development of a more rounded form of the brain is a relatively late development, but Weidenreich must have been aware that the dorsoventral diameter of the human brain is not equally increased in all racial types and that it reaches its greatest natural prominence among plano-occipitals such as the Armenoids and Tyrolese (the Vedas also had a relatively higher cerebrum, as Sarasin has shown), but he did not discuss this situation. Instead he saw in dorsoventral enlargement the possibility that "association" areas might have been selectively enlarged (the fact that they had to be simultaneously rostrocaudally compressed is glossed over), and a highly theoretical speculation of G. Elliot Smith is quoted (somewhat irrelevantly) to provide substance to Weidenreich's hypothesis.

Flechsig was the first to emphasize the supposed relationship between intelligence and what he called "association areas," a term applied to those portions of the brain that are tardy in myelinating and that do not receive any primary afferent system or emit any long motor projection. That such regions perform associative functions is more than probable. That they perform such functions to a greater extent than other portions of the brain is open to question. There is no reason at all to suppose that what are called intellectual functions are specifically dependent upon them.

Weidenreich included in his figures (his fig. 79) endocranial casts from a gorilla, *Pithecanthropus erectus,* Neanderthal man, and modern man, but if he had used the endocranial cast of a chimpanzee it would have been apparent that this animal has a relatively greater dorsoventral cerebral diameter than does modern man. The difference in the relative magnitude of the dorsoventral diameters of the brain of the gorilla and chimpanzee would seem to be explicable on the basis of difference in the craniocervical angle of these two anthropoids, for the head of the gorilla is carried more decidedly forward than that of the chimpanzee. It is by no means impossible, judging from the pelvic and femoral configuration of early hominids, that they also carried their heads on a wider craniocervical angle than does modern man, and all reconstructions of these forms, such as Coon's (1954) of *Sinanthropus,* show very wide craniocervical angles. Weidenreich did recognize the possibility that brachycephalization was due to adjustment of the head to the erect posture, but his emphasis was on the contention that broad-headedness is an advanced state of development which is still progressing and not on the purely mechanical aspects of the relationship.

While the proportion of short and broad to long and narrow skulls seems to have increased from Neolithic times, it does not seem that this is a universal, irreversible, forward trend that is completely gene-controlled, or that it is correlated with a superior degree of intelligence.

With regard to the tendency towards broad-headedness, it may be pointed out that among modern male Scots short, narrow crania are becoming more numerous (Scott, 1953). In view of the high incidence of anatomic variations (especially those due to modifying influences which operate in the genic environmental sphere or on peristatic fetal-maternal relationships; Fischer, 1952) more work like that of Lasker (1953) and of Otto (1953) needs to be done. May brachycephalization be one of the alterations in body form and size due to a shift in human reproductive habits or to changes in ecological conditions, such as Bartholomew and Birdsell (1953) have emphasized?

Even if we grant that brachycephalization has become an established, progressive feature of contemporary man, we must admit that many groups of earlier men also exhibited this feature. It is easy enough to point out that cultural growth was most rapid among the round-headed peoples of the Mediterranean, but this is merely an *ad hoc propter hoc* argument, and it is chastening to recall that a few decades ago the economically prosperous and supposedly dolichocephalic north Europeans were arguing that long-headedness was positively correlated with intellectual superiority.

In any case, for the original argument to have real weight, the condition of brachycephalization itself still would require to be correlated with superior intelligence. Thus far no data have been brought forward establishing such a correlation. Ordinarily, the basis for the argument in favor of brachycephalization is shifted to some intermediate ground as by Weidenreich's assumption that spherical-brainedness is positively correlated with an increase in the "association" regions of the brain and that these are particularly concerned with intellectual functions. As an example of an "association" region the rostral portion of the frontal lobe has been most frequently cited. There are no easily accessible data to prove that such an increase has occurred with a differential in favor of that region, but even if there were we would still be faced with the difficulty of validating the assumption that these regions are the substrate of intelligence.

Within the past decade a mass of data have accumulated which throw considerable doubt on that assumption. Towards the end of the nineteenth century Gottlieb Burckhardt had the idea that if psychotic persons are bothered by auditory hallucinations one way to get rid of these would be to remove that portion of the cortex in which he thought auditory sensation ended. Burckhardt's (1890–1891) results were not very conclusive, but in 1935 Egas Moñiz (1936) revised the surgical treatment of psychoses in accordance with the hypothesis that it might be profitable to disconnect those portions of the brain most intimately related with complex mental activity. Moñiz chose the frontal lobe, and by 1951 more than 18,600 persons had undergone one or another type of frontal lobe operations. We have had, therefore, considerable opportunity to examine the validity of the belief that intelligence is situated in the frontal lobe. Because this subject was approached with notable bias in favor of the long-accepted supposition that it does, it is not surprising that all the psychologic studies have not been in agreement. This in itself indicates that we are not dealing with the clear-cut correlation everyone supposed existed and expected to find substantiated. It is not necessary to go into the details of the recent findings, but enough is now known to make it clear that an individual lacking both frontal lobes can function quite satisfactorily in our society and that many of what we regard as intellectual traits are not notably impaired in such individuals. Consequently, it would appear that the frontal lobe, as such, is not the physical substrate of what our psychological tests of intelligence measure.

Here again it is interesting to enquire how this erroneous concept achieved currency. I have previously explored this curious question (F. A. Mettler, 1949), as follows:

The attribution of changes in personality to frontal lobe damage is not so old as might be supposed. Although some psychic disorders were attributed to cerebral dysfunction even in the early post-Galenic period (C. C. Mettler, 1947) is was not until the second half of the nineteenth century that any evidence was brought forward to suggest that the frontal lobe is specifically concerned with psychic processes. There is nothing in Greisinger's (1867) book to this effect and the suggestion that Harlow's (1848) patient, Phineas Gage, of the so-called "crow-bar case," owed his personality changes (the phrase that he was "no longer Gage," appears in the record; Harlow, 1869, p. 14) to frontal lobe damage was an afterthought on the part of Ferrier. (For Harlow and most of his contemporaries the most significant feature of the case was the survival of the patient, and others, overzealous to defeat the phrenologists, were almost willing to argue that the brain was practically useless in order to achieve their purpose. It is interesting to observe, in passing, that one of the first cases in which a personality change was observed to follow a brain injury was a psychotic case in which the psychosis disappeared after attempted suicide by shooting through the head; Nobele, 1835.)

Welt's (1888) case of Franz Binz of Zürich was probably the first verified example of serious alteration of character and moral behavior due to a frontal lesion, the extent of which was established at autopsy. Franz Binz, like Phineas Gage, changed from a peaceful, gay, polite, and cleanly person to a violently quarrelsome sloven. Goltz, Hitzig, and Ferrier had previously described similar changes. Ferrier (1890) believed that removal of cortex rostral to the electrically excitable area produced "a form of mental degradation which appears to me to depend on the loss of the faculty of attention, and my hypothesis is that the power of attention is intimately related to the volitional movements of the head and eyes," Ferrier attributed the opinion that intellectual degradation may follow lesion of the rostral part of the brain to a number of previous authors, including Brissaud. Welt had been unable to demonstrate any true degradation of intellectual capacity in the case of Binz. Hitzig (1884) also thought that intelligence is impaired by injury of the frontal lobe in the dog, a belief controverted by Loeb (1902), and Bruns could find no evidence of impairment of intellect in one extensive tumor case of his own.

An unpleasant, nasty character was one of the triad of symptoms of release which Goltz felt succeeded frontal lobe changes. [The full triad was (1) general excitement (the capstone of the theory that injury of the cortex brought about a phenomenon of "release" was laid by Charcot, 1876–1880), (2) lack of self-control, (3) violence of spinal and bulbar activity.]

Clownish behavior (*Witzelsucht, mania bel esprit, lazzi, moria*) as a symptom of rostral frontal lobe damage appeared in Jastrowitz's articles of 1888 (Jastrowitz, 1888; see also Leyden and Jastrowitz, 1888; and Bruns, 1892) and formed a part of Bruns' (1897) table of frontal lobe symptomatology. Jastrowitz referred to the condition as *moria*.

Difficulties in the associational process entered the symptomatology of the frontal lobe through the work of Flechsig, who argued that two (originally he said three) "association" centers existed in the brain (a large parieto-occipito-temporal and a smaller frontal one) which gave rise to no projections but only associational fibers, for the purpose of interrelating afferent impulses. Flechsig felt that the frontal association field was primarily concerned with the association of impulses of bodily sense, as contrasted with vision and audition as special senses (he thought of the frontal lobe as containing sensory as well as motor capacities, as indeed its caudal part does), and that injury of it produced defects in personality and self-awareness. Association fibers from it were supposed to deal especially with memory images (Flechsig, 1896). Flechsig's theory was not widely accepted (Oppenheim, 1900) but the theory that psychiatric disorders depend upon an essential difficulty in the associational process long endured in the literature. Thus Bolton (1911) divided psychotic processes into two categories: (1) those in which there is defective control of the processes of lower association, and (2) those in which there is independent activity of the "centers of lower association." He placed apathetic, hebephrenic, and manic syndromes in the first category and illusory and hallucinatory states in the second.

Loss of initiative or apathy as symptoms of frontal lobe disease appeared in Bruns' tabulation and loss of complex emotional behavior probably should also be included here together with defective recognition, due to a degradation in perceptual ability. In contrast to simple apathy, ambulatory hyperkinesia was attributed by Baraduc (1876) as, much earlier, by Magendie, to frontal lobe lesion—specifically by Baraduc to atrophy of the left inferior frontal convolution.

Persistence of fear and the occurrence of panic reactions have been described as signs of frontal damage, and apparently, in cases of thrombosis of the arteries supplying the frontal region, may be so severe as to amount to delirium tremens. Perhaps these phenomena are to be related with Goltz's listing of release phenomena, though this is far from clear.

Memory defects for the past without impairment of the ability to learn and lack of planning for the future (deterioration of insight) are also listed as results of frontal lobe damage.

It may be justifiably said that these so-called "higher" functions discussed in the foregoing paragraphs are so ill-defined as to be scarcely worth scientific consideration. This depends upon one's point of view. One common criticism of the scientific method as applied to the present sphere is that it has not yielded quantitative support of phenomena which anyone, using merely observation, can easily perceive. Since scientific tests answer only the questions they have been designed to ask, it is, of course, possible that the proper tests have not been devised. On the other hand, it is perfectly possible that these "higher" functions are not functions of the frontal lobe at all or, at best, require damage of very large parts of the frontal lobe in such a way as to compound simple functional deficits into complex patterns of deficit.

The premier question which must receive an affirmative answer in order to conclude that the "higher" functions under discussion are frontal lobe functions, is, Do such deficits invariably appear if the frontal lobe is quite dysfunctional? Under such scrutiny the allocation of most of the preceding phenomena (slovenliness is an exception) fails to be substantiated. We must therefore conclude either that special circumstances, beyond the factor of frontal lobe damage, must be present for their appearance or that they are not true functions.

It becomes clear then that behind the notion that damage of the frontal cortex produces intellectual damage and personality change is a body of data which must be interpreted in a somewhat different light than that which has been employed in the past. We may consider several possibilities. "Intelligence" may be a generalized function of the neural system, or, alternatively, it may be situated in some special locus which has thus far escaped notice. Finally, it is possible that it may not easily be correlated with structural characteristics at all. For example, intelligence must certainly depend on a variety of factors just as does excellence in sports, and excellence in sports depends on the conjunction of the fitness of the individual with the requirements of the sport chosen. Intelligence presumably also involves not merely an aspect of fitness but the utilization of such fitness in a situation for which it is appropriate. One may question whether there is such a condition as intelligence without specifying the circumstances under which the intellectual skill is to become manifest. Because these external circumstances are obviously very variable, the search for a particular structural substrate would have to be abandoned in favor of a search for a variety of substrata to match the conceivable spectrum of requirements. We may approach the consideration of the possibility that intelligence may be a generalized cerebral function by asking whether Parker's (1922) emphasis on the neurocyte provides us with a useful clue.

Is intellectual capacity directly correlated with the number of neurocytes in the cerebral cortex?

Still another approach to the problem of wherein the supposed superiority of the modern brain may lie is the assumption, already referred to above, that the functional elements of the cerebral cortex, notably its cells, and their functional capacities have increased in number as a result of an increased complexity of folding of cortical surface rather than as the result of an increase in mass. In other words, the free surface of the brain is said to have increased as the result of greater infolding without any increase in the spherical diameter of the cerebrum. Such a situation is certainly possible, and there is a difference among cerebra with regard to degree of convolutional complexity. It is further true that there is a difference between normal brains and the small cerebra of idiots (which are often relatively smooth), but, as in the case of weight or volume, no correlation can be established between degree of gyrencephaly and condition of sanity or intellectual proficiency.

There are two aspects to the problem of whether increased complexity of internal cerebral organization is of possible evolutionary significance. In the first place the fact of such increasing complexity must be established, and in the second place its relation to survival value must be demonstrated. Quantitative estimates of cortical complexity may be expressed in surface area measurements, which are very unreliable, or in terms of the relation of total volume of nerve cells to volume of cerebral cortex (gray cell coefficient; von Economo, 1926, 1929), or some equivalent of number, such as von Economo's photographic technique or a scanning densitometer measurement (Campbell, 1954). Simplified estimates of the gray cell coefficient can also be worked out on the basis of number, as well as volume, of cells in some arbitrary cubic unit of cortical tissue. Thus the argument that intelligence is related to number of nerve cells can be explored on a localized as well as generalized basis. Such volumetric work is still in its infancy and, I have already noticed, in connection with the discussion of total cerebral volume, some of the difficulties which have beset past computations involving volumetric units. Further, we have no information at all about earlier man and can argue only by comparison of what we find in the brains of different races of modern man and in animals. Obviously there is always a very real danger that superiority will be attributed to some causally unrelated but real concomitant difference which may be disclosed.

The psychologic correlates of the hypothesis that intelligence is a generalized brain function are the theories of vicarious cortical functioning and of mass action. Pavlov took the position that loss of one or another portion of the neural system, and especially of the cerebral cortex, could be compensated for by the extraordinary activity of other portions, the potentialities of which extended beyond their usual function. This principle is demonstrable, but it has limits. Extension of it to the proposition that any portion of the neuraxis (or cortex) can take over the functions of any other portion of the neuraxis (or cortex) is quite unwarranted. Moreover, when such a situation develops, the vicariously mediated activity is likely to be an obvious and, often, poor substitute for the original.

A similar criticism applies to the principle of mass action which is supportable to the extent that neural activity occurs in a frame of reference of totality of function which is distorted by truncation, often in seemingly inconsequential ways. The mass actionists have, however, been less interested in interaction than in the fact that much neural tissue is dispensable. Such a consideration of their work brings us close to the problem in hand. Unfortunately the fact that much neural tissue may be dispensed with does not demonstrate that the function of what has been removed exists elsewhere, as well as in what has been ablated. It may merely mean that the experimental enterprise is in irrelevant one.

Many persons in the United States not only have been subjected to psychosurgical operations that have removed more or less of the frontal lobe and therefore a considerable proportion of the "association" areas, but these operative procedures have also rendered enough brain non-functional to reduce these individuals to a functioning brain weight not greatly in excess of that of *Pithecanthropus,* depending on what the operated person's brain originally weighed. Nevertheless, as indicated above, such operations may not be followed by any alterations easily detected by psychologic tests. It is true that some patients give very poor performances after operations, but such a situation might be due to the progress of the original disorder for which the operation was done. It is much more significant that many mature patients show no such changes in our society as it is presently organized. The literature contains many impressionistic reports to the effect that such "psychosurgical" operations have adverse effects. Unfortunately we cannot rely on this type of report, but it is true that psychologic tests leave much to be desired by way of conclusiveness. There are limits to what psychologic testing can do, and many patients who refuse to cooperate in a psychologic test situation and cannot be included in statistical evaluations may easily provide the clue to what those portions of the brain that have been removed may "be good for." In social situations, such as those in which we customarily function, the shortcomings of the individual are often compensated for by the social conscience of his fellows. The simple fact that many rather deficient and essentially parasitic individuals move freely and in an undistinguished manner through our protective social structure should not be overlooked in any attempt to explain why persons who have little or no frontal lobe are not merely able to function in our society but are often able to earn very considerable salaries. In a truly competitive and less genteel society the individual who does not or cannot "pull his own weight" or whose wits are less than nimble is likely to succumb fairly early, and this is even more true of persons who do not bestir themselves in existences of a solitary nature. We cannot put this kind of pressure on individuals in psychologic test situations, and our tests consequently lack a certain depth and are devoid of the vitality which must be of importance to the student of survival values. Nevertheless, the lessons of psychosurgery are clear, and they are to the effect that we have overrated the importance of the frontal cerebral cortex in intellectual function. While it is likely that any one of us could ill afford to part with any cerebral substance if we were transported back to a situation in which we had to retrace the necessity of developing our culture all over again, our modern social system is so arranged that most of us can function at a very low level of efficiency most of the time. The "psychosurgical" data contain another clue of considerable importance and that is that we can more easily dispense with cortical gray matter than with subcortical cellular accumulations. I wish to return to this point farther along.

For the present then we may say that those authors who look for the progress of evolution in the direction of some generalized augmentation of cerebral function, such as might accompany an increase of nerve cells, may be correct, but there is no evidence at all to justify the assumptions that modern man has more such cells in fact than Cro-Magnon, Neanderthal, or even Swanscombe man, and it remains to be demonstrated that there is a positive correlation between number of neurocytes and what passes for intelligence. The position may be granted that a high degree of intelligence is a total function, but it is quite impossible for all or any portion of the cerebral cortex to subserve the function of all other parts.

A high degree of intelligence is certainly not localized in one particular portion of the neural system. It is, or should be, the sum of perfect functioning not merely of the neuraxis but of all other parts of the body. If it is true then that the future of our race depends on the most complete utilization of intelligence, we shall have to look for the most nearly perfect physical individual in order to find the most intelligent.

We all know that matters do not work out this way. We are all aware that the handsome matinee idol may be an unusually vapid individual and that beautiful blondes are often intolerable for protracted periods. The difficulty is, of course, not merely that a physical disability can be readily offset by a cultural advantage but that a disability may actually turn out to be an asset by virtue of its psychological activating quality. We cannot therefore look for survival of the race in over-all physical perfection. Moreover, as physical defects, such as myopia or a missing extremity, are very easily offset by technological devices, we must search for uncompensable limitations if we are to discover any areas wherein our development will be blocked in a progressive civilization.

Can man satisfactorily maintain a "large" brain?

Proponents of the theory that man's brain has been consistently enlarging have directed very little attention to the anatomic circumstances that are required for the maintenance of such a brain as modern man possesses or to what changes would be required if that brain were to undergo a future progressive increase in size.

Obstetrical difficulties

Obviously, at the very outset of independent existence the head of an infant must, under ordinary circumstances, pass through a birth canal the dimensions of which are unalterably fixed by the size and shape of the maternal pelvis. A not inconsiderable degree of obstetrical difficulty consists in the mismating of genotypically large males with females having a pelvic outlet too restricted for the uncomplicated delivery of the product of such a mating. The margin of obstetrical safety is not so great but that any appreciable increase in the size of the head of the infant would immediately influence the paranatal death rate adversely and markedly raise the incidence of brain injury among neonates. It is quite possible that increased head size and increased pelvic dimensions would occur together. This has been the course of events in the past (fig. 4), but pelvic size is an important selective factor with regard to magnitude of head size in any race and operates in favor of small-headedness.

Oxygen requirements of neural system

The oxygen requirements of the neural system of neonates are different from those of adults. Newborn animals can endure a surprising reduction in oxygen, as anyone who has ever tried to drown kittens can testify. Nevertheless, there are specific limits to such endurance, and it would be interesting to know whether, as seems reasonable, such limits become progressively lower for neural systems of larger size. I am unaware of any studies on this subject, but we do possess an impressive mass of data which demonstrates that a very considerable proportion of brain-injured children have been damaged because of failure to get oxygen to all portions of the brain during intra-uterine existence, as well as at birth or immediately afterward.

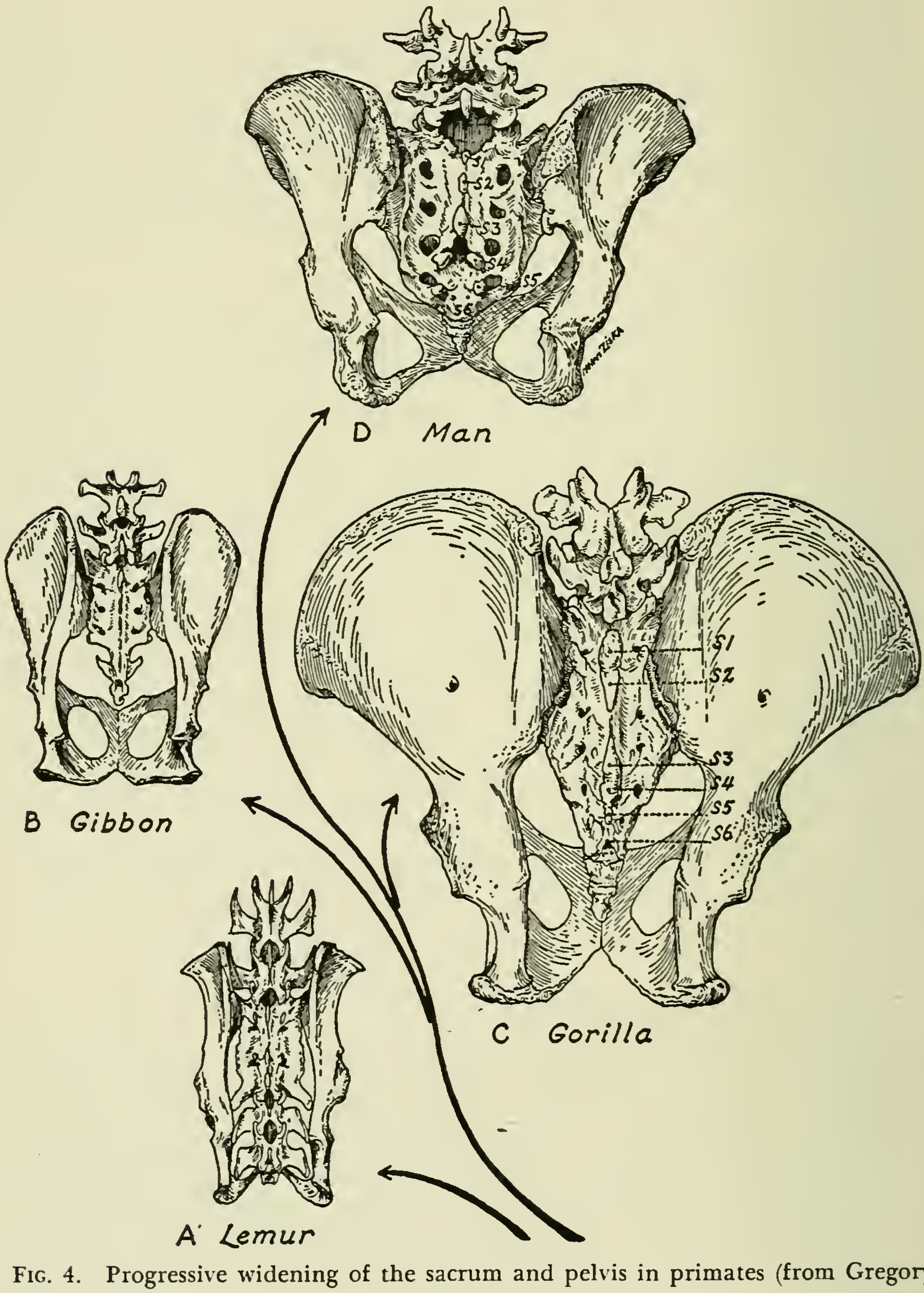

Fig. 4. Progressive widening of the sacrum and pelvis in primates (from Gregory, 1951, vol. 2).

It was long believed that most brain-injured children, the so-called cerebral palsy cases, were damaged during birth, but older doubts have been fortified in recent years by increasing evidence that a great many such children have been born without any notable difficulty in labor. Protracted and complicated labors do result in brain injuries and even deaths, as noted above, but much brain injury occurs before birth as well as during or afterward and as the result of processes the nature of which has only recently been elucidated. Two very important principles have emerged. These are, first, that gross malformations of the neural system almost always have their origin in the very earliest period of pregnancy (often before the mother is aware of her condition) and, second, that alterations in oxygen supply occurring in any part of pregnancy have very drastic effects. Almost any noxious influence that reaches the fetus in its very early, relatively undifferentiated period (especially during the first two weeks after conception) will result in a malformation but after the second month of pregnancy the neural system can withstand many insults, with the exception of oxygen deprivation, which would previously have done irreparable damage.

One possible reason for the precarious condition of the neural system with regard to variations in oxygen supply is probably to be sought in the manner in which blood is carried to the brain.

The brains of all primates are supplied with blood from two principal arterial reservoirs—the internal carotid and vertebral arteries. The ultimate branches of these two principal supplies anastomose at the base of the brain in a circulus arteriosus from which a crown of vessels penetrates and also embraces the brain itself. In very low forms, such as Amphibia, which have quite simple brains, the brain is supplied not only by vessels from a greater variety of sources, but the individual vessels of the brain itself exhibit many intercommunications (Herrick, 1948).

In herbivores and carnivores the situation is not so free as in *Ambystoma* nor so restricted as in the primates. The vascular net of the amphibian cerebrum has been replaced by the terminal vascular design seen in primates, but at the base of the brain the anastomotic pattern has been retained in what is called a rete mirabile, and this is supplied not merely from the vertebral and internal carotid arteries but also receives an abundant supply of blood from the external carotid through ophthalmic and meningeal branches which, in the human adult, do not ordinarily maintain any notable connection with the extracranial vascular arrangements.

In the human embryo an early, freely vascularized stage exists very briefly. During this period all the blood reaching the brain arrives via the internal and external carotid arteries, for no vertebral arteries exist until the end of the second month, at which time the arterial reservoir for the lower (infratentorial) part of the brain is shifted from the carotid to vertebral arteries and the external carotid contribution is gradually cut off.

Thus the arterial plan of the brain of the human infant passes through a series of changes which recapitulate those of lower phyla and, at the end of the second month, the embryo has already been committed to the primate pattern of supply. A very considerable number of developmental errors can occur in this process of recapitulation, but once it has been completed the pattern settled upon must prove adequate for all subsequent purposes, and it is not a pattern into which any considerable margin of safety has been built. From this time onward the brain enlarges and removes its internal substance farther and farther from its all important supply of blood and thus of oxygen. At the same time the tracery of vessels on the surface of the brain is progressively. stretched out, and ultimately a rigid encasement for the entire brain develops in which, with little room to spare, any considerable increase in intracranial pressure will serve to prevent blood from entering the skull.

We now know that the brain of the fetus cannot withstand pronounced drops in maternal blood pressure which are not fatal to the mother. The effect of such a drop is to reduce the oxygen exchange through the placenta to a point where the oxygen concentration in the fetal blood is inadequate to maintain nerve tissue situated in those regions where the physiologic factor of safety is small. Such regions are those in the interior of the brain and in the white matter where the vessels are few and thin. Ultimately, if the child does not perish during the period of deprivation, the neural tissues in these regions break down, the vessels traversing them rupture, and a true apoplexy occurs in the fetus.

Phenomena of this type are probably more common today than ever before. Such circumstances can and do occur when pregnant women undergo surgical operation by modern techniques and could conceivably happen in high speed transport. Other sources of difficulty are infectious processes which impair placental circulation, drugs, and an improper regulation of the atmosphere such as occurs in combustion failures in tight modern houses, or automobiles, or during the breakdown of refrigeration or air-conditioning apparatus.

The problem of cerebral oxygen supply is also a serious one for adults and can be a limiting factor in our further evolution. Many of us are unaware to what extent the necessities of earning a living expose a significant proportion of the working population to neural damage through oxygen lack.

The neural system is very vulnerable to a number of chemical substances. Some of these substances, such as lead and carbon monoxide, are constantly about us, and great vigilance is required to avoid being poisoned by them. Others, such as DFP (diisopropyl fluorophosphate), the still unused "nerve" gas of the Germans of World War II, are unusual compounds which probably are more destructive as military threats to morale than as practical hazards. In an intermediate position are substances such as carbon tetrachloride, methyl alcohol, ergot, and manganese which are potentially dangerous but the use of which is reasonably well controlled.

Approximately a million and a half Americans are chronically exposed to carbon monoxide as an *industrial* chemical hazard. It may be assumed that the number of individuals exposed to this substance, and hazards such as lead compounds, organic solvents, and several of the other chemicals and compounds, is at least twice as great as industrial figures indicate. Moreover, it is probably not without significance that the neural effect of substances like carbon monoxide seems to be due entirely to anoxemia rather than to any special neurotropic action. Even in lead poisoning the initial reaction of the toxic chemical is with inorganic phosphates, a combination that has a very serious effect on the erythrocytes. Primary pathology of the neural system, in lead poisoning, is practically unknown.

The problem of supplying the brain with oxygen is not, however, restricted to the very young or to industrial workers. The third principal cause of death in the United States is major brain stroke. Murphy (1954) has pointed out that "one-half million persons in this country sustain strokes each year, and . . . one and one-fourth million hemiplegic patients are surviving in the hospital or at home."

Study of figure 5 will reveal (incidence of neural vascular accidents) that the number of persons who have vascular lesions in the neural system is appreciably larger than those who show evi-

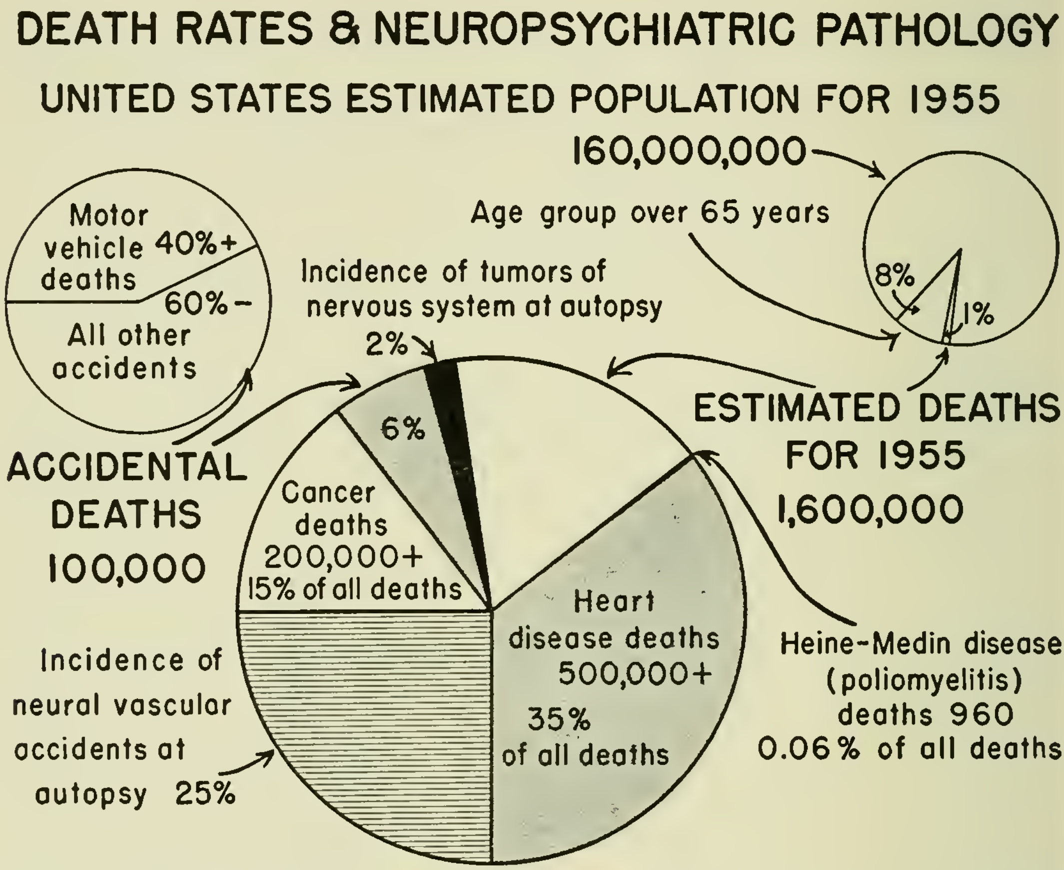

Fig. 5. Relative frequency of different causes of death and also of neuropathology.

dence of such lesions, for such lesions are found in every fourth person who dies. In other words, many persons who will die of other causes and who will show no signs of nervous system damage before they die have substantial damage of the vessels of the nervous system. Had these individuals lived longer they would unquestionably have gone on to show failure of the nervous system.

As our population grows older, an increasing proportion of individuals will inevitably come to a situation in which the vascular supply of the neural system will break down.

All of these considerations point to the possibility that a large brain may not necessarily be a desirable endowment. Indeed, it is possible to experience a certain amount of uneasiness about such a prospect for it is not at all inconceivable that if man's brain were to increase without substantial modifications, both in his structure and culture, he might be moving in the direction of extinction.

Culture and "intelligence"

It is not often that scientists expend great labor to correlate two variables when the second of these is known to show marked variation in terms of a third, unconsidered variable. Nevertheless, this is exactly what we do when we search for a direct correlation between brain structures and "intelligence," for it is a truism that what we call intelligence is at least as dependent upon nurture as upon nature.

When all the available data have been examined we are forced to admit that no evidence exists to support the contention that man's cultural advance has been due to, or has even been paralleled by, structural changes in his nervous system. The assumptions that the cerebral cortex has become more convoluted or more efficiently organized, by virtue of an increase in the number of nerve cells in it, or because of increase synaptic contacts, are unsupported conjectures, and the belief that human intracranial capacity has undergone steady enlargement is at variance with the actual facts. Since the beginning of the Eolithic period, mankind's neural system has displayed a number of variations on a central structural theme, but no clear trend has become established. Many modern persons seem not to be more abundantly supplied with cerebral substance than any of the Eolithic or Neolithic variants, and indeed most of us have less in the way of brain mass than did Cro-Magnon man who seems not to have been especially successful in the business of survival.

On the other hand it is quite clear that since the Eolithic period mankind has literally inherited the earth. That he owes this inheritance to his culture no one will question, but there has been a tendency to regard culture and structure as essentially separate and antithetical. We speak of physical and social anthropologists, of anatomists, physiologists, psychologists, and sociologists—a literal army of departmentalized scholars, each viewing man from the point of view of his own individual discipline and each insisting upon parcellation.

What in fact do we mean when we admit that, of course, man's progress has been due to his culture? We may agree (as many have) that this is due to the assumption of the "erect posture, his free-moving arms and hands, his sharp-focusing eyes, a brain capable of fine judgment and decision as well as of keen perception, and the power of speech," as Coon (1954), among others, has pointed out, but all these things were man's in the Eolithic. Man is where he is today not because he has evolved new structural attributes but because he has used the capacities he possessed to provide himself with the means to develop beyond those capacities.

The development of clothing, of tools, of improved means of locomotion, of ways to produce and store food must be looked upon as intellectual accomplishments of the first magnitude. They are especially important in that they came into being at a time when the patterns and mechanisms for intellectual activity so familiar to us were still unknown, when man was still beset by great dangers, could not move far from water, was at the mercy of the sun and snow, and had no accurate records of the past nor clear confidence in the future.

By taking these first steps man had passed beyond the necessity for personal change. He had embarked upon the process of supplementing his evolutionary progress by developing outside himself what other species must attain by personal structure change.

Cultural development nullifies the selective influence of natural environment, by protection from it

Man's forward progress has been characterized by what have been called conquests. In terms of the sciences the implication of such a word is that, whereas man has previously had to come to terms with a physical or biological phenomenon, he has now managed to make himself more or less independent of the influence of such phenomena by virtue of his ability to manipulate the circumstances on which such phenomena depend or that he is at least able to escape from their undesirable effects. In terms of survival, man's knowledge and culture have, consequently, removed him one step farther from the compulsion of his original environment. He is not, of course, freed from obedience to natural law, but he is no longer the inevitable victim of the simple inexorable phenomenon he has learned to manipulate or circumvent. Such a cultural acquisition is the equivalent of an effective structural modification, but it has the disadvantage that a higher degree of vigilance is required for its effective maintenance.

The cultural acquisitions that free man from dependency on his natural environment are those that protect him from it and that widen his course of action. Science and technological advances operate in this dual manner, and it is to these substitutes for, or supplements to, structural evolutionary change that I now wish to direct attention. Before doing so it is necessary to point out that when cultural continuity is maintained such cultural acquisitions act to all intents and purposes in a society just as though they were genetically determined.

Charles Galton Darwin, the British physicist, has touched upon the biologic equivalence of culture in a rather restricted manner in connection with what he calls "creeds" or what we might call established beliefs (whether rational or not) which result in habit patterns. "A creed," says Darwin (1953), "may have the quality, possessed by the genes of mankind, of being able to produce a permanent effect upon humanity."

Thus it is not merely that aspect of culture that produces science and technologic advances and that removes man from dependency on a restricted environment which may be the equivalent of, or a substitute for, a genetically determined trait, but so also is *any* established course of action, whether rational or irrational. It is obvious that instead of freeing man from the exigencies of his natural environment and increasing his scope of action such an evolutionary change supplement might substitute any kind of abnormal restrictive environment and greatly limit man's scope of behavior.

Evolutionary change supplement

It may be advisable to define more precisely what is meant here by the term evolutionary change supplement and to give some examples. The essential point to bear in mind is that, by virtue of their survival value, human cultural alterations, whether things or thoughts, have come to serve as equivalents or substitutes for structural evolutionary changes, that these cultural alterations, when of a positive nature, protect man from his environment and increase his functional scope, but that they can, from a negative point of view, constitute an adverse artificial environment and severely upset man's structural evolutionary process.

One of the difficulties in dealing with evolutionary changes of any type is encountered in an attempt to separate genetically determined factors from those due to environmental influences. We are all aware that not only are botanical forms severely affected by the climate and soil in which they grow but that the size of animals' bodies and the magnitude of egg clutches are directly influenced by latitude. It is clear that both constitution and environment are active in such variation and that the genetic factors can be operative over a wide, though still definitely limited, range. The non-hereditary influence can be viewed as an evolutionary change supplement.

An important and presently threadbare example of the difficulty in separating genetic and environmental factors is the supposed inverse relation between fertility and level of intelligence. Solution of this problem has been obstructed not merely by a lack of satisfactory methods of measuring intelligence but also by the absence of a clear definition of what is meant by fertility. Are we to understand by fertility the capacity to produce offspring or rather their actual production, i.e., the birth rate? The use of a term such as fertility rate suggests that we are dealing with a genetically determined trait, for that is the meaning of the term in animal husbandry. A moment's reflection soon discloses, however, that local variations in the human birth rate involve cultural, environmental, or, in other words, non-genetic influences to as great an extent as, if not greater than, the actual capacity to produce offspring. Moreover, even the capacity to produce offspring may be influenced by such environmental factors as diet or radiation.

We come therefore to the realization that not only can we not say that what we measure by intelligence tests is entirely genetically determined but that even the birth rate is notably influenced by environment. Viewed in such a light we become aware that what at first sight seemed an interesting correlation between two genetic traits turns out to be no more profound an expression than the simple statement that ignorant persons display their ignorance in reproductive habits as well as in other ways.

Another difficulty in distinguishing between nature and nurture arises when we deal with such behavioral phenomena as become manifest in the interaction of the individual and its milieu. Are these the result of heredity or environment, or do they occupy an ambivalent and intermediary position? Not all evolutionary changes are obviously structural, although probably all depend on some type of structural change. As an example of what is meant by saying that not all evolutionary changes are obviously structural, it may be pointed out that the migratory habits of birds are not directly structurally self-evident. Nevertheless such habits, like all physiologic behavior, depend on a morphologic substrate and are therefore genetically determined, to some degree at least. In some behavioral patterns of birds, as in the tumbling of pigeons, both hereditary and what might be termed cultural factors are involved. For practical purposes newly emergent behavioral phenomena (having survival value and appearing relatively constantly in a population) whether of a simple physiologic or complex and apparently social nature may be considered solely genotypically determined evolutionary changes if they manifest themselves in their essentially important character in individuals of the species which have been reared in isolation.

More interesting is the position occupied by non-transmissible behavior patterns. These form, of course, a large part of the material of social behavior and, in man, reach the complexity of a definite culture. Social anthropologists have made it clear that culture is itself a product of evolution and undergoes all the usual aspects of evolutionary development. More recently attention has been directed to the fact that the culture produced by man constitutes an artificial environment which exerts a selective factor upon its creator. In other words it becomes itself a selective determinant. Many examples of such a situation might be cited. Man has created many machines on which his present culture is dependent. These machines call for certain behavioral traits in their operators. Operators failing to exhibit these traits or exhibiting them in common with other inconsistent traits not only fail to derive any benefit from the machines (and therefore fall behind in the socio-economic struggle for supremacy) but may in fact injure themselves (and often other persons near them). Again, individuals residing in areas that have long served as emigration sources and never as attractions to immigrants display, as the result of progressive personality selection, psychologic traits essentially different from those seen in newly opened frontier or prospecting communities.

It is not necessary to belabor the point that culture is at once a product and a determinant of selection, and it certainly has been adequately emphasized that the culture of a species may protect individuals who would otherwise be unfit for survival. I am not so sure that the broader aspect of this principle, notably that it shifts the emphasis for selection from the structural to the cultural level, has been sufficiently emphasized among morphologically minded individuals. (The shift to a culturally determined environment tends to result in differential reproduction in selected genetical systems as a result of weighting cultural adaptation more heavily in the struggle for survival than physical adaptation.) The fact that the physically unfit have had increasing opportunity to survive has been a cause of concern to many writers, but the fact that even greater opportunities for survival have been provided for the culturally adept seem not to have been recognized.

A species that can enhance its sensory capacity by instrumentation and its motor capabilities by technology is under no selective stress at the structural level, and structural modifications in such directions will have little survival, and therefore selective, value. On the other hand the individual who fails correctly to interpret the indicators of our technological civilization will soon be eliminated from this in one way or another.

Not all cultural variants have survival value any more than do all structural variants, but to those cultural elaborations that transcend the selective effect of organic (or important genetically determined behavioral) changes I have chosen to apply the term evolutionary change supplements. Behavioral patterns, not genetically transmissible, that have definite survival significance for the species are evolutionary change supplements. Various names could be applied to such developments, and it could be said that they are merely culture. They certainly are cultural alterations, but it would not be sufficient to characterize them in such a way solely, for not all culture, as has just been pointed out, has positive or negative survival value for the species or even acts as a selective force. Moreover, such a name would obscure the fact that these particular aspects of culture tend to encourage structural variation and protect the total species from specialized evolution. Neither would it be correct to consider particular cultural features simple supplements of evolutionary structural changes, for they also supplement behavior patterns. To call them evolutionary supplements would be to ignore the fact that they are also determinants of evolutionary processes. The phrase evolutionary change supplements does not entirely satisfy me, and I am sure additional objections, beyond those I have pointed out, can be raised by others.

One of the most interesting aspects of evolutionary change supplements is that they not only free a species from the forces that result in structural evolution but, by tremendously increasing intraspecies variability, they make it possible to develop very great potentialities for structural evolution. This is the result of a variety of influences, among which preservation of many more mutations than would otherwise survive is only one. Another is, of course, the tendency for cross breeding which is seen in most protective and permissive environments. These two factors are mutually reënforcing, because with the genetic reservoir greatly expanded as the result of mutation, cross breeding will result in further intraspecies variation.

There has been an almost uniform tendency to look towards the most highly developed examples of *Homo sapiens* as holding the hope for the future of our species, and it is certainly true that, as our culture is presently organized, the ability to develop evolutionary change supplements seems to be the only requirement for progress. The more we can control our environment and devise new ways to manipulate it and make it work for us the less we shall have to do with our own soma. Nevertheless, I can conceive of a situation in the brightly burnished and explosive future in which the capacity to survive in a very primitive environment might be the most import characteristic *Homo sapiens* could display, and the most valuable members of the species may prove to be those who are presently far down the scale in social acceptability.

Types of neural system supplements

To list all the supplements that have been developed for the neural system would constitute a complete catalogue of our cultural necessities and conveniences, but it is worth paying some attention to the areas in which such supplementation has been maximal and minimal.

It is customary to divide neural function into various types of categories which more or less overlap. Thus we can speak of autonomic and central neural functions, of spinal and cranial nerve functions, or of sensory, internuncial, and motor activities.

One might suppose that the greatest cultural developments would be in those spheres characterized by the capacities for nicety of sensory discrimination or degree of motor performance. It is certainly true that little or no cultural sophistication exists in areas such as olfaction, gustation, or vestibular function or in pedal dexterity, as contrasted with manual, but the great mass of cultural developments seem to be primarily directed towards supplementing the autonomic functions of the body and to the avoidance of actual discomforts. Mankind appears to be more interested in homeostasis at the social as well as the biologic level than hustling, and in ease than exertion.

Another generality which emerges in connection with what types of neural system supplements have and what have not been developed is that relatively little development has occurred in those areas in which the race as a whole is not naturally proficient. Thus there is great variation in the ability of persons to discriminate between gustatory sensations, and gustatory or olfactory sensory experiences would make very poor communications media. As a consequence, such experiences play an almost completely nonobjective role in our culture. The implication seems clear that culture tends to develop around average natural attributes, which is in line with what we know about the tendency for social organizations to level off the hills of exceptional ability and fill up the valleys of deficiency.

The demands of the future

There have been many guesses advanced as to what the world of the future will be like (Shapiro, 1933). We can be sure of little in this regard except that we can confidently expect more of what we are already are aware. This being the case, it is safe to say that the world of the future will be full of technological advances, toxic hazards, high velocities, synthetic foods, and radiation dangers, all of which sum up to what man regards as improved material advantages and which result, in fact, in increased isolation from the natural environment of the physical world. It is an interesting observation that the nervous system is relatively resistant to many of these technological alterations. Notable exceptions exist with regard to oxygen deprivation, which we have already noticed, and with regard to nutrition.

The neural system has no capacity to store appreciable quantities of food substances, enzymes, and minerals, deficiencies of which produce not only pronounced reversible functional changes but actual structural deterioration which may not be entirely reversible

Man has been remarkably adaptable in connection with his diet, being exceeded, from the point of view of omniverousness, by the hog alone. It might be expected that quite low forms would exhibit a greater versatility in ability to absorb nutriment and therefore to survive than does man, but the case seems to be quite otherwise, for it is enough to place some insects upon an unfamiliar though satisfactory type of food in order to starve them to death. Still, man's very omniverousness seems to have been achieved at the cost of a loss in the ability to discriminate between good and bad, or even poisonous, food. It is very difficult to fool felines or canines about their food in spite of their domestication, and it is even more difficult to fool an ape, but man possesses little ability to select what is good, and reject what is bad, from natural sources. This ability is more notable in the very young than in older individuals. Taste and olfaction are both of rudimentary significance in man and deteriorate quite rapidly with age. Tests on primitive peoples and groups, such as the Lapps, who are located away from the central streams of culture do not support the notion that the olfactory or gustatory senses of these people are any more acute than those of people with more advanced and centralized cultures. Among all groups of modern man there is great individual variability in olfactory and gustatory sensitivity. In general about one-third of any population sample is practically anosmic and ageustic, but even those individuals who exhibit a good sense of smell and taste show little ability to live off an unfamiliar terrain. Modern man's nutrition provides an interesting example of the manner in which evolutionary change supplements function and is affected by a wide range of cultural and economic factors which will probably exert increasing degrees of pressure as the pressure of population density continues to increase. The essentially irrational role that culture plays in food habits and preferences has been explained by many serious and competent writers, and the extent to which processed, "substitute," and "supplementary" food products have supplanted natural foods has clearly been demonstrated to be dependent on the disinclination of people to expend the time and trouble in bringing the latter to the table. Psychiatrists have also shown the extent to which eating and eating habits have become substitutive functions unrelated to the actual bodily need for food as nutritive material. All these circumstances suggest areas requiring attention in the future in order to make certain that the neural system man has is adequately provided with the material it needs in order to function at peak capacity.

Another difficulty arising from foods, from the point of view of the neural system, is the not inconsiderable danger of actual poisoning

Here again the economic factors involved are especially compelling. Tremendous quantities of insecticides, fungicides, dye products, and hygroscopic agents are carried forward in food products brought to the table. It is rather pointless to inveigh against the possibility of poisoning ourselves, when our society is organized in such a manner as to force the producer to use dangerous materials in order to maintain the small margin of profit that keeps him in business, when we beat Federal, state, and county budgets down to such a level that no really efficient job of inspection can be done, and when the consumer himself (or shall I say herself) shows a strong disinclination to select safer food products which require time and labor in bringing them to the table.

The opportunity for modern mankind to poison himself does not begin with food and end with war. It covers a wide variety of possibilities encompassing practically all circumstances in which modern man comes in contact, from the cradle to the grave, in his technical environment.

The modern world is full of accident and technical hazards

As the individual grows older and becomes ambulatory, his neural system runs the risk of new conflicts with our culture. Although the death rate of children in the first decade of life has been greatly lowered, this lowering has been due to a reduction in the mortality from disease, not because of more satisfactory safeguards against accidents. One might suppose that the children of well-educated, solicitous, and careful parents would have a lower death rate than the children of parents with little or no education, but what little information we have on this subject (and it is old) does not bear out that common assumption (Lennox, 1924). There is, of course, a higher death rate in slum areas, but many factors other than the lack of protection of children are involved in such communities. There can be little doubt but that the pattern of development of the nervous system (the insatiable and direct curiosity and lack of care and foresight as well as of understanding, all directly related to the manner in which the human neural system develops ontogenetically) is responsible for the high death rate from accidents.

Infection

The period about 10 years of age is one at which neurological infections are especially likely to occur. At that time the individual has attained, in most modern cultures, full adult mobility but only partial immunity. It is, moreover, an age at which intracranial neoplasms, which may have been present from birth, now begin to become manifest. The brain reaches its maximum volume about the tenth year of life, but the cranium does not acquire its fullest size with the end of the second decade at which time the brain occupies about two-thirds of the endocranial volume. There is therefore a critical period of maximum endocranial filling at about the end of the first decade.

Behavioral disorders

With the advent of adolescence, psychiatric disorders become distressingly more frequent and, for those who see in such conditions overt manifestations of biochemical disturbances, the metabolic shifts attendant upon a changing hormonal situation are conceived to provide the basis for this rise in incidence. While it is probable that the origin of severe psychiatric disturbances begins long before adolescence, it does seem to be true that in many endocrine disorders, such as myxedema, which begin with birth the more serious aspects of intellectual deficit are cumulative.

Thus, the myxedematous child who has not received thyroid medication prior to the second decade of life usually has a permanently damaged neural system.

The witlessness of childhood passes into the riskiness of adolescence

It takes the human being a long while to develop a sense of caution and to achieve a respect and understanding for, and of, destructive machinery. The primary killer of the first decade of our race continues as the principal cause of death throughout the second decade. If childhood is the age of simple curiosity and exploration, adolescence is the period of experiment and manipulation. It is at this latter age that the neural system is exposed to a new and serious though still fortunately minor peril—habituation to drugs. All such habituations (whether heroin addiction, alcoholism, barbiturates, or phenanthrene habituation—the smoking or coffee habits) are all essentially neural habituations, and the only real difference between the coffee drinker and morphine addict lies in the urgency and nature of his dependency, both dependencies being dictated through and by the nervous system.

With the development of adulthood and the acquisition of full muscular power certain inadequacies of our evolutionary state become apparent

Sensory acuity has already begun to fail before the individual has gone far into the third decade, and there is a marked degree of deterioration in the condition of the teeth which, if it were not offset by cultural skill, would soon exert a marked limiting influence upon many individuals.

Sensory deterioration, though perceptible, is not yet incapacitating, but the active physical life of the second and third decade soon discloses that man's assumption of the upright posture has been achieved at the risk of an essentially unstable vertebral column. In quadrupedal infraprimate species the vertebral column forms a rather simple horizontal arch of the classical type in which the highest point is in the center and the central vertebrae behave much like keystones. In the lower primates such as the fossil lemur, *Notharctus,* or recent baboon the vertebral column has not become organized in such a way as to introduce any appreciable risk into its stability. In man, however, the situation is greatly altered, and a double or sigmoid curvature has replaced the original arch. Where this curvature is free, as in the cervical and lumbar regions, anteroposterior displacements in the elements of the column are not uncommon, with the result that the contained spinal cord and nerves may be damaged. Sudden compressive forces, such as may occur in directional change in high speed travel, greatly increase the probability of such structural failures. It may be asked why this feature of human structure should be a greater hazard at the present time than it was in an equestrian society. There is no doubt that ruptured or herniated nucleus polposus, as this condition is called, was a common cause of trouble for our carriage-riding predecessors, but a torso well-splinted by abdominal and back muscles properly developed by horseback riding is not particularly vulnerable to this disability. We are not, however, making comparisons here between the twentieth and nineteenth centuries but between the quadrupedal, semiquadrupedal, and erect postures. Sciatica, the name by which this condition was known to our forbears, has been a familiar feature of the literature of medicine from earliest times, and there is every indication that the unstable dynamics of our vertebral column, although long known, constitute a definite contemporary hazard to the safety of the neural system in view of the demands of high speed travel and the lack of opportunity to maintain a properly exercised axial musculature.

Radiation

While it is probable that all of the population of the future will be subjected to more or less potentially dangerous radiation, it seems likely that adults will be subjected to more intense and prolonged exposure than the young or aged. Fortunately the neural system is peculiarly resistant to the effects of radiation, and it is only by radiation during early intra-uterine life that any notable effect would be produced.

Warfare

There seems to be no particular reason to suppose that the neural system would be particularly vulnerable to bacterial or biologic warfare. We are not well prepared from the point of view of public defense against biologic attack, but (with the exception of certain improbable parasitic infections, such as by trypanosomes or cysticerci) most populations are naturally well protected, as the result of natural, or easily acquired, immunity against infections of the neural system. The case is quite otherwise with regard to chemical warfare.

Physical disturbances

One might suppose that physical disturbances would adversely affect the neural system, and they do but not preferentially and, in the case of some agents (such as vibration caused by pneumatic drills), to a lesser extent than joint surfaces, tendon sheaths, and bony structures. Some physical disturbances, notably decompression and the thermal extremes of runaway industrial processes, may disturb the neural system extensively though in an indirect manner. Heat stroke and freezing occur only after there has been a breakdown in the heat-regulating mechanism, such as sweat-gland fatigue or failure of the metabolic processes to cope with a reduction in environmental temperature. Aviation black-out is due either to lack of oxygen or to gravitational or centrifugal force manifesting itself differentially with regard to the body and its circulating blood, and in such a way as to result in regional anemia.

Character of the nerve cell

Although the neural system is the physical substrate for many delicate perceptual and adaptive processes, it is not a fragile and precarious tissue but a tough apparatus. Nevertheless it must have the means to maintain itself by food and oxygen in a minimum condition. In respect to the need for food and oxygen, we have not advanced far in 500 million years. Our nerve cells still require to be bathed in an aqueous, nutrient, oxygen-containing medium much like their Cambrian progenitors required, and this would appear to continue as a definite limitation upon the future.

Until quite recently we were of the opinion that mature nerve cells of the central neural system could not regenerate. We knew that the distal processes of neurocytes could and did regenerate, but it seemed as though the fibers inside the spinal cord and brain were devoid of this property. Moreover, when cells situated there were seriously damaged they seemed to be unable to recuperate and usually perished.

Such a situation now appears to be due to factors outside the nerve cell itself. Probably it is caused by the overenthusiastic activity of elements associated with the more sedately behaving nerve cells which are as frequently thwarted by the reparative activity of these associated elements as by the original traumatic situation. Anyone who is blessed with well-meaning but meddlesome relatives will appreciate the predicament of the neurocytes!

We now know that neurocytes will survive in tissue culture when removed not only from the body of embryos but even from that of adult humans. Moreover, such cells regenerate their broken processes and attempt to establish a kind of communal relationship. In my own laboratory we have found that such cells do not merely survive but are capable of being excited by electrical stimulation. Electrodes so small their tips cannot be seen under the microscope can be constructed and inserted within the cell in order to study its internal behavior! The study of the electrophysiology of single nerve cells grown outside the body has therefore become an actuality, and we have a tool with which to study the metabolism of the various elements of the nervous system *in vitro*. In this way the effect of drugs, vitamins, and other chemicals on such cells can be investigated directly. The possibility of the isolation of individual cell types is also within our grasp, and the construction of an artificial nervous system from real, living neural elements is a very definite possibility of the future.

How the nervous system breaks down

There is another way in which we can approach the problem of what the future has in store for the nervous system. Instead of attempting to identify the substances and conditions that place definite limits on its ability to function, we can try to determine what the most common types and causes of neural disintegration have in common. We have three major sources of information on this subject—mortality and morbidity statistics and autopsy findings. The figures on morbidity statistics can be profitably augmented by data on industrial hazards, absenteeism, the incidence of accidents, and the manner in which medical (and dental) services are utilized.

Necropsy statistics (fig. 5) lead us to believe that of the persons who will presumably die this year one-third will have notable damage of the nervous system. Mortality statistics are misleading, because the actual cause of death in a case of apoplexy may be pneumonia. It is for this reason that the autopsy findings on unselected cases are more informative as to the true extent of neural damage. By far the largest number of these neural lesions are the result of failures of blood supply to the nervous system. One-quarter of all dead persons show notable damage of this nature. Of such cases one-third have had actual hemorrhages, whereas the remain-

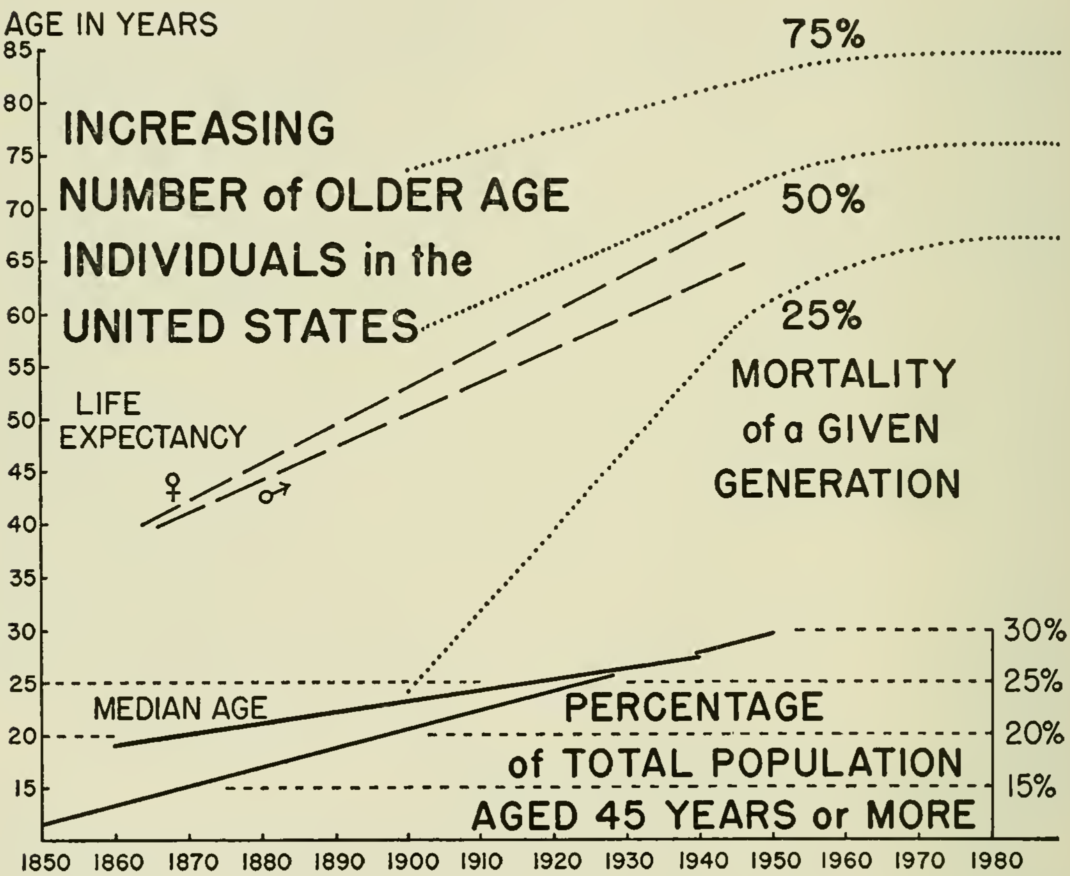

Fig. 6. Composite of three more or less independent graphs (data obtained from Joseph Zubin from Dublin, Lotka, and Spiegelman, 1949; and from Statistical Bulletin of the Metropolitan Life Insurance Co., 1949, vol. 30, no. 10, pp. 1–3; 1952, vol. 33, no. 3, pp. 1–3; 1953, vol. 34, no. 4, pp. 1–2). Lowermost line on lowermost graph shows percentage of total population aged 45 or more from 1850 through the present; median age for same period shown in upper left line in same area. Life expectancy for individuals of both sexes and born in various years shown by two dashed lines in center of graph. In upper right quadrant, three dotted lines show times at which generations born in various years from 1900 through the present exhibited a 25, 50, and 75 per cent mortality. Thus, of the generation born in 1900, 25 per cent were dead at age 25 (or 1925), and half are dead now. By 1972 three-quarters of that generation presumably will have died.

der exhibit softening and death of neural tissue as a result of inadequacy of blood flow.

Of the 33 per cent of autopsy cases with neural lesions, about 25 per cent is therefore accounted for on the above basis and the remaining 8 per cent is accounted for by approximately equal proportions (2%) of tumors, trauma, malformations, and infections of the neural system.

Six per cent of all deaths are due to accidents each year, and a large proportion of these must be considered due (in more than one sense) to neural failure or inadequate function from the point of view of natural selection.

In summary then, although trauma of the neural system is especially lethal and although a surprisingly high percentage of tumors and malformations are found in the neural system and it is rather susceptible to infection, the overwhelming cause of destruction of neural tissue is failure in blood supply.

Morbidity statistics reveal a much higher percentage of persons to be affected by neuropsychiatric disorders than are found to contain evidence of neuropathology at death. This is not due to such a simple matter as the fact that not all neuropsychiatric disorders depend on obvious organic substrate, for there are many lesions demonstrable after death that are not accompanied by obvious interference with function. This is because the nervous system, like other bodily tissues, contains a certain amount of spare material.

About 3 per cent of the population of the United States suffers from neuropsychiatric disorders which are ongoing and serious (table 9), other than deafness, blindness, and old age. Of this number of persons by far the largest proportion suffer from psychiatric or convulsive disorders.

Although advanced age is not in itself a disease, in the common sense of the word, there are few persons who have passed the age of 65 who do not exhibit a certain amount of psychomotor deterioration. At the present time about 8 per cent of the population is 65 years or older (fig. 5).

A figure of 10 per cent would therefore be a very conservative one for persons exhibiting impaired neural function. If one included persons who are deaf, mute, and/or blind, or who are suffering from some temporary neuropsychiatric impairment, an estimate of 20 per cent would not be too high for that proportion of the population which at any moment must be considered unable to participate in the true type of activity on which survival would depend if the protective mechanisms of society were to break down. If, because of military urgency, such protective mechanisms were ineffectual for a protracted period, this entire segment of the population might very well succumb.

While the effect of morbidity due to neuropsychiatric disorder is non-adaptive behavior, it is not easy to explain what the most important cause or causes for such disorders may be, because when we speak of a psychiatric disease we really are only applying the term to non-adaptive behavior and the term must necessarily

TABLE 9

Prevalence of Ongoing Serious Neuropsychiatric Disorders in the United States

Demyelinizing diseases		
Total	8,000	5/100,000
In northern latitudes	6,000	10/100,000
Cerebral palsy (major congenital defects)	500,000	300/100,000
Born annually	11,000	
Expected mortality in infancy	1,500	
Expected life institutionalization	3,000	
Remaining in society	6,500	
Convulsive disorders (epilepsy)	750,000+	500/100,000
Serious psychiatric disorders	2,800,000	1,750/100,000

be relative. It is sometimes said that complexity in civilization "causes more mental breakdowns." This is probably not true, but it is certainly true that non-adaptive behavior has less social significance in less complex societies and that what Coon has called the paleolithic organization of social life can tolerate such behavior more easily than a highly specialized urban culture. The incidence of psychiatric morbidity rises in urban communities not because such communities contain or produce more "breakdowns" but because they extrude non-adaptive individuals more vigorously than do agricultural communities and because such individuals succumb in non-supportive environments. This is just another way of saying that culture exerts its own selective effect, and we have therefore come again upon the ubiquitous manner in which evolutionary change supplements operate. In very primitive, unorganized societies psychiatrically ill individuals soon perish. In simple, organized societies they may not only survive but may be treated as privileged persons. In highly competitive societies they are protected but extruded if they possess no useful skill or creative ability. It is surprising to what extent society is able to absorb aberrant behavioral patterns which are not merely non-contributory but frankly aberrant, providing the individual exhibiting the pattern has something useful to offer the community.

Ordinarily an environmental situation admits of only one directional developmental tendency. There is only one "ideal." In a regulated, variable environment a number of different ideals may be tolerable and the individual traits which go towards the development of such different ideals may be mutually contradictory or even antagonistic or destructive.

A scientifically organized, mechanistic society must necessarily depend on the creative ability of its reflective minds, and these must operate in the relatively free and unhurried milieu which is itself destroyed by the very machine and increased productivity which the reflective mind creates. We all know creative engineering geniuses whose preoccupations with generalities and principles result on the one hand in constant and almost daily scientific and mechanical advances and whose preoccupations, on the other hand, also make them practically unfit to drive a simple automobile. Traits such as rapid reaction time and the ability to develop generalities, both of great value to our society, are not necessarily present in the same individual, nor does the same individual necessarily exhibit one of these traits throughout his lifetime.

In a rigid and obligatory environment individuals departing from the requirements of the environment are ultimately obliterated. In our social organization the accident-prone driver can travel in public conveyances, obtain a chauffeur, stay at home, move to an isolated community, or even obtain repeated respite from obliteration through the technical skills of the medical profession.

Not only does the manipulation of environment lead to great intraspecies variation by the preservation of variants and mutants and provision for these to procreate, but interbreeding among all the members of the species is facilitated.

For the individual who considers himself the prototype of the future and the fittest human this is a dismal prospect indeed. For the biologist such shuffling about constitutes no real alteration in the species, because the moment such an elaborated species is brought into direct contact with a compulsive environment all the irrelevant variants are promptly eliminated.

It would appear that while man's cultural development has tended on the one hand to preserve variants that will ultimately prove to have been useless it will also have the effect of guarding the species by having protected it from the commitment of specific evolutionary specialization. Not only has average man remained unspecialized but he has, in the process of domestication, become a result as well as a manipulating factor of that process and now presents a bewildering degree of variation not merely at the structural but also at the behavioral level, to the consternation of obstetricians and delight of psychologists.

Conclusion

Attention has been drawn to the fact that there is no good evidence to support the assumption that man's neural system has undergone any progressive alteration in the direction of greater size or complexity since the middle of the Pleistocene. It was at this period that cultural development became manifest, and the hypothesis is advanced that, with the advent of culture, man achieved a degree of independence from his environment and was therefore no longer under the necessity of developing structural modifications to survive. Consideration is drawn to the fact that the culture man has created has itself become a selective factor in his development and has resulted in great variation in the species.

It is pointed out that man's nervous system has some definite structural and functional limitations and that structural evolution in the direction of a larger or more complex neural system would require the movement of the species form into a direction in which the factors of structural and physiologic safety are already very narrow. Evolution of the species, in the sense of improvement in living conditions and extended and continued manipulation of the environment, would consequently appear to have to occur at a cultural rather than structural level. The specific structural limitations placed on man's neural system appear to be those that animal forms have inherited from the earliest Paleozoic, notably the necessity of a cell living in an aqueous medium to obtain oxygen and food.

In its broadest sense structural evolution may be regarded as a process that really gathered momentum and significance when unicellular organisms became combined into complex bodies in which the component cells assumed specialized functions. In so far as later forms are concerned, this process appears to have been extended by the cooperation of complex individuals in social systems. There is nothing novel about a comparison of the social order in which individuals are the subsidiary units to biologic bodies in which cells are the units, but, within the culture man has developed, there seems to be no clear, general recognition of the fact that a social order implies that individuals must accept the principle of specialization and cooperation and that neither the individual nor the system can achieve maximum efficiency if the subsidiary elements of the system insist that they can accomplish any and all tasks in the social order. Certainly, if there is to be any considerable evolution in which the neural system is to participate, it is quite clear that individual neural systems must draw upon the cultural reserves of the order, and this implies specialization on the part of particular individuals.

Before putting down the subject in hand, I should like to call attention to the fact that a recognition of the cooperative function of the individual involves a radical revision on the part of the individual in the concept of the "I" and "not I." A high degree of cooperative activity cannot be achieved in the presence of a strong sense of distinction between what is the concern of the individual and what is not. On the other hand a marked weakening in the ability to distinguish between the "I" and "not I" can have serious psychiatric consequences.

How does the neural system determine what is a part of the self and what is not? It is not possible to develop this consideration to any extent at this place, but it is not difficult to demonstrate that identification of the self with substance involves to a very large extent the degree of personal satisfaction the individual can obtain from such substance. Under such circumstances my glasses are much more significant to me than the last toe of my left foot. Our cultural development has progressed therefore to the point where we can easily place a higher evaluation on an item of technological achievement than on a part of our own body. This would seem to be a rather interesting way of raising the question whether evolutionary progress may not be moving not only faster but more significantly in the area of culture than structure.

LITERATURE CITED

Baraduc

1876. Troubles cérébraux analogues à ceux de la paralysie générale. Bull. Soc. Anat. Paris, pp. 277–279.

Bartholomew, G. A., and J. B. Birdsell

1953. Ecology and the protohominids. Amer. Anthrop., vol. 55, pp. 481–498.

Blomquist, H. E.

1953. Über die aus dem 5–6 Jahrhundert n. Chr. stammenden Knochenfunde von Kjeldamäki (im Kirschspiel Wöra, Süd-Ostbothnien, Finnland). Ann. Acad. Sci. Fennica, vol. 36, pp. 5–37.

Bolton, J. S.

1911. A contribution to the localization of cerebral function based upon the clinico-pathological study of mental disease. Brain, vol. 33, pp. 26–148.

Bonin, G. von

1934. On the size of man's brain as indicated by skull capacity. Jour. Comp. Neurol., vol. 59, pp. 1–28.

Broca, P.

1862. Sur la capacité des crânes parisiens des divers époques. Bull. Soc. d'Anthrop. Paris, ser. 1, vol. 3, pp. 102–116.

Bruns, L.

1892. Ueber Störungen des Gleichgewichtes bei Stirnhirntumoren. Deutsche med. Wochenschr., vol. 18, pp. 138–140.

1897. Die Geschwülste des Nervensystems. Berlin.

Burckhardt, G.

1890–1891. Ueber Rindenexcisionen. Allg. Zeitschr. f. Psychiat., vol. 47, pp. 463–548.

Campbell, B.

1954. The organization of the cerebral cortex. Jour. Neuropathol. Exp. Neurol., vol. 13, pp. 407–416.

Charcot, J. M.

1876–1880. Leçons sur les localisations dans les maladies du cerveau et de la moelle épinière faites à la faculté de médecine de Paris. Paris, 2 vols.

Cobb, W. M.

1955. The age incidence of suture closure. Anat. Rec., vol. 121, p. 277.

Conel, J. LeR.

1939–1955. The postnatal development of the human cerebral cortex. Cambridge, Massachusetts, Harvard University Press, 5 vols.

Coon, C. A.

1954. The story of man. New York, Alfred A. Knopf.

Craik, K. J. W.

1952. The nature of explanation. Cambridge, Cambridge University Press.

Darwin, C. G.
1953. The next million years. Garden City, New York, Doubleday and Co., Inc.
Donaldson, H. H.
1895. The growth of the brain. London, Walter Scott, Ltd.
Dublin, L. I., A. J. Lotka, and M. Spiegelman
1949. Length of life. Revised edition. New York, Ronald Press Co.
Dubois, E.
1914. Die gesetzmässige Beziehung von Gehirnmasse zu Körpergrösse bei den Wirbeltieren. Zeitschr. f. Morphol. u. Anthrop., vol. 18, pp. 323–350.
Economo, C. von
1926. Ein Koeffizient für die Organisationshöhe der Grosshirnrinde. Klin. Wochenschr., no. 14.
1929. Wie sollen wir Elitegehirne verarbeiten? Zeitschr. f. d. g. Neurol. u. Psychiat., vol. 121, pp. 324–409.
Ferrier, D.
1890. The Croonian lectures on cerebral localization. London, Smith, Elder and Co., p. 151.
Fischer, E.
1952. Über das Wesen der anatomischen Varietäten. Zeitschr. f. menschliche Vererbungs- u. Konstitutionslehre, vol. 31, pp. 217–242.
Flechsig, P.
1896. Gehirn und Seele. Auflage 2. Leipzig.
1896. Die Localisation der geistigen Vorgänge, insbesondere der Sinnesempfindungen des Menschen. Leipzig.
Gregory, W. K.
1951. Evolution emerging. A survey of changing patterns from primeval life to man. New York, The Macmillan Co., 2 vols.
Greisinger, W.
1867. Mental pathology and therapeutics. Translation by C. L. Robertson and J. Rutherford. London, The New Sydenham Society.
Harlow, J. M.
1848. Passage of an iron rod through the head. Boston Med. and Surg. Jour., vol. 39, pp. 389–393.
1869. Recovery from the passage of an iron bar through the head. Boston, D. Clapp and Son, p. 20.
Herrick, C. J.
1948. The brain of Amblystoma punctatum. Chicago, The University of Chicago Press.
Hitzig, E.
1884. Zur Physiologie des Grosshirns, Wandervers. d. Südwestd. Neurol. u. Irrenärzte in Baden, 17 Juni, 1883. Arch. f. Psychiat., vol. 15, pp. 270–275.
Jastrowitz, M.
1888. Beiträge zur Localisation im Grosshirn und über deren praktische Verwerthung. Deutsche med. Wochenschr., vol. 14, pp. 81–83, 108–112, 125–128, 151–153, 172–175, 188–192, 209–211 (see especially p. 111).
Keith, A.
1925. The antiquity of man. London.
Lasker, G. W.
1953. Environmental growth factors and selective migration. Human Biol., vol. 24, pp. 262–289.

LeGros Clark, W. E.
1954. The fossil evidence for human evolution. Chicago, The University of Chicago Press.
Lennox, W. G.
1924. Child mortality with reference to the higher education of parents. Amer. Jour. Hygiene, vol. 4, pp. 52–61.
Leyden, E., and M. Jastrowitz
1888. Beiträge zur Lehre von der Localisation im Gehirn. Leipzig, Thieme, p. 82.
Loeb, J.
1902. Comparative physiology of the brain and comparative psychology. New York, G. P. Putnam Sons.
Lull, R. S., H. B. Ferris, G. H. Parker, J. R. Angell, A. G. Keller, and E. G. Conklin
1922. The evolution of man. New Haven, Yale University Press.
Martin, R.
1928. Lehrbuch der Anthropologie. Auflage 2. Jena, G. Fischer, 3 vols.
Mettler, C. C.
1947. History of medicine. Philadelphia, The Blakiston Co.
Mettler, Fred A. (ed.)
1949. Selective partial ablation of the frontal cortex. New York, Paul B. Hoeber, Inc.
Moñiz, Egas
1936. Les premières tentatives opératoires dans le traitement de certaines psychoses. Encéphale, vol. 31, no. 2, pp. 1–29.
Murphy, J. P.
1954. Cerebrovascular disease. Chicago, The Year Book Publishers, Inc.
Nobele
1835. Ann. Med. Belge, Fevrier, Compte Rendu. *Cited by* Haeser, H., 1836, Fall einer bedeutenden Gehirnverletzung. Schmidt's Jahrbücher, vol. 9, pp. 321–322.
Oppenheim, H.
1900. Diseases of the nervous system. Translated by E. E. Mayer. Philadelphia, J. B. Lippincott, p. 399.
Otto, W.
1953. Über Geburtenverteilung der verschiedenen Wuchsformen. Zeitschr. f. Altersforschung, vol. 7, pp. 130–139.
Parker, G. H.
1922. The evolution of the nervous system of man. *In* Lull, R. S., and others, The evolution of man. New Haven, Yale University Press, pp. 80–102.
Retzius, G.
1915. Wächst noch die Grösse des menschlichen Gehirns? Zeitschr. f. Morphol. u. Anthrop., vol. 18, pp. 49–64.
Roche, A. F.
1953. Increase in cranial thickness during growth. Human Biol., vol. 25, pp. 81–92.
Rowland, Lewis P., and Fred A. Mettler
1949. Cell concentration and laminar thickness in the frontal cortex of psychotic patients. Jour. Comp. Neurol., vol. 90, pp. 255–280.
Scott, J. H.
1953. The variability of cranial and facial dimensions in modern skulls. Brit. Dental Jour., vol. 94, pp. 27–31.

SHAPIRO, H. L.
1933. Man—500,000 years from now. Nat. Hist., vol. 33, pp. 582–595.
SKERLJ, B., AND Z. DOLINAR
1950. Staroslovanska okostja z Bleda. Monogr. Slovene Acad. Sci. Arts, Ljubljana, cl. 1, no. 2, pp. 67–104.
STRAUS, W. L., JR.
1954. Some problems of human evolution. Anat. Rec., vol. 121, p. 371.
TILNEY, FREDERICK, AND H. A. RILEY
1928. The brain from ape to man. New York, Paul B. Hoeber.
TORGERSEN, J., B. GETZ, U. HAFSTEN, AND H. OLSEN
1953. Steinaldersmannen fra Bleivik, Skåre, Rogaland. Årbok Univ. Bergen, Naturvitenskap. Rekke, no. 6, pp. 1–53.
VIERORDT, H.
1893. Anatomische physiologische und physikalische Daten und Tabellen. Jena, Gustav Fischer.
WEIDENREICH, FRANZ
1924. Die Sonderform des Menschenschädels als Anpassung an den aufrechten Gang. Zeitschr. f. Morphol. u. Anthrop., vol. 22, pp. 51–282.
1946. Form and qualities of the human brain and skull in the light of evolution. *In his* Apes, giants and man. Chicago, The University of Chicago Press.
WELT, L.
1888. Ueber Charakterveränderungen des Menschen infolge von Läsionen des Stirnhirns. Deutsches Arch. f. klin. Med., vol. 42, pp. 339–390.