

Cerebro-Cortical Surface Areas, Volumes, Lengths of Gyri and their Interdependence in Mammals, Including Man¹

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Eingang des Ms. 5. 3. 1970

The importance of brain size from the standpoint of evolution and of "intelligence" has been emphasized by numerous authors. Good reviews of the subject are those by BLINKOV and GLEZER (1968) and by HOLLOWAY (1968).

The major points of emphasis in the past have been the ratio of brain weight or brain volume to body weight and the line of evolution leading from the insectivores to man.

Less easily accessible to measurement than weight and volume has been the surface area of the cerebral cortex and especially of the paleo- and neocortex. This parameter is of great significance because together with measurements of cortical thickness, the number of possible synapses would depend on the cortical surface area and on cell density per volume (now being determined by Dr. Herbert HAUG in Kiel). This surface area depends on the total volume of the telencephalon and its degree of folding.

It seemed of interest to compare representatives of several, taxonomically far separated mammalian classes, rather than to confine ourselves to the customary approach of following a line of evolution within a restricted group of mammals.

The determination of cortical surface areas was a task which presented our predecessors with enormous technical difficulties. Nevertheless, the problem has been tackled successfully and with superhuman patience and industry by BAILLARGER (1895), H. WAGNER (1864), R. WAGNER (1864), HENNEBERG (1910, 1911), ARESU (1914), LÉBOUCQ (1929), NAYRAC (1930) and others.

The development of stereological methods permitted us to analyze 48 brains within a period of two years.

Some of our early results have been published (ELIAS, KOLODNY and SCHWARTZ, 1967, ELIAS, HAUG, LANGE, SCHLENSKA and SCHWARTZ 1969 and ELIAS and SCHWARTZ 1969). But in the present paper everything is coordinated.

The human brain served as a standard with which other brains might be compared. Measurements were undertaken on 20 adult human brains, most from cases with well documented histories. Since most of them were accident and murder cases, the majority of the victims were physically healthy.

The following is a brief survey of taxonomical units studied: Marsupials: Mouse Opossum 1 case; Opossum 3 cases; Kangaroo 2 cases; Wallaby 1 case.

Carnivores: Coyote 2 cases; Fox 3 cases; Raccoon 3 cases; Dog 2 cases..

Primates: Man 20 cases.

Toothed Whales: Baird's Dolphin 2 cases; Bottlenose Dolphin 4 cases; Risso's Dolphin 1 case; Pilot Whale 3 cases; False Killer 1 case.

We are indebted to Drs. AUGUST HENNIG and MELVIN DIPERT for much important advice.

Methods

Most of the brains were immersed in 20% formalin made up with saline and kept in the fixative for 2 to 3 months. A few were fixed by perfusion through the carotid and vertebral arteries from the arch of the aorta.

¹ Supported By USPHS grant NB-7104.

Table 1
Calf brains

	Whole brains				Blocks cut out of brains	
	Fresh		After 2 months in 20 % formalin in saline		After fixation	After paraffin embedding
	g	cm ³	g	cm ³	cm ³	cm ³
Calf 1	235	220	240	225	6.744	4.390
Calf 2	203	189	190	175	7.359	4.530
Calf 3	195	180	195	180	11.665	6.388
Calf 4	203	200	200	200	5.905	3.517
Calf 5	240	220	225	220	4.212	2.559
Sum	1076	1009	1050	1000	35.885	21.384
Average	215	201	210	200	7.177	4.276
Average Shrinkage	0.9 % by volume				41 % by volume	

Volumes were determined by water immersion. A container was partially filled with water and its weight recorded. The brains were, then, immersed into the water, but kept suspended by a string. The difference of weight recorded by the scale in grams equals the volume of the brains. Subsequently the brain was permitted to drop to the bottom of the container. The new difference of scale readings equals the weight.

Five brains of calves were measured before and after formalin fixation. Some shrank slightly while others became a little larger. The volume change averaged 0.9% (table 1) a difference smaller than the accuracy of the scale. Among the human brains whose fresh volume could be determined the change averaged 13% (table 2). However, when fresh human brains are immersed in water for volume determination, the ventricles can be filled excessively. This cannot be avoided, because these precious specimens must be handled with great gentleness. Later when the brains are immersed in the fixative, and suspended in the refrigerator in a plastic bag to prevent distortion, the walls of the bag press the excess fluid out of the ventricles. Therefore, we assume the shrinkage observed in the calf brains to be more realistic than the volume differences in human brains. In fact, in a few cases we immersed fresh human brains up to three times and obtained a different reading each time, the differences reached 12% in one individual brain, again due to different filling of the ventricles.

The volume of a single human lateral ventricle, after fixation, is given by BLINKOV and GLEZER (1968) as ranging between 4.3 and 56.6 cm³. Our comparisons between fresh and

Table 2
Human brains — fresh vs. fixed volume

	Apparent fresh volume (including filled ventricles)	Fixed volume (ventricles mostly emptied through compression)
	cm ³	cm ³
Case 4	1364	1135
Case 14	1025	965
Case 15	1256	1100
Case 16	1303	1120
Case 18	1174	965
Case 19	985	825
Case 20	1060	996
Sum volume	8167	7106
Average	1166	1015
Apparent reduction in volume		13 %

fixed human brains would imply that one lateral ventricle can reach 300 cm³ in volume, a number much higher than the maximum quoted by BLINKOV and GLEZER. We can account for this great apparent volume as follows: A lateral ventricle has a cross-section similar to a crescent. Since fresh brain is very soft, the walls can be made to recede to such an extent that the cross section becomes circular, thus greatly exceeding a crescent in area. This great expansion is not possible when the brain is enclosed in the cranium or in a hanging plastic bag.

It should be emphasized that, according to the Archimedian principle it is indifferent, whether the ventricles are filled with water or with air, as long as the total specific gravity remains above 1.

A much greater shrinkage was to be expected with our paraffin and celloidin embedded brains. A shrinkage factor was determined, using the same 5 calf brains, by cutting parallelepipeds out of the fixed brain and measuring their edges with calipers. The volume was then computed as the product of length · height · width. After embedding, the parallelepiped's new volume was again determined and the average shrinkage was found to be about 41 % (see table 1). Since paraffin and celloidin embedded material is subject to such enormous shrinkage all the measurements on which this paper reports concern wet, formalin fixed specimens, except for the extremely small *Marmosa* which was paraffin embedded. In the quantitative table, the values are corrected for the shrinkage, of the *Marmosa* brain.

After removal of the brainstem by a cut through the level of the superior colliculi, the cerebrum was divided into the two hemispheres. In the case of human and cetacean brains, the hemispheres were cut into slices of equal thickness by means of an electric meat slicer, and each slice was sealed with some formol in a plastic bag.

In the case of smaller brains, slicing was performed with a straight razor and the slices were embedded side by side in gelatine. After cooling the gelatine slab was, likewise, sealed with some formol in a plastic bag. No shrinkage or swelling occurred during or after gelatine embedding.

One hemisphere was cut into "frontal" slices, the other into "horizontal" slices. The designation of frontal versus horizontal is made in analogy to the human brain. In reality, in the marsupials and carnivores the true frontal plane (parallel to the forehead) is practically horizontal. In the whales, the brain is tilted almost 90° forward when compared with the human brain. Therefore the words "frontal" and "horizontal" can be taken literally only for human brains. In cetacean and carnivore cases, our term "frontal" means perpendicular to the body of the corpus callosum and the word "horizontal" means parallel to the body of the corpus callosum. But in the marsupials, in which the corpus callosum is represented by a cylindrical bundle, "frontal" means perpendicular to the long axis of the brain, while "horizontal" means parallel to the lower edge of the maxilla.

Stereological Procedures

A. Surface Area Determination

If a solid is penetrated by several straight lines, the number of points in which these lines intersect its surface is proportional to the surface area (fig. 1).

After slicing, penetrating lines can be substituted by lines superimposed upon the cut surfaces of the slices (fig. 2).

Surface determination by the method of line intersections was introduced by SMITH and GUTTMANN (1953). According to a formula especially useful for brain measurements, derived by HENNIG (1957),

$$S = 2 \cdot P \cdot t \cdot h, \quad (1)$$

where S is the absolute value of the surface area to be measured, t is the average thickness of the slices and h is the distance between parallel test lines (h stands for height because the letter d is used for another parameter in stereology).

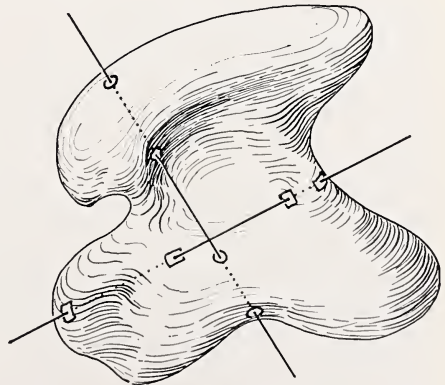


Fig. 1. A solid pierced by test-lines

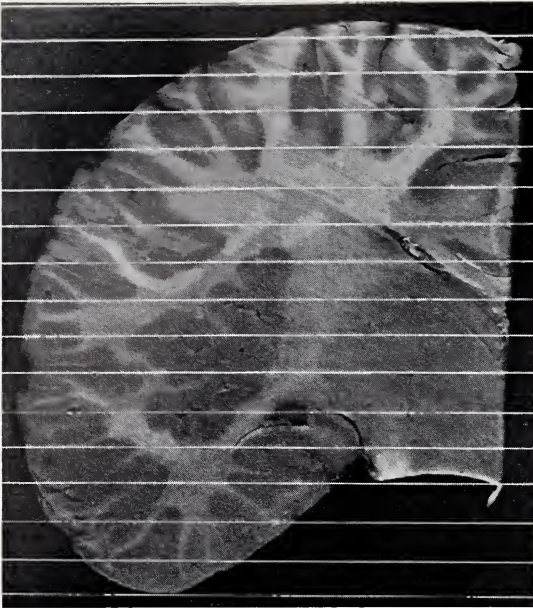


Fig. 2. Slice through the right cerebral hemisphere of a brain of *Delphinus bairdii*, with equidistant, transverse lines, engraved on a plate of plexiglas, superimposed

In practice, we superimpose a plastic plate upon the brain slices. The plastic plate has parallel, equidistant lines engraved into it. "Engraving" of the lines is done with a sharp kitchen knife along a metal ruler. The plastic plate is layed upon the plastic bag, the lines in contact with it, to avoid parallax. The plastic bag prevents filling of the engraved lines with liquid.

Prior to slicing, the length and height of the brain are measured with calipers (a very large, wooden pair of calipers was constructed to measure human and cetacean brains). Though the slicer is set to the approximate desired thickness (3–10 mm according to brain size) the average thickness is found by dividing the measured length (for frontal cuts) or height (for horizontal cuts) by the number of slices.

The calculation of t may be slightly incorrect for the following reason:

Slight deviations of cutting (i. e. whether perpendicular or parallel to the corpus callosum) are inevitable, because slicing is accomplished with the medial surface laying down, so that the person who operates the slicer does not see the corpus callosum. As a consequence of a deviation from the correct angle of sectioning, an error in the computation of slice thickness may result; for, as stated above, t in formula (1) is found by dividing the measured length or height of the hemisphere by the number of slices, it being assumed that this length or height had been measured at the exact angle of 90° to the direction of cut.

To evaluate the error due to a faulty cutting direction several brains were measured for height and length by means of calipers determining at first the length and height with exact reference to the corpus callosum. Then the calipers were tilted by 10° in both directions, a deviation in cutting direction greater than ever committed.

In 5 out of 6 such tests, a deviation of the cutting direction from the horizontal produced as would be expected, a greater number of slices in oblong brains and hence lead to a smaller calculated t . Therefore the estimate of the surface area would be too low.

Conversely, tilting of the cutting direction against the true frontal plane reduced the number of slices in 5 out of 6 experiments, leading to a calculated t higher than the true thickness. This will produce a surface estimate greater than the true value.

For the broad brains of Cetacea the effect is the reverse.

Therefore, errors due to faulty t determination are largely compensated when both hemispheres are averaged.

Consider a sagittal section through a cerebral hemisphere as an ellipse with the corpus callosum parallel to its long axis. Let a be the long and b the short axis. Precise "horizontal" cutting will produce $\frac{b}{t}$ slices; precise frontral sections $\frac{a}{t}$, slices, a is

the longest, b the shortest caliper diameter of the ellipse. Thus when tilting the ellipse about a transverse axis (perpendicular to the sagittal plane), we obtain a caliper diameter d , so that $b < d < a$. Since t is calculated under the tacit assumption that $d = b$, the calculated t will be higher than real for most frontal slices and lower than real for most horizontally cut brains.

Figure 3 attempts to visualize this effect schematically. If cutting in the correct direction, we obtain 3 horizontal and 7 frontal slices out of the model. When tilted by 35° the model yields 5 horizontal and 6 "frontal" slices. In our practical work, the tilting is, of course, minimal compared to this model. Since real brains are not accurate ellipsoids, the deviations by tilting in opposite direction are not symmetrical.

Only in human brains no such faulty cutting angle appears, because instead of the corpus callosum, the human brain offers a base line which remains always in sight, and which can be aligned with the ridges of the meat cutter. This line connects the lowest point of the temporal lobe with the lowest point of the occipital lobe, with the pre-occipital notch in between.

In a cetacean brain (*Tursiops truncatus* 2) the true height measured was 10.05 cm. Tilting the calipers 10° forward, the apparent height was 10.17 cm, tilting it 10° backward, it measured 10.17 cm. The maximum variance is then 0.12 cm. This would affect the calculated t maximally by $+\frac{0.12}{n}$ or by $+0.12\%$. A

statistically acceptable estimate of the standard deviation for t would be $1/6$ of this value, i. e. $\sigma_{t \text{ horizontal}} \cong +0.02\%$.

By the same method the standard deviation for frontal section thickness is found to be $\sigma_{t \text{ frontal}} \cong \pm 0.05\%$. For a dog $\sigma_{t \text{ horizontal}} \cong +0.0166\%$ and $\sigma_{t \text{ frontal}} \cong 0.015\%$; for a raccoon $\sigma_{t \text{ horizontal}} \cong -0.0066\%$ and $\sigma_{t \text{ frontal}} \cong -0.0166\%$.

Since in 5 out of 6 measurements, the length appeared shorter than real after rotation and the height appeared greater than real in the same number of tests, we believe that in practice, discrepancies between the two hemispheres due to faulty t determination compensate each other when the calculated surface areas of both hemispheres are added.

The average of the deviation among the various kinds of animals is $\sigma = 0.0209$.

Intersection counts are made on every slice. The point counts of intersections of the lines with the pia-cortex boundary yields P in the above formula. Where a test line crosses a sulcus, 2 points are counted, because two portions of cortex are in contact with the pia at such a location. Tangent points and external points are counted once (fig. 4).

Only one direction of lines would be needed, if the sulci and gyri were arranged at random. However, this is usually not the case. In marsupials and in some of the carnivores, the brains are oblong; and the sulci and gyri show a preferential longitudinal arrangement (fig. 5).

For example, if the surface area of one hemisphere of coyote 1 were determined from longitudinal lines, it would be 60 cm^2 , were it derived from vertical lines it would be 119 cm^2 and from transverse lines (average from both hemispheres), 121 cm^2 . The brains of odontocete whales are broader than long (fig. 6), and there is a slight tendency for sulci and gyri to run transversely. In *Delphinus* 3, for example, longitudinal lines yielded 968.4 cm^2 vertical lines gave 882.7 cm^2 and transverse

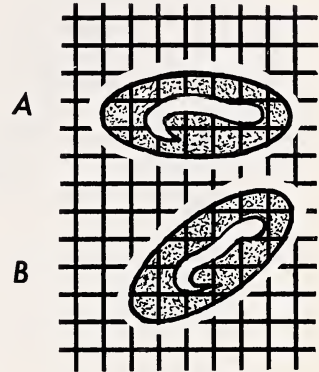


Fig. 3. A model for the cause of possible incorrect thickness determination of slices by involuntary tilting

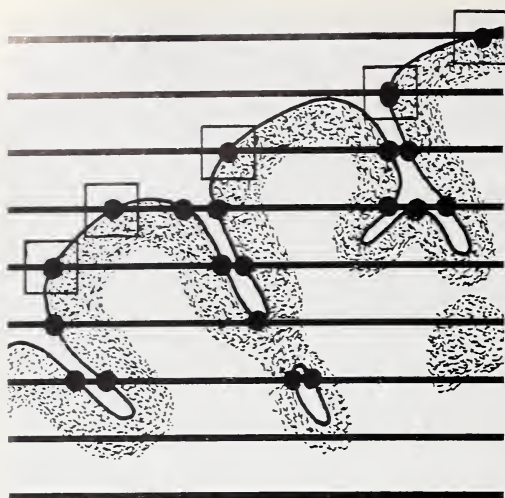


Fig. 4. Diagram to illustrate the point count method for the determination of total surface (black dots) and of external surface (squares)

from all three directions must be averaged. Vertical lines can be laid over frontal slices only (fig. 7, B), transverse lines (fig. 7, A) can be laid over both frontal and horizontal slices. Longitudinal lines can be laid over horizontal slices only (fig. 7, C). Even a superficial inspection of figure 7 shows that a surface estimate based on longitudinal lines only would be too low for the coyote, an animal whose brain is oblong; while transverse and vertical lines would yield too high a figure. Therefore, the values obtained for the three directions of space must be averaged.

In cetacean brains which are broader than long and high, transverse lines yield

lines indicated a surface area of 862.7 for one hemisphere. These differences indicate preferred orientation of gyri in a transverse direction. But the anisotropy is much lower than in the coyote. In the human brain, such anisotropy, though present, is even less obvious.

Although, to our knowledge, no numerical index for preferred orientation has been worked out, one can gain a superficial impression of anisotropy by comparing point counts in two directions made on series of slices through individual hemispheres (table 3).

To eliminate errors in surface determination due to preferential orientation (anisotropy), test lines must be layed through the brain in three directions perpendicular to each other (fig. 7), and the counts

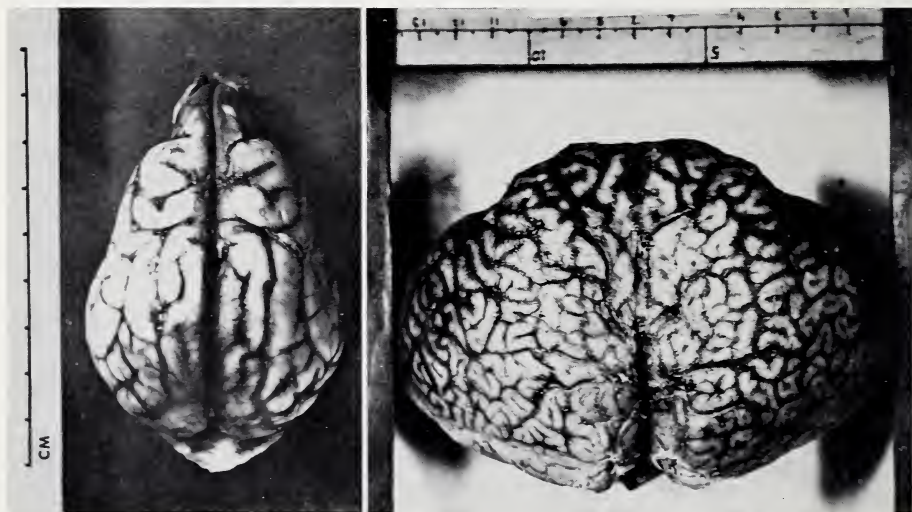


Fig. 5 (left). Brain of a coyote (*Canis latrans*) — Fig. 6 (right). Brain of a pacific dolphin (*Delphinus bairdii*)

Table 3

Surface areas (cm²) of individual hemispheres calculated from point counts in each of the two possible orientations of the line grid

L = Left hemisphere R = Right hemisphere

		Hemisphere	Longitudinal	Transverse	% deviation	Hemisphere	Vertical	Transverse	% deviation
<i>Globicephala</i>									
<i>scammoni</i>	3	R	2519	2378	6	L	3039	2591	15
<i>Tursiops gillii</i>	1	R	1436	1416	2	L	1432	1398	2
<i>Tursiops truncatus</i>	2	R	2062	1686	18	L	1742	1590	8
<i>Delphinus bairdii</i>	3	R	955	887	8	L	845	861	2
<i>Vulpes</i> (Fox)	3	L	46	88	48	R	92	74	10
<i>Procyon</i> (Raccoon)	3	L	66	81	19	R	70	85	18
<i>Canis latrans</i>									
(Coyote)	1	L	59	105	44	R	119	140	15
<i>Didelphys</i>	2	L	3.9	8.7	55	R	6.0	7.8	23
(Opossum)									
<i>Marmosa mitis</i>		R	0.69	1.35	49	L	1.42	1.62	12
(Mouse opossum)									
<i>Homo. Case</i>	7	L	1228	1288	3	R	960	927	3
<i>Homo. Case</i>	12	R	1242	1202	4	L	1373	1361	1
<i>Homo. Case</i>	16	R	1146	1182	3	L	1265	1249	1

the lowest surface area estimate. In human brains which are moderately oblong, this discrepancy is low. Among our sample, the raccoon's brain provides the greatest uncertainty about its cortical surface area because the left hemisphere is, in each of our three cases, wider than the right; and one can cut each of the two hemispheres in one direction only. Thus the compensation from the combination of both hemispheres is imperfect. Is this an expression of "dominance"?

The number of intersections depends to a small degree on the accidental position of the superimposed grid. In figure 8 we see 10 intersections for the thick lines and 11 intersections for the thin test lines. Since in practical work counts must be made on every slice, the error is not great. To determine the accuracy of these point counts, we made the following test on one *Tursiops* brain, one human and one raccoon.

The test plate was layed over each slice in the specified direction, and a point count was made; then the grid was displaced, in the direction perpendicular to the test lines, by one third the distance between lines ($\frac{h}{3}$), the lines remaining parallel to themselves. A second count was made and the procedure repeated. The results are shown in table 4. This test executed by two observers was used to determine the error of P in the equation for S.

These data were then analyzed with a computer by rows, columns and also by the individual „cells“ of three counts apiece. The standard deviation (now a function of these 14 separate analyses) was reported out as 22. This standard deviation can be assumed to be representative of our method as a whole. 22 out of 1823 amounts to an error of less than $\pm 1.2\%$.

We are now ready to put the computed standard deviations into the formula, coming from the theory of error propagation,

$$\sigma_S = 2(P \cdot h \cdot \sigma_t + P \cdot t \cdot \sigma_h + h \cdot t \cdot \sigma_p);$$

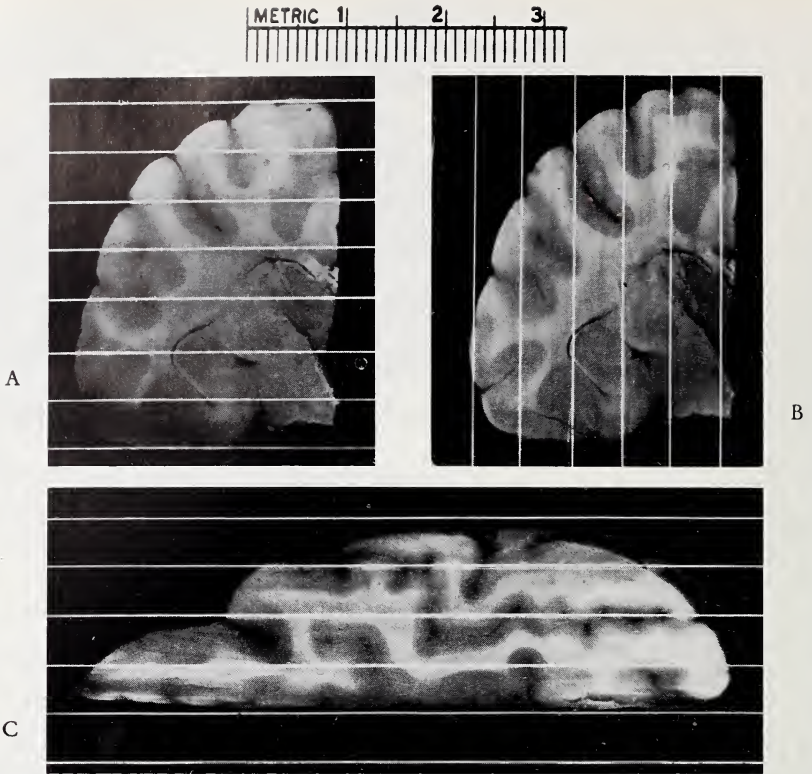


Fig. 7. Slices through individual hemispheres of a coyote brain with test-lines superimposed but since $h = 1$ and $\sigma_h = 0$, the middle term in this equation disappears so that

$$\sigma_S = 2 (P\sigma_t + t\sigma_p).$$

The average σ_t has been found to be 0.021. The average σ_p was 22. Again using Tursiops as representative of all the measurements, we insert $P = 1823$ and $t = 0.578$.

$$\text{Thus, } \sigma_S = 2(1823 \cdot 0.01 + 0.578 \cdot 22) = 102,$$

resulting in a probable error of $\pm 5\%$ for one hemisphere. But for human brains in which t determination is more accurate than in others, for reasons explained above, the final error is less than this.

This statistical analysis was carried out for us by Dr. MERLIN DIPERT, Chief, Computer Center, Department of Biology, Argonne National Laboratories.

B. Length of externally exposed gyri

It might be of interest to provide a method for the coarse estimation of the cerebrocorti-

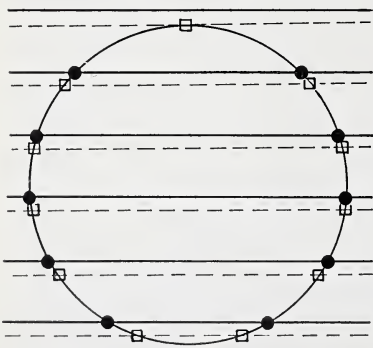


Fig. 8. A circle with test-lines superimposed, showing that a slight displacement of the test-lines can alter the intersection count. A tangent point has the value one.

Table 4
Personal bias

Intersection Counts	Left Longit.	Left Transv.	Right Transv.	Right Vertical
Worker				
<i>Tursiops gillii</i> 2	1977	1733	1840	1903
	D. S.	2014	1732	1817
	1972	1710	1830	1892
	1805	1883	1673	1755
H. E.	1770	1888	1742	1734
	1786	1902	1701	1748
Raccoon 1	D. S.		451	380
	H. E.		397	342
Human case 19			772	829
	D. S.		765	839
				770
H. E.			784	826
			773	819
			795	790

cal surface area from a measurement of the total length of superficially exposed gyri, so that paleontologists could obtain more quantitative information from endocranial casts. Therefore, we determined the length of the superficially exposed gyri in 17 human and 20 animal brains. The results are shown in fig. 9. Those gyri touching the falx and the tentorium were not measured, because they cannot, as a rule, yield impressions on the inside of the skull. Only in those few animals with an ossified tentorium (such as the toothed whales, the mink and the raccoon) and with a partially ossified falx cerebri might skeletal impressions be seen in fossils at these deep locations. Nevertheless, even in those animals tentorial and falcine surfaces were not included in length determinations. We fully realize that in the case of man and in some dolphins, the subarachnoid space is so wide that distinct impressions of gyri are not created on the inside of the cranium. But in many kinds of mammals such impressions are distinct enough to be useful.

To measure the length of these gyri, one can use a curvimeter (map-reading wheel) both for casts and for actual brains. But for the latter there is a better stereological method: The number of convexities in the external cortical surface is counted on each slice. If P is the number of convexities and t the average thickness of the slices, the total length of these gyri is

$$L = 2 P t \quad (2).$$

(ELIAS, HENNIG and SCHWARTZ 1971).

On several brains, the curvimeter was used before cutting and the point count method was applied after cutting. As table 5 shows, the results of both kinds of length determination agree very well. This double measurement provides, at the same time, experimental evidence for the accuracy of the formula.

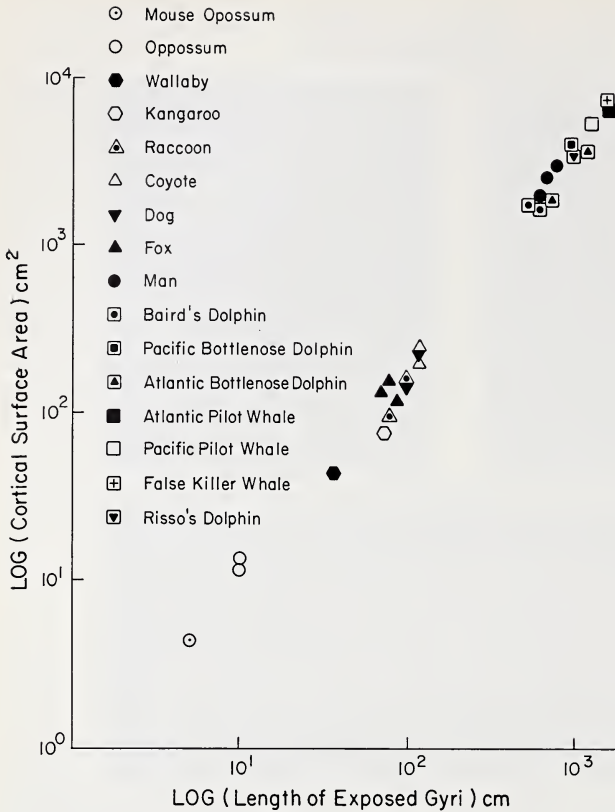


Fig. 9. Logarithms of the lengths of externally exposed gyri plotted against the logarithms of the cerebrocortical surface area of various mammals

the same test lines with only the perimeter of each slice. If the latter point count is given the value p , then, without calculating the surface areas, the index of folding is found immediately as

$$I = \frac{P}{p} \quad (3),$$

(the ratio of black dots to white squares in figure 4).

Results

A. Human Brains

The length of superficially exposed gyri in our sample of 20 human brains ranges from 548 cm to 787 cm. The surface area of the neocortex ranges from 1952 cm² to 3031 cm². The index of folding ranges from 2.25 to 3.07.

The data of 20 human cases are given in table 6, arranged in the order of size of the cortical surface.

The study includes 9 males and 11 females. In the upper half size class (50%),

C. Index of Folding

LEBOUCQ (1929) introduced the very useful concept of the "rapport" between the actual surface of a hemisphere and the calculated surface of a sphere of equal volume. The more complex the folding, the greater is this ratio. VON BONIN (1941), improved on this concept, substituting for it, the index of folding = that is the ratio of the entire surface area to the externally exposed surface area. He derived his values partially from disconnected data published in the literature and from his own measurements (still conducted with conventional slow methods). Stereologically, this index is found rapidly by making the above described point counts of line intersections with the entire pia-cortex boundary and a point count of intersections of

Table 5

	Length of gyri Determined with			
	Curvimeter		Stereological Methods	
	D. S.	H. E.	D. S.	H. E.
<i>Globicephala scammoni</i>	617 cm left	590 cm right	634 cm left	689 cm right
<i>Tursiops gillii</i> 1	424 cm left	429 cm right	416 cm left	412 cm right
<i>Tursiops gillii</i> 2	524 cm left	452 cm right	525 cm left	411 cm right
<i>Vulpes fulva</i> 2	66.1 cm total	76.2 cm total	64.7 cm total	

there were 5 male and 5 female brains. The most extensive cortical surface was that of a male. Also the least extensive cortex belonged to a male. Among the five largest brains (25%) there was 1 male and 4 females.

Admittedly a sample of 20 cases is too small for valid conclusions. Nevertheless we are taking the liberty of making a few remarks concerning these numeral data.

The average cortical surface area of paleo- plus neocortex together was 2268 cm². The cortical surface averaged 2297 cm² in 9 males and 2257 cm² in 11 females, a difference of 0.9% from the total average. In other words, there is no difference of cortical surface area between males and females in this sample, the probable error of all measurements being $\pm 5\%$ (see above).

The question of whether there exists a correlation between cortical area and intellectual accomplishment appears, at first sight, to be answerable in the affirmative, since the two persons in this sample who had reached the highest intellectual level had the largest cortical area.

Among them was a man and a woman. Should future studies confirm this cursory impression it should be kept in mind that it is probable that greater brain surface and higher intelligence are mutually interdependent. For BENETT, ROSENZWEIG and DIAMOND (1969) have shown that rats exposed to an enriched environment developed, postnatally, larger brains than their litter mates who grew up under impoverished conditions. On the other hand, BRESLER and BITTERMAN (1969) obtained better learning performance in fish whose brain volume they had surgically increased during early embryonic stages.

The third largest cortex was possessed by a „feable minded“ woman, an inmate of an asylum. Her brain, however, showed bilateral depressions in areas 40, 44 and 45. It may be assumed that there existed a deficiency of white matter under these cortical areas resulting in loss of auditory coordination and aphasia, by deficiency in short and medium-long association fibers.

B. Non-human Brains

Among non-primate mammals we selected three taxonomic groups very distant from each other; and within each group we investigated a variety of species. The results of the marsupial brains will be found in table 7, those of carnivore brains in table 8 and those of the Odontoceta (toothed whales, including dolphins) in table 9.

Among the four taxonomic groups included in this work, only the marsupials are represented by extremes in the evolutionary scale, the opossums and the kangaroos (the wallaby is very closely related to the kangaroos and would be identified as such

Table 6
Human brains

Case	Body height m	Sex	Age	Personality	Volume of whole brain (fixed) cm ³	Volume of cere- brum only (rostral from red nucleus) cm ³	Surface area of cerebral cortex cm ²	Length of exposed gyri cm	Index of folding	Remarks
1	1.65	M	40	University graduate. Health Administrator.	1265	1015	3031	787	3.04	
2	1.81	F	55	Physician. Many hobbies.	1320	1160	2672	716	3.04	Unusually extensive striate cortex
3	1.58	F	26	Idiotic inmate of asylum, epileptic.	1310	1170	2530	678	3.06	Trigone and operculum (arcas 44 & 45), laryngeal field of area 4, and portion of supramarginal gyrus (area 40) sunken in on both sides.
4	1.64	F	20	Medical technician, excellent in sports, group leader, excellent school and personality record.	1275	1135	2491	678	2.84	
5	1.76	F	19	Allegedly intelligent housewife, good dancer.	1100	965	2439	569	2.70	
6	1.78	M	24	Schizophrenic, had harassed childhood, never a steady job, cirrhosis.	1220	1185	2407	760	2.84	
7	1.81	M	45	No character information was available.	1290	1160	2403	654	3.06	
8	1.83	M	77	Aggressive business tycoon, civic leader, few intellec- tual interests.	1360	1220	2359	616	2.99	
9	1.60	F	45	No personality information available.	1200	1080	2328	581	2.66	
10	1.78	M	48	Retired army colonel, reportedly un-intelligent.	1275	1120	2294	724	3.07	Pronounced dolichocephalic

Table 6 (continued)

Case	Body height m	Sex	Age	Personality	Volume of whole brain cm ³ (fixed)	Volume of cere- brum only (rostral from red nucleus) cm ³	Surface area of cerebral cortex cm ²	Length of exposed gyri cm	Index of folding	Remarks
11	1.58	F	25	Little information.	1170	1040	2240	600	2.50	
12	1.67	M	59	Owner and manager of bowling alley, one yr. college. Read business jour- nals frequently.	1100	979	2193	644	2.71	
13	1.58	M	21	Thief, shot by police.	1400	1246	2142		2.63	Specimen lost while moving. Length of gyri can not be determined
14	1.76	M	25	Not very intelligent	1025	965	2128	620	2.66	
15	1.51	F	22	Social worker, very kindly, average intelligence.	1100	990	2119	554	3.03	
16	1.62	F	20	Kindergarten teacher. Early, low intelligence, later intelligence improved steadily. Competent, cons- cientious worker, coopera- tive, unimaginative. Can not correlate knowledge with practical application. Successful in her profession and well liked.	1120	980	2101	613	3.01	Degenerated fibers in dorsal third of posterior half and dorsal portion of splenium of corpus callosum.
17	1.73	F	36	Hotel desk clerk, 2 yrs. coll- ege, average intelligence.	1170	1040	2024	574	2.85	
18	1.73	F	22	Nurse, high average intelli- gence, resourceful, conscient- ious, efficient.	1080	965	1952	612	2.76	
19		F	53	Emaciated at death.	1110	985	1937	548	3.06	
20	1.66	M	35	Bigamist, migrant.	1060	996	1715	658	2.25	

Table 7
Brains of Marsupialia

		Body weight kg	Body length cm	Total length cm	Brain volume cm ³	Cerebral volume cm ³	Cortical surface cm ²	Length of exposed gyri cm	Index of folding
<i>Marmosa</i> <i>mitis</i> (Mouse opossum)		0.020	17	39	1.37	1.24	4.38	5.24	1.03
<i>Didelphys</i> <i>virginiana</i> (Opossum)	1	2.16	47	70	4.00	3.75	14.33		1.15
<i>Didelphys</i>	2	3.90	39	65	4.7	4.42	13.23	10.2	1.09
<i>Didelphys</i>	3	4.62	47	78	4.5	3.9	11.93	10.2	1.11
<i>Wallabia</i> (<i>Protemnodon</i>) <i>rufogrisea</i> (Wallaby)		2.4	45	78	32.7	22.6	61.02	36	1.23
<i>Macropus</i> <i>melanops</i> (Black-faced kangaroo) young adult	1	2.5	47	83	37.0	29.2	74.9	75	1.41
<i>M. melanops</i>	2	13.5			49.1	34.0	101	63	1.42

Table 8
Carnivora

		Body weight g	Body length cm	Total length cm	Brain volume cm ³	Cerebral volume cm ³	Cortical surface cm ²	Length of exposed gyri cm	folding Index of
<i>Procyon</i> <i>lotor</i> (Raccoon)	1	6361	54	78	36.6	29.4	96.0	79	1.79
<i>Procyon</i> <i>lotor</i>	2	4960	52	77	42.1	34.6	120	84	1.86
<i>Procyon</i> <i>lotor</i>	3	5910	60	81	49.1	40.0	151	97	1.89
<i>Vulpes</i> <i>fulva</i> (fox)	1	4000	72	94	46.5	36.6	138	71	1.98
<i>Vulpes</i> <i>fulva</i>	2	3270	59	87	37	31	118	88	2.16
<i>Vulpes</i> <i>fulva</i>	3	3840	70	91	45	42	150	78	1.89
<i>Canis</i> <i>latrans</i> (Coyote)	1	11500	120	155	84.5	76.5	213	117	1.82
<i>Canis</i> <i>latrans</i>	2	12500	81	127	102.5	87	240	119	1.85
<i>Canis</i> <i>familiaris</i> (toy poodle)	1	685	16	20	36.6	35.0	144	101	2.14
<i>Canis</i> <i>familiaris</i> (shepherd x labrador)	2	37000	109	158	84.9	75.1	221	115	2.02

Table 9

Cetacea

		Average length of species m	Whole brain cm ³	Cerebrum cm ³	Surface cm ²	Length cm	Index of folding
<i>Delphinus</i> <i>bairdii</i>	1	2.15 (Hall; Kelson)	710	550	1684	612	4.13
<i>Delphinus</i> <i>bairdii</i>	2	2.15 (Hall; Kelson)	795	660	1750	547	3.87
<i>Tursiops</i> <i>truncatus</i>	1	2.0 (actual)	1040	854	1868	700	4.25
<i>Tursiops</i> <i>truncatus</i>	2	2.13	1234	1000	3532	1170	4.60
<i>Tursiops</i> <i>gillii</i>	1		1230	1005	2869	841	4.68
<i>Tursiops</i> <i>gillii</i>	2		1750	1440	4210	956	4.82
<i>Grampidelphus</i> <i>griseus</i>		2.50 (actual)	1500	1250	3522	1045	4.25
<i>Globicephala</i> <i>macrorhyncha</i>	1	6.10 (Hall; Kelson)	3065	2460	6674	1562	4.88
<i>Globicephala</i> <i>macrorhyncha</i>	2	6.10 (Hall; Kelson)	2620	2015	5914	1373	6.21
<i>Globicephala</i> <i>scamoni</i>	1	4.9 (Hall; Kelson)	2580	2150	5335	1360	5.03
<i>Pseudorca</i> <i>crassidens</i>		3.25—6 (Hall; Kelson)	3650	2940	7392	1544	4.97
		5.5 (Walker)					

by a layman. There is no essential increase in body size and weight from the Virginia opossum to these two kangaroo like creatures. But there is a 7.7 fold and 7.9 fold increase in brain volume and a 3.3 fold and 5.8 fold increase in cortical surface in wallaby resp. black-faced kangaroo, as compared to the Virginia opossum. Can the erect posture of kangaroo and wallaby account for this?

No attempt was made to compare species "low" and "high" within one of the other groups. But they represent, in general, terminal twigs of a few branches of the genealogical tree of mammals.

Discussion

There exists, as was hoped, a very useful and better than expected relationship between the length of superficially exposed gyri and the surface area of the cerebral cortex. This relationship is presented graphically in figure 9, where the logarithms of those lengths are plotted on the abscissa and the logarithms of the surface areas on the ordinate. The specimens are found remarkably close to a straight line having the equation

$$\log S \cong 1.35 \log L - 0.45.$$

An equally strict relationship, illustrated in figure 10 exists between the volume of the entire brain and the cerebrocortical surface area:

$$\log S \cong 0.94 \log V + 0.53.$$

These two formulae were derived as follows: A straight line was drawn through the centers of gravity of the plotted groups of points (figs. 9 and 10). The angle which

this line formed with the abscissa was measured with a protractor. The tangent of that angle provided the coefficient of the first expression in each of the formulae. The point of intersection of the line with the ordinate furnished the constant.

Using the simple relationships one can estimate the cerebrocortical surface area of a brain, when the length of superficially exposed gyri and the total volume of a brain are known. This procedure will be of importance when a specimen is too precious to be sliced or when endocranial casts are to be evaluated.

Summary

Stereological methods were used to determine the surface areas of the cerebral cortex and the lengths of superficially exposed gyri in 48 mammalian specimens including toothed whales, man, carnivores and marsupials. Unexpectedly strict relationships were found to exist between these two parameters and the volume of the cerebrum. These mathematical interdependences can be used to estimate two of the three parameters (including volume) if one of them is known.

Zusammenfassung

Zur Bestimmung der Oberflächen des Cortex und der Längen der oberflächlich exponierten Gyri werden stereologische Methoden angewendet. Untersucht wurden 48 Säugetiergehirne, darunter Zahnwale, Mensch, Raubtiere und Beuteltiere. Zwischen den beiden genannten Parametern und dem Hirnvolumen bestehen sehr enge Beziehungen. Diese Abhängigkeiten können benutzt werden, zwei der 3 Parameter (einschließlich Volumen) zu schätzen, wenn einer von ihnen bekannt ist.

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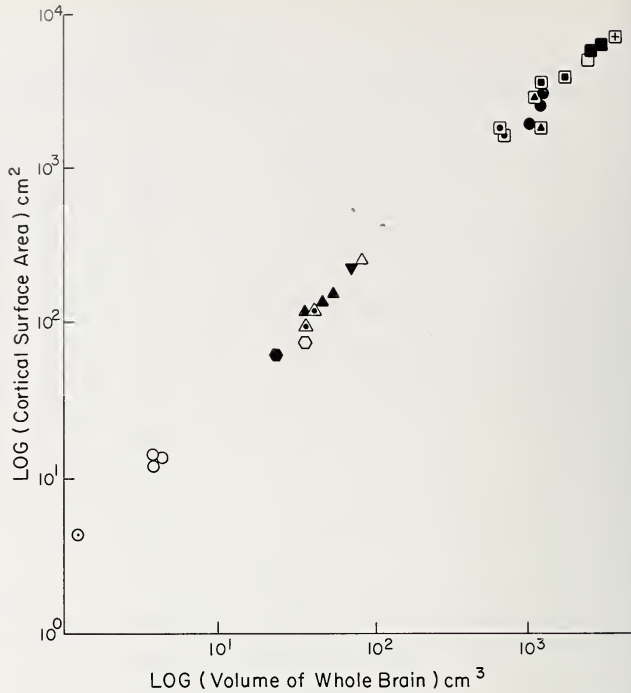


Fig. 10. Logarithms of the volume of the cerebrum plotted against the logarithms of the cerebrocortical surface area of various mammals

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Strahlenwirkung auf die Embryonalentwicklung bei Goldhamstern

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Eingang des Ms. 21. 6. 1970

Trächtige Goldhamster (*Mesocricetus auratus* Waterhouse) wurden während verschiedener Phasen der Embryonalentwicklung bestrahlt. Einer ersten Gruppe (I) von je 12 Muttertieren wurde am 6., 8., 10., 12. und 14. Tag der Schwangerschaft eine Dosis von 100 r verabreicht. Die zweite Gruppe (II) von ebenfalls 12 Muttertieren wurde an den gleichen Trächtigkeitstagen mit 200 r bestrahlt.

Die Ganzkörper-Bestrahlung erfolgte in Narkose („Numal-Roche“, 10 mg/100 g Körpergewicht, i.-p.). Die technischen Bedingungen waren folgende: Siemens-Röntgenapparat 220 KV, 15 mA, 1,5 Cu-Filter; Fokus — Tierabstand: 50 cm, Dosis 45 r/Min. Am letzten Tag der Tragzeit wurden die Feten dem Uterus entnommen und sofort in Bouin fixiert.

In der vorliegenden Arbeit wird nur über die makroskopisch faßbaren Veränderungen berichtet. Der Bericht über die noch nicht abgeschlossenen mikroskopischen Aus-

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Zeitschrift/Journal: [Mammalian Biology \(früher Zeitschrift für Säugetierkunde\)](#)

Jahr/Year: 1970

Band/Volume: [36](#)

Autor(en)/Author(s): Elias H., Schwartz David

Artikel/Article: [Cerebro-Cortical Surface Areas, Volumes, Lengths of Gyri and their Interdependence in Mammals, Including Man 147-163](#)