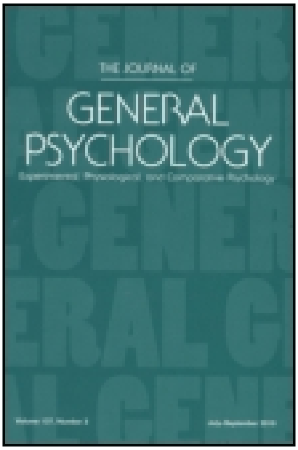

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BRAIN-WEIGHT AND BODY-WEIGHT OF MAMMALS*

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Much thought and labor of anatomists as well as of psychologists has been spent on the relation of brain-size and body-size in the animal kingdom, and especially in the class of mammals.

The reason for this is not far to seek. It is the widely accepted belief that the development of mind or of intelligence is correlated with the mass of the brain.

> If there is throughout nature a parallelism between mass and force and if this particularity is true of the other organs of the animal or human body, and if the faculties of the mind are a function of the brain, then there can be no doubt whatever that there must also exist a parallelism between the mass of the brain and the degree of mental gifts and faculties (3).[1]

All modern authors appear to have started from this assumption, and hence have differentiated between a part of the brain needed for somatic functions, the somatencephalon, and another part connected with the exercise of intelligence, the psychencephalon. The difficulties in making such a definite division were still clearly realized by Manouvrier (1885) in his fundamental memoir:

> The methods . . . to divide abstractly the weight of the brain into two quantities cannot be of great practical use. It is only a provisional application of conclusions about the possibilities of analyzing the influence upon the brain of the two classes of cerebral functions: the psychic and the motor function, intimately associated with each other (15).[2]

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[1]Wenn der Parallelismus zwischen Masse und Kraft in der ganzen Natur and speziell auch bei den übrigen Organen des tierischen und menschlichen Körpers besteht, und wenn die geistigen Tätigkeiten eine Funktion des Gehirns sind, so kann prinzipiell gar kein Zweifel darüber bestehen, dass swischen der Masse des Gehirns und der Grösse der geistigen Befähigung und Leistung dieser Parallelismus sich findet.

[2]Le moyen . . . pour diviser abstraitement le poids de l'encephale en deux quantités ne peut acquerir une grande utilité pratique. Ce n'est qu'une application provisoire de conclusions relatives à la possibilité d'analyser l'influence exercée sur le developpement du cerveau par celui des deux grands ordres de fonctions cérébrales: la fonction psychique et la fonction motrice, intimement associées l'une à l'autre.

The general conclusion at which Manouvrier arrived was that increase of body-weight leads to an increase of absolute, but to a decrease of relative brain-weight. In a subsequent memoir he tried to push the analysis further by comparing brain-weight with weight of the femur.

We shall not cite even all the more important authors who have contributed to this problem, particularly since Anthony (1) has done this only a few years ago.

In a short paper, Snell (17) argued theoretically that the brain-weight should increase by somewhat more than the 2/3 power of body-weight, and that deviations from this rule were due to different developments of the psychic functions. He wrote down the formula: $E = K\ S^r$ (using a different notation, however), putting r as about 0.68.

Again a few years later, Dubois (4) published his first paper on this problem, which has since become almost unquestioned. While using the same formula as Snell, he rejected the purely theoretical point of view of that author, and proceeded to determine the value of r "empirically." For that purpose he picked out a number of pairs of animals of the same class, of different body-weight but of the *same degree of intelligence.* He thus found r consistently to be 5/9 (instead of higher than 6/9, as Snell had thought). After having thus obtained r, his relative exponent, he determined for all animals the "cephalization coefficient" which he assumes to be a measure of the development of the "psychencephalon"—or, as he implies, of intelligence. It must indeed be admitted that the order in which this cephalization coefficient arranges the mammals agrees with our impression of their intelligence, although some discrepancies remain which Dubois himself was the first to note.

While Manouvrier's work shows all the care and critical self-control that are the signs of a great mind, Snell's and Dubois' work had laid itself open to criticism on several points. First, as Manouvrier had already admitted, the psychic and somatic functions of the brain are intimately connected with each other. It is true that brain physiology had lost sight of this fact towards the end of the nineteenth century, but the recent works of Lashley in America, of Goldstein in Germany, and of Head in England, to name but a few, have led away from the "diagram makers" and have shown that intelligence is a function of the cortex as a whole, thus reinstating the teachings of Flourens. The details are still far from being understood, but we have, at any rate, no right to introduce such conceptions as psychencephalon and somatencephalon as measurable quantities. Secondly, it is tacitly assumed that higher intelligence is due to (or associated with) greater brain-weight or greater weight of the psychencephalon, and the cephalization coefficient is then taken as a measure of intelligence. But nobody has ever satisfactorily defined intelligence in such a way as to include animals, and, moreover, we know the behavior of only a very few animals with some degree of accuracy (13). To suppose, therefore, as Dubois does, that each one of certain pairs of mammals has the same intelligence as the other one, is merely begging the question. Clearly, we shall have to avoid all references to intelligence and all preconceived hypotheses about the relation of mind to the brain and define our task thus: to find out whether there is any law regarding the relation between body-weight and brain-weight expressible in numerical terms.

Even a cursory glance at a table of these constants (several have been published) will show that there is no strict correspondence, that the search for a well-defined function will, therefore, be in vain, that, in other words, brain-weight depends not only on body-weight. We are thus confronted with the problem to determine just how much brain-weight does depend on body-weight. It need hardly be emphasized that all this work should be based on the whole of the available data, not on a selected few as was done by Dubois.

Both questions, this last one as well as the search for a function, can be determined by the calculus of correlation. But at first sight a new difficulty arises. Brain-weight is not a linear function of body-weight, and thus it may seem as though the correlation calculus (from which a linear regression formula can be determined) were unsuited for our purpose. But we may investigate whether brain-weight is related to body-weight by a function of the form $E = k\, S^r$, as most authors have maintained. Throwing this into logarithmic form, we have:

$$\log E = \log k + r \log S$$

which is precisely the type of regression formula we can determine from a correlation table.

This formula has been widely used for the analysis of embryological data on growth. This material has recently been collected by Julian Huxley (12) who has also discussed its applicability to problems of comparative morphology. In the case of the brain (12, p. 215), it has already been noted that the value of r is different according to whether mammals as a whole or whether only individuals of one species of mammals are under consideration. We may add further that it is not applicable to the ontogeny of at least the human brain, as a perusal of Dunn's (6) paper will show. The physical (or biological) significance of our parameter is, therefore, still hidden.

For the arithmetical work, the data collected by Warncke (18) have mainly been used, and for primates Hrdlička's (11) tables have been included. All juvenile specimens were left out and only those adults were taken for whom both brain-weight and body-weight is given. Whenever possible, means have been calculated and used. Warncke and Hrdlička have both weighed fresh brains. Warncke's longer list (which has been used) contains both his own determinations and those previously collected by Dubois. The material actually used is found in Table 1. Two widely discrepant sets of observations found in Warncke's tables have not been included: man with his exceptionally high brain-weight has been left out, for he undoubtedly represents a one-sided specialization; on the other hand, the whales were excluded because in them an enormous amount of subcutaneous fat, a special adaptation to life in the cold waters of the oceans, enters into their body-weight.

Plotted on a double logarithmic scale, we obtain the diagram given in Figure 1. From a correlation table (Table 2) we obtain a correlation between the logarithms of brain-weight and body-weight of $r = .83459$. By any test this correlation is significant, and we conclude that brain-weight depends indeed to a large extent on body-weight. But before proceeding further, it may be well to show that this correlation is linear; in other words, that we were on the right path in our choice of formula. For this purpose we calculate the correlation ratio η, and we obtain $\eta = .9449$. By Blakeman's (2) test we have $\xi = .196 \pm .053$, and by R. A. Fisher (7) we have $N\ (\eta^2 - r^2) = 22.56$ for 18 areas which leads to $P > .10$

TABLE 1

Species	Brain-weight	Body-weight	N	Log E	Log S	k
Primates						
Simia satyrus	400	63400	2	2.60	4.80	.29
Anthropopithecus troglodytes	345	22045	1	2.54	4.34	.50
Gorilla gorilla	425	90525	1	2.63	4.96	.24
Hylobates synd.	130	9490	2	2.11	3.98	.32
Hylobates lar	97.3	5628	3	1.99	3.75	.34
Hylobates pileatus	103	5454	1	2.01	3.74	.36
Hylobates leuciscus	94.5	6237	2	1.98	3.79	.32
Semnopithecus entellus	111.5	7010	1	2.05	3.85	.34
Lophopithecus obscurus	64.4	5461	10	1.81	3.79	.23
Lophopithecus melalophus	77.3	8967	1	1.89	3.95	.20
Trachypithecus maurus	73.5	9270	7	1.87	3.97	.19
Semnopithecus pruinosus	56	5100	1	1.75	3.71	.21
Cercopith. callith.	77.8	3571	3	1.89	3.55	.36
			W + H			
Cercopith. cynosurus	72	2920	1	1.86	3.47	.39
Cercocebus fuliginosus	103.4	4112	5	2.01	3.61	.45
			W + H			
Cynomolgus fascicularis	74.7	4877	4	1.87	3.69	.28
Nemestrinus nemestricus	117	6625	1	2.07	3.82	.37
Nemestrinus leoninus	90	2050	1	1.95	3.31	.60
Macacus assamensis	90.5	3655	1	1.96	3.56	.43
Macacus ocreatus	84	5100	1	1.92	3.71	.31
Cercopithecus cynomolgus	72	11156	1	1.86	4.05	.16
Alouata nigra	45.6	2955	1	1.66	3.47	.25
Ateles ater	120	2550	1	2.08	3.41	.71
Ateles spec. (?)	110	2800	1	2.04	3.45	.60
Ateles marginatus	97	3201	1	1.99	3.51	.49
Lagothrix lagotrica	88.5	2252.5	2	1.95	3.35	.58
Cebus capucinus	65.25	1602.8	2	1.81	3.20	.52
Saimiris sciurea	22.35	346.75	2	1.35	2.54	.49
Nyctopithecus trivirgatus	15.5	480	1	1.19	2.68	.27
Ateles geoffroyi	94.75	2211.5	2 (H)	1.98	3.34	.62
Callitrix jacchus	7.7	205	7	0.89	2.31	.24
Oedipomidas oedipus	9.3	213	2	0.97	2.33	.28
Leontopithecus rosalea	12.7	407	1	1.10	2.61	.25
Midas ursulus	8.4	225	1	0.92	2.35	.24
Papio doguerra	182	4990	1 (H)	2.26	3.70	.70
Papio anubis	212.7	6810	1 (H)	2.33	3.83	.66
Papio sphinx	174.5	4763	1 (H)	2.24	3.68	.68
Papio hamadryas	142	12020	1 (H)	2.15	4.08	.30
Papio babuin	179.5	10546	1 (H)	2.25	4.02	.42
Papio spec.	213	22220	1 (H)	2.33	4.35	.30

TABLE 1 (*continued*)

	Brain-weight	Body-weight	N	Log E	Log S	k
Prosimiae						
Lemur macaco	23.5	1792.8	3	1.37	3.25	.17
Lemur rufiventer	24.9	1015	1	1.40	3.01	.27
Lemur —	28.3	1790	1	1.45	3.25	.21
Lemus albifrons	22.3	1540	1	1.35	3.19	.18
Lemur mongoz	24.0	1559	3	1.38	3.19	.20
Galago galago	7.9	515	1	0.90	2.71	.13
Nycticebus tardigradus	14.4	572	1	1.16	2.76	.22
Pterodicticus potto	10.76	684	4	1.03	2.84	.15
Microcebus minimus	1.9	62	1	0.28	1.79	.13
Chiroptera						
Pteropus Edwarsi	7.3	375	7	0.86	2.57	.15
Pteropus edulis	10.6	1261.4		1.03	3.10	.10
Rhinolophus	0.35	23.45		—.46	1.37	.04
Vespertilio serotinus	0.31	23.4		—.51	1.37	.04
Insectivora						
Tupaja javanica	2.3	80		0.41	1.90	.50
Erinaceus europaeus	3.8	747.8		0.58	2.87	.05
Talpa europaea	1.5	77		0.18	1.89	.09
Carnivora						
Ursus arctos	407	196900		2.61	5.29	.14
Canis lupus	119.5	36328		2.08	4.56	.12
Vulpes adustus	47.4	7888.4		1.68	3.90	.14
Vulpes vulpes	50.4	4235		1.70	3.63	.21
Hyaena hyaena	85	23127	2	1.93	4.36	.12
Crocotta crocuta	168	43500		2.23	4.64	.16
Crossarchus zebra	10.8	930		1.03	2.97	.12
Genetta pardina	15.4	1032		1.19	3.01	.17
Paradoxurus hermaphrodytus	23.7	3047		1.37	3.48	.12
Herpestes galera	28.8	2675		1.46	3.43	.16
Herpestes cafer	24.1	1764		1.38	3.25	.18
Herpestes smithi	14.6	1205		1.16	3.08	.14
Uncia leo	216	94000	2	2.33	4.97	.12
Leopardus pardus	135	21140	3	2.13	4.33	.20
Leopardus onca	149	29000	1	2.17	4.46	.18
Uncia concolor	127.7	37000	2	2.11	4.57	.13
Uncia tigris	246	57800		2.39	4.76	.19
Felis domestica	30.3	370.5	12	1.48	2.57	.64

TABLE 1 (*continued*)

	Brain-weight	Body-weight	N	Log E	Log S	k
Rodentia						
Parasciurus indicus	11.4	1935		1.06	3.29	.08
Sciurus cintreus	7.2	328		0.86	2.52	.16
Parasciurus rufivent.	6.7	365	2	0.83	2.56	.14
Sciurus vulgaric	6.0	389		0.78	2.59	.12
Castor canadensis	35.6	19500		1.55	4.29	.06
Cricetus cricetus	2.46	366	5	0.39	2.56	.05
Epimys norwegicus	8.75	465		0.94	2.67	.16
Mus musculus*	.475	24.32	5	—.32	1.39	.06
Mus wagneri*	.424	18.92	5	—.37	1.28	.06
Myopotamus coypus	18.53	5700		1.27	3.76	.06
Spalax hungaricus	3.0	122		0.48	2.09	.13
Alactaga saliens	3.5	193		0.54	2.29	.11
Jaculus orientalis	2.5	98		0.40	1.99	.13
Viscacia viscacia	15.1	2370	4	1.18	3.57	.10
Coelogenys paca	35.8	5635		1.55	3.75	.12
Cavia porcellus	5.05	498	2	0.70	2.70	.09
Oryctolagus cuniculus	12.15	2530.5	2	1.08	3.40	.07
Ungulata						
Procavia capensis	19.2	3500		1.28	3.54	.09
Elephas africanus	4370	1,642,000		3.64	6.22	.37
Elephas indicus	5045	2,547,000	2	3.70	6.41	.32
Tapirus indicus	169	160,000		2.23	5.20	.07
Equus caballus	587	260,000		2.77	5.41	.17
Hippotigris zebra	674	166,500		2.83	5.22	.26
Hippotigris Boehmi	612	250,000		2.79	50.4	.18
Asinus asinus	419	187,972.5	2	2.63	5.27	.15
Hippopotamus amphibius	582	1,749,730		2.76	6.24	.05
Tragulus Stanleyi	17.2	2099	5	1.25	3.32	.12
Cervus canadensis	409.3	200,000		2.61	5.30	.14
Bos taurus	446	175,000		2.65	5.24	.17
Cetacea						
Phocaena communis	460	53,800	2	2.66	5.24	.37
Lagenorrhynchus albirostris	1126	67,560		3.05	4.83	.78
Tursiops tursio	1886	278,000		3.28	5.44	.53
Globiocephalus melas	2458	983,000	2	3.39	5.99	.30
Megaptera boops	3531	42,372,000		3.54	7.63	.04
Balaenoptera rostrata	2490	62,250,000		3.40	7.79	.02
Balaenoptera rostrata	7000	73,997,000		3.85	7.87	.05
Balaenoptera musculus	3636	50,904,000		3.56	7.71	.03

*After Fortuyn.

TABLE 1 (*continued*)

	Brain-weight	Body-weight	N	Log E	Log S	k
Edentata						
Bradypus tridactylus	24.9	4097		1.40	3.61	.11
Myrmecophaga jubata L	85.2	2553	3	1.93	3.41	.51
Dasypus sexcinctus	33.5	7990		1.53	3.90	.10
Manis javanica	11	3500		1.04	3.54	.05
Marsupials						
Trichosurus vulpecula	11.4	1620		1.07	3.21	.09
Onychogale frenata	13.5	1433		1.13	3.16	.12
Didelphys marsup.	6.3	1700		0.80	3.23	.05
Didelphys cancrivorus	5.8	1370		0.76	3.14	.05

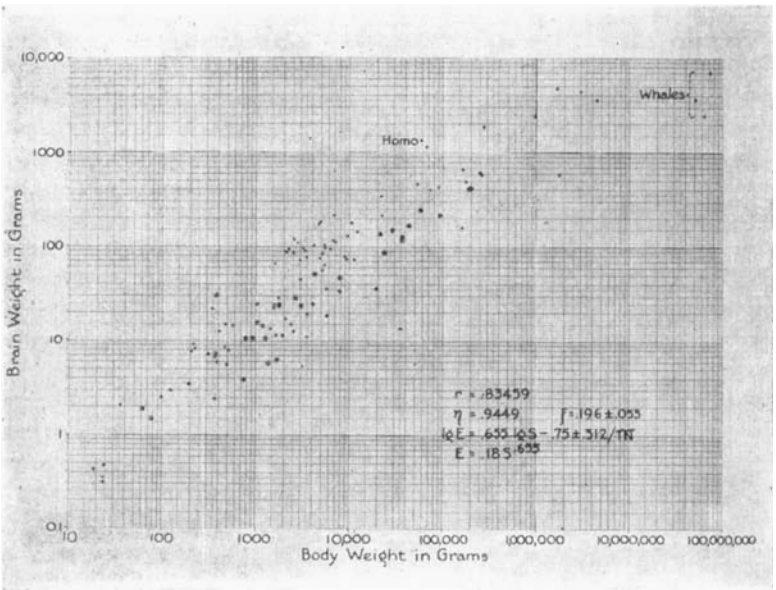

FIGURE 1

. Primates.
⊙ Carnivora.
⊕ Marsupials.
+, × Other Orders.

TABLE 2

CORRELATION TABLE FOR BRAIN-WEIGHT AND BODY-WEIGHT OF MAMMALS

Horizontal rows: logarithms of brain-weight.
Vertical columns: logarithms of body-weight.

	1.2 — 1.5	1.5 — 1.8	1.8 — 2.1	2.1 — 2.4	2.4 — 2.7	2.7 — 3.0	3.0 — 3.3	3.3 — 3.6	3.6 — 3.9	3.9 — 4.2	4.2 — 4.5	4.5 — 4.8	4.8 — 5.1	5.1 — 5.4	5.4 — 5.7	5.7 — 6.0	6.0 — 6.3	6.3 — 6.6
3.6 — 3.9																	1	1
3.3 — 3.6																1		
3.0 — 3.3													1		1			
2.7 — 3.0														1	2		1	
2.4 — 2.7											1	1	2	4				
2.1 — 2.4									3	3	3	3	1	1				
1.8 — 2.1							1	10	9	3	1	1						
1.5 — 1.8								1	3	2	1							
1.2 — 1.5					2		6	4	2									
.9 — 1.2				2	3	4	5	3										
.6 — .9				1	4	1	3											
.3 — .6			3	1	1	1												
.0 — .3		1	1															
—.3 — —.0																		
—.6 — —.3	4																	

for the probability of the correlation being linear. On the basis of the material at present available, the relation of brain-weight and body-weight is, therefore, adequately described by the formula given above.

We can now proceed to construct our regression formula, and we obtain:

$$\log E = 0.655 \log S - 0.75 \pm .312/\sqrt{N}$$

or,

$$E = .18\ S^{0.655}$$

E and S both being determined in grams.

This formula differs from that given by Dubois in the value of the exponent. In a point of fact, the exponent is very close to two-thirds and thus agrees quite well with Snell's value. It should be emphasized once more, however, that our value has been found on a strictly empirical basis.

Accepting the value of the exponent as 0.655, it becomes possible to classify the various species as regards brain-weight by the coefficient k. Although not much more than a curious coincidence, this coefficient[8] for man is practically 1; that of all animals is a true fraction. Thus, our scale is shorter than Dubois' which goes from 2.89 to .05, due, of course, to the way in which the regression line has been fitted. The order, too, differs somewhat from that given by Dubois. The greatest change has occurred in the case of the cat, which has moved up considerably. Another interesting point in our scheme is the position of the big anthropoid apes as compared with that of the cynomorpha and platyrhine monkeys. Averages may not mean very much, yet it is interesting to see that the mean value of k for the first group is .34, for the second one .40, while it is .20 for the lemuroidea, and .18 for the carnivora and for the ungulata.

It is clear from all that has been said above that the figures given here are nothing but a description of facts, a description which, in the mathematical sense of the term, is the "best" one. It does not pretend to make any enunciation about the relation of intelligence and brain-weight. For that purpose, we need a much broader psychological basis than we have at present.

Former attempts to analyze the relation between body-weight and brain-weight suffer from three deficits: (1) they presuppose a correlation between intelligence and brain-weight, (2) they make suppositions about the intelligence of animals which are unproven, and (3) they are based on a conception of cortical functions which can no longer be considered valid. The attempt has here been made to work out the correlation between brain- and body-weight, using the same formula ($E = k\ S^r$) of relative growth as former authors, but taking into account the complete mass of data at present available. There is a close correlation between the logarithms of brain- and body-weight, and this correlation is linear. Brain-weight increases as the 0.655th power of body-weight. The value of the cephalization coefficient k differs from species to species. Whether or not this is an indication of the intelligence of animals must be left to the psychologist to answer.

[8]Its exact value is .99. We have thought it permissible to round off this figure, particularly in view of the uncertainty of the original data [our value is based on Vierordt's data taken from Dubois, but the brain-weight for ♂ and ♀ Bohemians, after R. Pearl (16) is 1404.9 g].

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