

Within-Species Brain-Body Weight Variability: A Reexamination of the Danish Data and Other Primate Species

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ABSTRACT A restudy of the Danish brain weight data published by Pakkenberg and Voigt ('64), using partial correlation techniques, confirms and extends their earlier conclusions regarding a much stronger allometric relationship between height and brain weight than between body weight and brain weight. The relationship is particularly strong in males, and not in females, which is hypothesized to be related to higher fat components in the latter. Comparative data for smaller samples of *Pan*, *Gorilla*, *Pongo*, *Macaca*, *Papio*, and *Saimiri* using body weights, suggest that such relationships also hold more strongly in males than females, although more reliable data are greatly needed. In addition to providing within-species ranges of variability for variously derived neural statistics (e.g., encephalization quotients, "extra neurons," etc.), for "normal" primates, it is suggested that while allometric trends do exist within species, and particularly males, evolutionary pressures leading to larger brain size were probably very diverse, and that any one homogenistic theory is unlikely.

In recent years, a considerable degree of interest has emerged with regard to the significance of allometry in brain evolution for many taxa of vertebrates (Jerison, '73), and in particular, the Primates (Jerison, '73; Passingham '73, '75; Passingham and Ettlinger '73; Gould '75; Holloway, in press a, b, '76a, b, '75, '74; Bauchot and Stephan, '69, Stephen et al., '70, to mention but a few). It is a well appreciated fact that a complete data base for many primates does not exist, particularly at the species-level where relationships between body weights, body lengths, brain weight, age, and sex cannot be rigorously examined for possible underlying mathematical relationships. Indeed, most researchers regard allometry as well-defined for between taxa comparisons (above the level of the genus), weak but definite at the level of the genus, and either too weak or nonexistent to demonstrate within species (on the basis of present sample sizes).

Human autopsy materials are quite numerous as the excellent paper by Dekaban and Sadowsky ('78) indicates, but to date, little attempt has been made to go beyond the usual

statistical surveys of brain and body weights, ages, and sex, or to provide data on interactive effects between the variables. With regard to nonhuman primates, the situation is far worse, and given the enormous expenditures of money and energies in collecting vital statistics in numerous primate centers and research institutions in this and other countries, it seems a pity that such data are not available. In the course of two years in collecting this data, only two primate research centers were willing to provide any information on healthy, adult autopsy findings.

The purpose of this article is to examine the possibilities of existing allometric relationships within certain primate species in the hope that such an exercise might 1) suggest certain relationships heretofore regarded as obscure; and 2) to stimulate similar studies by those scientists who have accumulated such relevant data. The major data base analyzed herein is

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that of the Danish population previously published by Pakkenberg and Voigt in 1964, kindly furnished to me by the senior author, and which is probably the best sample of a modern population of *Homo* published to date in terms of complete data recording. In addition, selected samples of *Gorilla gorilla*, *Pan troglodytes*, *Pongo pygmaeus*, *Macaca* and *Saimiri*, will also be analyzed, but less completely. The major focus of these studies is to provide a comparative base for understanding brain-body weight relationships within species of healthy, mature individuals, and the range of variability of derived "statistics" such as: encephalization coefficients and "extra neuron" numbers which do not appear in the literature (e.g., Jerison, '73; Bauchot and Stephan, '69); sexual dimorphic differences or similarities; interactive effects between age, height (or body length), body weight, brain weight, and sex by the technique or partial correlations; and to provide a more secure theoretical basis appropriate to the goal of synthesis between genetics, size, and evolutionary selection pressures.

MATERIALS AND METHODS

The Danish sample of Pakkenberg and Voigt ('64)

In their original publication, 1,090 brains were weighed from bodies brought to the University Institute of Forensic Medicine, Copenhagen, which included 765 males, 325 females, ranging in age from infancy to 95 years, broken down into nine categories of death: 1) Poisoning, 2) Cardiac failure, 3) Hemorrhage, 4) Hanging, 5) Shock, 6) Other anoxias, 7) General pathology, 8) Brain disease, and 9) Head trauma. These data also included information on degree of oedema, or swelling of the brain, body weight and height, brain weight, sex, age. Thus, the material included a number of cases where death was sudden and without pathological involvement to the brain, an advantage over previous publications reviewed by the authors where most of the material came from pathological institutes.

Since my interest was to gain a better understanding of "normal" variability within modern human populations, I decided to exclude from the original 1,090 cases all those which might be judged as abnormal. To begin, all cases under 18 years of age, and those older than 65 were excluded, since it is common knowledge that brain weights (and body heights) decline significantly after age 65, and that brain size has not reached full weight prior to age 18.

A second set of strictures on sample inclusion was followed: exceptionally underweight and overweight cases were excluded, as were extremes of low or high stature. In the sample analyzed by Pakkenberg and Voigt ('64), body weights varied from 10 to more than 130 kg in males, and 8 to more than 105 kg for females; from 100–199 cm in height for males, and from 100–184 cm in height for females. In order to examine whether allometric trends might exist within normal samples, it was decided to eliminate the extremes in weight and stature from analysis. Thus, for females, weights lower than 40 kg and higher than 89 kg were excluded; for males, weights lower than 46 kg and higher than 106 kg were excluded. With regard to stature, female heights lower than 148 cm and higher than 182 cm were excluded; for males, heights lower than 153 cm and greater than 194 cm were dropped.¹ In culling this sample, I was particularly intent in avoiding extreme outliers which could shift the regressions and overemphasize brain-body size relationships. In other words, these criteria become an extremely robust test for underlining relationships within the normal sample.

The third basis for sample exclusion was cause of death. Thus, all cases of "brain disease" were eliminated, as well as those, which according to Pakkenberg and Voigt, produced brain swelling, such as "Hanging." These strictures reduced the samples for males and females, respectively, to 502 and 165 cases which were judged as normal.

Prior to sample selection, the data for all 1,090 cases were punched onto IBM data cards, and the total set broken down into two data decks, the normal described above, and a pathological group. These decks were then statistically analyzed by using the following subroutines from SPSS (Statistical Package for the Social Sciences '75): 1) *Condescriptive*, yielding averages, SD variance, SE skewness, kurtosis, range, minimum, and maximum values; 2) *partial correlation*; 3) *scattergram*; 4) *multiple regression*. Each skewness and kurtosis figure was tested using the test for departure from normality given by Sokal and Rohlf (69:137, 171–172), which is essentially a t-test

¹The choice of what constituted an "extreme" was admittedly done on an ad hoc judgmental basis. That is, for females, I regarded heights under 4' 10" and over 5' 11" as extremes, and under 5' 0" or over 6' 4" as extremes for males. For body weights, I selected 88 and 196 pounds as the "normal" female range, and between 101 and 233 pounds as normal for males. The cm and kg figures are simply metric conversions of the English system equivalents. It is probable, then, that some truly "normal" part of the sample was eliminated.

using standard errors of g_1 and g_2 (skewness and kurtosis, respectively). No departures were significant at the 0.05 level.

In addition, a number of compute operations were performed on the data to provide variability statistics on \log_{10} values for age, brain weight, body weight, body height; Jerison's ('73) E.Q. or encephalization coefficient, his N_c or "extra neurons;" Bauchot and Stephan's ('69) "progression index;" and brain/body weight ratios. These sexual dimorphic differences in neural parameters between males and females were tested using the Student-t test for significance by comparing not only the total samples for males and females, but also the portions of each sexed sample above and below their respective mean body weights, in that the differences in E.Q., N_c , and ratios were quite different.

Since the male normal sample was roughly three times as large as the female sample, the male sample was also run using a random select operation which chose approximately $\frac{1}{3}$ of the male cases. In addition, the data were also analyzed by 10-year cohorts to see if particular trends were taking place within parts of the sample.

The other primate samples

Adequate data for normal, adult, healthy primates simply do not exist in clear published form. The values for brain and body weights used in this study were carefully culled from three primary sources: 1) Kennard and Wilner's ('41) listings for rhesus macaques,² (encephalization quotients) and N_c 's, along with given; 2) Bauchot and Stephan's ('69) compilations of values for various primate species, which are based on their literature search of previously published values and their own collected specimens; 3) autopsy materials from Yerkes, kindly furnished to this author by Dr. H. McClure. The statistics in Tables 6 and 7 are based on selected sample for healthy, normal adults. The data for *Macaca* and *Saimiri* were given to this author by Dr. D. McClure at Yerkes, and represent this author's cutting from those lists of all individuals noted as non-adult, "emaciated," or "dehydrated." The chimpanzee data set are a combination of Bauchot and Stephan's ('69) listings, Kennard and Wilner's ('46) listing, and an additional few specimens from the Yerkes laboratory, where the same criteria for selection were used. In the use of chimpanzee, a minimal body weight of 20.4 kg was used; *Gorilla* female minimal weight was 58 kg; *Gorilla* male, 108 kg; *Pongo*

male, 53.6 kg; *Pongo* female 20.2 kg; *Saimiri*, both sexes, 0.470 kg; *Macaca*, male, 4.27 kg; *Macaca* female, 3.93 kg. The species selected for which data appeared maximal and reliable, were: 1) *Macaca mulatta*, 2) *Saimiri sciurius*, 3) *Pan troglodytes*, 4) *Gorilla gorilla*, and 5) *Pongo pygmaeus*. Table 7 shows the number of cases for males and females in all of the primate species studied.

It should be stressed that these sample sizes for the nonhuman primates are very small, but until carefully documented variability of vital statistics are published, this represents the best data base available at this time.³

RESULTS AND DISCUSSION

The Danish sample

Basic univariate statistics

Table I provides the results of the SPSS descriptive runs for the Danish sample for the original variables, as well as those for E.Q.s (encephalization quotients) and N_c 's along with skewness and kurtosis figures, the latter indicating that these samples can be regarded as essentially normally distributed. The figures in parentheses in the male sample are those for a randomly selected sample of approximately $\frac{1}{3}$ of the original $N = 502$ male sample. As can be seen, the two male samples do not differ in any significant way. The differences between both male and female samples reflect sexually dimorphic characters, and are significant. The female sample, as indicated by the CV (coefficient of variation) figures is only slightly more variable than either the total or selected male samples. On the other hand, judging from the CVs for height, (and assuming an average figure of 10%), it would appear that the selection process has been perhaps too narrow. However, as will become clearer later, this narrowing of range of height values does not effect the original conclusions of Pakkenberg and Voigt ('64) on the stronger relationship between brain size and height, than between brain size and body weight.

² All of the Kennard and Wilner data had very low body-weights, which became significantly so once the data was compared to that from Yerkes. In plotting \log_{10} brain vs \log_{10} body-weights, it was apparent there were two almost nonoverlapping populations. In this report, the Kennard and Wilson data were eliminated, except for some of the Chimpanzee, Gorilla, and Pongo values, which appeared within the ranges published by Bauchot and Stephan ('69).

³ Some 30,000 nonhuman primates are sacrificed every year in biomedical and space research. I regard the nonavailability of data as a pathetic, illplanned, and unconscionable waste.

TABLE 1. Basic univariate statistics for the Danish data

Samples and variables							
Male, normal, N = 502 (N = 165)							
	Age yrs.	Brain weight grams	Body weight grams	Height cm	E.Q.*	N _e s* × 10 ⁷	Brain/body ratio
Mean	48.4 (48.1)	1,457.2 (1,450.8)	72,137 (72,316)	173.7 (174.7)	7.145 (7.036)	912.2 (908.4)	0.021 (0.020)
SD	11.64 (11.90)	119.8 (124.0)	11,398 (11,692)	6.97 (6.49)	0.856 (0.824)	55.1 (56.63)	0.003 (0.003)
SE	0.519 (0.929)	5.35 (9.68)	(508.72) (886)	0.311 (0.507)	0.038 (0.064)	2.46 (4.42)	0.000 (0.000)
Kurtosis	-0.172 (-0.296)	-0.06 (-0.099)	-0.242 (-0.317)	0.025 (0.197)	0.143 (0.398)	-0.131 (-0.007)	0.233 (0.534)
Skewness	-0.703 (-0.619)	0.146 (-0.231)	0.408 (0.391)	-0.046 (-0.162)	0.289 (0.439)	0.123 (0.213)	0.354 (0.457)
Min	18 (18)	1,160 (1,180)	46,000 (46,000)	153 (158)	5.05 (5.24)	777.15 (785.7)	0.013 (0.014)
Max	65 (65)	1,850 (1,850)	106,000 (104,000)	194 (192)	10.2 (10.14)	1,089.76 (1,089.8)	0.033 (0.033)
Range	47 (47)	690 (670)	60,000 (58,000)	41 (34)	2.535 (4.93)	312.61 (304.04)	0.020 (0.019)
C.V.%	24	8.2	15.8	4.0	11.98	6.04	14.3
Female, normal, N = 165							
	Age yrs.	Brain weight grams	Body weight grams	Height cm	E.Q.	N _e s × 10 ⁷	Brain/body ratio
Mean	46.2	1,317.9	62062	163.7	7.154	853.18	0.022
SD	12.72	109.8	9878	6.07	0.955	52.95	0.004
SE	0.99	8.55	769	0.47	0.074	4.12	0.000
Kurtosis	0.677	0.447	-0.083	-0.01	0.440	0.453	0.550
Skewness	-0.464	0.560	0.350	0.092	0.628	0.527	0.669
Min	18	1,040	40,000	148	5.08	711.8	0.014
Max	65	1,650	89,000	182	10.4	1012.72	0.036
Range	47	610	49,000	34	2.62	300.92	0.022
C.V.%	27.5	8.3	15.9	3.71	13.38	6.20	18.2
% of male	95.45	90.4	86.03	94.24	100	93.5	104.8

() parenthesized figures are for the smaller male sample.
* per Jerison ('73).

It is interesting to note that while male brain weights are heavier than those of females, the E.Q.s are practically identical between the two sexes when the total sample is considered. As the N_e "extra neuron" numbers indicate, the male has more extra neurons, reflecting greater body weight.⁴ Using Student-t tests on the large male and female samples, the age difference was barely significant at the 0.046 level. Height and body weight differences were highly significant (P = 0.001). Interestingly, the E.Q. differences was totally insignificant (P = 0.91), while the difference in brain/body ratio was highly significant (P = 0.001, P = 0.0218 (females), P = 0.0206 (males)). When the samples for both males and females were further partitioned, by using the averages

for both male and female body weights, it became apparent that the pattern of significant differences was quite changeable. (See Table 8, and Fig. 1.) That is, when large males were compared with small females, neither E.Q.

⁴The formulas used to calculate neural statistics are as follows:
E.Q. (Jerison, '73) = $\frac{\text{Brain weight}}{0.12 \text{ body weight}^{0.666}}$
E.Q.s. (Stephan and Bauchot, '69) = $\frac{\text{Brain weight}}{0.0429 \text{ body weight}^{0.653}}$
N_es (extra neurons) = $\frac{\text{Brain weight}^{0.666} - (0.03 \text{ body weight}^{0.666})}{0.006} \times 8 \times 10^7$

I am aware that these "statistics" were not devised for intersex comparisons. Still, the comparisons have heuristic value, and have been computed herein more for the questions they raise than for the answers they yield. . . . All three of the above statistics are residuals, and in this article, no claim is made that they represent any variable representing behavioral effectiveness.

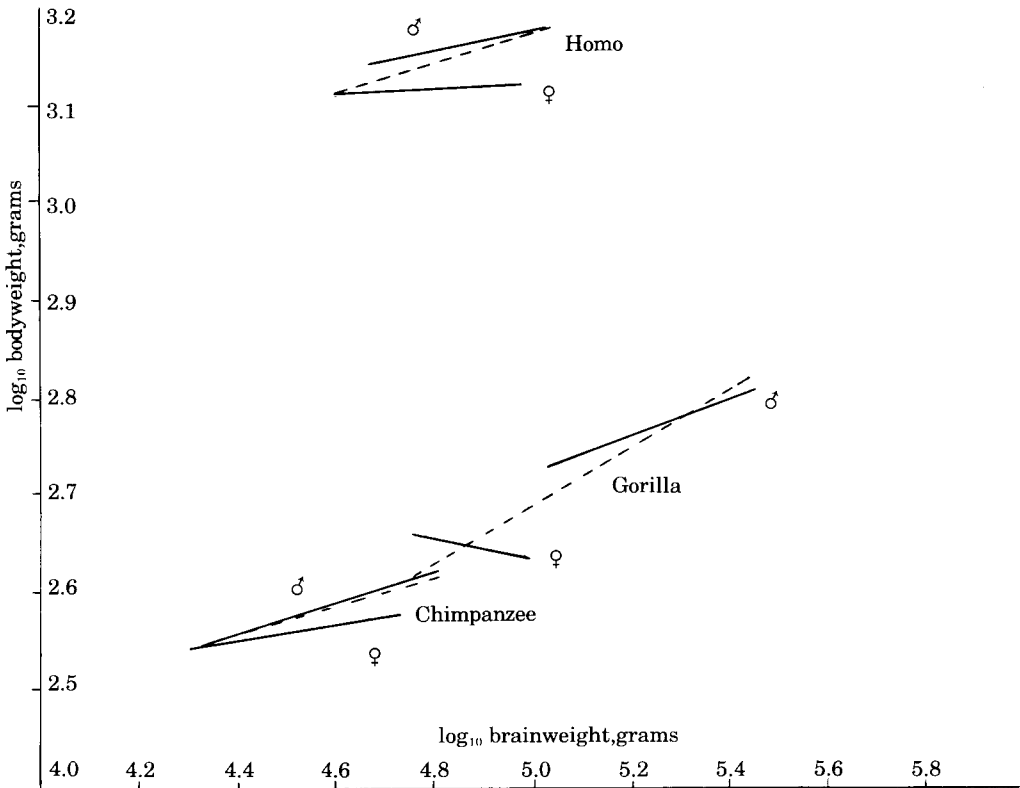


Fig. 1. is a plot of the \log_{10} values for brain and body weights in *Homo*, *Pan*, and *Gorilla*, for each sex. The equations for these lines are given in Table 6. The dashed lines represent the lines for male and females combined. It should be remembered that only the male and combined lines are significant with regard to their slopes and correlations. It can be seen that the vertical distance between chimpanzee and gorilla is slight, but that extending the lines (allometric correction) does not transform the one into the other.

score was significantly different, while the brain/body ratio was (large males, mean = 0.0226; small females, mean = 0.0244). Reversing the partition, i.e., small males and large females, all differences but age were highly significant, and all in favor of the males. For large male-large female, the E.Q.s were larger in males (as were N_c 's) and significantly so, including the brain/body ratio. When small males were compared to large females, all differences were highly significant, with females having the higher E.Q.s and brain/body ratio, but not N_c 's. The precise meaning of those shifts is unclear, but will be discussed later with regard to possible selection paradigms when considering the evolution of brain-size in *Homo sapiens*.

Correlation statistics

Zero-order. In their original 1964 study, Pakkenberg and Voigt showed that "... brain

weight depends significantly on height, but not on body weight," (p. 303), but did not publish correlation coefficients aside from regression coefficients using linear regression analysis. The present study confirms their findings, but applies both standard Pearson correlation and partial correlation techniques. In addition, effects of age are taken into account. Table 2 provides the zero-order correlations for the combined sample and the individual male and female samples.

As expected, brain weight shares a negative correlation with age, but interestingly, is less pronounced in the female sample, being almost $2\frac{1}{2}$ times higher in males. Also expected is the negative correlation of height with age, and a positive correlation with body weight. The correlations of brain weight with height are obviously stronger than with body weight, and this correlation increases in the first and second order partial correlations when age and body weight are controlled. By and large, all corre-

TABLE 2. Zero-order correlations for the Danish data

Sample		Combined = 667					Female = 165					Male N = 502					Male = 166				
	Age	Brain	Body	Hgt.	Age	Brain	Body	Hgt.	Age	Brain	Body	Hgt.	Age	Brain	Body	Hgt.	Age	Brain	Body	Hgt.	
Age	—	-0.2241 (0.001)	0.0897 (0.010)	-0.1740 (0.001)	—	-0.1393 (0.037)	0.2993 (0.001)	-0.2440 (0.001)	—	0.3467 (0.001)	-0.0076 (0.433)	-0.2661 (0.001)	—	-0.3598 (0.001)	-0.0143 (0.427)	-0.2772 (0.001)	—	—	—	—	
Brain	—	—	0.2914 (0.001)	0.4661 (0.001)	—	—	0.0440 (0.287)	0.0698 (0.186)	—	—	—	0.1775 (0.001)	—	—	0.1779 (0.011)	0.3516 (0.001)	—	—	—	—	
Body wt	—	—	—	0.5284 (0.001)	—	—	—	0.2504 (0.001)	—	—	—	0.4641 (0.001)	—	—	—	0.5130 (0.001)	—	—	—	—	
Hgt	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	

() indicates significance level.

TABLE 3. Partial correlations for the Danish data

Relationship	Combined sample (variables controlled)					Male sample					Female sample				
	Age	Brain	Body	Height	Age	Brain	Body	Height	Age	Brain	Body	Height	Age	Brain	Body
Brain-body	0.3210 (0.001)	—	—	0.0601 (0.061)	0.1864 (0.001)	—	—	0.0173 (0.350)	0.0907 (0.124)	—	—	0.0274 (0.364)	—	—	—
Brain-height	0.4450 (0.001)	—	0.3843 (0.001)	—	0.2868 (0.001)	—	0.3087 (0.001)	—	0.0373 (0.318)	—	0.0608 (0.220)	—	—	—	—
Age-brain	—	(N.S.)	-0.2676 (0.001)	-0.1641 (0.001)	—	—	-0.3504 (0.001)	-0.2800 (0.001)	—	—	-0.1599 (0.020)	-0.1264 (0.053)	—	—	—
Age-height	—	-0.0806	-0.2618	—	—	-0.1644 (0.001)	-0.2965 (0.001)	—	—	-0.2372 (0.001)	-0.3453 (0.001)	—	—	—	—
Age-body	—	0.1663	—	0.2173	—	0.0584	—	0.1358 (0.001)	—	0.3087 (0.001)	—	0.3839 (0.001)	—	—	—
Body-height	0.5547 (0.001)	0.4639 (0.001)	—	—	0.4794 (0.001)	0.4361 (0.001)	—	—	0.3496 (0.001)	0.2482 (0.001)	—	—	—	—	—

() indicates significance level.

lations are stronger in the male sample, except for age and body weight, which reflects a real dimorphic tendency towards obesity in aging females. Of particular interest, I believe, is the marked difference between males and females with respect to the brain weight-height correlation, which is both high and significant in the male samples, but not in the female sample. Needless to say, a positive and significant correlation occurs between body weight and height in all samples, but is again much stronger in the male samples.

Partial correlation statistics. Table 3 indicates the partial correlations (1st order) for the combined, large male and female samples. The smaller male sample is omitted since no significant differences exist between it and the larger male sample. Examining the male sample first, it is clear that the relationship (0-order) between brain and body weights decreases considerably from 0.1775 to 0.0173 (N.S.) when controlling for height; in the female sample, the effect of controlling for height remains insignificant. In males, the relationships between brain weight and height decreases slightly (0.3515 to 0.3087, both significant at the 0.001 level) when body weight is controlled; in females, this relationship changes only slightly and remains insignificant. When age and brain weight are examined by controlling for height, there is a slight rise in correlation in the male sample from (-0.2661 to -0.2800), but there is a drop in the female sample from -0.1393 to -0.1264, although these are not significant in this sample. Concomitantly, in the male sample, the correlation between brain and height decreases somewhat from 0.3515 to 0.2868 when controlling for age, thus indicating that there is definitely an age effect; the same decreases occur in the female sample, but the relationship between brain and height is still insignificant. The relationship between age and height in males decreases from -0.2661 to -0.1644 when brain weight is controlled for, thus corroborating a brain-age decline, and a height-age decline. These changes are insignificant in females.

This effect can also be seen in the 2nd order correlations between brain and height when age and body weight are controlled together; in males, the 0-order correlation between brain and height decreases from 0.3515 to 0.2290, the latter still significant at the 0.001 level. In females, the change is from 0.0698 (N.S.) to 0.006 (N.S.), suggesting that age effects do exist in females, but that they are far stronger in males, and comparatively stronger than the

weight effects, although weight (body) and age are correlated.

Multiple regression. Multiple linear regression was applied to combined and separate large male and female samples to provide an equation of best fit to the data and to account for the greatest amount of combined variance from age, body weight, and height variables. This does not impart much in the way of additional information, since the technique essentially depends on the use of partial correlations which have been presented in the above sections. The main reasons for presenting such results here are to underline the sexual dimorphic differences in variable strength toward accounting for variance, and *not* as a predictive technique per se.

Table 4 shows the relevant statistics and order of variable inclusion for the three samples. As can be seen, height does not enter the formula for the female sample, and age is the 1st order variable selected for this sample. As can also be seen, the Multiple-R for the combined sample reaches 0.496, showing the effects of sexual dimorphic inclusion when the two samples are combined.

Age-group analysis. Having examined the correlations between the variables for each sample, it is necessary to consider the question of possible varying coefficient strengths within age groups. Table 5 shows these results for brain-body and brain-height relationships.

In almost all cases, males show significant correlations between brain weights and body weights and heights, but at different strengths at different ages, whereas only the oldest female age group, 56-65, shows any significant effects. With males, there is an interesting decline in coefficient value during ages 36-55, in the brain-body height data, and a jump to 0.4431 in the 56-65 age group. As the same occurs with regard to brain-body weight correlations, it is tempting to suggest more variability within the middle age groups than at young or old extremes. Since it is well known that both height and brain size decline in the later years, this might explain the strength of the coefficients in the oldest part of the sample. In any event, despite the uneven sample sizes of these groups, these tables should underline the fact that age-groups vary in their relationships, and that the broad spectrum analysis inclusive of ages 18-65 may be too gross to pinpoint underlying age effects.

The other primate data

As the Danish data have thus far shown,

TABLE 4. Multiple regressions for the Danish data

Combined sample, N = 667			
Variable	Multiple R	B, coefficient	Beta-unstandardized (corr.)
(1) Hgt.	0.466	6.267	0.3816
(2) Age	0.488	-1.844	-0.1671
(3) Body weight	0.496	0.116 D-02	0.1048
(Constant)		356.83	
Male Sample, N = 502			
(1) Hgt.	0.3515	4.284	0.2495
(2) Age	0.4384	-2.875	-0.2793
(3) Body weight	0.4415	0.6259 D-03	0.0595
(Constant)		806.47	
Female Sample, N = 165			
Hgt.			
(1) Age	0.1393	-1.445	-0.1674
(2) Body weight	0.1657	0.104 D-02	0.0904
(Constant)		1,319.73	

TABLE 5. Age-cohort correlations for the Danish data

	Ages	Sex	N	Corr.	Signif.
Brain-body weight	18-25	F	15	0.1058	0.354
		M	29	0.3178	0.049
	26-35	F	21	0.1041	0.331
		M	47	0.2461	0.048
	36-45	F	37	0.1678	0.160
		M	98	0.1173	0.125
	46-55	F	45	0.0620	0.343
		M	168	0.1057	0.086
	56-65	F	47	0.2960	0.022
		M	160	0.2850	0.001
Brain-height	18-25	F	15	0.1663	0.277
		M	29	0.3072	0.053
	26-35	F	21	-0.0034	0.494
		M	47	0.3062	0.018
	36-45	F	37	0.1522	0.184
		M	98	0.2596	0.005
	46-55	F	45	-0.0262	0.432
		M	168	0.1694	0.014
	56-65	F	47	0.3015	0.020
		M	160	0.4431	0.001

The italicized significance figures are those P's less than 0.05. Note that almost all are for male.

there are body size relationships with brain size, particularly significant in males. Do any of these effects exist in other primates species for populations of mature, healthy individuals?

Table 6 shows these effects, although the very small sample sizes must be taken into consideration. Unfortunately, not only are the sample sizes small, but there are not sufficient data to analyze body length, which one suspects would correlate more strongly with brain size, particularly in males, as it did in the Danish sample. Next, Table 7 is given here to provide some indication of species variability with respect to certain neural parameters commonly

encountered in the literature (e.g., Jerison, '73, Stephan et al., '70) and which are sometimes used when discussing hominid evolution. As far as I am aware, variation figures for N_c , or extra neurons, and encephalization quotients, E.Q.s, have not been previously published. Figure 1 is included to show the actual slopes for the *Hominoidea*, and to test for possible allometric transformations between certain species.

DISCUSSION

While there are a large number of issues to which these data could be applied, this discussion is in the main limited to within-species

TABLE 6. Tentative brain-body weight relationships in mature, healthy nonhuman primates

Species	N	R	Sig.	Equation		Source
				Intercept	Slope or exponent	
<i>Macaca mulatta</i>						
Male	37	0.3958	0.0076	38.49 × Body	0.1005	Kennard and Wilner, '41; Bauchot and Stephan, '69; Yerkes
Female	24	0.0934	0.3321	55.75 × "	0.05111	
Both	29	0.3798	0.054	4.82 × "	<i>0.34950</i>	
<i>Saimiri Sciurius</i>						
Male	16	0.2486	0.1766	13.37 × "	0.09221	K&W; B&S, Yerke's
Female	22	-0.1002	0.3286	28.08 × "	-0.03209	
Both	38	0.3953	0.007	10.54 × "	<i>0.12410</i>	
<i>Pan troglodytes</i>						
Male	14	0.68198	0.0036	70.03 × "	0.16132	K&W; B&S, Yerke's
Female	16	0.34214	0.0973	160.06 × "	0.07834	
Both	30	0.5997	0.0023	83.05 × "	<i>0.1434</i>	
<i>Gorilla gorilla</i>						
Male	10	0.61824	0.0284	61.93 × "	0.18601	K&W; B&S
Female	10	-0.4165	0.1156	1351.5 × "	-0.0994	
Both	20	0.8705	0.00001	16.50 × "	<i>0.29380</i>	
<i>Pongo Pygmaeus</i>						
Male	16	0.0542	0.42	280.32 × "	0.02841	K&W; B&S
Female	24	0.0367	0.43	261.8 × "	0.01713	
Both	40	0.6977	0.00001	31.13 × "	<i>0.2229</i>	
<i>Homo sapiens</i>						
Male	502	0.195	0.00001	463.1 × "	0.10228	Pakkenberg and Voigt, '64.
Female	165	0.049	0.26554	993.5 × "	0.02532	
Both	667	0.308	0.00001	218 × "	<i>0.16805</i>	

Italicized slope values are for sexes combined.

allometric relationships. Admittedly, the data bases are incomplete, and some of the selection criteria for "healthy mature" specimens could be questioned. These results could well be changed by adding cases to any of the species discussed above. On the basis of these data, however, it is clear that for males, there are relationships between brain and body size that appear very much stronger than they do in female samples. It is tempting to try to offer a uniform explanation, such as more lean body mass in males, or concomitantly, more body fat in females which is not directly innervated. While I strongly suspect this to be the case in the *Homo sapiens* Danish data set (and probably *Pongo*), I hesitate to suggest it for all the remaining species, although it seems a reasonable hypothesis for further testing.

Thus far and without exception, males in all of the taxa examined show higher correlations between brain and body weights than do females, whether the relationships are significant or not. As expected, all significance figures are concomitantly higher in males, and, in all cases, the slope is higher for males. When sexes are combined, the effects of sexual dimorphism are very pronounced in terms of the correlation coefficients, significance, and slope, being strongest in the most dimorphic taxa, such as *Gorilla*, *Pongo*, and *Macaca*. In my estimation,

it is far too early to speculate regarding the theoretical significance of these findings until

1) the data bases are enlarged and carefully culled, and 2) we have some firmer conceptualizations of how to synthesize within-in species variation and trends with between-taxa and evolutionary shifts through time. Furthermore, at least at the present, there is no evidence which securely links any behavioral variables with brain size per se. Bodysize in males may be related in some species to dominance variables, and thus possibly differential reproductive success, but it is far too early in our understanding of these complex questions to make such assertions. It is tempting, however, on the basis of the Danish *Homo sapiens* age-cohort analysis, to expect certain cohorts to be particularly important in terms of brain-body size relationships and reproductive activity.

Several years ago, Van Valen ('74) discussed the theoretical possibilities for selection for larger brain sizes if there were weak relationships between brain and body sizes, and brain weight and intelligence. These data herein suggest to me that selection for increased body size in males could well provide the impetus for larger-brained males and thus species without selection on behavioral parameters per se. On the other hand, while this admittedly male-

TABLE 7. Ranges and means of neural statistics for nonhuman primates and homo

Taxon	N	E.Q. J		E.Q. S		N _c × 10 ⁶		Brain weight, ratio	
		Mean	Range	Mean	Range	Mean	Range	Body weight	Mean
Chimp.	14	2.799	1.97-3.78	11.45	8.21-15.15	3.38	3.07-3.82		0.010
"	16	3.12	2.19-3.99	12.65	9.0-15.97	3.27	2.88-3.58		0.006-0.016
Gorilla	10	1.60	1.17-1.96	6.91	5.16-8.33	3.93	3.64-4.49		0.007-0.017
Gorilla	10	2.05	1.70-2.55	8.59	7.21-10.58	3.47	3.23-3.71		0.002-0.005
Orang	16	1.87	1.54-2.36	7.84	6.51-9.78	3.11	2.66-3.48		0.004-0.008
Orang	24	2.56	1.93-3.46	10.42	7.92-13.83	2.89	2.51-3.28		0.004-0.007
Macaca	37	2.10	1.41-2.90	8.10	5.52-10.97	0.12	0.11-0.14		0.006-0.015
"	24	2.29	1.85-3.15	8.75	7.09-11.88	0.12	0.10-0.14		0.007-0.021
Saimiri	16	2.42	2.01-2.98	8.61	7.21-10.53	0.053	0.047-0.569		0.012-0.024
"	22	2.73	1.96-3.36	9.60	7.01-11.79	0.051	0.046-0.058		0.0031
Homo sapiens	502	7.145	5.05-10.20	29.87	21.33-42.12	9.12	7.77-10.90		0.024-0.042
♂	165	7.154	5.08-10.40	29.74	21.36-42.62	8.53	7.12-10.13		0.039
♀									0.024-0.050
									0.013
									0.015
									0.012-0.024
									0.0218
									0.014-0.036

TABLE 8. Student's t-tests on partitioned male and female Danish data

Combination	Variable	Males small		Males big		Males big		Males small	
		♂ mean	♀ mean (sig. ²)	♂ mean	♀ mean	♂ mean	♀ mean	♂ mean	♀ mean
Age, years		N = 283	N = 86	N = 219	N = 79	N = 219	N = 86	N = 283	N = 79
		48.3	(0.001)	48.6	50.4	48.6	42.3	48.3	50.4
Height, cm		171.6	(0.001)	176.4	164.3	176.4	163.1	171.6	164.3
Brainweight grams		1,438.9	(0.001)	1,480.8	1,316	1,480.8	1,316.0	1,438.9	1,319.7
Bodyweight grams		64,032	(0.001)	82,612	54,514	82,612	54,514	64,032	70,278
E.Q. (J)		7,578	N.S.	6,586	6,533	6,586	7,725	7,578	6,533
E.Q. (S)		31.56	N.S.	27.68	27.30	27.68	31.99	31.56	27.30
N.s × 10 ⁷		909.1	(0.001)	916.3	857.7	916.3	857.75	909.1	848.2
Brain/body ratio		0.0244	(0.001)	0.018	0.019	0.018	0.024	0.0244	0.019

¹Averages in grams.
²Two-tailed significance figures, based on separate variance estimates.

biased framework could have obtained, the data also suggest that a) if females were allometrically corrected for body size, and b) their (females) larger brain/body ratios, and c) larger E.Q. values taken into consideration, one could as easily argue that the female contribution to increasing brain size in hominid evolution was at least equally, if not more important than that of the males. Table 8 shows that if selection were theoretically oriented toward increasing E.Q., brain/body ratio and N_c , more or less simultaneously, the combination of small female-small male offers the highest values of these parameters. On the other hand, however, the combination of large female-large male provides the highest gains in absolute brain weight, and the lowest brain/body ratios. The combination of small males-big females is curious, in that the brain/body ratio for males is significantly higher than females, as are the E.Q. and N_c statistics. Again, as interesting as these exercises may be, their only present value is to indicate a plurality of choices or hypotheses for consideration.

I most specifically *do not* suggest that increases in brain size in any or all primate species has occurred through any of these mechanisms. I believe the warnings of Maruyama ('78) regarding Prigogine's ('76) multicausal models and heterogenistic logic should be seriously considered. Large-bodied males could have been selectively favored for different reasons in different environments and at different times, and similar selection favoring females could likewise have occurred. At present, I know of no primate data which relates the size of the brain to behavioral (and thus natural selection) effectiveness, at least within a species, nor is there any adequate data to show selection favoring differential reproduction within females with higher brain/body ratios. If there are mathematical relationships between brain and body weights, there are also relationships between the obverse, i.e., body weight and brain weight. All of our analyses use the paradigm of brain weight as the dependent variable, and body weight or stature as the independent variable. Perhaps the degrees of dependence and independence vary for different species. Admittedly, the exponents given in Table 6 for each primate species could vary if the samples were larger. They are each different, however, albeit the scale is always lower than the exponents found if multiple genera of higher taxonomic categories are used.

I see no reason why there should not be species-specific growth constraints operative

between brain and body sizes, and it is these that change in the course of evolution. It would be nonsensical, on the basis of our present data, to attempt to argue the primacy of either sex toward a set of interactions so complex and so poorly understood. It is allometry at the species level which has synthesizable potential with our knowledge of growth, genetics, and evolution. The remainder is descriptive and misleading, in that it leads to speculations, almost accepted as dictates, that all of brain evolution is purely allometric, a proposition which is untestable.⁵

Each of the major primate taxonomic categories scales somewhat differently considering the range of exponents, which vary from 0.5775 in Old World monkeys to 0.7985 in New World monkeys. As I attempted to point out before (Holloway, '76a, b), there is a relativity to all relative brain measures (outside of brain/body weight ratio) as reflected by E.Q.s (Jerison, '73) or "Progression indices" (Bauchot and Stephan, '69), depending on the equations used. Using these on fossil australopithecine hominids, for example, as does McHenry ('74, '75), leads to different interpretations of their relative position with regard to modern *Pan* or *Homo*, depending on the exponent utilized (Holloway, '76a; Holloway and Post, MS.) Jerison's ('73) exponent of 0.66 is a fine fit to all of the modern mammal data, but this assemblage does not (and is not meant to) reflect evolutionary relationships. In that regard, Bauchot and Stephan's "basal insectivore" equation, with an exponent of about 0.63, has more to recommend it, since primates possibly evolved from such a stem rather than from whales, camels, mice, lions, bovids, etc.

Indeed, perhaps each primate species should have its E.Q. calculated from whichever taxonomic group could be considered ancestral to it (Holloway and Post, MS.). Pilbeam and Gould ('74) warned: "We cannot judge adaptation until we separate such changes into those required by increasing size and those serving as special adaptations to changing environments." (p. 900). Yet they concluded that the robust form of australopithecine was simply an allometric version of the smaller-sized gracile form, at least with regard to teeth and brain size. Perhaps so, but a line is determined only by two points, and if each evolved from a common ancestor (*Australopithecus afarensis*?)

⁵ While I have never seen any outright reference to a "0.66 gene," I have the impression that many biologists believe it to exist!

TABLE 9. Results of allometric corrections

Chimpanzee from gorilla							
	Av. brain size (grams)	Av. body size (grams)	Gorilla equation		Predicted (grams)	Actual (grams)	% diff.
Gorilla male	585	178,432	$61.93 \times \text{body}$	0.18601	452	390	15.9
" female	441	78,848	$1351.5 \times \text{body}$	0.0994	481	361	33.2
" Both	513	128,635	$16.5 \times \text{body}$	0.29380 (Both)	365	374	2.4
(Chimpanzee body weights placed in Gorilla equations)							
Gorilla from chimpanzee							
Chimpanzee equation							
Chimpanzee male	390	43,540	$70.03 \times \text{body}$	0.16132	492	585	15.9
" female	361	32,658	$160.06 \times \text{body}$	0.07834	387	441	12.2
" Both	374	37,736	$83.05 \times \text{body}$	0.1434 (Both)	449	513	12.5
(Gorilla body weights placed in Chimpanzee equations)							
Female <i>Homo</i> from Male <i>Homo</i> , and visa versa							
Male equation							
	1,457	72,137	$463.1 \times \text{body}$	0.10228	1,431.8	1,318	8.6
Female equation							
	1,318	62,062	$993.5 \times \text{body}$	0.02532	1,318.8	1,457	9.5
Combined equation							
			$281.0 \times \text{body}$	0.16805			
♂ wt. used in equation					1,428	1,457	2.0
♀ wt. " " "					1,393	1,318	5.7

(Johansen and White, '79), each would have a different slope to the ancestral condition. I only note that when I correct for allometry between brain volumes and radial measures on endocasts for pongids and hominids, and use the residuals in discriminant analysis, the robust and gracile forms tend to classify at the 100% level as distinct taxa (Holloway, in press b; and in '76b). If they are simply allometric variants of the same beast, the discrimination of shape differences should become random, or classification should approach 50%. Nor do I find convincing evidence from those studies that chimpanzee and gorilla endocasts are simply allometric variants of one another.

In this regard, we might ask if the data accumulated thus far suggest any simple transformations between species. For example, are gorillas most simply explained as larger bodied-chimpanzees—i.e., that the one is simply an allometric version of the other? As Table 9 indicates, using allometric corrections from either chimpanzee to gorilla or the reverse does yield estimated brain sizes not far from actual averages. If one wanted to pursue this argu-

ment to its logical extreme, one would suppose that the scenario of chimpanzee being derived from gorilla is the most likely, since the prediction is the closest, i.e., 2.4% as against 12.5% for chimpanzee to gorilla. This is, to my mind at least, rather simple-minded, and not just because the beasts are different in adaptations to niche resources, over-all morphology, and behavior. As Figure 1 illustrates, an allometric correction based on mean values from the male and female combined regression equations will give % deviations that are intuitively tolerable, but the slopes are considerably different for the two groups, and their extensions beyond their own present ranges become increasingly divergent. Indeed, each group remains exactly in its position. That is, the chimpanzee predicted values are consistently under the gorilla ones; the gorilla predicted values consistently larger than the chimpanzee ones; female *Homo* is less than predicted, and male *Homo* more than predicted. Again, these exercises prove nothing.

It is not my intention here to question the existence of allometric trends within or between species of primates, since with only two

variables, brain and body weights (or lengths), there is no adequate test for what must be taken as a correlation rather than a true regression (or causal relationship). Nor do I doubt that some allometric explanations hold for some mammalian species, fossil and living, and perhaps even within particular phases of human evolution. It is my intent, however, to show that allometric scalings could have a plurality of causal mechanisms behind them, and that with our present inadequate data base, homogenistic, deterministic theories are only useful as a starting point, and are presently descriptive, rather than causal models.

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