Medical Hypotheses (2002) **58**(4), 284–290

doi: 10.1054/mehy.2001.1516, available online at http://www.idealibrary.com on IDEAL®

Primate encephalization and intelligence

M. F. Williams

Oakland, USA

Summary The amount of brain mass exceeding that related to an animal's total body mass is called encephalization. And quantifying encephalization has been argued to be directly related to an animal's level of intelligence. In this study, the legitimacy of the encephalization hypothesis was tested for encephalization slopes 0.28, 0.67, and 0.75 in Snell's equation of simple allometry by determining the intersexual encephalization similarity for humans and 18 other primate species and by comparing the encephalization quotients for humans and six other primate species against the learning ability evaluations for their intelligence. Results suggest that the most accurate means for quantifying the encephalization of humans and other adult primate species requires the use of Lapicque's universal exponent of 0.28 in Snell's equation of simple allometry. Since Lapicque's slope was derived from various vertebrate groups, this equation may potentially be universally applicable for determining relative adult vertebrate encephalization and intelligence. © 2002 Published by Elsevier Science Ltd

INTRODUCTION

Brain mass exceeding that related to total body mass is known as encephalization. And the importance of accurately quantifying encephalization stems from the hypothesis that this excess in brain matter is somehow related to the level of an animal's intelligence (1,2). As early as 1871, Charles Darwin wrote in his book '*The Decent of Man*': 'No one, I presume, doubts that the large proportion which the size of man's brain bears to his body, compared to the same proportion in the gorilla or orang, is closely connected with his mental powers.'

But as far back as 1812, it was recognized that smaller animals tended to have proportionately larger brain masses relative to their body masses than larger animals. And in 1871, Snell conceived his equation of 'simple allometry':

$$\text{brain weight} = k(\text{body weight})^{a};$$

where a represents the exponential slope and k the constant, as a means for evaluating the allometric relationship between brain and body mass (3,4), as the basic formula for measuring encephalization.

It was originally argued that vertebrate brain masses sloped at a two thirds rate (0.67) in relation to the body (1,3–7). But a later expansion in the database led to estimates of 0.75 for the slope for vertebrates (7–9).

However, back in the 1890s, both Lapicque and Dubois independently derived exponential slopes ranging from 0.2 to 0.4 for closely related species or subspecies of adult birds and mammals (3,6,9,10). And L. Lapicque cited a 'universal' slope of 0.28 for closely related animals (3) and a slope of 0.20 for individual animals within a species (9). But it has also been observed that allometric slopes tend to be higher at higher taxonomic levels (10) which has led Pagel and Harvey (9) to argue that measures of encephalization should only be made with reference to a particular baseline group.

Received 25 May 2001
Accepted 31 October 2001

Correspondence to: **Marcel F. Williams**, 748 Oakland Avenue #306, Oakland, CA 94611-4523, USA. Phone: 510-547-1661;
E-mail: newpapyrus@yahoo.com

To test whether such taxonomic constraints are necessary and to evaluate the fundamental legitimacy of the encephalization hypothesis, the relationship between encephalization and intelligence was examined by comparing learning ability evaluations for primate intelligence, at high confidence levels, against their resulting encephalization quotients for the exponential slopes: 0.67, 0.75, and 0.28 in Snell's equation of simple allometry. Under the assumption that there is no significant difference in intelligence between the genders of a species, the legitimacy of using encephalization formulas was also tested by measuring the encephalization similarity between the genders of the same species.

MATERIALS AND METHODS

Nomenclature

The following taxonomic terminology was used throughout this article to refer to the major primate groups: Prosimii (prosimians) = lower primates; Anthropoidea (anthropoids) = old world monkeys and apes; Catarrhini (catarrhines) = old world monkeys and apes; Cercopithecoidea (cercopithecoids) = old world monkeys; Hominoidea (hominoids) = ape/human clade; hylobatidae (hylobatids) = lesser apes (gibbons and siamangs); hominidae (hominids) = great ape (chimpanzee, bonobo, gorilla, orangutan)/humans; Ponginae (ponginines) = orangutan; Homininae(hominines) = Africanape(gorilla,chimpanzee)/human clade; Hominini (hominin) = humans (11,12).

Learning capacity and intelligence in primates

Fundamentally, biological intelligence is the ability of an organism to memorize and to cross-associate sensory perceptions; and to be able to recall and reassociate those memories and cross associations in order to utilize them in their adaptive behavior. And in theory, the capacity of intelligence in an organism can be demonstrated by how complexly an organism can utilize such perceptual memories and associations in its behavior. Since intelligence is viewed to be synonymous with learning ability, it has, therefore, been argued that the level of intelligence in an organism can be demonstrated by the level of its ability to learn (13).

Mirror and video self-recognition test are methods utilized by researchers to determine if an animal is intelligent enough to self identify its own reflective, or recorded, images (17). Self-cognition (self-recognition, self-awareness, or self-conciousness) is basically defined as the ability of an organism to recognize itself as an object distinct from all other objects in its perceptual universe (14).

While partial self-cognitive behavior in front of mirrors has been detected in some individuals within the species *Macaca fuscata* and *Macaca nemestrina*, full self-cognitive behavior in front of mirrors or in videos has never been detected in non-hominid (great ape/human clade) primates. So full self-cognitive behavior appears to be exclusive to humans and great apes amongst the primates (15–18).

Learning set, reversal task, and transfer index test have been devised by researchers to measure not only an animal's ability to learn, but also an animal's ability to learn how to learn more efficiently (13). The application of such tests on primates has reflected the self-recognition test in showing that all great apes performed at a higher level of intelligence than monkeys and lesser apes. While the great apes perform well below the adult human level in learning capacity, these learning ability tests have consistently shown that the bonobo (*Pan panicus*), chimpanzee (*Pan troglodytes*), gorilla (*Gorilla gorilla*), and orangutan (*Pongo pygmaeus*) perform equally well amongst themselves and are, therefore, equally intelligent species (13,19–26).

While learning ability tests tend to show that monkeys perform better than prosimians, there is some degree of ambiguity as to the relative levels of learning ability and intelligence amongst non-self-cognitive primates species. However, learning set, reversal task, transfer index test and language studies have consistently shown that the rhesus monkey (*Macaca mulatta*) outperforms the squirrel monkey (*Saimiri sciureus*) in its ability to learn (13,24,26–28) and is, therefore, on a higher level of intelligence.

A synthesis of the results from self-cognitive, learning set, reversal task, and transfer index test on primates with the highest confidence levels allows us to distinguish at least two different levels of self-cognitive intelligence and two different levels of intelligence below the self-cognitive level. This, therefore, gives us four different levels of intelligence, as determined through the learning ability test, for seven different primate species: *Homo sapiens*, *Pan troglodytes*, *Pan panicus*, *Gorilla gorilla*, *Pongo pygmaeus*, *Macaca mulatta*, and *Saimiri sciureus*.

If the encephalization quotients (EQ) resulting from an encephalization formula are truly reflective of relative animal intelligence then, amongst the seven primates in this study:

1. Humans (*Homo sapiens*) should receive the highest encephalization quotients amongst these seven primate species;
2. The great apes (*Pan*, *Gorilla*, and *Pongo*) should be given the highest levels of encephalization next to humans;
3. All species of great apes: *Pan troglodytes*, *Pan panicus*, *Gorilla gorilla*, and *Pongo pygmaeus* should receive approximately the same level of encephalization with each other.
4. The rhesus monkey, *Macaca mulatta*, should be given a lower encephalization than humans and great apes but

a higher level of encephalization than the squirrel monkey, and
5. The squirrel monkey, *Saimiri sciureus*, should receive the lowest encephalization quotient amongst these seven learning ability tested primate species.

The statistical accuracy of an encephalization formula can also be assessed if we assumed that there is no significant difference in intelligence between the genders within a primate species, even though some degree of brain and body size dimorphism may be exhibited. The mean encephalization quotients for each gender of a primate species, therefore, should reflect such an intersexual equivalence if such indices are truly related to intelligence. Therefore, genders who are approximately equal in intelligence should also have approximately equal encephalizations if the encephalization quotients derived from an encephalization formula are truly reflective of intelligence.

In this paper, the encephalization formulas:

$$EQ = E/P^{0.67};$$
$$EQ = E/P^{0.75}; \text{ and}$$
$$EQ = E/P^{0.28};$$

where E = the brain weight, P = the body weight, and EQ = the the level of encephalization, were used to determine the relative encephalizations for the learning ability tested primates: *Homo sapiens*, *Pan panicus*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus*, *Macaca mulatta*, and *Saimiri sciureus*. These encephalization formulas were also used to determine the encephalization quotients, and the intersexual encephalization similarity, between the genders of 19 primate species.

The adult brain and body weight data for extant and extinct primate species and genders used in this article and in Tables 1 through 7 were derived from Schultz (29,30); Tobias (2); Pilbeam and Gould (3); Bronson (31); McHenry (32); Wood and Richmond (33) and Stephan, Frahm, and Baron (34).

RESULTS AND DISCUSSION

Primate encephalization and learning ability

While encephalization formula $EQ = E/P^{0.67}$, corresponds with the learning ability assessments for seven primates in Table 1 by giving both genders of *Homo sapiens* the largest encephalization quotients, it paradoxically gives female squirrel monkeys encephalizations above all other monkeys and great apes. Male rhesus monkeys are also paradoxically given larger encephalizations than the chimpanzee, gorilla, and male orangutan.

A similar lack of correspondence with learning ability levels in Table 1 is found in encephalization formula $EQ = E/P^{0.75}$. Both male and female squirrel and rhesus monkeys are given larger encephalizations than the great apes despite the fact that these monkeys don't even have the cognitive ability to recognize their own reflective images.

However, in formula $EQ = E/P^{0.28}$, the encephalization quotients correspond precisely with the learning ability evaluations in Table 1 giving humans larger encephalizations than the great apes, great apes higher encephalizations than the monkeys, and rhesus monkeys a larger encephalization than the squirrel monkey with the squirrel monkey genders having the lowest encephalization quotients amongst the seven primate species listed.

And amongst the great apes, the encephalization similarity in Tables 2 and 3 ranges from 96.8 to 99.5% in males, and 96.2 to 100% in females. This suggest that the encephalization in all great ape species on this scale are

Table 1 Encephalization and learning capacity in 7 primate species

Species	E (grams)	P (grams)	EQ (0.28)	EQ (0.67)	EQ (0.75)	LAL
Homo sapiens (M)	1400	65,000	62.9	0.835	0.344	A
Homo sapiens (F)	1300	58,000	60.3	0.836	0.349	A
Gorilla gorilla (M)	535	175,000	18.2	0.164	0.063	B
Gorilla gorilla (F)	443	85,000	18.5	0.221	0.089	B
Pongo pygmaeus (M)	416	75,000	18.0	0.225	0.091	B
Pongo pygmaeus (F)	338	37,000	17.8	0.294	0.127	B
Pan troglodytes (M)	381	48,000	18.6	0.278	0.117	B
Pan troglodytes (F)	350	42,000	17.8	0.280	0.119	B
Pan panicus (M)	356	38,500	18.5	0.301	0.130	B
Pan panicus (F)	329	32,000	18.0	0.315	0.138	B
Macaca mulatta (M)	91	5,210	8.29	0.294	0.148	C
Macaca mulatta (F)	85	4,880	7.88	0.287	0.146	C
Saimiri sciureus (M)	25	720	3.96	0.304	0.180	D
Saimiri sciureus (F)	23	580	3.87	0.324	0.195	D

EQ (0.28) = $E/P^{0.28}$; EQ (0.67) = $E/P^{0.67}$; EQ (0.75) = $E/P^{0.75}$; where EQ = the encephalization quotient, E = brain weight; and P = body weight. LAL = the level of measured learning ability where A > B > C > D. M = male and F = female mean body weights.

Table 2 The mean male encephalization indices for great apes of equal learning ability

Species	E (grams)	P (grams)	EQ (0.28)	EQ (0.67)	EQ (0.75)
Gorilla gorilla	535	175,000	18.2	0.164	0.063
Pongo pygmaeus	416	75,000	18.0	0.225	0.091
Pan troglodytes	381	48,000	18.6	0.278	0.117
Pan panicus	356	38,500	18.5	0.301	0.130
Highest % of encephalization similarity			99.5	92.4	90.0
Lowest % of encephalization similarity			96.8	54.5	48.5

EQ (0.28) = $E/P^{0.28}$; EQ (0.67) = $E/P^{0.67}$; EQ (0.75) = $E/P^{0.75}$; where EQ = the encephalization quotient, E = brain weight; and P = body weight. The percentage of EQ similarity = EQ1/EQ2, where EQ1 < EQ2.

Table 3 The mean female encephalization indices for great apes of equal learning ability

Species	E (grams)	P (grams)	EQ (0.28)	EQ (0.67)	EQ (0.75)
Gorilla gorilla	443	85,000	18.5	0.221	0.089
Pongo pygmaeus	338	37,000	17.8	0.294	0.127
Pan troglodytes	350	42,000	17.8	0.280	0.119
Pan panicus	329	32,000	18.0	0.315	0.138
Highest % of encephalization similarity			100.0	95.2	93.7
Lowest % of encephalization similarity			96.2	70.2	64.5

EQ (0.28) = $E/P^{0.28}$; EQ (0.67) = $E/P^{0.67}$; EQ (0.75) = $E/P^{0.75}$; where EQ = the encephalization quotient, E = brain weight; and P = body weight. The percentage of EQ similarity = EQ1/EQ2, where EQ1 < EQ2.

approximately equal and are in agreement with the learning ability evaluations on the higher apes.

For slope 0.67, on the other hand, the encephalization similarity amongst the great apes was as low as 54.5% in males and 70.2% in females. And for encephalization slope 0.75, it was as low as 48.5% in males and 64.5% in females. This demonstrates that encephalization slopes 0.67 and 0.75 are clearly not good measures of learning ability, or intelligence, in the great apes.

Primate intersexual encephalization similarity

Table 6 lists the intersexual encephalization similarity for 19 primate species. The highest encephalization similarity was again found in encephalization quotients derived from encephalization slope 0.28. The average intersexual encephalization similarity was 96.6% with the lowest intersexual encephalization similarity at 87.2%.

Table 6 gave a mean intersexual encephalization similarity of 92% for slope 0.67 with the lowest intersexual encephalization similarity at 72.2% on this scale. The mean intersexual encephalization similarity for slope 0.75 was even lower at 90.8% with the lowest intersexual encephalization similarity at only 69%.

Despite the significantly higher intersexual encephalization similarity for slope 0.28 compared to slopes 0.67 and 0.75, a maximum range of accuracy as low as 87.2% still appears to be rather large. However, 16 out of the 19 primates in Table 6 received encephalization similarities at least 95.1% or higher. And there are some indications that the three lowest intersexual encephalization similarities for slope 0.28 in Table 6 may be skewed due to the fact that the mean brain and body weights for the genders of *Cercopithecus aethiops*, *Ateles panicus*, and *Papio anubis* were derived from a very small number of individuals.

The data for the primate with the lowest intersexual encephalization similarity (87.2%) (*Cercopithecus aethiops*) appear to be obviously skewed (Table 6). This is apparent by the fact that while both genders receive a mean cranial mass of 66 grams, the mean male body mass is paradoxically 60% larger than the mean female body mass. This may be due to the fact that the mean male brain and body weights for *Cercopithecus aethiops* were determined from only 10 individuals (Table 4) while the mean female brain and body weights were determined in Table 5 from only six individuals (31).

Another primate with a relatively low intersexual encephalization similarity (94.4%) for slope 0.28 is *Ateles panicus*. In this case, the gender with larger mean body weight paradoxically has the smaller mean brain weight. While the mean female brain and body weights were derived from 15 to 17 individuals, the mean brain and body weights for males in Table 4 were derived from only six individuals (31) which may have possibly skewed the results.

Table 4 The mean male encephalization indices for 19 primates

Species	E (grams)	P (grams)	EQ (0.28)	EQ (0.67)	EQ (0.75)
Homo sapiens	1400	65,000	62.9	0.835	0.344
Gorilla gorilla	535	175,000	18.2	0.164	0.063
Pongo pygmaeus	416	75,000	18.0	0.225	0.091
Pan troglodytes	381	48,000	18.6	0.278	0.117
Pan panicus	356	38,500	18.5	0.301	0.130
Papio anubis	175	16,060	11.6	0.266	0.123
Symphalangus syndactylous	126	11,100	9.28	0.245	0.117
Macaca arctoides	102	7,810	8.29	0.251	0.123
Hylobates lar	104	5,700	9.23	0.317	0.159
Cercopithecus aethiops	66	5,230	6.00	0.213	0.107
Macaca mulatta	91	5,210	8.29	0.294	0.148
Ateles panicus	106	5,040	9.74	0.350	0.177
Ateles geoffroyi	108	4,760	10.1	0.371	0.188
Macaca fascicularis	70	4,740	6.54	0.241	0.123
Cebus apella	71	2,770	7.72	0.351	0.186
Cebus albifrons	65	1,770	8.01	0.433	0.238
Aotus trivirgatus	17	720	2.69	0.207	0.122
Saimiri sciureus	25	720	3.96	0.304	0.180
Sanguinus oedipus	9.2	370	1.76	0.175	0.109

EQ = $E/P^{0.28}$; EQ = $E/P^{0.67}$; EQ = $E/P^{0.75}$; where EQ = the encephalization quotient, E = brain weight; and P = body weight.

While there are no obvious indications that the low encephalization similarity for slope 0.28 for *Papio anubis* at 90.5% may have been skewed, the mean brain and body weights for baboon females in Table 5 were derived from only 5 to 7 individuals (31) which may suggest that the low encephalization for females relative to males may be skewed by the low number of female individuals measured.

Table 5 The mean female encephalization indices for 19 primates

Species	E (grams)	P (grams)	EQ (0.28)	EQ (0.67)	EQ (0.75)
Homo sapiens	1300	58,000	60.3	0.836	0.349
Gorilla gorilla	443	85,000	18.5	0.221	0.089
Pongo pygmaeus	338	37,000	17.8	0.294	0.127
Pan troglodytes	350	42,000	17.8	0.280	0.119
Pan panicus	329	32,000	18.0	0.315	0.138
Papio anubis	148	12,900	10.5	0.261	0.122
Symphalangus syndactylous	123	10,200	9.28	0.254	0.121
Macaca arctoides	100	7,450	8.24	0.254	0.125
Hylobates lar	101	5,300	9.15	0.323	0.163
Cercopithecus aethiops	66	3,220	6.88	0.295	0.155
Macaca mulatta	85	4,880	7.88	0.287	0.146
Ateles panicus	101	5,220	9.19	0.326	0.164
Ateles geoffroyi	108	4,680	10.1	0.375	0.191
Macaca fasicularis	62	3,360	6.38	0.269	0.140
Cebus apella	63	1,810	7.71	0.414	0.227
Cebus albifrons	60	1,470	7.79	0.453	0.253
Aotus trivirgatus	17	630	2.80	0.226	0.135
Saimiri sciureus	23	580	3.87	0.324	0.195
Sanguinus oedipus	9.7	370	1.85	0.185	0.115

$EQ = E/P^{0.28}$; $EQ = E/P^{0.67}$; $EQ = E/P^{0.75}$; where EQ = the encephalization quotient, E = brain weight; and P = body weight.

If the possibly skewed data from the three primates with the lowest intersexual encephalization similarity are removed from the results for 19 primates in Table 6, the mean intersexual encephalization similarity for slope 0.28 rises from 96.6% to 97.7% with the lowest intersexual encephalization similarity rising from 87% to 95.1%. This may suggest that species that are equivalent in intelligence have encephalization similarities at least 95% or above while encephalization similarities that fall as low as 87% may represent the range of differences in levels of intelligence within a primate species.

Relative primate encephalization

The resulting encephalization quotients from various extant and extinct catarrhine, platyrrhine, and prosimian primates on the 0.28 encephalization scale (Table 7) show some interesting results and patterns.

As earlier noted, the high encephalization similarity amongst the great apes would seem to suggest that the last common ancestors of the hominines (African ape/human clade) and the last common ancestors of the hominids (great ape/human clade) must have had a similar degree of encephalization.

The hylobatid genders display mean encephalization quotients ranging from 9.15 to 9.28 with the lowest degree of encephalization similarity at 98.6%. This appears to suggest that the gibbon and siamang are equally

Table 6 Primate intersexual encephalization similarity for 19 species

Species	Percentage of intersexual encephalization similarity		
	EQ (0.28)	EQ (0.67)	EQ (0.75)
Homo sapiens	95.9	99.9	98.6
Gorilla gorilla	98.4	74.2	70.8
Pongo pygmaeus	98.9	76.5	71.7
Pan troglodytes	95.7	99.3	98.3
Pan panicus	97.3	95.6	94.2
Papio anubis	90.5	98.1	99.2
Symphalangus syndactylous	100.0	96.5	96.7
Macaca arctoides	99.4	98.8	98.4
Hylobates lar	99.1	98.1	97.5
Cercopithecus aethiops	87.2	72.2	69.0
Macaca mulatta	95.1	97.6	98.6
Ateles panicus	94.4	93.1	92.7
Ateles geoffroyi	100.0	98.9	98.4
Macaca fascicularis	97.6	89.6	87.9
Cebus apella	99.9	84.8	81.9
Cebus albifrons	97.3	95.6	94.1
Aotus trivirgatus	96.1	91.6	90.4
Saimiri sciureus	97.7	93.8	92.3
Sanguinus oedipus	95.1	94.6	94.8
Mean % of intersexual similarity	96.6	92.0	90.8
Highest % of intersexuual similarity	100.0	99.9	99.2
Lowest % of intersexual similarity	87.2	72.2	69.0

The percentage of intersexual encephalization similarity = EQ1/EQ2; where EQ1 < EQ2 as derived from Table 4 for males and Table 5 for females.

Table 7 EQs for 22 primate species using encephalization slope 0.28

Species	E (grams)	P (grams)	EQ (0.28)
Homo sapiens (M)	1400	65,000	62.9
Home erectus (Choukoutien)	1050	53,000	49.9
Homo habilis	680	35,000	36.3
Australopithecus afarensis	470	37,000	24.7
Australopithecus africanus	450	32,000	24.6
Australopithecus robustus	500	40,500	25.6
Australopithecus boisei	510	47,500	25.0
Gorilla gorilla (F)	443	85,000	18.5
Pan troglodytes (F)	350	42,000	17.8
Pan panicus (M)	356	38,500	18.5
Pongo pygmaeus (M)	416	75,000	18.0
Symphalangus syndactylous (F)	123	10,200	9.28
Hylobates lar (M)	104	5,700	9.23
Papio anubis (M)	175	16,060	11.6
Macaca mulatta (M)	91	5,210	8.29
Cercopithecus aethiops (M)	66	5,230	6.00
Ateles panicus (M)	106	5,040	9.74
Saimiri sciureus (F)	23	580	3.87
Callithrix jacchus	8.6	215	1.91
Lemur fulvus	23.3	1,400	2.41
Indri indri	38.3	6,250	3.31
Tupaia glis	3.2	170	0.760

$EQ = E/P^{0.28}$; where EQ = the encephalization quotient, E = brain weight; and P = body weight. M = mean brain and body weights for males and F = mean for females.

encephalized and, therefore, equally intelligent and suggest that the gibbon and siamang probably had an equally encephalized common ancestor.

All of the australopithecine species: *A. afarensis*, *A. africanus*, *A. robustus*, and *A. boisei* are given encephalization quotients in Table 7 significantly above the great ape level. The lowest level of encephalization similarity amongst the australopithecines was approximately 96.1% which suggests that not only were all of the australopithecine species on a higher level of intelligence than the great apes but they were also equivalent with each other in intelligence which would suggest that they all had an equally encephalized common ancestor.

All species of *Homo* were given higher encephalization indices in Table 7 than the australopithecines with *Homo erectus* having a significantly lower encephalization than *Homo sapiens*, and *Homo habilis* having a significantly lower encephalization than *Homo erectus*.

Not surprisingly, the tree shrew (*Tupaia glis*) receives the lowest encephalization quotient amongst all primates listed in Table 7 with an encephalization quotient of 0.760. The tree shrew is, therefore, the only primate in this study with an encephalization that falls below 1.0 on the 0.28 encephalization scale.

Body size and cerebral expansion

Lapicque argued that the universal slope of 0.28 represents a brain that enlarges old neurons without adding new ones (3). However, neuron density is lower in the larger brained human males relative to the smaller brained human females (35). This suggests that the slope of 0.28 actually represents an expansion of non-neuron cerebral tissue.

Arguments have been made for a relationship between brain size and the metabolic constraints on venous system that delivers oxygen and glucose to the brain (7,8). So it is interesting that the functional mechanisms (heart and lungs) directly related to the delivery of oxygen and nutrients to the body also appear to slope at a rate of 0.28 in animals (36,37). Since the frequency of breathing and heart beats decline at a slope of 0.28 relative to the increase in body mass, the expansion in non-neuron brain tissue may be related to an expansion of the venous delivery system and structural neural glia cells to compensate for the reduced frequency of oxygen and nutrients delivered to the brain in larger animals.

CONCLUSION

Of the three encephalization slopes (0.28, 0.67, and 0.75) applied in Snell's equation of simple allometry, only Lapicque's universal exponent 0.28 gave resulting encephalization quotients (EQ) that closely reflected the learning ability determinations of intelligence for seven adult primate species on four different levels of learning ability and intelligence. Encephalization slope 0.28 also gave the highest encephalization similarities between the genders of 19 primate species as would be expected if it is assumed that there is no significant difference in intelligence between the genders within a species.

Therefore, amongst adult primate species, the encephalization formula:

$$EQ = E/P^{0.28};$$

where E = the brain weight, P = the body weight, and EQ = the the level of encephalization, appears to be the most accurate method for determining the encephalization and, therefore, the intelligence of one primate species relative to another primate species.

Since Lapicque derived the universal exponent of 0.28 from the encephalization slopes from various bird and mammal species (3,6,9,10), the use of this encephalization slope may be universally applicable for determining relative encephalization and intelligence in adult vertebrate species.

ACKNOWLEDGEMENTS

The author would like to thank the Georgia State University Language Research Center for generously providing me with their most recent research materials on primate cognition and learning ability. I am also extremely grateful to Dr. Duane M. Rumbaugh for his correspondence and for his encouraging comments and reviews of earlier drafts of this paper.

REFERENCES

1. Jerison H. J. Paleoneurology and the evolution of the mind. *Scientific American* 1976; **234**: 90–101.
2. Tobias P. V. *The Brain in Hominid Evolution.* New York and London: Columbia University Press, 1971.
3. Pilbeam D., Gould S. J. Size and scaling in human evolution. *Science* 1974; **186**: 892–901.
4. Macphail E. M. *Brain and Intelligence in Vertebrates.* Oxford: Claredon Press, 1982.
5. Jerison H. J. *Evolution of the Brain and Intelligence.* New York: Academic Press, 1973.
6. Lande R. Quantitative genetic analysis of multivariate evolution, applied to brain:body size allometry *Evolution* 1979; **33**(1): 402–406.
7. Armstrong E. Relative brain size in monkeys and prosimians. *AJPA* 1983; **66**: 263–273
8. Harvey P. H., Bennett P. M. Brain size, energetics, ecology and life history patterns. *Nature* 1983; **306**: 314–315.
9. Pagel M. D., Harvey P. H. Taxonomic differences in the scaling of brain on body weight among mammals *Science* 1989; **244**: 1589–1593.
10. Riska B., Atchley W. R. Genetics of growth predict patterns of brain-size evolution, *Science,* 1985; **229**: 668–671.
11. Simons E. L. *Primate Evolution: An introduction to Man's Place in Nature.* New York: MacMillan, 1972.
12. Andrews P. Evolution and environment in the Hominioidea. *Nature* 1992; **360**: 641–646.
13. Essock S. M., Rumbaugh D. M. (1978) Development and measurement of cognitive capabilities in Captive nonhuman primates. pp. 161–208. In H. Markowitz and V. J. Stevens (eds): *Behavior of Captive Wild Animals.* Chicago: Nelson-Hall, 1978.
14. Dobzhansky T. *Mankind Evolving: The Evolution of the Human Species.* New Haven and London: Yale University Press, 1962.
15. Gallup G. G. Chimpanzees: Self-recognition. *Science*, 1970; **167**: 86–87.
16. Anderson J. R. Responses to mirror image stimulation and assessment of self-recognition in mirror-and-peer-reared stumptail macaques. *Quarterly Journal of Experimental Psychology*, 1983; **35B**: 201–212.
17. Parker S. T. (1991) *Evolved mechanism for cognitive construction: imitation as a learning and teaching-incentive device; Circular reactions as self-teaching devices*, presented at the 21st annual symposium of the jean piaget society. Philadelphia, PA, May, 1991.
18. Patterson F. *Mirror behavior and self-concept in the lowland gorilla.* Videotape and paper given at the Symposium on Gorilla Cognition and Communication at the 13th annual meetings of the American Society of Primatologist. Davis, CA, 1990.
19. Rumbaugh D. M., McCormack C. The learning skills of primates: A comparative study of apes and monkeys. In D. Starke, T. Schneider, and H. J. Kahn. (eds) *Progress in Primatology.* Stuttgart: Fischer, 1967.
20. Rumbaugh D. M. Learning skills of anthropoids. In L. A. Rosenblum (ed) *Primate Behavior: Developments in Field and Laboratory Research*, New York: Academic Press, 1970.
21. Bourne G. H. *The Ape People.* New York: G. P. Putnam's, 1971.
22. Rumbaugh D. M., Gill T. V. The learning skills of great apes. *Journal of Human Evolution.* 1973; **2**: 171–179.
23. Rumbaugh D. M. Primate language and cognition: common ground, *Social Research*, 1995; **62**(3): 711–730.
24. Rumbaugh D. M., Savage-Rumbaugh S., WashburnD. A. Toward a new outlook on primate learning and behavior: complex learning and emergent processes in comparative perspective. *Japanese Psychological Research* 1996; **38**(3): 113–125.
25. Hillix W. A., Rumbaugh D. M. Language in animals. pp. 837–847. In G. Greenberg and M. M. Haraway (eds) *Comparative Psychology: A Handbook.* Garland Publishing, Inc: New York and London, 1998.
26. Beran M. J., Gibson K. R., Rumbaugh D. M. Predicting hominid intelligence from brain size. pp. 88–97. In M. C. Corbalillis and S. E. G. Lea (eds) *The Descent of Mind: Psychological Perspectives on Hominid Evolution*, Oxford University Press, Inc, 1999.
27. Miles R. C. Learning-set formation in the squirrel monkey. *Journal of Comparative Physiology and Psychology* 1957; **50**: 356–357.
28. Hodos W. Evolutionary interpretation of neural and behavioral studies of living vertebrates. In F. O. Schmidt (ed) *The Neurosciences: Second Study Program.* New York: Rockerfeller University Press, 1970.
29. Schultz A. H. The recent hominoid primates. In S. L. Washburn and P. C. Jay (eds): *Perspectives on Human Evolution.* pp. 122–195. New York: Holt, Rinehart and Winston, 1968.
30. Schultz A. H. *The Life of Primates.* New York: Universe Books, 1969.
31. Bronson R. F. Brain weight–body weight relationships in 12 species of nonhuman primates. *AJPA*, 1981; **56**: 77–81.
32. McHenry H. M. Body size and proportions in early hominids. *Am J Phys Anthropol* 1992; **87**(4): 407–31.
33. Wood B., Richmond B. G. Human evolution: taxonomy and paleobiology. *Journal of Anatomy* 2000; **197**(Pt 1): 19–60.
34. Stephan H., Frahm H., Baron G. New and revised data on volumes of brain tructures in insectivores and primates. *Folia primatol* 1981; **35**: 1–29.
35. Witelson S. F., Glezer I. I., Kigar D. L., Kigar, Women have greater density of neurons in posterior temporal cortex. *J Neurosci* 1995; **15**: 3418–28.
36. Gunther B., Guerra E. Biological similarities. *Acta Physiologica Lantinoamerica* 1955; **5**: 169–86.
37. Gould S. J. *The Panda's Thumb: More Reflections in Natural History.* New York and London: W.W. Norton and Company, 1980.

