News and Views

Chimpanzee neonatal brain size: Implications for brain growth in *Homo erectus*

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Introduction

Some 30,000 nonhuman primates are sacrificed every year in biomedical and space research. I regard the nonavailability of data as a pathetic, ill-planned, and unconscionable waste.
—Ralph Holloway (1980) on the scarcity of data on brain masses in nonhuman primates.

It has long been argued that, relative to nonhuman primates, humans experience a large percentage of brain growth postnatally (Schultz, 1940, 1941; Count, 1947; Jordaan, 1976; Gould, 1977; Passingham, 1982; Martin, 1983; Dienske, 1986; Smith and Tompkins, 1995; Coqueugniot et al., 2004; Hublin and Coqueugniot, 2006). Recent work, however, has suggested that humans and chimpanzees experience comparable or even identical percentages of their total brain growth postnatally (Fragaszy and Bard, 1997; Fragaszy et al., 2004; Kennedy, 2005; Vinicius, 2005). For example, Vinicius (2005) stated that chimpanzee brain growth in utero has been overestimated and prenatal human brain growth has been underestimated. He suggested that humans and chimpanzees experience an overlapping 24–31% and 30–36.5% of their brain growth in utero, respectively. Additionally, three recent papers presenting different values for the percentage of total brain growth that occurs in utero in chimpanzees

and humans have reached conflicting interpretations regarding brain development in *Homo erectus* (Coqueugniot et al., 2004; Leigh, 2006; Hublin and Coqueugniot, 2006). Based on the Mojokerto specimen, Coqueugniot et al. (2004) and Hublin and Coqueugniot (2006) argued that *H. erectus* had not yet evolved a humanlike trajectory of brain growth and, therefore, that this species had not developed the cognitive skills or the language capacity present in modern humans. In contrast, Leigh (2006) found both the proportional and absolute size of the Mojokerto specimen to be consistent with brain-growth patterns in modern humans.

There is a wide range of values cited for the percentage of chimpanzee brain size achieved by birth: from 31% (e.g., Fragaszy and Bard, 1997) to 50% (e.g., Dienske, 1986). The size of the brain at birth in chimpanzees has been compared to that of humans and has been used to make inferences about (1) primate life history (Sacher and Staffeldt, 1974; Hofman, 1983; Martin, 1983; Harvey and Clutton-Brock, 1985; Dienske, 1986; Smith and Tompkins, 1995; Fragaszy and Bard, 1997; Kennedy, 2005); (2) hominid brain growth, development, and cognitive ability (Holt et al., 1975; Passingham, 1975; Gould, 1977; Passingham, 1982, Passingham, 1985; Cunnane and Crawford, 2003; Coqueugniot et al., 2004; Hublin and Coqueugniot, 2006); and (3) early hominid obstetrics (Leutenegger, 1987; Häusler and Schmid, 1995; Tague and Lovejoy, 1998). However, as Vinicius (2005) noted, the chimpanzee neonatal brain-mass value cited in all of the above papers can be traced to a single male neonate with a 128-cc brain (Schultz, 1941) and/or to a chimpanzee with a 171-cc brain who was already 74 days old at death (Schultz, 1940). Furthermore, the use of different adult chimpanzee brains

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from the literature alters the percentage of brain growth estimated to have occurred at birth, since chimpanzee adult brains can vary from 290 cc to 500 cc (Zuckerman, 1928). Finally, it is important to note that the very use of brain mass as a measure has been questioned by Tobias (1970), although many of his objections to brain-mass comparisons concern intraspecific, rather than interspecific, studies.

Recent studies on chimpanzee brain-growth trajectories (Vrba, 1998; Herndon et al., 1999; Rice, 2002; Leigh, 2004) did not use the two neonatal chimpanzees from Schultz (1940, 1941), but instead used neonatal brain mass data from Yerkes National Primate Research Center (NPRC). Only Herndon et al. (1999) reported individual data, which consisted of nine individuals who were under three weeks old and had an average brain mass of 142.4 g (range 82–172 g). Hublin and Coqueugniot (2006) suggested that the chimpanzee with an 82-g brain might be premature and calculated a prenatal brain growth of 39% for the remaining eight neonatal chimpanzees. They also used endocranial volumes of three other neonatal chimpanzees (between 0 and 19 days of age) to estimate the prenatal brain-growth percentage at 42% (Hublin and Coqueugniot, 2006). Using only the four individuals that were less than a week old from the Herndon et al. (1999) data set, Leigh (2006) calculated an average brain mass of 123.5 g (range 82–170 g) and a percentage of prenatal brain growth for chimpanzees of 32%.

We suggest that the difference in estimates for the percentage of brain size achieved at birth in the chimpanzee can be attributed to the scarcity of reliable data on the size of the neonatal brain at birth in the genus *Pan*. Here, a larger sample size of 17 neonatal brain masses of *Pan troglodytes* from the Yerkes NPRC are reported. Using resampling statistics, we calculate the percentage of brain growth achieved at birth in chimpanzees and compare this to human brain growth in utero. The advantage of using resampling techniques to generate this percentage is to produce distributions, mean values, and ranges for a measure that has previously only been reported as an average and has been plagued by small sample sizes. In addition, we use these values to estimate the size of the neonatal brain in *Homo erectus*.

Materials

Brain and body masses of 17 newborn chimpanzees (*Pan troglodytes*) were generously provided by the Yerkes NPRC and added to data on seven neonatal chimpanzees previously reported by Herndon et al. (1999) (Table 1). All of the animals were reported to be full term. Seven were stillborn, nine died the day they were born, and eight died within two weeks of their birth.

Herndon et al. (1999) excluded any stillborn chimpanzee or any neonate that did not reach 1 day old from their analysis, wary that stillborn infants may have suffered from an illness or trauma that could have impacted the mass of the newborn brain. However, data provided to us by Yerkes NPRC on three other anthropoid species, *Macaca nemestrina*, *Cercocebus atys*, and *Saimiri sciureus*, suggest that stillborn infants do not have brains that are any larger or smaller than the brains of

Table 1
Neonatal brain and body masses for 24 chimpanzees (*Pan troglodytes*)

Sex	Neonatal brain mass (g)	Neonatal body mass (g)	Age at death
Female	157.23	1710	Stillbirth
Female	169.00	1870	Stillbirth
Female	146.64	1270	Stillbirth
Female	148.04	1240	Stillbirth
Female	150.58	1670	Newborn
Female	165.43	1500	Newborn
Female	151.15	1790	Newborn
Female	129.34	900	Newborn
Female	129.19	1450	Newborn[+]
Female	169.79	1820	2 days*
Female	109	1400	~4 days*
Female	133	900	~4 days*
Female	172	1500	~11 days*
Male	205.34	2380	Stillbirth[#]
Male	147.60	1520	Stillbirth
Male	180.85	1520	Stillbirth
Male	145.55	1350	Newborn[+]
Male	148.70	1385	Newborn
Male	169.64	1770	Newborn
Male	160.28	1980	Newborn
Male	144.00	1360	3 days
Male	82	700	~4 days*[#]
Male	136	1300	~11 days*
Male	156	1400	~11 days*

* Previously reported by Herndon et al. (1999).
[+] Twins.
[#] Individuals not used in the analysis due to extremely large or small birth masses.

nonstillborns (Table 2). There is a difference ($t = 1.96$, $p = 0.06$) in brain mass between the stillborn and nonstillborn chimpanzees listed in Table 1. However, this difference is driven by two male neonatal chimpanzees: a stillborn with a brain of 205.3 g and a body mass of 2380 g, and a live newborn with a brain of 82 g and a body mass of 700 g. These two individuals, one an unusually small neonate, the other an unusually large neonate, have neonatal body masses almost three standard deviations away from the mean body mass for the remaining 22 infant chimpanzees used in this study. For this reason, we feel it is reasonable to exclude these individuals from our analysis. When they are excluded, stillborn chimpanzees no longer have significantly larger brains at birth than nonstillborns.

The newborn chimpanzees were sexed at birth (13 females and 9 males). The sample of adult brain masses consists of 71 chimpanzees that were at least seven years old and of known sex that died at the Yerkes NPRC. Data from 42 individuals were reported by Herndon et al. (1999) and the other 29 brain and body masses were provided to us directly from Yerkes NPRC. Using adult and neonatal data sets from the same facility reduces the error that extrinsic factors, such as sample, nutrition, and measurement differences (Tobias, 1970; Peters et al., 1998), may impose on brain-mass data. The procedure for extracting and weighing the brain after birth is detailed in Herndon et al. (1999). Endocranial volumes (EV) from adult chimpanzees (Zuckerman, 1928) were used to assess the congruence between EV and brain mass.

Table 2
Difference in brain mass between stillborn and nonstillborn primates

Species	Stillborn		Nonstillborn		P-value[+]
	n	Brain mass (g)	n	Brain mass (g)	
Macaca nemestrina	29	64.0 ± 8.9	64	60.9 ± 8.6	0.11
Cercocebus atys	13	52.8 ± 15.4	28	59.6 ± 8.4	0.07
Saimiri sciureus	9	16.0 ± 1.8	15	14.9 ± 2.2	0.21
Pan troglodytes	7	165.0 ± 21.9	17	144.2 ± 23.4	0.06
*Pan troglodytes**	6	158.2 ± 6.0	16	148.1 ± 16.0	0.22

* With two male outliers removed from the analysis (a stillborn with a brain of 205.3 g and a body mass of 2380 g, and a live newborn with a brain of 82 g and a body mass of 700 g).

[+] P-value based on a Student's *t*-test.

Individual human neonatal and adult brain masses were taken from Bischoff (1880) and Marchand (1902) and were compared to averaged data sets from the literature (Thurnam, 1866; Ellis, 1920; Feer, 1922; Craig, 1929; Blackfan, 1933; Coppoletta and Wolbach, 1933; Schultz, 1941; Blinkov and Glezer, 1968; Dekaban and Sadowsky, 1978; Holloway, 1980; Ho et al., 1980, 1981; Jit, 1988; Sahni et al., 1998). These papers were used because they reported both neonatal and adult brain masses, avoiding the possible error introduced by differences in brain extraction or measurement techniques. Cranial capacities for 38 adult *Homo erectus* specimens were obtained from Lee and Wolpoff (2003) and Wolpoff (pers. comm.).

Methods

Because of the limited number of neonatal chimpanzee brain masses reported, we employed a resampling technique to estimate the percentage of brain mass achieved by birth in chimpanzees. This allowed us to use cross-sectional data to estimate a longitudinal relationship. We assumed that any of the nine male neonatal brain sizes could develop into any of the 34 male adult brains, and that any of the 13 female neonatal brains could develop into any of the 37 female adult brain sizes. A single neonatal brain mass of known sex was chosen at random and divided by a randomly selected adult brain mass of the same sex to calculate a possible percentage of brain at birth for chimpanzees. This was repeated until all of the possible male combinations (306) and all of the possible female combinations (481) had been calculated.

This exact permutation resampling procedure was repeated using Zuckerman's (1928) wild-shot adult cranial capacity data from chimpanzees. These data were multiplied by the specific gravity of brain tissue, 1.036 (Blinkov and Glezer, 1968), to convert the endocranial volumes into brain masses.

Random resampling was performed on the human data from Bischoff (1880) and Marchand (1902) to generate a distribution of values for the percentage of brain growth that occurs in utero in humans. A single human neonatal brain mass of known sex was chosen at random and divided by a randomly selected adult brain mass of the same sex to calculate a possible percentage of brain growth at birth for humans. This procedure was repeated 10,000 times. The mean and standard deviation of this distribution were then compared to the average percentage of brain size achieved at birth, as reported in the literature (Table 3).

Resampling statistics were also used to estimate the neonatal brain mass in *Homo erectus*. Adult cranial capacities for *H. erectus* were converted to brain masses as described above for the chimpanzee cranial capacities (multiplied by 1.036). In order to estimate the size of the *H. erectus* brain at birth, we multiplied the adult *H. erectus* brain mass by the percentage of brain growth achieved at birth, first using a chimpanzee model and then a modern human model. A model of *H. erectus* neonatal brain mass based on chimpanzee brain-growth patterns was constructed by randomly sampling a chimpanzee percentage of brain growth in utero and multiplying it by a randomly selected *H. erectus* adult brain mass. This procedure was repeated 50,000 times. A human model was obtained by repeating this protocol using human proportions of brain growth in utero.

Results

Chimpanzees are born with an average brain mass of 150.9 ± 17.0 g, which grows to an average of 381.7 ± 37.2 g by adulthood (Table 4). Using these averages, chimpanzees achieve 39.5% of their brain growth by birth. Using resampling statistics, chimpanzees experience 40.1% (S.D. = 5.7%) of their brain growth in utero. The mean difference

Table 3
Percentage of brain size achieved at birth in human studies

Author	Neonate n	Adult n*	Male %	Female %	Total %
Thurnam (1866)	155	1424	27.2	26.0	26.9
Bischoff (1880)[+]	41	902	27.7	31.7	29.2
Marchand (1902)[++]	24	781	26.7	28.7	27.4
Ellis (1920)	Not given	1367	28.8	29.1	29.0
Blackfan (1933)	293	3579	26.0	28.4	26.8
Schultz (1941)	2	20	—	—	25.9
Dekaban and Sadowsky (1978)[+++]	404	3447	27.3	28.7	27.9
Ho et al. (1980, 1981)	252	1261	28.3	30.9	29.5
Jit (1988); Sahni et al. (1998)	73	388	28.7	28.7	28.4

* Individuals at least 16 years old.

[+] Neonates ranged from newborn to up to 10 days old.

[++] Neonates ranged from newborn to up to 7 days old.

[+++] Neonates ranged from newborn to up to 12 days old.

Table 4
Descriptive statistics for brain size at birth and as adult in chimpanzees (*Pan troglodytes*) from the Yerkes National Primate Research Center

	Male		Female		All	
	n	Brain mass (g)	n	Brain mass (g)	n	Brain mass (g)
Adult[+]	34	395.2 ± 37.5	37	369.4 ± 32.8	71	381.7 ± 37.2
Neonate	9	154.3 ± 14.0	13	148.5 ± 19.0	22	150.9 ± 17.0
% brain growth by birth		39.0%		40.2%		39.5%
% brain growth by birth using resampling	306*	39.4%	481*	40.5%	787*	40.1%

* Number of permutations.
[+] Adult defined as greater than seven years of age following Herndon et al. (1999).

between male chimpanzees (39.4% ± 4.9%) and female chimpanzees (40.5% ± 6.1%) was statistically significant using a permutation test on the resampled data.

There was a statistically significant difference between the adult brain mass from Yerkes NPRC and Zuckerman's data (1928) on endocranial volume ($t = 2.20$, $p = 0.03$), and a permutation test indicated that the difference between the percentage of chimpanzee brain growth in utero calculated from the Yerkes data and the Zuckerman endocranial volume data was significant ($p = 0.004$).

Resampling from the Bischoff (1880) data set found that humans experience 29.9% (S.D. = 4.7%) of their brain growth in utero. The Marchand (1902) data set resulted in a slightly lower range of brain size achieved at birth in humans (28.0% ± 5.0%). These results can be seen in Figure 1. These values are similar to the average brain size at birth achieved in humans, as calculated using mean values (Table 3). Using permutation tests, human values are statistically distinct from chimpanzee values with strong significance. After 1000 permutation trials, not a single mean difference between randomly generated distributions exceeded the mean difference between humans and chimpanzees (11.2%).

We applied these results to 38 adult *Homo erectus* crania with a mean brain mass of 986.6 g ± 169.4 g and a range of 621 g to 1275 g. A chimpanzee model of brain growth predicts a *H. erectus* neonate with a brain mass of 394.5 ± 87.8 g. Using a human model of brain growth predicts a *H. erectus* neonate with a brain mass of 295.8 ± 68.4 g.

Discussion

This study used only two data points (neonatal and adult brain sizes) to compare chimpanzee and human brain-growth strategies. However, postnatal brain growth is not linear (Vrba, 1998; Rice, 2002; Leigh, 2004), and information about the size of the brain throughout postnatal development is necessary to fully characterize the trajectory of brain growth in humans and chimpanzees. For instance, Leigh (2004) plotted the size of the brain throughout postnatal development in humans and chimpanzees and found that, although the two species had postnatal brain growth for a similar length of time (5–6 years), they grew at significantly different rates. Nevertheless, using only the size of the brain at birth and the size of the adult brain, it is clear that human infants experience both proportionately and absolutely more of their brain growth postnatally compared to chimpanzees. Recent suggestions that humans and chimpanzees achieve roughly the same proportion of brain growth in utero (Fragaszy and Bard, 1997; Kennedy, 2005; Vinicius, 2005) are not supported when a larger data set is used (Fig. 1). Any interpretations that have assumed this equal pattern of brain growth between humans and chimpanzees should be reassessed in light of these results.

Although chimpanzees do not achieve half of their brain size at birth as some have suggested (Dienske, 1986; Smith and Tompkins, 1995), they experience more than a third of their brain growth in utero, contrary to the findings of some other authors (Fragaszy and Bard, 1997; Kennedy, 2005; Leigh, 2006). The average chimpanzee brain growth calculated here (40.1%) is also greater than the 30–36.5% range suggested by Vinicius (2005).

The proportion of the human brain achieved at birth is remarkably consistent considering that these studies employed different techniques across three continents and three centuries. The lowest percentage of adult brain size at birth calculated for a sufficiently large sample size is 26.8%, while the largest reported is 29.5% (Table 3). This consistency suggests to us that when the sample size is large enough, the percentage of brain growth achieved at birth is an informative index, especially when addressing interspecific questions.
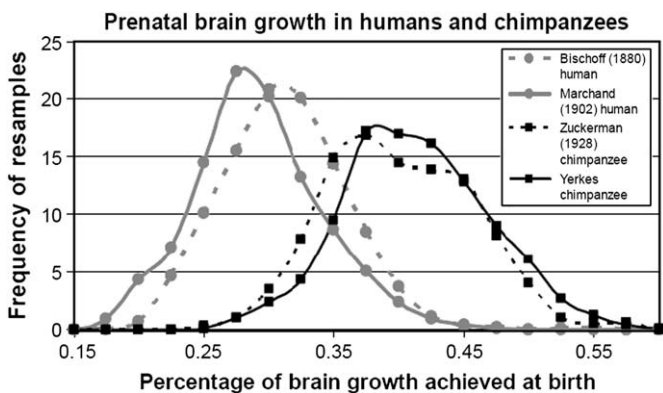

Fig. 1. Resampling results for percentage of brain growth in utero in humans and chimpanzees. Humans and chimpanzees show different distributions for the percentage of brain growth achieved by birth using resampling statistics. The results remain generally consistent through the use of different data sources (for humans: Marchand, 1902; Bischoff, 1880; for chimpanzees: Yerkes NPRC and Zuckerman, 1928). The use of cross-sectional data may overestimate the range of variation shown in these graphs.

Hublin and Coqueugniot (2006) raised some concern over the use of the Marchand (1902) data set and the use of brain masses instead of endocranial volumes in calculating the percentage of brain growth by birth. However, we have found that the Marchand (1902) data set used by Leigh (2006) produces results that are consistent with all of the human brain studies in which both neonates and adults are reported (Table 3). The difference between the Yerkes brain-mass data and Zuckerman's (1928) cranial-capacity data in chimpanzees, however, suggests that the concern regarding the conversion of endocranial volumes to brain masses may have some merit. These results suggest to us that the measure of proportional brain size at birth should ideally be calculated on brain data that is collected in a consistent manner, preferably by the same researchers at the same facility using consistent methods.

Although the tails of the distributions of brain growth in utero of humans and chimpanzees cross (Fig. 1), humans experience more of their brain growth postnatally when compared to chimpanzees. By using resampling methods, we produced the maximum range of values for the percentage of brain growth in utero in humans and chimpanzees. However, it is known that measured brain mass can be influenced by a great many factors (Tobias, 1970), and imposing restrictions on the resampling procedure so that certain resampled pairs are excluded would reduce the variation of values generated by our methods. For instance, Hublin and Coqueugniot (2006) reported a relationship between the head circumference at one month of age and the head circumference at 15 years of age in a longitudinal study of 137 individuals ($r = 0.57$). If brain size at birth is correlated with brain size as an adult, such that any neonate brain mass may not necessarily develop into any adult brain mass, as we had assumed during the resampling procedure, then the standard deviations of brain growth in utero presented here would be overestimates. This would further reduce the amount of overlap in the distributions of percentage of brain growth achieved by birth in humans and chimpanzees.

Finally, these data are relevant to understanding the evolution of the life history of humans. Application of a chimpanzee brain-growth pattern results in a *Homo erectus* newborn with a brain of 394.5 ± 87.8 g, within the range of a modern human neonate. Marchand (1902) reported human neonatal brains ranging from 255 g to 540 g, while Bischoff (1880) measured human neonatal brains from 295 g to 443 g. The Mojokerto specimen has recently been used to approximate the pattern of brain growth in *H. erectus* (Coqueugniot et al., 2004; Leigh, 2006; Hublin and Coqueugniot, 2006). However, estimates of the age of the Mojokerto individual range from 0.5–1.5 years old (Coqueugniot et al., 2004) to 4–6 years old (Antón, 1997). Because the Mojokerto specimen best fits a chimpanzee model of brain growth if it is one year old, but a human model of growth if it is older (Balzeau et al., 2005), it is currently unclear how this specimen can inform the discussion of brain growth in *H. erectus* without a better understanding of its age at death.

Therefore, the most applicable fossil for assessing brain development and life history in *H. erectus* is currently the Nariokotome skeleton. After correcting for age and sex, Walker and Ruff (1993) estimated from the morphology of the Nariokotome
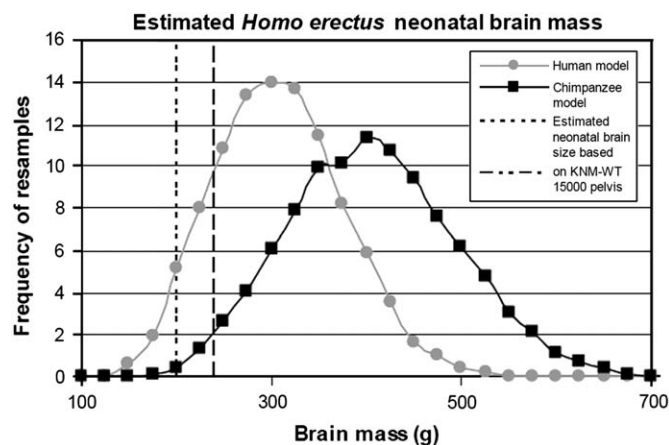

Fig. 2. Resampling results estimating the neonatal brain mass in *Homo erectus*. A chimpanzee model of brain growth produces a distribution of potential *Homo erectus* neonatal brain masses with an average of 394.5 ± 87.8 g, whereas a human model of brain growth produces a distribution with a mean neonatal brain mass of 295.8 ± 68.4 g. Using the size of the pelvic inlet and adjusting for age and sex, Walker and Ruff (1993) estimated that the neonatal brain mass in *H. erectus* is between 200 and 240 g, as demarcated by vertical lines in the graph. The human model for neonatal brain growth appears to be a better fit for this range. In order to support the chimpanzee model, the *H. erectus* neonate would require a brain exceeding 330 g. This value would imply that even after adjusting for the age and sex of the KNM-WT 15000 pelvis, Walker and Ruff (1993) underestimated the size of a neonatal *H. erectus* brain by 30–40%.

pelvis that a newborn *H. erectus* would have a brain that is, at most, approximately 200–240 g, significantly smaller than the 394.5 ± 87.8 g estimated from a chimpanzee model of brain development (Fig. 2). Walker and Ruff's (1993) calculation is instead more consistent with the estimate of the size of the *H. erectus* brain at birth calculated using a human model (295 ± 68.4 g). Despite the potential sources of error in estimating neonatal brain size in *H. erectus* from the Nariokotome pelvis (e.g., from estimating sex, age, and pelvic volume), our findings support the conclusions of Walker and Ruff (1993) and Leigh (2006) that *Homo erectus* may not have been characterized by a chimpanzee-like prenatal brain-growth pattern.

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