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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 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 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.