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The Evolution of Brain Size and Intelligence

J. Philippe Rushton and C. Davison Ankney

6

In this chapter, we update our earlier reviews of the literature (Rushton & Ankney, 1996, 1997) on the relation between whole brain size and general intelligence (IQ). In 55 samples in which IQ scores (or their proxy) were correlated with external head size measures, the mean r was 0.20 (N = 62,602; $P < 10^{-10}$); in 27 samples using brain imaging techniques the mean was 0.40 (N = 1,341; $P < 10^{-10}$); and in 5 samples using the method of correlated vectors to extract g, the general factor of mental ability from test scores, the mean was 0.57. Further, we update our review of brain size/cognitive ability correlations with age, sex, social class, and race, which provide further information about the brain-behavior relationship. Finally, we examine the evolution of brain size from a behavior genetic and life history perspective.

Throughout the nineteenth and early twentieth centuries, the relation between brain size and intelligence was almost universally accepted (Broca, 1861; Darwin, 1871; Morton, 1849; Topinard, 1878). The renowned French neurologist Paul Broca (1824–1880), for example, made major contributions to refining early techniques for estimating brain size by measuring external and internal skull dimensions and weighing wet brains at autopsy. He concluded that variation in whole brain size was related to intellectual achievement, observing that mature adults had larger brains than either children or the very elderly, skilled workers had larger brains than unskilled workers, and eminent individuals had larger brains than those less eminent.

Broca's studies were cited by Charles Darwin (1871) in support of the theory of evolution in *The Descent of Man*, where he wrote:

No one, I presume, doubts that the large size of the brain in man, relatively to his body, in comparison with that of the gorilla or orang, is closely connected with his higher mental powers. We meet the closely analogous facts with insects, in which the cerebral ganglia are of extraordinary dimensions in ants; these ganglia in all the Hymenoptera being many times larger than in the less intelligent orders, such as beetles....

The belief that there exists in man some close relation between the size of the brain and the development of the intellectual faculties is supported by the comparison of the skulls of savage and civilized races, of ancient and modern people, and by analogy of the whole vertebrate series.

Darwin's cousin, Sir Francis Galton (1888), was the first to guantify the relation between human brain size and mental ability in living subjects. He multiplied head length by breadth by height and plotted the results against age (19-25 years) and class of degree (A, B, C) in more than 1,000 male undergraduates at Cambridge University. He reported that (1) cranial capacity continued to grow after age 19, and (2) men who obtained high honors degrees had a brain size 2%-5% greater than those who did not. Years later, Karl Pearson (1906) reanalyzed Galton's data and found a correlation of 0.11 using the Pearson coefficient he had invented for this type of analysis. Pearson (1924, p. 94), who was also Galton's disciple and biographer, reported Galton's response: "He was very unhappy about the low correlations I found between intelligence and head size, and would cite against me those 'front benches' [the people on the front benches at Royal Society meetings whom Galton perceived as having large heads]; it was one of the few instances I noticed when impressions seemed to have more weight with him than measurements."

Following World War II (1939–1945) and the revulsion evoked by Hitler's racial policies, however, craniometry became associated with extreme forms of racial prejudice. After the U.S. civil rights movement became prominent in the 1950s, along with the cold war struggle for the hearts and minds of the Third World, research on brain size and intelligence virtually ceased, and the literature underwent vigorous critiques, notably from Philip V. Tobias (1970), Leon Kamin (1974), and Stephen Jay Gould (1978, 1981). As we shall show, however, modern studies confirm many of the nineteenth-century observations.

Tables 6.1 and 6.2 update and extend several recent reviews of the brain size/IQ literature (Gignac, Vernon, & Wickett, 2003; Gray & Thompson, 2004; Jensen & Sinha, 1993; McDaniel, in press; Rushton & Ankney, 1996, 1997; Vernon, Wickett, Bazana, & Stelmack, 2000). All samples were nonclinical. To be included, the published reference had to report an actual correlation; personal communications, unpublished papers, and works merely cited were excluded. The average or most

Study	Sample	Head Size Measure	IQ Measure	Correlation
Pearl (1906)	935 German male soldiers	Perimeter	Officers' rating	0.14
Pearson (1906)	2,398 British boys aged 3–20 years, standardized to age 12	Length	Teachers' estimate	0.14
Pearson (1906)	2,188 British girls aged 3–20 years, standardized to age 12	Length	Teachers' estimate	0.08
Pearson (1906)	1,011 British male university students	Length	Grades	0.11
Murdock & Sullivan (1923)	291 American boys aged 6–17 years, standardized by age	Perimeter	Various IQ tests	0.20
Murdock & Sullivan (1923)	395 American girls aged 6–17 years, standardized by age	Perimeter	Various IQ tests	0.27
Reid & Mulligan (1923)	449 Scottish male medical students	Capacity	Grades	0.08
Sommerville (1924)	105 white male university students	Capacity	Thorndike	0.08
Estabrooks (1928)	172 white boys age 7	Capacity	Binet IQ test	0.23
Estabrooks (1928)	207 white girls age 7	Capacity	Binet IQ test	0.16
Porteus (1937)	200 white Australian children	Perimeter	Porteus Maze	0.20
Schreider (1968)	80 adult Otomi Amerindians from Mexico	Perimeter	Form board	0.39

 Table 6.1

 Head Size and IQ Relationships Determined in Neurologically Normal Subjects

	0 1	Head Size	IQ	C 1 ·
Study	Sample	Measure	Measure	Correlation
Schreider (1968)	158 French farmers of unreported sex	Perimeter	Raven's Matrices	0.23
Klein et al. (1972)	172 Guatemalan Amerindian boys aged 3–6 years	Perimeter	Knowledge tests, with age standardized	0.23
Klein et al. (1972)	170 Guatemalan Amerindian girls aged 3–6 years	Perimeter	Knowledge tests, with age standardized	0.29
Susanne & Sporcq (1973)	2,071 Belgian male conscripts	Perimeter	Raven's Matrices	0.19
Weinberg et al. (1974)	334 white boys aged 8–10 years	Perimeter	WISC	0.35
Passingham (1979)	415 English villagers (212 men, 203 women) aged 18–75 years	Capacity	WAIS	0.13
Susanne (1979)	2,071 Belgian male conscripts	Perimeter	Matrices	0.19
Pollitt et al. (1982)	91 boys and girls aged 3–6 years	Perimeter	Stanford- Binet	0.23
Majluf (1983)	120 boys and girls aged 8–20 months	Perimeter	Bayley Motor Development Test	0.35
Ounsted et al. (1984)	214 boys age 4	Perimeter	Language Test	0.06
Ounsted et al. (1984)	167 girls age 4	Perimeter	Language Test	0.07
Henneberg et al. (1985)	151 Polish male medical students aged 18–30 years	Capacity	Baley's Polish language IQ test	0.09
Henneberg et al. (1985)	151 Polish female medical students aged 18–30 years	Capacity	Baley's Polish language IQ test	0.19

Table 6.1 (continued)

Study	Sample	Head Size Measure	IQ Measure	Correlation
Sen et al. (1986)	150 16- to 18- year-old males in India	Perimeter	Raven's Matrices	0.02
Sen et al. (1986)	150 16- to 18- year-old females in India	Perimeter	Raven's Matrices	0.54
Broman et al. (1987)	18,907 black boys and girls age 7 years	Perimeter	WISC	0.19
Broman et al. (1987)	17,241 white boys and girls age 7 years	Perimeter	WISC	0.24
Ernhart et al. (1987)	257 3-year-old boys and girls	Perimeter	Stanford- Binet	0.12
Bogaert & Rushton (1989)	216 white Canadian male and female university students, adjusted for sex	Perimeter	MAB	0.14
Lynn (1989)	161 Irish boys aged 9–10 years	Perimeter	PMAT	0.15
Lynn (1989)	149 Irish girls aged 9–10 years	Perimeter	PMAT	0.23
Lynn (1990)	205 Irish children aged 9 years	Perimeter	Raven's Matrices	0.26
Lynn (1990)	91 English children aged 9 years	Perimeter	Raven's Matrices	0.26
Osborne (1992)	106 European– American boys aged 13–17 years, controls for height and weight	Capacity	Basic	0.16
Osborne (1992)	84 African– American boys aged 13–17 years, controls for height and weight	Capacity	Basic	0.34

Table 6.1 (continued)

Study	Sample	Head Size Measure	IQ Measure	Correlation
Osborne (1992)	118 European– American girls aged 13–17 years, controls for height and weight	Capacity	Basic	0.23
Osborne (1992)	168 African– American girls aged 13–17 years, controls for height and weight	Capacity	Basic	0.13
Rushton (1992b)	73 Asian– Canadian male and female university students	Perimeter	MAB	0.14
Rushton (1992b)	211 white Canadian male and female university students	Perimeter	MAB	0.21
Lynn & Jindal (1993)	100 9-year-old boys from northern India	Perimeter	Matrices	0.14
Lynn & Jindal (1993)	100 9-year-old girls from northern India	Perimeter	Matrices	0.25
Reed & Jensen (1993)	211 European– American male college students	Capacity	Raven's Matrices	0.02
Wickett et al. (1994)	40 white Canadian female university students	Perimeter	MAB	0.11
Furlow et al. (1997)	128 undergraduates, 60% female	Perimeter	CFIT	0.19
Rushton (1997)	100 East Asian– American 7- year-olds, 54% female	Perimeter	WISC	0.21

Table 6.1 (continued)

Study	Sample	Head Size Measure	IQ Measure	Correlation
Tramo et al. (1998)	20 individuals (10 pairs of identical twins) aged 24–43 years	Perimeter	WAIS-R	0.14
Tan et al. (1999)	54 female university students in Turkey	Capacity	CFIT	0.55
Tan et al. (1999)	49 male university students in Turkey	Capacity	CFIT	0.29
Ivanovic et al. (1996)	4,124 school- children of both sexes aged 6–17 years, in Chile	Perimeter -for-age	School grades	0.24
Ivanovic et al. (2000)	4,509 5- to 22- year-old male and female students in Chile	Perimeter -for-age	Raven's Matrices	0.22
Wickett et al. (2000)	68 individuals (34 pairs of brothers) aged 20–35 years	Perimeter	g from MAB and other tests	0.19
Ivanovic et al. (2004)	47 male 18- year-old high school students in Chile selected from the richest and poorest counties	Perimeter -for-age	WAIS-R	0.50
Ivanovic et al. (2004)	49 female 18- year-old high school students in Chile selected from the richest and poorest counties	Perimeter -for-age	WAIS-R	0.40

Table 6.1 (continued)

Table 6.1 (contin	able 6.1 (continued)
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Study	Sample	Head Size Measure	IQ Measure	Correlation
Number of s	*			
Total N: 62,6 Unweighted				
<i>n</i> -weighted n				

Abbreviations: CFIT, Culture-Free Intelligence Test; MAB, Multidimensional Aptitude Battery; NART, New Adult Reading Test; PMAT, Primary Mental Abilities Test; WAIS-R, Wechsler Adult Intelligence Scale–Revised; WISC, Wechsler Intelligence Scale for Children.

representative correlation has been reported from those studies providing multiple correlations. When possible, data were coded separately by sex. Corrections for body size typically were not included because many studies did not report this statistic, although age effects often were controlled for. Double entries were eliminated, particularly those emanating from the U.S. National Collaborative Perinatal Project (Broman, Nichols, Shaughnessy, & Kennedy, 1987). Also not included were typological studies showing that gifted people often have larger brains than average (Terman, 1926), whereas people with mental disabilities have smaller heads than average (Broman et al., 1987).

Table 6.1 shows the results of 55 studies that recorded external head measurements in a total of 62,602 children, adolescents, and adults. The correlations with cognitive ability measures ranged from 0.02 to 0.55, with an unweighted mean of 0.21 (when weighted by sample size, 0.20). Table 6.2 shows the results of 27 studies that used brain imaging techniques such as magnetic resonance imaging (MRI) and computed tomography (CT) in a total of 1,341 normal (nonclinical) subjects. The correlations range from 0.04 to 0.69, with an unweighted mean of 0.39 (when weighted by sample size, 0.37). We obtained the exact *P* values of all correlations in tables 6.1 and 6.2 using Fisher's (1970, pp. 99–101) method for combining independent probabilities, and calculated the overall *P* values, which are less than 10^{-10} in both cases.

Five studies that used the method of correlated vectors to distill g, the general mental ability factor, from the subtests of an IQ test (Jensen, 1998) found that correlation with brain size is even higher (mean r = 0.57). This procedure consists of correlating the rank of a group of subtests' factor loadings on g with that same group of subtests' ranked

Table 6.2

Reported Correlation Between Brain Volume and IQ in Neurologically Normal Subjects, Determined Using Established Psychometric Tests

Source	Sample	IQ Measure	Correlation
Willerman et al. (1991)	20 European-American male university students with mean age = 18 years	WAIS-R	0.51
Willerman et al. (1991)	20 European–American female university students with mean age = 18 years	WAIS-R	0.33
Andreasen et al. (1993)	37 European–American males aged 18–75 years	WAIS-R	0.40
Andreasen et al. (1993)	30 European-American females aged 18-75 years	WAIS-R	0.44
Raz et al. (1993)	29 European-American adults (17 men, 12 women) with mean age = 43.8 (SD = 21.5)	CFIT	0.43
Egan et al. (1994; corrected by Egan et al., 1995)	40 British military personnel (unreported sex and race backdown) with mean age = 23 (SD = 5), corrected for height, weight, and restricted range	WAIS-R	0.48
Castellanos et al. (1994)	46 children aged 5–19 years of unknown background	WISC-R subscales	0.33
Harvey et al. (1994)	34 healthy male and female British hospital staff and locals (62% Caucasian; 38% Afro- Caribbean) used as control group	NART	0.69
Jones et al. (1994) Wickett et al.	67 healthy male and female British, aged 16–60, some Afro-Caribbean used as community control group 40 white Canadian women	NAT or verbal subset of the WAIS	0.30
(1994)	aged 20–30 years; height and weight partialed out and corrected for restriction of range	MAB	0.40
Kareken et al. (1995)	68 Caucasian and non- Caucasian adults of both sexes aged 18–45	Average of various subtest	0.25
Reiss et al. (1996)	12 boys, mainly white, aged 5–17 years	WISC-R	0.52
Reiss et al. (1996)	57 girls, mainly white, aged 5–17 years	WISC-R	0.37

Table 6.2	2 (continued)
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Source	Sample	IQ Measure	Correlation
Flashman et al. (1998)	90 healthy normal volunteer controls (47% female) with mean age = 27 (SD = 10)	WAIS-R	0.25
Tramo et al. (1998)	20 individuals (10 pairs of identical twins) aged 24–43 years; we use their total cortical surface area as the estimate of brain size	WAIS-R	0.20
Gur et al. (1999)	40 men with mean age = 26 years (SD = 5.5)	various	0.40
Gur et al. (1999)	40 women with mean age = 26 years (SD = 5.5)	various	0.39
Tan et al. (1999)	54 female university students in Turkey, aged 18–26 years	CFIT	0.62
Tan et al. (1999)	49 male university students in Turkey, aged 18–26 years	CFIT	0.28
Wickett et al. (2000)	68 individuals (34 pairs of brothers) aged 20–35 years	g from MAB and other tests	0.38
Pennington et al. (2000)	96 individuals (48 pairs of MZ and DZ twins), mean age = 17 (SD = 4.1)	WISC-R and WAIS-R	0.42
Pennington et al. (2000)	36 individuals (18 pairs of MZ and DZ twins), mean age = 19 (SD = 3.7)	WISC-R and WAIS-R	0.31
Schoenemann et al. (2000)	72 individuals (36 pairs of sisters) aged 18–43 years	g, from 11 diverse cognitive tasks, including Raven's Matrices, with corrections for age	0.45
Aylward et al. (2002)	83 white men and women aged 8-46 years used as healthy controls	Unspecified IQ test	0.04
MacLullich et al. (2002)	97 healthy men aged 68 years (SD = 1.3)	g, from various tests, including NART and Raven's Matrices	0.42

Source	Sample	IQ Measure	Correlation
Ivanovic et al. (2004)	47 male 18-year-old high school students in Chile selected from the richest and poorest counties	WAIS-R	0.55
Ivanovic et al. (2004)	49 female 18-year-old high school students in Chile selected from the richest and poorest counties	WAIS-R	0.37
Number of samp	oles: 27		
Total N: 1,341			
Unweighted mea	n r = 0.39		
<i>n</i> -weighted mear	r = 0.37		

Table 6.2 (continued)

Abbreviations: CFIT, Culture-Free Intelligence Test; MAB, Multidimensional Aptitude Battery; MRI, Magnetic Resonance Imaging; NART, New Adult Reading Test; PMAT, Primary Mental Abilities Test; WAIS-R, Wechsler Adult Intelligence Scale-Revised; WISC, Wechsler Intelligence Scale for Children.

correlations with any other variable, a procedure known as a Jensen effect (Rushton, 1998). Jensen (1994) found a simple correlation of 0.19 between head circumference and g on 17 cognitive tests among 286 adolescents, but when he used the method of correlated vectors he obtained a correlation of 0.64. When Wickett, Vernon, and Lee (2000) correlated brain volume by means of MRI in 68 adult subjects, they found r = 0.38, with g extracted from an extensive cognitive ability battery that also included mean and standard deviation (SD) reaction time measures, but when they used the method of correlated vectors, they found the correlation rose to 0.59. Similarly, the head perimeter measure went from 0.19 to 0.34. Schoenemann, Budinger, Sarich, and Wang (2000) obtained a simple correlation of 0.45 between brain volume and g, which Jensen (1998, p. 147) found to be 0.51 using the method of correlated vectors. Finally, Jensen (personal communication, August 8, 2002) carried out a vector analysis of the MRI study of MacLullich et al. (2002) in older persons and raised the correlation between g and cognitive ability from 0.42 to 0.78.

The evidence shows that external head size is a good proxy for brain volume. Head perimeter correlates with brain mass at autopsy from birth through childhood at correlation values of 0.80 to 0.98 (Brandt, 1978; Bray, Shields, Wolcott, & Madsen, 1969; Cooke, Lucas, Yudkin, & Pryse-Davies, 1977). It correlates with MRI brain volume at an average value of 0.66, based on five studies (0.55 in 10 pairs of identical twins aged 24–43 years, Tramo et al., 1998; 0.66 in 34 pairs of brothers aged 20–35 years, Wickett et al., 2000; 0.74 in 103 university students of both sexes in Turkey, Tan et al., 1999; 0.56 in 83 normal controls aged 8–46 years in the United States, Aylward, Minshew, Field, Sparks, & Singh, 2002; and 0.79 in 96 high school graduates of both sexes in Chile, Ivanovic et al., 2004).

Additional findings shown in table 6.2 are of interest. For example, the brain volume–IQ correlation is equally strong in males and females (e.g., Andreasen et al., 1993; Wickett, Vernon, & Lee, 1994, 2000). It is also found for people of East Asian, East Indian, European, Turkish, African, South American, and Amerindian descent. Age, although it plays a role in brain size and intelligence, does not confound the results. Studies using a narrow age range or younger or older samples show the same magnitude of correlations (e.g., Egan et al., 1994; MacLullich et al., 2002; Reiss et al., 1996). Several studies have examined whether different regions of the brain would show differential correlations with IQ; these studies appear to show that the size effects are manifest throughout the brain and are not specific to any particular region (Andreasen et al., 1993; Egan et al., 1994; Haier, Jung, Yeo, Head, & Alkire, 2004; Reiss et al., 1996), notwithstanding a study by Duncan et al. (2000) showing it centered in the lateral frontal cortex.

A functional relation between brain size and cognitive ability has been implied in three studies showing that the correlation between brain size and IQ holds true within families as well as between families (Gignac et al., 2003; Jensen, 1994; Jensen & Johnson, 1994) (although one study that examined only sisters failed to find the within-family relation: Schoenemann et al., 2000). The within-family finding is of special interest because it controls for most of the sources of variance that distinguish families, such as social class, styles of childrearing, and general nutrition.

The number of neurons available to process information may mediate the correlation between brain size and cognitive ability. Haug (1987, p. 135) showed a correlation of r = 0.479 (N = 81, p < 0.001) between number of cortical neurons (based on a partial count of representative areas of the brain) and brain size, including both men and women in the sample. The regression equating the two was given as: number of cortical neurons (in billions) = 5.583 + 0.006 (cm³ brain volume). This means that a person with a brain size of $1,400 \text{ cm}^3$ has, on average, 600 million fewer cortical neurons than an individual with a brain size of $1,500 \text{ cm}^3$. The difference between the low end of normal $(1,000 \text{ cm}^3)$ and the high end $(1,700 \text{ cm}^3)$ works out to be 4.283 billion neurons (a difference of 27% more neurons from a 41% increase in brain size). Subsequently, Pakkenberg and Gundersen (1997) found a correlation of r = 0.56 between brain size and number of neurons (0.56). The human brain may contain up to 100 billion (10^{11}) nerve cells classifiable into 10,000 types, resulting in 100,000 billion synapses (Kandel, 1991). Even storing information at the low average rate of one bit per synapse, which would require two levels of synaptic activity (high and low), the structure as a whole would generate 10^{14} bits. Contemporary supercomputers, by comparison, command a memory of about 10^9 bits of information.

It is also predictable, however, that correlations between IQ and overall brain size will be modest. First, much of the brain is not involved in producing what we call intelligence; thus, variation in the size or mass of that tissue will lower the magnitude of the correlation. Second, IQ, of course, is not a perfect measure of intelligence, and thus variation in IQ scores is an imperfect measure of variation in intelligence.

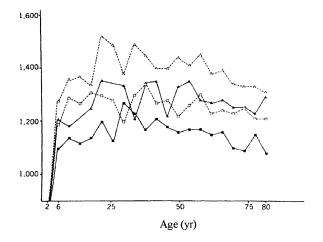
Brain size and IQ are also correlated with body size. Results from autopsy studies such as the one by Dekaban and Sadowsky (1978) of 2,773 men and 1,963 women, as well as the one by Ho, Roessmann, Straumfjord, and Monroe (1980) of 644 men and 617 women, suggest a correlation of about 0.20 between brain mass (grams) and stature and body mass. Similarly, MRI studies find an average correlation of about 0.20 (Pearlson et al., 1989; Wickett et al., 1994). The relationship is higher (0.30-0.40) with measures of the skull (cm³), estimated either from endocranial volume or from external head measures. In a stratified random sample of 6,325 U.S. servicemen, cranial capacity correlated, on average, 0.38 with height and 0.41 with mass in 2,803 women and 3,522 men (Rushton, 1992a). There is also a correlation of about 0.25 between IQ and height. However, this correlation may involve no causal or intrinsic functional relation but may occur instead as a result of the common assortment of the genetic factors for both height and intelligence, which in North American society are desirable characteristics, so that there is a fairly high degree of positive assortative mating for both. The result is a between-families genetic correlation between height and IQ, while the best evidence is that there is no *within-family* correlation between the traits (Jensen & Sinha, 1993).

There is, however, disagreement about whether or not brain size should be corrected for body size before examining brain size/IQ correlations. As noted by Rushton and Ankney (1996), controlling for body size obviously changes the question from "Is IQ correlated with absolute brain size?" to "Is IQ correlated with relative brain size?" Although these are quite different questions, evidence shows that the answer to both is yes. Controlling for body size can be regarded to some degree as an overcorrection because head size itself is part of stature and body weight.

Group (age, sex, social class, and race) differences exist in average brain size and cognitive ability. Because group distributions overlap substantially on the variables in question, with average differences amounting to between 4% and 34%, it is impossible to generalize from group averages to individuals. Nonetheless, significant among-group variation in brain size and cognitive ability does exist, and therefore a review is required if a full understanding of the relation between brain size and IQ is to be achieved. We emphasize that enormous variability exists within each of the populations to be discussed. We also emphasize that the relationships reported are correlational.

Age Differences

Autopsy studies show that brain mass increases during childhood and adolescence and then, beginning as early as 20 years, slowly decreases through middle adulthood, and finally decreases more quickly in old age (Dekaban & Sadowsky, 1978; Ho et al., 1980; Pakkenberg & Voigt, 1964; Voigt & Pakkenberg, 1983). Broca first showed these relationships in the nineteenth century (see reanalysis by Schreider, 1966). The data of Ho et al. (1980), collated for 2,037 subjects from autopsy records, for various subgroups, 1,261 of them between the ages of 25 and 80, are shown in figure 6.1. All brains were weighed on the same balance at the Institute of Pathology at Case Western Reserve University after excluding those brains with lesions or other abnormalities. The average mass of the brain increases from 397g at birth to 1,180g at 6 years. Growth then slows, and brain mass peaks at about 1,450g before age 25 years. The mass declines slowly from age 26 to 80 at an average of 2g per year. The decrease after age 80 years is much steeper, the loss



Mean brain weight for four-year age periods in various subgroups. Brain weight is plotted at the midpoint of each age period (e.g., the point at age 6 years represents the average for subjects between 4 and 8 years) (white men, open triangles; black men, solid triangles; white women, open squares; black women, solid squares). Differences in brain weights among various groups become apparent at age 6 years. (From Ho et al., 1980, p. 636, Figure 2.)

being 5 g per year. As shown in figure 6.1, although the rate of decrease varies slightly, it is essentially similar for various subgroups.

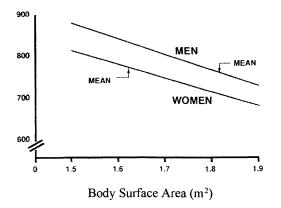
MRI investigations also show a curvilinear pattern of growth and change, with an overall decrease in brain volume following the late teens as gray matter is replaced with cerebrospinal fluid (CSF) (range of r values = -0.32 to -0.71; Gur et al., 1991; Jernigan et al., 1991). Pfefferbaum et al. (1994) demarcated cell growth, myelination, pruning, and atrophy. With a sample of 88 male and female subjects aged 3 months to 30 years, cortical gray matter volume (mainly cell bodies) peaked at around age 4 years and then declined steadily throughout the life span; cortical white matter volume (myelin sheath) increased steadily until about age 20 years and appeared stable thereafter; and the volume of cortical CSF remained stable from 3 months to 20 years. In a sample of 73 male subjects aged 21-71 years, CSF increased exponentially over the five decades of adulthood studied. Ventricular enlargement between ages 20 and 30 years suggested a possible marker for the onset of atrophy, whether it be due to cell loss or cell shrinkage. In the Baltimore Longitudinal Study of Ageing, participants aged 59-85 years showed significant annual increases of 1,526 mm³ in ventricular volume (Resnick et al., 2000). A Danish study by Garde et al. (2000) reported significant increases in white matter hyperintensities (WMHs) in a 30-year longitudinal study of 68 healthy 50- to 80-year-olds. These WMHs were significantly related to concomitant IQ declines.

General intelligence shows concomitant increases during childhood and adolescence and then (slow) decreases between ages 25 and 45, and (faster) decreases after age 45. It once was claimed that this age-related decline in IQ was spurious because early longitudinal studies contradicted findings from cross-sectional studies; thus, the cross-sectional observations were derogated as a generation or "cohort" effect, perhaps due to "more favorable" environments for younger cohorts. However, several subsequent longitudinal studies, reviewed by Brody (1992) and Deary (2000), have corroborated results from cross-sectional studies. Brody (1992, p. 238) concluded, "Declines in fluid ability over the life span up to age 80 might well average 2 standard deviations." The 68 healthy Danes in the study by Garde et al. (cited above) similarly showed a decrease in IQ by 14 points (1 SD) from age 50 to 80.

Sex Differences

An absolute difference in average brain size between men and women has not been disputed since at least the time of Broca (1861). It is often claimed, however, that this difference disappears when corrections are made for body size or age of people sampled (Gould, 1981, 1996). However, Ankney (1992) demonstrated that the sex difference in brain size remains after correction for body size in a sample of similarly aged men and women (following tentative results by Dekaban & Sadowsky, 1978; Gur et al., 1991; Hofman & Swaab, 1991; Holloway, 1980; Swaab & Hofman, 1984; Willerman, Schultz, Rutledge, & Bigler, 1991).

Ankney (1992) suggested that the large sex difference in brain size went unnoticed for so long because earlier studies used improper statistical techniques to correct for sex differences in body size and thus incorrectly made a large difference "disappear." The serious methodological error was the use of brain mass/body size ratios instead of analysis of covariance (see Packard & Boardman, 1988). Ankney (1992) illustrated why this is erroneous by showing that, in both men and women, the ratio of brain mass to body size declines as body size increases. Thus, as

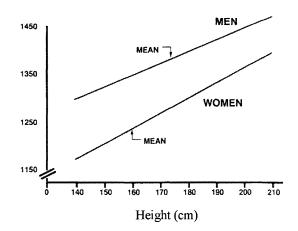


The relation between the ratio of brain mass/body surface area and body surface area in white men and women. Ankney (1992) calculated the ratios by estimating brain mass at a given body surface area using the equations in Ho et al. (1980, Table 3): men, brain mass = $1,077g (\pm 56) + 173 (\pm 31) \times body$ surface area (r = +0.27, P < 0.01); women, brain mass = 949g (±52) + 188 (±32) × body surface area (r = +0.24, P < 0.01). (From Ankney, 1992, p. 331, Figure 1. Copyright 1992 by Ablex Publishing Corp. Reprinted with permission.)

can be seen in figure 6.2, larger women have a lower ratio than smaller women, and the same holds for larger men compared with smaller men. Therefore, because the average-sized man is larger than the average-sized woman, their brain mass to body size ratios are similar. Consequently, the only meaningful comparison is that of brain mass to body size ratios of men and women of equal size. Such comparisons show that at any given size, the ratio of brain mass to body size is much higher in men than in women (figure 6.2).

Ankney reexamined autopsy data on 1,261 American adults (Ho et al., 1980) and found that at any given body surface area or height, brains of white men are heavier than those of white women, and brains of black men are heavier than those of black women. For example, among whites 168 cm (5'7") tall (the approximate overall mean height for men and women combined), the brain mass of men averages about 100g heavier than that of women (figure 6.3), whereas the average difference in brain mass, uncorrected for body size, is 140g. Thus, only about 30% of the sex difference in brain size is due to differences in body size.

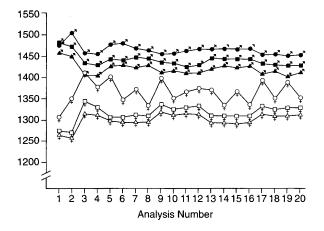
Ankney's results were confirmed in a study of cranial capacity in a stratified random sample of 6,325 U.S. Army personnel (Rushton,



The relation between brain mass and body height in white men and women. Lines are drawn from equations in Ho et al. (1980, Table 1): *men*, brain mass = 920g (\pm 113) + 2.70 (\pm 0.65) × body height (r = 0.20, P < 0.01); *women*, brain mass = 748g (\pm 104) + 3.10 (\pm 0.64) × body height (r = +0.24, P < 0.01). (From Ankney, 1992, p. 333, Figure 4. Copyright 1992 by Ablex Publishing Corp. Reprinted with permission.)

1992a). After adjusting, by means of analysis of covariance, for effects of age, stature, weight, military rank, and race, men averaged $1,442 \text{ cm}^3$ and women $1,332 \text{ cm}^3$. This difference was found in all of the 20 or more separate analyses (shown in figure 6.4) conducted to rule out any body size effect. Moreover, the difference was replicated across samples of East Asians, whites, and blacks, as well as across officers and enlisted personnel. Parenthetically, in the army data, East Asian women constituted the smallest sample (N = 132), and it is probable that this caused the "instability" in estimates of their cranial size when some corrections were made for body size (figure 6.4). The sex difference of 110 cm^3 found by Rushton, from analysis of external head measurements, is remarkably similar to that (100g) obtained by Ankney, from analysis of brain mass (1 cm³ = 1.036 g; Hofman, 1991).

Studies using MRI have also confirmed the sex difference in adult brain size (Gur et al., 1991; Harvey, Persaud, Ron, Baker, & Murray, 1994; Reiss et al., 1996; Willerman et al., 1991). Thus, Ivanovich et al. (2004) carried out a study that controlled for body size in 96 18-year-old male and female high school graduates in Chile and found that the males averaged $1,480 \text{ cm}^3$ (SD = 125) before body size adjustments and $1,470 \text{ cm}^3$ (SD = 40) after adjustments, while the females



Cranial capacity for a stratified random sample of 6,325 U.S. Army personnel. The data, grouped into six sex-by-race categories, are collapsed across military rank (East Asian men, closed circles; white men, closed squares; black men, closed triangles; East Asian women, open circles; white women, open squares; black women, open triangles). The data show that, across the 19 different analyses controlling for body size, men averaged larger cranial capacities than women, and East Asians averaged larger cranial capacities than whites or blacks. Analysis 1 presents the data unadjusted for body size and shows no difference between East Asian and European men. (Adapted from Rushton, 1992a, p. 408, Figure 1. Copyright 1992 by Ablex Publishing Corp. Reprinted with permission.)

averaged $1,394 \text{ cm}^3$ (SD = 89) before and $1,404 \text{ cm}^3$ (SD = 37) after adjustments.

A stereological investigation by Pakkenberg and Gundersen (1997) found that men had about 4 billion more cortical neurons than did women, and this was not accounted for by differences in height. The average number of neocortical neurons was 19 billion in female brains and 23 billion in male brains, a 16% difference. In their study, which covered the age range from 20 years to 90 years, approximately 10% of all neocortical neurons were lost over the life span in both sexes. Sex and age were the main determinants of the total number of neurons in the human cortex, whereas body size per se had no influence on neuron number.

From birth through the early months, Rushton and Ankney (1996) found the sex difference held across several autopsy studies when, following Ankney's (1992) procedure (see figure 6.3), brain masses of boys and girls were compared after matching them for stature (Dekaban

& Sadowsky, 1978; Pakkenberg & Voigt, 1964; Voigt & Pakkenberg, 1983). From 7 to 17 years, sex differences in cranial capacity are in the range of 60–100 cm³ (Lynn, 1993; Rushton & Osborne, 1995).

The sex differences in brain size present a paradox. Women have proportionately smaller average brains than do men but apparently have the same intelligence test scores. According to Kimura (1999), women excel in verbal ability, perceptual speed, and motor coordination within personal space, whereas men do better on various spatial tests and on tests of mathematical reasoning. A review by Voyer, Voyer, and Bryden (1995) showed that on the "purest" spatial measures, such as rotating an imaginary object or shooting at a moving rather than a stationary target, the sex difference approaches 1 SD. Ankney (1992, 1995) therefore hypothesized that the sex difference in brain size relates to those intellectual abilities at which men excel; that is, spatial and mathematical abilities require more "brain power." Analogously, whereas increasing word-processing power in a computer requires some extra capacity, increasing three-dimensional processing, as in graphics, requires a major increase in capacity.

Unfortunately for this hypothesis, what little information there is from the two MRI studies to date suggests that brain size is not significantly related to results on purely spatial tests (such as mental rotation) in either men or women (Wickett et al., 1994, 2000). Yet in the same studies, brain size did correlate significantly with IQ. However, one of these studies looked at only women and the other looked at only men. It would be more informative to know what happens in a *combined* sample of men and women, since the hypothesis that the extra brain size relates to men's better spatial scores would predict a correlation that should appear across sexes. So far, no comparison of brain size and spatial scores has been made in a mixed-sex group.

Baron-Cohen (2003) hypothesized that men on average tend to be systemizers (seeking to analyze, explore, and construct systems) while women tend to be empathizers (seeking to identify with another person's emotions and thoughts). Baron-Cohen speculates that having more brain cells allows storing of more information and greater attention to detail, which itself would lead to better systematizing.

The nineteenth-century proposition that men average slightly higher in general intelligence than women (e.g., Broca, 1861, p. 153) is not without contemporary exponents. Lynn's (1994, 1999) resolution of the brain size/sex difference paradox, which he dubbed "the AnkneyRushton anomaly" (1999, p. 1), was to produce evidence that contradicts the consensus view that there is no difference in general intelligence. He reviewed data from Britain, Greece, China, Israel, the Netherlands, Norway, Sweden, and Indonesia, as well as the United States, to show that men averaged about 4 IQ points higher than women on a number of published intelligence tests.

Subsequently, Lynn and Irwing (2004) carried out a meta-analysis of 57 studies of sex differences in general population samples on the Standard and Advanced Progressive Matrices. Results showed that while there is no difference among children aged 6-14 years, males do obtain higher means from the age of 15 through old age. Among adults, the male advantage is equivalent to 5 IQ points. These results disconfirm the frequent assertion that there is no average sex difference on the Progressive Matrices and support a developmental theory, namely, that a male advantage appears from the age of 15 years, around when brain size differences peak. Lynn and Irwing also carried out a meta-analysis of 15 studies of child samples on the Colored Progressive Matrices and found that among children aged 5-11 years old, boys had an advantage of 3 IQ points. They suggest that the Raven tests measure two cognitive skills, "visualization" and logical reasoning, that the Colored Matrices measure visualization even more than the Standard Matrices, and that it is this difference in what is tested that gives the younger boys their advantage over girls on this test.

Socioeconomic Differences

Nineteenth- and early twentieth-century data from Broca (1861) and others (Hooton, 1939; Sorokin, 1927; Topinard, 1878) suggested that people in higher-status occupations averaged a larger brain or head size than those in lower ones. For example, Galton collected head measurements and information on the educational and occupational background of thousands of individual visitors to the South Kensington Natural Science Museum in London. However, he had no statistical method for testing the significance of the differences in head size between various occupational or educational groups. Nearly a century later, Galton's data were analyzed by Johnson et al. (1985), who found that professional and semiprofessional groups averaged significantly larger head sizes (in both length and width) than unskilled occupational groups. Subsequently, Rushton and Ankney (1996) calculated cranial capacities from the summary by Johnson et al. (1985) of Galton's head size data and found that cranial capacity increased from unskilled to professional classes from 1,324 to 1,468 cm³ in men and from 1,256 to 1,264 cm³ in women. These figures are uncorrected for body size.

The relationship between head size and occupational status has also been found after correcting for body size. Jensen and Sinha (1993) reviewed much of the literature. They drew an important distinction between a person's socioeconomic status (SES) of origin (the SES attained by the person's parents) and the individual's attained SES (the SES attained by the person in adulthood). Correlations of IQ, head size, and other variables are always smaller when derived from the SES of origin than when derived from attained SES. Thus, Jensen and Sinha analyzed the head circumference data from the National Collaborative Perinatal Project (Broman, Nichols, & Kennedy, 1975) of approximately 10,000 white and 12,000 black 4-year-old children and found a small but significant correlation with social class of origin within both the white and black populations, after height was controlled for (r = 0.10). Jensen and Sinha also reanalyzed autopsy data reported by Passingham (1979) on 734 men and 305 women and found an overall correlation between brain mass and achieved occupational level of about 0.25, independent of body size.

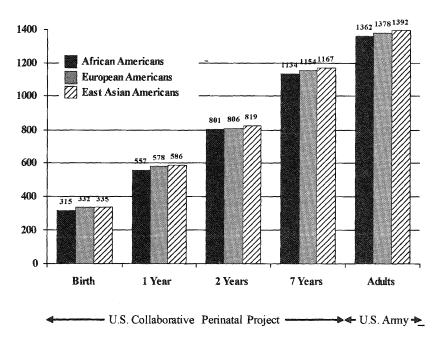
Studies using brain imaging techniques have also reported significant main effects of brain size on occupational status and education level; higher-status subjects had, on average, a larger brain than lower-status subjects (Andreasen et al., 1990; Pearlson et al., 1989). Rushton (1992a) used the externally measured cranial size of 6,325 U.S. servicemen and found that officers averaged significantly larger cranial capacities than enlisted personnel either before or after adjusting for the effects of stature, weight, race, and sex (1,384 vs. 1,374 cm³ before adjustments; 1,393 vs. 1,375 cm³ after adjustments). The differences between officers and enlisted personnel were found for both men and women, as well as for East Asians, whites, and blacks, and in fact were in the opposite direction from predictions based on body size.

IQ test scores are significantly correlated with the socioeconomic hierarchies of modern Europe, North America, and Japan (Herrnstein & Murray, 1994; Jensen, 1998). The basic finding is that there is a difference of nearly 3 SD (45 IQ points) between average members of professional and unskilled classes. These are group mean differences with considerable overlap of distributions. Nonetheless, the overall correlation between an individual's IQ and his or her SES of origin is between 0.30 and 0.40, and the correlation between IQ and attained SES, or occupational level, is about 0.50 (Herrnstein & Murray, 1994). In studies of intergenerational social mobility, Mascie-Taylor and Gibson (1978) and Waller (1971) obtained IQ scores of fathers and their adult sons. They found that, on average, children with lower test scores than their fathers had gone down in social class as adults, but those with higher test scores had gone up. A within-family study was also conducted by Murray (1998), who found that among the 1,074 sibling pairs in the National Longitudinal Survey of Youth who had taken the Armed Forces Qualification Test, the sibling with the higher IQ achieved a higher level of education, a higher occupational status, and greater take-home pay than the sibling with the lower IQ.

Race Differences

The races differ in average brain size, and this shows up at birth. Rushton (1997) analyzed the Collaborative Perinatal Project's head circumference measurements and IQ scores from 40,000 children followed from birth to age 7 years (Broman et al., 1987). The results showed that at birth, 4 months, 1 year, and 7 years, the East Asian American children in the study averaged larger cranial volumes than the white American children, who averaged larger cranial volumes than the black American children (figure 6.5). Within each race, the children with the larger head sizes obtained higher IQ scores. By age 7, the East Asian children an IQ of 90. Moreover, the East Asian children, who averaged the largest craniums, were the shortest in stature and the lightest in weight, whereas the black children, who averaged the smallest craniums, were the tallest in stature and the legter cranial to body size.

Dozens of studies from the 1840s to the 1990s, using different methods on different samples, reveal the same strong pattern. Four different methods of measuring brain size—MRI, endocranial volume measured from empty skulls, wet brain weight at autopsy, and external head size measurements—all yield the same results. Using MRI, for example, Harvey et al. (1994) found that 41 Africans and West Indians had a smaller average brain volume than did 67 Caucasians, although Harvey et al. provided no details on how, or if, the samples were matched for age, sex, or body size. In another study from the same mixed-race area of South London, Jones et al. (1994) found a (not significant) trend for



Mean cranial capacity (cm³) for African Americans, European Americans, and East Asian Americans from birth through adulthood. Data for birth through age 7 are from the U.S. Perinatal Project; data for adults are from the U.S. Army data in figure 6.4. (From Rushton, 1997, p. 15, Figure 2. Copyright 1997 by Ablex Publishing Corp. Reprinted with permission.)

whites to have a 30 cm³ larger intracranial volume but smaller ventricles than Afro-Caribbeans.

Using the method of measuring endocranial volume, the American anthropologist Samuel George Morton (1849) filled over 1,000 skulls with packing material and found that blacks averaged about 5 cubic inches less cranial capacity than whites. These results have stood the test of time (Todd, 1923; Gordon, 1934; Simmons, 1942). Subsequently, Beals, Smith, and Dodd (1984) carried out the largest study of race differences in endocranial volume to date, with measurements of up to 20,000 skulls from around the world. Their study found that East Asians, Europeans, and Africans averaged cranial volumes of 1,415, 1,362, and 1,268 cm³, respectively. The skulls from East Asia were 3 cubic inches larger than those from Europe, which in turn were 5 cubic inches larger than those from Africa. Using the method of weighing brains at autopsy, Broca (1873) found that whites averaged heavier brains than blacks, and had more complex convolutions and larger frontal lobes. (He corroborated the black-white difference using endocranial volume and also found that East Asians averaged larger cranial capacities than whites.) Subsequent studies have found an average black-white difference of about 100g (Bean, 1906; Mall, 1909; Pearl, 1934; Vint, 1934). Some studies have found that the more white admixture (judged independently from skin color), the greater the average brain weight in blacks (Bean, 1906; Pearl, 1934). In their autopsy study of 1,261 American adults, Ho et al. (1980) found that 811 white Americans averaged 1,323g and 450 black Americans averaged 1,223g—a difference of 100g. Since the blacks and whites in the study were similar in body size, differences in body size cannot explain away the differences in brain weight.

As yet unpublished, the largest cross-racial autopsy study carried out to date, at Columbia University Medical School, is by physical anthropologist Ralph Holloway (personal communications, February 21, 1997, March 16, 2002, and August 26, 2004). Holloway found that black and white men between ages 18 and 65 years differed by about 80g in brain weight, the samples being of very similar body size. The amount was less for women, about 40g. The data showed that 615 blacks, 153 Hispanics, and 1,391 whites averaged brain weights of 1,222, 1,253, and 1,285g, respectively. There were also a very large number (N = 5,731) of autopsied brain weights from 15- to 50-year-old Chinese from Hong Kong and Singapore that averaged 1,290g. Holloway himself remains agnostic as to the cause of these differences and whether they are related to general intelligence.

A final means of estimating brain size is by cranial volume calculated from external head size measurements (length, width, height). The results again confirm the racial differences. Rushton (1991, 1992a, 1993, 1994; Rushton & Osborne, 1995) carried out a series of studies estimating brain size this way from five large archival data sets. In the first of these studies, Rushton (1991) examined head size measures in 24 international military samples collated by the U.S. National Aeronautics and Space Administration (NASA) and, after adjusting for the effects of body height, weight, and surface area, found the cranial capacity for East Asians was 1,460 cm³ and for Europeans was 1,446 cm³. In the most comprehensive of these studies, Rushton (1992a) calculated average cranial capacities for East Asians, whites, and blacks from a stratified random sample of more than 6,000 U.S. Army personnel. The East Asians, whites, and blacks averaged 1,416, 1,380, and 1,359 cm³, respectively. The East Asians averaged 36 cm³ more capacity than the whites, and the whites averaged 21 cm³ more capacity than the blacks. This study allowed precise adjustments for all kinds of body size measures. Yet adjusting for these or other variables did not erase the average racial differences in cranial capacity.

No exact solution is possible, of course, to the question of how large the racial differences are in brain size. There is much variability from sample to sample, with a clear overlap of distributions. Nonetheless, the consistency of results found even with the use of different procedures is noteworthy. Rushton (1995) reviewed the world database from (1) autopsies, (2) endocranial volume measurements, (3) head measurements, and (4) head measurements corrected for body size. The results in cm³ or equivalents were: East Asians = 1,351, 1,415, 1,335, 1,356 (mean = 1,364); whites = 1,356, 1,362, 1,341, 1,329 (mean = 1,347); and blacks = 1,223, 1,268, 1,284, and 1,294 (mean = 1,267). The overall mean for East Asians was 17 cm³ more than that for Europeans and 97 cm³ more than that for Africans. Within-race differences, due to method of estimation, averaged 31 cm³.

To reduce the uncertainty about race differences in brain size still further, Rushton and Rushton (2003) extended the parameters of the debate by examining race differences in 37 musculoskeletal variables shown in standard evolutionary textbooks to change systematically with increments in brain size in the hominoid line from chimpanzees to australopithecenes to Homo erectus to modern humans. The 37 variables included cranial traits (such as jaw size and shape, tooth size and shape, muscle attachment sites on the head, and indentations in the skull for muscles to run along), and postcranial traits (such as pelvic width, thighbone curvature, and knee joint surface area). Across the three populations, the correlations between brain size and the 37 morphological traits averaged a remarkable r = 0.94. It is noteworthy that the correlation for 12 lower limb traits was as high (r = 0.98) as the correlation for the 11 cranial traits (r = 0.91). If the races did not differ in brain size, these correlations with the concomitant musculoskeletal traits could not have been found. It must be concluded that the race differences in average brain size are securely established. They were acknowledged by Ulric Neisser, chair of the American Psychological Society's Task Force on Intelligence, who noted that, with respect to "racial differences in the mean measured sizes of skulls and brains (with East Asians having the largest, followed by whites and then blacks)... there is indeed a small overall trend" (Neisser, 1997, p. 80).

Racial differences in measured intelligence around the world parallel those found in brain size (Jensen, 1998; Lynn & Vanhanen, 2002; Rushton, 2000). In the United States and around the world, East Asians, measured in North America and in Pacific Rim countries, typically average IQs in the range of 101–111. Caucasoid populations in North America, Europe, and Australasia typically average IQs of 85–115, with an overall mean of 100. African populations living south of the Sahara, in North America, in the Caribbean, and in Britain typically have mean IQs of 70–90.

Serious questions have been raised about the validity of using IQ tests for racial comparisons. However, because the tests show similar patterns of internal item consistency and predictive validity for all groups, and because the same differences are found on relatively culture-free tests, many psychometricians have concluded that the tests *are* valid measures of racial differences, at least among people sharing the culture of the authors of the test (Herrnstein & Murray, 1994; Jensen, 1998). This conclusion was endorsed by an American Psychological Association Task Force's statement: "Considered as predictors of future performance, the tests do not seem to be biased against African Americans" (Neisser et al., 1996, p. 93).

Subsequent work has been carried out on the construct validity of IQ tests in Africa. For example, the study by Sternberg et al. (2001) of Kenyan 12- to 15-year-olds found that IQ scores predicted school grades with a mean r = 0.40, P < 0.001 (and continued to do so after controlling for age and SES, r = 0.28, P < 0.01) just as they do for white children in Europe and America. Similarly, Rushton, Skuy, and Bons (2004) found that among engineering students at the University of the Witwatersrand, the test items "behave" in the same way for African students as they do for non-African students, thereby indicating the test's internal validity, while concurrent validity was demonstrated by finding that the test scores correlated as highly with other test scores (an English Comprehension test, the Similarities subscale from the South African Wechsler Adult Intelligence Scale, end-of-year university grades, and high school grade point average) for Africans as they do for non-Africans.

The same three-way pattern of race differences has been found using the simplest culture free cognitive measures such as reaction time tasks, which are so easy that 9- to 12-year-old children can perform them in less than 1 second. On these simple tests, children with higher IQ scores perform faster than children with lower scores, perhaps because reaction time measures the neurophysiological efficiency of the brain's capacity to process information accurately—the same ability measured by intelligence tests (Deary, 2000; Jensen, 1998). Children are not trained to perform well on reaction time tasks (as they are on certain paper-andpencil tests), so the advantage of those with higher IQ scores on these tasks cannot arise from practice, familiarity, education, or training. Lynn and Vanhanen (2002) found that East Asian children from Hong Kong and Japan were faster than European children from Britain and Ireland, who in turn were faster than African children from South Africa. Using similar tasks, this pattern of racial differences was also found in California (Jensen, 1998).

Behavioral Genetics and Evolution

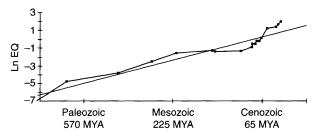
Heritabilities for mental ability range from 50% to 80% and have been established in numerous adoption, twin, and family studies (Bouchard & McGue, 2003). Noteworthy are the 80% heritabilities found in adult twins raised apart. Genetic influence is also found in studies of nonwhites, including African Americans (Osborne, 1980; Scarr, Weinberg, & Waldman, 1993) and Japanese (Lynn & Hattori, 1990).

Both brain size and its relation to general intelligence are also highly heritable-80% or higher (Pennington et al., 2000; Posthuma et al., 2002; Thompson et al., 2001). In the largest and most recent of these studies, Posthuma et al. (2002) scanned the brains of 258 Dutch adults from 112 extended twin families using MRI and found high heritability for whole-brain gray matter volume (82%), whole-brain white matter volume (87%), and general intelligence (86%). The high heritability of gray matter implies that interindividual variation in cell-body volume is not modified by experience. Similarly, the high heritability of white matter, which reflects the degree of interconnections between different neurons and might be expected to be more influenced by experience, suggests that either experience barely contributes to interindividual variation therein or, alternatively, exposure to relevant environmental experience is under strong genetic control. Posthuma et al. also found rvalues = 0.25 (*P* values < 0.05) between gray matter volume, white matter volume, and g. The genetic correlations (the cross-trait/cross-twin correlations) showed that the relation between both measures of brain volume and g was mediated entirely by genetic factors.

These results on heritability may or may not pertain to race and other group differences because heritability studies have typically undersampled people from the most deprived segments of society, where lower heritabilities might be expected due to harmful environmental effects damaging brains and lowering IQs. Thus, in a study of cranial capacity in 236 pairs of black and white adolescent twins aged 13–17 years, Rushton and Osborne (1995) found a lower heritability for blacks (12%-31%) than for whites (47%-56%) and a higher within-family environmental effect for blacks than for whites (42%-46% vs. 28%-32%).

Nonetheless, transracial adoption studies do show some genetic contribution to the between-group differences in IQ. Studies of Korean and Vietnamese children adopted into white American, Belgian, and Dutch homes have shown that, although as babies many had been hospitalized for malnutrition, they grew to excel in academic ability, with IQs 10 points or more higher than their adoptive national homes (Clark & Hanisee, 1982; Frydman & Lynn, 1989; Stams, Juffer, Rispens, & Hoksbergen, 2000; Winick, Meyer, & Harris, 1975). By contrast, black and mixed-race children adopted into white middle-class families performed at a lower level than the white siblings with whom they had been raised (Scarr et al., 1993). Multifarious other sources of evidence suggest that racial differences in intelligence are partly genetic (Jensen, 1998; see Rushton & Jensen, 2005, for a full review).

It is reasonable to hypothesize that bigger brains evolved based on natural selection for increased intelligence (Jerison, 1973). Over the last 575 million years of evolutionary history, neural complexity and brain size have increased in vertebrates and invertebrates alike (figure 6.6), little of which can be explained by body size increases. Russell (1983) calculated encephalization quotients, or EQs, a measure of actual brain size to expected brain size for an animal of that body weight (following Jerison, 1973; EQ = Cranial capacity $(cm^3)/(0.12)$ (body weight in grams)^{0.67}). Russell found that the mean EQ was only about 0.30 for mammals living 65 million years ago, compared to the average of 1.00 today. EQs for molluscs varied between 0.043 and 0.31, and for insects between 0.008 and 0.045, with the less encephalized species resembling forms that appeared early in the geological record and the more encephalized species resembling those that appeared later. Russell (1989) also demonstrated how," over 140 million years, dinosaurs showed increasing encephalization before going extinct 65 million years ago





Average encephalization quotient (EQ; natural log), a measure of neural tissue corrected by body size, plotted against elapsed geological time in millions of years (After Russell, 1983.)

(probably because of an asteroid impact or other catastrophic event). He extrapolated the data to suggest that if dinosaurs had continued on, they would have progressed to a large-brained, bipedal descendant. The tripling in size of the hominoid brain over the last 5 million years (chimpanzees $\approx 380 \text{ cm}^3$, australopithecenes $\approx 450 \text{ cm}^3$, Homo erectus $\approx 1,000 \text{ cm}^3$, and Homo sapiens $\approx 1,350 \text{ cm}^3$) may be a special case of the more general trend to larger brains.

Others have also shown the value of an evolutionary perspective on brain size relations. Bonner (1980, 1988) reviewed naturalistic data and found that the more recently an animal species had evolved, the larger was its brain and the more complex was its culture. Passingham (1982) reviewed experimental studies of "visual discrimination learning" that measured the speed with which children and other mammals abstracted such rules as "pick the same object each time to get food." More intelligent children, assessed by standardized IQ tests, learned faster than did those with lower IQ scores, and mammals with larger brains learned faster than did those with smaller brains (i.e., chimpanzees > rhesus monkeys > spider monkeys > squirrel monkeys > marmosets > cats > gerbils > rats > squirrels). Madden (2001) found that species of bowerbirds that build more complex bowers have larger brains than species that build less complex ones.

Metabolically, the human brain is an expensive organ. Representing only 2% of body mass, the brain uses about 5% of basal metabolic rate in rats, cats, and dogs, about 10% in rhesus monkeys and other primates, and about 20% in humans (Armstrong, 1990). Moreover, as large brains evolved, they required more prolonged and complex life histories to sustain them. For example, across 21 primate species, Smith (1989) found that brain size correlates 0.80-0.90 with life span, length of gestation, age of weaning, age of eruption of first molar, age at complete dentition, age at sexual maturity, interbirth interval, and body weight. Similarly, Rushton (2004) found that across 234 mammalian species, brain weight correlated with longevity (0.70), gestation time (0.67), birth weight (0.46), litter size (-0.22), age at first mating (0.50), duration of lactation (0.54), body weight (0.61), and body length (0.63). Remarkably, even after the effects of body weight and body length were controlled for, brain weight still correlated with longevity (0.59), gestation time (0.66), birth weight (0.16), litter size (-0.18), age at first mating (0.63), and duration of lactation (0.61). From an adaptationist perspective, unless large brains substantially contributed to evolutionary fitness (defined as increased survival of genes through successive generations), they would not have evolved.

The sexual dimorphism in cranial size and cognitive ability likely originated partly through evolutionary selection of men's hunting ability (Ankney, 1992; Kolakowski & Malina, 1974) and partly through the reproductive success socially dominant men have traditionally enjoyed (Lynn, 1994). Race differences in cranial capacity may have originated from evolutionary pressures in colder climates for greater intelligence (Rushton, 1995). Of course, brain size and intellectual performance are also affected by nutrition and experience (Sternberg, 2004).

Conclusion

The preponderance of evidence demonstrates that brain size is correlated positively with intelligence and that both brain size and cognitive ability are correlated with age, sex, social class, and race. Correlation does not prove cause and effect, but, just as zero correlations provide no support for a hypothesis of cause and effect, non-zero correlations do provide support. We are convinced that the brain size/cognitive ability correlations that we have reported are in fact due to cause and effect. This is because we are unaware of any variable, other than the brain, that can directly mediate cognitive ability.

Numerous issues still require research, and several paradoxes require resolution. For example, the average brain size of white women is equal to or less than the average brain size of black men (see figures 6.1 and 6.4), but white females obtain a higher average mental test score than do black males. We hypothesize that, within race, at least some of the additional brain tissue/neurons that men have, as compared with women, are related to the average male advantage in dynamic spatial abilities (not measured on standard IQ tests), such as in throwing balls and the like at stationary or moving targets. If so, that could untangle the aforementioned paradox. Additional research using MRI with a wider array of cognitive tasks may shed light on this puzzle.

Although it is established that the correlation between brain volume and g is mediated by common genetic factors, this is only the first step in unveiling the relation between them. One important next step will be to identify specific genes that influence both brain volume and g. Since genes have been identified that regulate brain size during development, particularly in the ape lineage leading from mammals to humans (Evans, Anderson, Vallender, Choi, & Lahn, 2004), these might be useful candidates for examining the underlying process.

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