AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 101:217–236 (1996)

How and Why Humans Grow Thin Skulls: Experimental Evidence for Systemic Cortical Robusticity

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KEY WORDS Skull, Neurocranium, Cortical bone, Robusticity, *Homo,* Pigs, Armadillos

ABSTRACT To what extent is cranial vault thickness (CVT) a character that is strongly linked to the genome, or to what extent does it reflect the activity of an individual prior to skeletal maturity? Experimental data from pigs and armadillos indicate that CVT increases more rapidly in exercised juveniles than in genetically similar controls, despite the low levels of strain generated by chewing or locomotion in the neurocranium. CVT increases in these individuals appear to be a consequence of systemic cortical bone growth induced by exercise. In addition, an analysis of the variability in vault thickness in the genus *Homo* demonstrates that, until the Holocene, there has been only a slight, general decrease in vault thickness over time with no consistent significant differences between archaic and early anatomically modern humans from the Late Pleistocene. Although there may be some genetic component to variation in CVT, exercise-related, non-genetically heritable stimuli appear to account for most of the variance between individuals. The thick cranial vaults of most hunter-gatherers and early agriculturalists suggests that they may have experienced higher levels of sustained exercise relative to body mass than the majority of recent, post-industrial humans.

> Nature is not greatly concerned over the precise thickness of the cranium.
> Todd (1924:255)

Why modern humans have generally thinner bones and, in particular, thinner skulls than archaic humans has long been a subject of speculation for clinical and hominid palaeontological research. The degree of cortical robusticity throughout the skeleton and, more specifically, in the cranial vault is often considered a major morphological distinction between anatomically modern *Homo sapiens* and earlier taxa of *Homo* (e.g., Wolpoff, 1980; Stringer, 1988). Weidenreich (1943), for example, noted that the mean parietal thickness at bregma of modern Europeans, 5.5 mm, is 60% thinner than that of the *Sinanthropus pekinensis* fossils from Zhoukoudian and 40% thinner than that of Neanderthals. Cranial vault thickness (CVT) is frequently used as a character to make inferences about the phylogenetic relationships among recent taxa of *Homo* (e.g., Stringer, 1984, 1987; Thorne and Wolpoff, 1981; Groves, 1989; Frayer et al., 1993), and to make inferences about the behavioral differences between modern and archaic humans (e.g., Coon, 1962; Brace, 1979).

CVT is an interesting character to examine in depth because the vault grows somewhat differently than long bones that have traditionally been the focus of most research on cortical robusticity. Unlike bones that form within a cartilagenous framework, the bones of the neurocranium—the parietals

Received August 29, 1995; accepted April 29, 1996.

and the squamous portions of the occipital, frontal and temporal—all develop intramembranously from the membranes that surround the inside and outside, respectively, of the vault. Early in development, osteoblasts in these membranes rapidly deposit highly vascularized woven bone within numerous ossification centers (Ohtsuki, 1977). As growth slows after birth, both the inner membrane, the endocranium, and the outer membrane, the pericranium, switch to depositing vascularized lamellar bone, forming the inner and outer tables of the neurocranium (Sperber, 1989). Osteoclasts and then osteoblasts begin to invade the center of the vault at around age four, resorbing and remodeling the woven bone and the earliest formed lamellae into the trabecular bone of the diploë, which comes to contain haemopoietic cells (Williams et al., 1989). It is important to note that, unlike most limb bones and other cranial bones, both the endocranial and pericranial surfaces of the superior half of the vault constitute depository growth fields in human and nonhuman primates (Duterloo and Enlow, 1970; Enlow, 1990). Consequently, the vast majority of the neurocranial cavity does not expand though drift (resorption of the inner layer and deposition of the outer layer) but instead expands from tension-induced growth within the sutures of the vault. A small amount of drift does occur, however, at the sutural margins of the neurocranial bones, preventing steeply angled sutures (Enlow, 1990). The bones of the superior half of the vault, therefore, can grow only thicker and do so independently of any increases in cranial capacity.

This paper asks to what extent as a character CVT is strongly linked to the genome and to what extent it reflects epigenetic responses to exogenetic stimuli. Despite information on the proximate cellular processes by which CVT develops, there is little understanding of the mechanisms that cause some individuals or taxa to have thicker cranial vaults than others. Three hypotheses have been proposed to account for variability in nonpathological cranial vault thickness in humans.[1] The most common hypothesis is that CVT is subject to selection. Wolpoff (1980:333), for example, points out that thick vaults are a possible adaptation for protecting the skull from injury, suggesting that "the technological innovations of the Late Stone Age, including the use of efficient long-distance hunting weapons such as bows with poisoned arrows reduced the necessity for large size and skeletal robustness in hunting populations." According to this hypothesis, the recent decline in vault thickness most likely reflects a relaxation of selection pressures to maintain thick vaults, presumably because thin vaults are metabolically less expensive to grow or support. Similar arguments are found in Brace (1979:67), Stringer (1988:268), and elsewhere.

A second hypothesis is that differences in CVT reflect nonheritable, in vivo responses to mechanical force. Bone tissue interacts dynamically with its mechanical environment. Force applied to a bone (quantified per unit area as stress, σ), generates strain (deformation, ϵ) whose cumulative effects, if sufficient in magnitude, can damage its microstructure and mechanical integrity (Carter, 1987; Martin and Burr, 1989, Martin, 1992.). Controlled experiments on both limb bones that form endochondrally (e.g., Biewener et al., 1986; Woo et al., 1981; Rubin and Lanyon, 1984, 1985) and facial bones that form intramembranously (e.g., Corruccini and Beecher, 1982, 1984; Bouvier and Hylander, 1981; Yamada and Kimmel, 1991) demonstrate that high levels of strains induce local osteoblastic responses that increase cortical bone mass. Such remodeling can be adaptive because it increases the distribution of mass in the plane(s) of deformation, thereby reducing the amount of strain generated by a given force (Biewener et al., 1986; Frost, 1986, 1987, 1988). The most important sources of mechanical force on the cranial vault are clearly those from chewing. It is a reasonable hypothesis that strains from the tension produced by the *m. temporalis* on the outer table of the vault or strains generated from other chewing-related forces generated elsewhere in the cranium may af-

[1] A variety of pathologies, including haemolytic blood dysplasias associated with sickle cell anemia and thalassemia, can cause unusual thickening of the diploic layer of the cranial vault (Webb, 1990). Such cases, however, are rare in the fossil record and are not considered here.

fect the rate of bone growth in the cranial vault (Weidenreich, 1941; Washburn, 1947; Moss, 1954; Moss and Young, 1960; Nawrocki, 1991, 1992). As Hylander (1986) has shown, chewing harder foods generates more strain in the mandible and face than chewing soft foods, so variation in CVT may reflect responses to diets of different hardness. Locomotion may also generate strains in the cranium, resulting in the prediction that humans who run more may have thicker skulls (Bhanba, 1961).

Finally, a few researchers (e.g., Twiesselmann, 1941; Kennedy, 1985; Nawrocki, 1991; Nelson and Gauld, 1994) have pointed out that differences in the levels of certain circulating hormones may also influence CVT. All bone growth is mediated by hormones on both local and systemic levels. Growth hormone (GH) in particular has well-documented effects on CVT and overall cortical robusticity. For example, acromegalics who have persistent and high levels of GH have significantly thicker cranial vaults than normal individuals, whereas sufferers from GH deficiencies (e.g., hypopituitarism) have thinner-than-average cranial vaults (Randall, 1989; Vogl et al., 1993; Pirinen et al., 1994). Other circulating hormones such as insulin-like growth factor (IGF-I), parathyroid hormone (PTH), calcitonin, and even insulin could also have similar effects (Buchanan and Preece, 1992). Levels of circulating hormones such as GH might be higher in taxa with thicker vaults because of the influence of selection on the activities of the endocrine system or because of other nonheritable factors that induce endocrine responses. Exercise, for example, substantially elevates circulating GH levels in humans (Felsing et al., 1992).

Each of these hypotheses, which are not exclusive, makes predictions that can be tested in the laboratory on nonhuman animals and/or using comparative data on living and fossil human samples. If CVT variation is a consequence of selection in relation to cultural factors, then human crania from Upper Palaeolithic contexts should have thinner vaults than those from Middle or Lower Palaeolithic contexts. In addition, CVT would have to be a predominantly heritable trait for it to be a target of natural selection. If, however, CVT variation is an in vivo, exogenetic response to higher mechanical forces, then such strains should be sufficient to replicate them in laboratory conditions. In addition, this hypothesis would predict that humans who eat soft diets will have thinner vaults than those who eat harder diets. Finally, if CVT is merely a consequence of elevated circulating hormones that stimulate osteogensis, then thickened cranial vaults will develop in laboratory animals who have elevated GH levels, and such individuals will also have an overall high degree of cortical robusticity. An additional, related question is whether a thin cranial vault is a derived character of anatomically modern humans or whether it is a more recent phenomenon. Although generally cited as a defining character of modern humans, there has been little systematic investigation of variability in CVT among recent human taxa (see, however, Nawrocki, 1991).

This paper, therefore, presents the results of two interrelated analyses. First, it reports details of controlled laboratory studies on the effects of exercise on local and systemic cortical bone growth in nonhuman animals. These experiments demonstrate that significant differences in overall cortical robusticity, including the thickness of the cranial vault, can occur in genetically identical and/or closely related animals who experience different levels of exercise during their development. These results indicate that there is a strong nonheritable component to CVT variability. Second, these conclusions are supported by an analysis of changes in cortical vault thickness in Pleistocene *Homo* which reveals that, despite a slight trend towards thinner skulls, there are not many significant differences over time or between taxa until the Holocene.

MATERIALS AND METHODS

The processes that cause variation in CVT were studied in controlled laboratory experiments in which confounding factors such as age, nutrition, sex, and genetic variance were controlled among the subjects. I report here the results of separate experiments on two species of laboratory animals: the miniature domestic pig (*Sus scrofa*) and the

TABLE 1. Experimental protocols

	Pigs (*Sus scrofa*)	Armadillos (*Dasypus novemcinctus*)
N	2 females, 4 males 3 runners, 3 controls	2 males 1 runner, 1 control
Relatedness	Inbred siblings	Identical twins
Age at start	1 month	2 months
Age at stop	4 months	8 months
Exercise	3.0 mph AM, 30 min 3.0 mph PM, 30 min	1 mph AM, 60 min
Dyes	Calcein, 1 month Tetracycline, 2 months Alizarin, 3 months	Calcein, 2 month Tetracycline, 4 months Alizarin, 6 months
Longitudinal data	Weight (kg) Lateral X-rays of tibia, crania	Weight (kg)
Strain data	Tibia (proximal medial) Supraoccipital (lateral to sagittal suture)	Tibia (proximal medial)

common nine-banded armadillo (*Dasypus novemcinctus*). The protocols for both experiments are summarized in Table 1. For a variety of reasons (discussed below), more data was acquired from the six pigs; the data from the two armadillos are less comprehensive but are included because the subjects were genetically identical twins.

Pigs

The subjects were two female and four male piglets, all siblings from a single litter of an inbred strain of miniature swine (Charles River Laboratories, Wilmington, MA). At weaning, 1 month after birth, the pigs were almost identical in weight (see Table 3) and were arbitrarily divided into an exercise group of runners and a control group, each of which consisted of one female and two males. The exercise group was trained to run on a treadmill for 30 min each morning and 30 min each afternoon; after 1 month they were able to run comfortably at a speed of 3.0 mph. These levels of exercise approximate what a pig might habitually experience in wild conditions. In addition, the exercise group was kept in a large pen (13.5 m^2), whereas the controls were confined to a smaller pen (2.25 m^2). The control animals were not kept immobile but spent most of each day walking about their pen. All other aspects of their conditions were identical, including diet, exposure to light, and temperature. The experiment ran for 3 months, and the animals were sacrificed at the age of 4 months, after the cessation of neural growth. At the beginning and end of the experiment and every 2 weeks in between, the animals were anaesthetized (6 mg/kg Telazol and 0.04 mg/kg Atropine) in order to weigh them, take blood samples, and radiograph their heads and right hind limbs in lateral view to document longitudinal growth rates in the cranium and tibia. A record of longitudinal bone growth was also provided by intraperitoneal injections of fluorescent dyes that incorporate rapidly into bone mineral (Frost, 1969, 1983; Skinner and Nalbadian, 1975). Calcein (20 mg/kg), which appears green under flourescent light, was injected at age 1 month; oxytetracycline (70 mg/kg), which appears orange under flourescent light, was injected at age 2 months, and alizarin red (50 mg/kg), which dyes the bone red, was injected at age 3 months.

Close to the end of the experiment, (Tokyo Sokki Kenkyujo Co., Tokyo, Japan) 45° rectangular strain gauges with 120 $\pm$ 0.5 ohm resistance (FRA-1-11) were placed in two locations on one of the exercised animals. One gauge was placed on the dorso-medial aspect of the proximal end of the left tibia where there are no muscle attachments; the other gauge was placed on the squamous portion of the occipital (the supraoccipital) just lateral to the midsagittal line. For these procedures, anaesthesia was induced by telazol (6.0 mg/kg) and atropine (0.04 mg/kg) and maintained with halothane (Muir and Hubbell, 1989). To affix the gauges, a roughly 4 $\times$ 4 mm window was cut in the periosteum to expose the surface of the bone, the bone surface was degreased with chloroform, and the gauge was bonded with super-glue

(methyl-2-cyano-acrilate). Each gauge was connected with insulated wire to a Vishay 2120 amplifier to form one arm of a Wheatstone bridge circuit. Bridge excitation was 1 V, and voltage outputs were recorded on a Bell and Howell CPR 4010™ magnetic tape recorder at 15 in/s.

Strain levels were recorded 2 days after surgery; at this time, the pig had no limp and was able to move its head freely and without any evidence of pain. Recordings were made when the animal was running at 3.0 mph and when it was chewing hard pellets. Gauges were periodically calibrated and balanced when the animal was not active to record zero levels of strain. The subject was filmed in lateral view in normal light at 100 frames/s with Kodak 16 mm Plus-X reversal film (no. 7276) in order to correlate strain gauge activity with footfall during running. A voltage pulse triggered by the camera shutter was recorded by the tape recorder, allowing precise synchronization of frames with the strain data. After each experiment, still X-ray photographs were taken to pinpoint gauge location and the orientation of the gauge axes. Selected portions of the strain gauge data were played through an A-D converter into a Macintosh II™ computer at 500 points/s and analyzed using Labview II software (program developed by K. Johnson, Duke University). These data were integrated to calculate microstrain units ($\mu\epsilon$)[2] of tension (ϵ_1), compression (ϵ_2), shear (ϵ_1-ϵ_2), and the orientation of tension in degrees relative to the axis of the A element of each gauge (for fomulae and discussion, see Dally and Riley, 1978; Biewener, 1992).

Immediately after the animals were killed, the bones were defleshed and cleaned, and samples from the supraoccipital and the right tibia were fixed in 10% formaldehyde solution. The rest of the skeleton was cleaned using dermestid beetles and degreased with a 25% ammonia solution. For each individual, sections were cut from the supraoccipital just to the left of the sagittal suture and from the midshaft, proximal third, and distal third of the left femur, tibia, fibia, and metatarsal bones. Sections were embedded in Epotek™ epoxy, cut with an Isomet™ low speed saw, affixed to slides, and ground down to approximately 100 micron thickness with a Beuhler Petrothin™. Sections were examined in plain and cross-polarized transmitted light and reflected flourescent light using an Olympus™ SZH stereomicroscope and then were digitally captured for computer image analysis using a color video camera connected to a Quick Capture™ video input board in a Macintosh II™ computer. Each image was analyzed using Image (version 1.52).

Armadillos

The protocol for the armadillo experiment was similar to that used for the pigs but with several important differences. Only one pair of genetically identical armadillo twins was available. As with the pigs, one armadillo exercised by running on a treadmill every day for 60 min but at 1.0 mph. The duration of the experiment was for 6 months after weaning, which occurred at the age of 2 months. Dyes were administered in the same sequence and at the same doses but every 8 weeks. Close to the end of the experiment, a strain gauge was placed on the dorsomedial aspect of the proximal end of the left tibia of the exercised animal as described above. Longitudinal weight data were recorded every 2 weeks, but lateral radiographs of the skull were only taken at the end of the experiment. Immediately after being sacrificed, the animals were defleshed and their skulls and tibia fixed in a 5% gluteraldehyde solution buffered to pH 7.0. These bones were then dehydrated in ethyl alcohol, cleared in xylene, embedded in Osteobed™ polymer, and sectioned as described above.

Measurements and analysis

For the cranial vaults, total thickness was measured directly from sections of the anteromedial corner of the left supraoccipital (where a strain gauge was attached in the pigs). In addition, a specially modified version of Image 1.52 (by B. Guilford, University of Arizona) was used to measure cortical

[2]Strain (ϵ) is defined as $\Delta L/L$, in which L is the original length of an object and ΔL is its change in length when a force is applied. By convention, strain is calculated in dimensionless units of microstrain ($\mu\epsilon$) which equal 1×10^{-6} mm/mm (or in/in).

and medullary areas as well as the second moment of inertia, I, around the mediolateral (x) and dorsoventral (y) planes from cross-sections of the limb bones. I_x and I_y are calculations of the distribution of mass around the neutral axis of the bone in these planes (see Wainright et al., 1976; Ruff and Hayes, 1983a; Biewener, 1992; Ruff, 1992). Other measures of CVT were taken on the dried skulls using Mitutoyo™ digital calipers (accurate to 0.01 mm) at the following locations: the center of the frontal along the midsagittal axis, bregma (average of parietal and frontal), the parietal eminences, and the maximum thickness of the nuchal region in the midsagittal plane. A number of other comparative measurements were taken on dried bones using calipers. These measurements include the dorsoventral and mediolateral thickness of the last and second-to-last ribs and the first and fourth caudal vertrebrae at their midpoints, the maximum width of the mandibular corpus at dp_4 in the pigs and M_1 in the armadillos, the total maximum width of the maxilla at M^1, the length of the mandible, the maximum mediolateral width of the zygomatic arch at its midpoint, and the buccolingual and mesiodistal dimensions of M^1 and dp_4 in the pigs and M_1 in the armadillos. In all cases, measurements were made twice and averaged; wherever relevant, measurements were also averaged from the left and right sides.

Comparisons of bone thickness of various characters in the exercised and control animals these data were analyzed using StatView 4.1, mostly as Mann-Whitney U-tests to avoid assuming that the data were normally distributed. The power of the U-test is limited because of the necessarily small sample size for the pig experiment (three pairs). Consequently, a few of the *P* values suggest a high degree of significance but do not satisfy conventional 95% degree confidence limits. No statistical analysis was possible for the armadillo data as there was only one pair of subjects. Note, however, that the armadillos used in the experiment were genetically identical twins kept in exactly the same conditions with the exception of their levels of daily exercise. It is reasonable to interpret any differences between them as the consequence of non-genetically heritable influences related to exercise.

Comparative fossil hominid data

In addition to testing the effects of strain and exercise on vault thickness in pigs and armadillos, CVT values were compared in adult human and fossil hominid crania at two locations: bregma, the intersection of the frontal and parietal bones where the coronal and sagittal sutures meet, and the parietal eminence (tuberosity), which marks the initial center of ossification of the bone. The fossil sample (Table 2), all from the genus *Homo,* are divided into five groups: 1) *H. erectus,* 2) early archaic humans (which includes non-Neanderthal fossils attributed to *Homo sp. indet.* from Africa Asia and Europe, 3) Neanderthals, 4) early anatomically modern *H. sapiens* from the Pleistocene, and 5) recent anatomically modern *H. sapiens* from the Holocene. All the data from Pleistocene fossils were generously provided by S. Nawrocki, who compiled them from published measurements (for details see Nawrocki, 1991). The comparative data on Holocene modern human populations comes from several published sources which are indicated in Table 2.

RESULTS

Comparisons of cortical robusticity in experimental animals

Before comparing the differences in vault thickness between the exercised and control animals, it is useful to examine the variation in robusticity elsewhere in the cranium and postcranium of the experimental subjects. Table 3 summarizes the metrical variation for tooth size, body mass, and several craniofacial sites that are likely to generate and/or withstand masticatory forces. Tooth dimensions are included for comparison because crown dimensions are highly heritable and form prior to eruption (Garn et al., 1965). As one might expect for the genetically identical armadillos and the inbred sibling pigs, dental dimensions are statistically indistinguishable between the two groups. In addition, several features of the mandible and maxilla, whose growth and shape are known to be strongly influenced by mastica-

TABLE 2. Cranial vault thickness of fossils from the genus Homo *(from Nawrocki (1991) unless otherwise indicated)*

Fossil	Bregma (mm)	Parietal eminence (mm)	N
H. erectus			
Olduvai Hominid 9	—	10.0	1
Olduvai Hominid 12	10.0	7.5	1
Sale	8.0	6.4	1
Ternifine	—	9.0	1
Trinil	9.0	9.0	1
Sangiran 2	8.8	11.0	1
Sangiran 3	10.5	8.5	1
Sangiran 4	5.5	9.3	1
Sangiran 10	8.0	11.0	1
Sangiran 12	9.0	9.5	1
Sangiran 13	10.0	—	1
Sangiran 17	9.0	—	1
Sangiran 18	11.0	10.5	1
Hexian	—	13.5	1
Lantian	16.0	—	1
Zhoukoudian 1	—	5.0	1
Zhoukoudian 2	7.5	9.75	1
Zhoukoudian 3	9.5	11.25	1
Zhoukoudian 4	10.5	10.0	1
Zhoukoudian 5	9.0	—	1
Zhoukoudian 6	—	10.5	
Zhoukoudian 10	10.0	9.25	1
Zhoukoudian 11	7.0	16.0	1
Zhoukoudian 12	9.5	8.75	1
Ngandong 1	9.0	—	1
Ngandong 3	10.0	8.0	1
Ngandong 5	7.0	—	1
Ngandong 6	12.0	—	1
Ngandong 9	9.0	—	1
Ngandong 11	11.0	—	1
Early archaic humans			
Xujiayao 10	8.5	12.6	1
Xujiayao 6	6.5	7.0	1
Xujiayao 4.5	9.0	10.8	1
Maba	7.0	9.0	1
Dali	—	12.0	1
Melka Kunture	—	15.0	1
Bodo 1	13.0	—	1
Ndutu	—	11.5	1
Florisbad	12.0	12.0	1
Omo 2	9.0	—	1
Kabwe	8.8	9.5	1
Laetoli 18	12.0	—	1
Bilzingsleben	9.0	—	1
Swanscombe	7.0	10.5	1
Steinheim	6.0	6.5	1
Petralona	10.5	9.0	1
Fontechevade 5	7.0	8.0	1
Neanderthals			
Ehringsdorf 1	—	10.0	1
Ehringsdorf 2	—	17.0	1
Kulna	—	11.3	1
La Chapelle	5.5	7.5	1
La Quina 5	5.0	5.3	1
La Quina 13	—	7.1	1
La Ferrassie	6.0	7.0	1
Monte Circeo	—	7.0	1
Le Moustier	6.0	6.8	1
Spy 1	8.0	9.5	1
Spy 2	7.0	9.0	1
Gibraltar	7.0	9.5	1
Neanderthal	7.5	10.0	1
Amud 1	9.0	8.0	1
Tabun 1	4.0	5.0	1
Shanidar 1	—	8.0	1
Shanidar 2	—	8.2	1
Shanidar 4	—	8.1	1
Shanidar 5	—	9.0	1
Vindija 204	—	8.3	1
Vindija 261	5.9	—	1
Vindija 293	—	9.1	1
Krapina C	—	8.5	1
Krapina D	8.5	7.0	1
Krapina E	—	7.5	1
Krapina 16	7.0	7.5	1
Krapina Par. 5	—	7.5	1
Krapina Par. 20	—	8.0	1
Krapina Par. 21	—	6.0	1
Krapina Par. 32	—	8.0	1
Krapina 34.1	—	7.0	1
Early modern humans			
Cro-Magnon 1	8.0	9.5	1
Cro-Magnon 2	—	6.5	1
Cro-Magnon 3	—	5.5	1
Predmosti 1	—	5.0	1
Predmosti 3	7.5	6.0	1
Predmosti 4	—	6.0	1
Predmosti 9	4.5	6.0	1
Predmosti 10	—	5.0	1
Predmosti 14	—	7.5	1
Cotte de St. Brelade	12.0	6.0	1
Oberkassel 1	10.0	5.0	1
Oberkassel 2	8.0	7.0	1
Mladec 1	3.5	3.5	1
Mladec 5	—	7.0	1
Mladec 6	—	8.0	1
Mungo 1	4.5	—	1
Mungo 3	7.0	—	1
Kow Swamp 16	7.5	—	1
Keilor	9.0	—	1
Tandou 2	8.0	—	1
Wadjak 1	8.0	—	1
Omo 1	8.0	—	1
Boskop	—	14.0	1
Lukenya	—	12.0	1
KRM41658	7.0	7.0	1
Qafzeh 3	—	10.0	1
Qafzeh 5	—	8.0	1
Qafzeh 6	—	8.0	1
Qafzeh 7	—	5.0	1
Qafzeh 9	6.0	6.5	1
Skhul 2	—	10.5	1
Skhul 4	—	10.0	1
Skhul 5	7.5	4.5	1
Skhul 9	—	11.0	1
Holocene humans			
French[1,5]	5.4	5.7	200
Yuendumu[2]	7.4	4.3	20
Africans[1]	6.7	7.7	64
Chinese[1]	6.4	6.0	49
Phillipines[1]	6.7	5.7	22
Hebrides[1]	7.0	6.9	16
American, white[3,5]	5.88[6]	3.6	445
American, white[4,5]	—	2.9	32
Belgian[1,5]	5.3	5.7	200
Byblos[1]	7.4	6.9	13
Sialk Copper Age[1]	7.1	6.4	10
Hastière[1]	6.4	6.7	24
French Neolithic[1]	6.8	6.7	15
Sialk Iron Age[1]	5.7	5.3	20
Susa[1]	6.5	6.6	14
Palmyra[1]	6.4	7.2	19

[1] Tweisselmann, 1941.
[2] Brown et al., 1979.
[3] Todd, 1924.
[4] Roche, 1953.
[5] Postindustrial population.
[6] Measured at vertex.

TABLE 3. Comparative dental, cranial and bodyweight data from experimental pigs and armadillos

	Pigs						Armadillos		
	Controls (n = 3)	S.D.	Runners (n = 3)	S.D.	P^1	%diff	Control	Runner	%diff
Dental characters (mm)									
M_1 b-l	9.9	0.1	9.8	0.1	0.51	1.0	1.6	1.6	0.0
M_1 m-d	13.5	0.1	13.6	0.1	0.51	0.2	2.2	2.3	4.5
dp_4 b-l	7.9	0.1	8.0	0.1	0.01	1.3	na	na	na
dp_4 m-d	18.2	0.2	18.3	0.3	0.83	0.5	na	na	na
Maxillary and mandibular characters (mm)									
Corpus width at dp_4/M_1	15.9	0.1	15.8	0.1	0.28	0.6	4.2	4.2	0.0
Maxilla width at M_1	49.5	0.2	49.3	0.5	0.66	0.5	19.4	19.2	1.0
Mandible length	156.3	1.5	154.7	1.2	0.19	1.0	68.0	67.9	0.1
Mid-zygomatic width	6.4	0.2	6.3	0.3	0.99	0.6	1.6	1.5	4.6
Body weights (kg)									
Experiment start	4.1	0.2	4.1	0.5	0.51	1.5	0.25	0.25	0
Experiment middle	10.8	0.9	10.9	0.9	0.99	0.8	1.1	1.13	2.7
Experiment end	28.0	1.04	26.5	2.3	0.51	5.6	2.88	2.79	3.2

[1] Mann-Whitney U-Test.

tory forces, were also statistically indistinguishable in size between the exercised and control animals of both species. These characters include the width of the mandibular corpus at dp_4 in the pigs and M_1 in the armadillos, the width of the maxilla at M^1, the length of the mandible, and the mediolateral thickness of the zygomatic arch at its midpoint (see Herring, 1993). As with the teeth, such metrical similarities are predicted among the subjects because of their high genetic similarity and because they ate the same diets. Animals fed artifically softened diets develop maxillae and mandibles that are significantly less tall, wide, and deep than those of controls fed hard but otherwise nutritionally identical diets (Corruccini and Beecher, 1982; Bouvier and Hylander, 1981). Table 3 also summarizes longitudinal weight data. It is important to note that there were never any statistically significant differences in weight for the pigs or armadillos during the experiment. While the exercised animals may have had slightly more bone and muscle mass in their limbs (see below), these differences were apparently offset by lowered fat deposits.

Measures of cortical robusticity in the limbs of the exercised and control animals, however, reveal predictable contrasts. Unlike gnathic characters, the weight-bearing limb bones of the exercised animals were significantly thicker than those of the controls in both species. Table 4 summarizes several midshaft dimensions for the tibia including cortical area and the second moment of inertia, I, around the mediolateral (x) and dorsoventral (y) axes and the minimum (I_{min}) and maximum (I_{max}) moment areas. As Table 4 indicates, the limb bones of the exercised animals are not only significantly thicker in cortical area and linear dimensions, but they also have a significantly greater distribution of mass around the neutral axis of the bone. With the exception of the size of the medullary cavity, the high degree of statistical significance for these measures is to be expected given the well-established principle that bones model in response to higher levels of habitual strain, particularly in growing animals (Lanyon, 1984; Biewener et al., 1986; Lieberman and Crompton, in press). Similar responses to strain have been documented in many species, including pigs (Woo et al., 1981) and turkeys (Lanyon, 1984; Lanyon et al., 1986; Rubin and Lanyon, 1985; Loitz and Zernicke, 1992) as well as humans (Jones et al., 1977; Ruff et al., 1994).

Perhaps the most surprising metrical differences in cortical robusticity between the exercised and control animals are found in the cranial vault. Table 5 presents CVT data at five locations: the center of the frontal along the midsagittal axis, bregma, the parietal eminences, the maximum thickness of the nuchal region in the midsagittal plane, and the anteromedial corner of the left supraoccipital (where a strain gauge was attached in the pig). Despite the small sample sizes, there are highly significant contrasts in thickness between the two groups at each location. On average, the vaults of

TABLE 4. Comparative midshaft tibia data from experimental pigs and armadillos

	Pigs						Armadillos		
	Controls (n = 3)	S.D.	Runners (n = 3)	S.D.	P^1	%diff	Control	Runner	%diff
Tibia midshaft									
I_x (mm^4)	843.7	21.7	1,523.3	222.8	0.05	80.5	107.0	224.0	209.3
I_y (mm^4)	1,506.7	158.9	2,130.0	185.2	0.05	41.4	38.9	65.1	67.4
Imin (mm^4)	820.3	26.3	1,480.0	198.0	0.05	80.4	114.0	230.0	201.8
Imax (mm^4)	1,530.0	148.0	2,173.3	198.6	0.05	42.0	31.7	59.7	88.3
Cortical area (mm^2)	96.8	3.1	119.5	0.4	0.05	23.4	23.4	31.7	35.5
Medullary area (mm^2)	22.9	1.0	25.3	3.6	0.28	10.5	2.0	3.3	60.7

[1] Mann-Whitney U-Test.

TABLE 5. Comparative cranial vault, rib and vertebral data from experimental pigs and armadillos

	Pigs						Armadillos		
	Controls (n = 3)	S.D.	Runners (n = 3)	S.D.	P^1	%diff	Control	Runner	%diff
Cranial thickness (mm)									
Frontal, center, midsagittal	8.3	1.5	11.0	1.0	0.08	32.5	0.74	0.93	24.3
Bregma	6.6	0.8	8.8	0.4	0.05	33.3	0.66	0.80	21.2
Euryon	6.2	1.2	7.5	0.5	0.19	21.0	1.30	1.50	15.4
Supraoccipital	8.1	0.9	10.9	0.5	0.05	34.6	1.07	1.31	22.4
Nuchal (maximum)	10.2	0.2	12.6	1.1	0.05	23.5	0.34	0.50	47.0
Ribs, midpoint dimensions (mm)									
Fifteenth rib dorsoventral	3.8	0.1	4.6	0.3	0.05	20.9	na	na	na
Fifteenth rib mediolateral	8.8	0.2	5.8	0.5	0.83	1.7	na	na	na
Eighth rib dorsoventral	na	na	na	na	na	na	2.5	2.9	16.8
Eighth rib mediolateral	na	na	na	na	na	na	4.6	5.3	15.2
Sixteenth rib dorsoventral	3.3	0.1	4.0	0.2	0.05	20.3	na	na	na
Sixteenth rib mediolateral	4.5	0.2	5.8	0.2	0.05	28.2	na	na	na
Ninth rib dorsoventral	na	na	na	na	na	na	2.2	2.4	9.0
Ninth rib mediolateral	na	na	na	na	na	na	4.2	4.4	4.8
Caudal vertebrae (mm)									
C1 mediolateral	24.5	2.7	31.2	1.5	0.05	27.1	10.5	11.8	12.4
C1 dorsoventral	10.5	0.5	11.8	1.0	0.13	12.7	9.4	10.2	8.5
C4 mediolateral	14.4	0.4	16.2	0.9	0.05	12.3	9.2	10.5	14.1
C4 dorsoventral	6.4	0.2	7.2	0.2	0.05	11.5	8.6	9.2	7.0

[1] Mann-Whitney U-Test.

the exercised animals are about 28% thicker than those of the controls. Analysis of parasagittal sections through the parietal bones just lateral to the sagittal suture demonstrated the vault bones of the two groups to be histologically indistinguishable. The greater vault thickness of the exercised animals is entirely a consequence of more lamellar deposition, particularly from the pericranium.

Finally, Table 5 also presents the differences in cortical robusticity between the exercised and control animals for several locations elsewhere in the postcranium that are unlikely to experience high levels of strain from habitual masticatory or locomotor activities. These characters are the mediolateral and dorsoventral thickness of the first and fourth caudal vertebrae and the mediolateral and dorsoventral thickness of the last and penultimate ribs at their midpoints. These characters make no significant contribution to supporting body mass during locomotion because in neither species is the tail used when running, and the most caudal ribs do not extend to the ventral aspect of the abdomen. With the exception of one dimension (the mediolateral width of the fifteenth rib in the pigs), the contrasts in thickness between the two groups for these characters are highly statistically significant. Many of the differences in robusticity between the exercised and control animals therefore appear to be systemic.

Strain. Table 6 summarizes the results of the strain gauge analyses. The strain levels in the tibia for the pig and the armadillo,

TABLE 6. Strain gauge data from experimental pigs and armadillos

			Tibia strains (με)			Cranium strains (με)		
Subject	Activity	n	Tension	Compression	Shear	Tension	Compression	Shear
Pig	Running 3.0 mph	24	1,243.0 ± 446.0	−561.3 ± 172.4	1,804.3 ± 602.5	73.3 ± 21.9	−64.2 ± 11.4	137.4 ± 28.4
Armadillo	Running 1.0 mph	21	1,260.5 ± 193.7	−230.8 ± 78.0	1,491.3 ± 181.2	na	na	na
Pig	Chewing hard food	23	na	na	na	86.7 ± 45.2	−86.0 ± 29.3	172.7 ± 51.0

approximately 1,500–2,000 με of shear, are very similar to each other and to those documented for the tibia of other medium-sized mammals (Biewener and Taylor, 1986; Lieberman and Crompton, in press). Such levels of strain are well within the range of minimum effective strains that Frost (1986) predicts will elicit the type of bone modeling responses reported above. In contrast, the peak levels of strain measured in the pig vault during locomotion and chewing, both well under 200 με of shear, are roughly an order of magnitude lower than the levels of strain measured in the tibia, despite the close location of the gauge to both the nuchal crest and to the posterior fibers of the *m. temporalis*. According to most models (Frost, 1986; Carter, 1987; Beaupré et al., 1990; Turner, 1992), such low strains might be expected to induce resorption. In vivo strain levels were not measured in the armadillo cranium, but it is unlikely that locomotion generated high strains in the vault given their head posture (like pigs, armadillos do not move their heads in synchrony with their limbs as they run). The greater CVT in the exercised animals is, therefore, either a result of a lower threshold at which loading induces bone growth in the cranial vault than in the tibia or from systemic responses to exercise unrelated to strain (discussed below).

Comparative hominid data

In addition to comparing differences in cortical robusticity in laboratory animals as described above, hypotheses concerning the processes by which CVT develops in humans can also be tested with data from the hominid fossil record and from recent humans. I studied how CVT within the genus *Homo* has changed over time and tested whether CVTs differ significantly between taxa, and/or between humans with contrasting subsistence strategies. Figure 1A,B plots changes in CVT at bregma and the parietal eminences, respectively, over time for the adult fossils and populations listed in Table 2. The data from the 17 recent human populations are included only as sample means in order to avoid statistical biases from the large number of recent human skulls available for analysis. Figure 1A,B clearly indicates that while there has been a slight, general trend towards thinner skulls over the last 1 million years, the enormous degree of variability prior to the Holocene precludes any strong relationship between time and vault thickness at bregma and only a slight trend at the parietal eminences. Including the Holocene populations, r^2 is 0.13 for bregma and 0.28 for the parietal eminences; excluding the Holocene populations, r^2 for a least squares regression analysis is 0.19 for bregma and 0.35 for the parietal eminences.

If one breaks down CVT by taxon, as in Figure 2A,B, it is apparent that there are few simple statistically significant differences between Late Pleistocene hominid taxa in terms of vault thickness (see also Nawrocki, 1991). A single factor analysis of variance (ANOVA) reveals that at bregma *H. erectus* fossils are thicker than Neanderthals ($P < 0.001$) but not other early archaic humans and that neither the Neanderthals nor early anatomically modern humans have significantly thicker vaults at bregma than Holocene populations. Non-Neanderthal archaic humans, however, do have significantly thicker vaults at bregma than Pleistocene anatomically modern humans ($P < 0.02$). At the parietal eminence, *H. erectus* fossils are not significantly thicker than either Neanderthals or other archaic humans, and Neanderthals are not significantly thicker than Late Pleistocene early anatomically modern humans. It is interesting to note, however, that early archaic humans have significantly thicker parietal em-

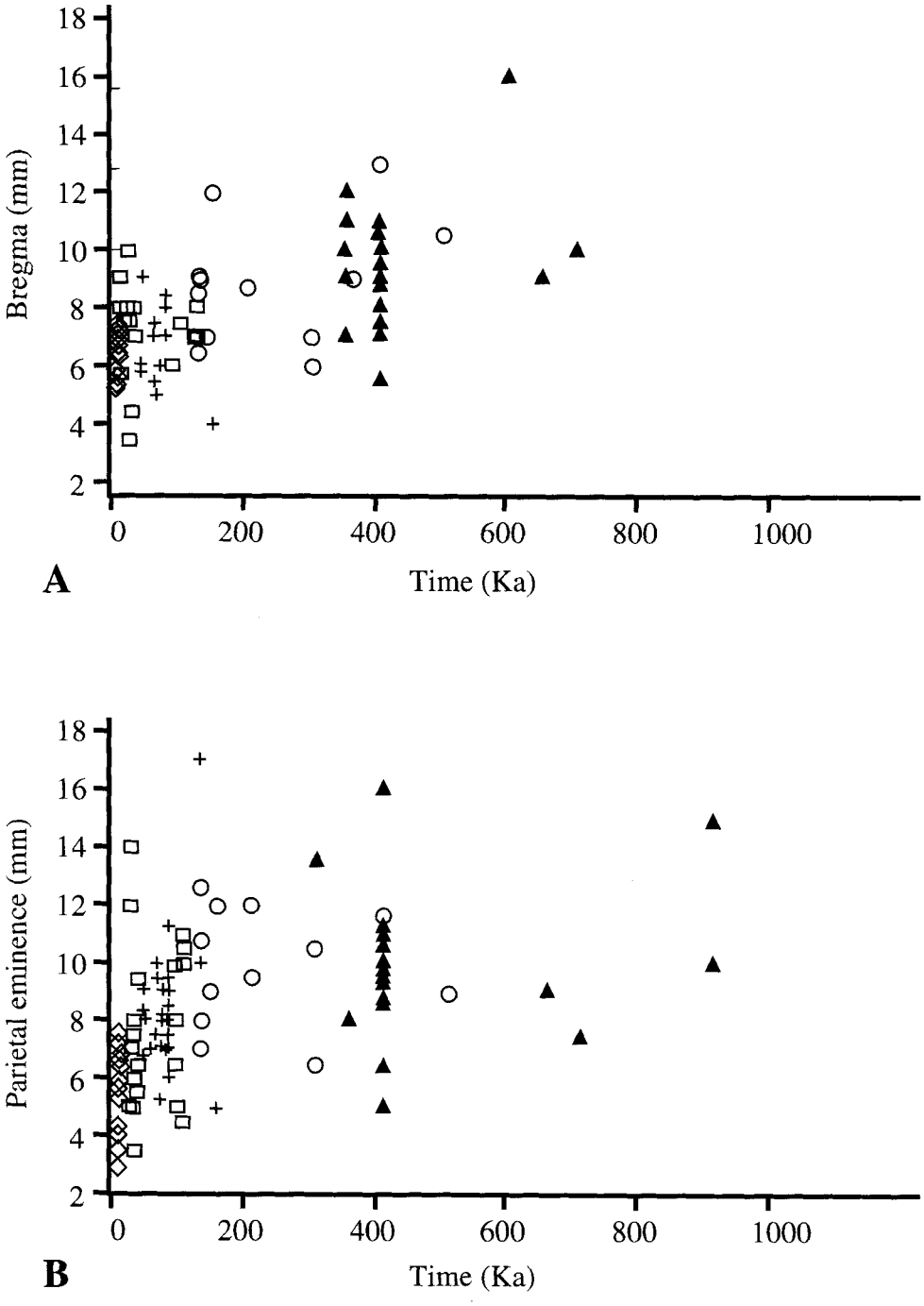


Fig. 1. Change in thickness over time at bregma **(A)** and the parietal eminences **(B)** for taxa within the genus *Homo*. See text for discussion of measurements and Table 2 for specimens included. Least square regression for bregma is 7.23 + 0.06x, $r^2 = 0.19$; least square regression for the parietal eminences is 6.7 + 0.007x, $r^2 = 0.35$.

inences than both Neanderthals ($P < 0.008$) and Pleistocene modern humans ($P < 0.0002$) and that Pleistocene modern humans have significantly thicker parietal eminences than Holocene modern humans ($P < 0.02$).

A thin cranial vault is clearly not a derived character unique to modern *Homo sapiens* relative to other taxa within the genus *Homo*. Subsistence strategy, however, does appear to have an effect on CVT. Among the post-Neolithic Holocene populations from Europe (and North America) and the Middle East listed in Table 2, seven are preindustrial farmers and four are postindustrial (as indicated in Table 2). A Student's *t*-test comparison of these two groups reveals that the populations of preindustrial farmers have significantly thicker vaults ($P < 0.02$) at both bregma and the parietal eminence than the more recent, industrial populations. Brown et al. (1979) have also documented significant differences in cranial vault thickness between recent sedentary Australian aborigines and earlier, more mobile aborigines. These data do not support the null hypothesis that CVT does not vary by subsistence strategy. Pleistocene hunter-gatherers tend to have thicker skulls than Holocene farmers (not enough data, however, are currently available to compare Holocene hunter-gatherers with farmers), and recent postindustrial populations tend to have thinner skulls than preindustrial farming populations.

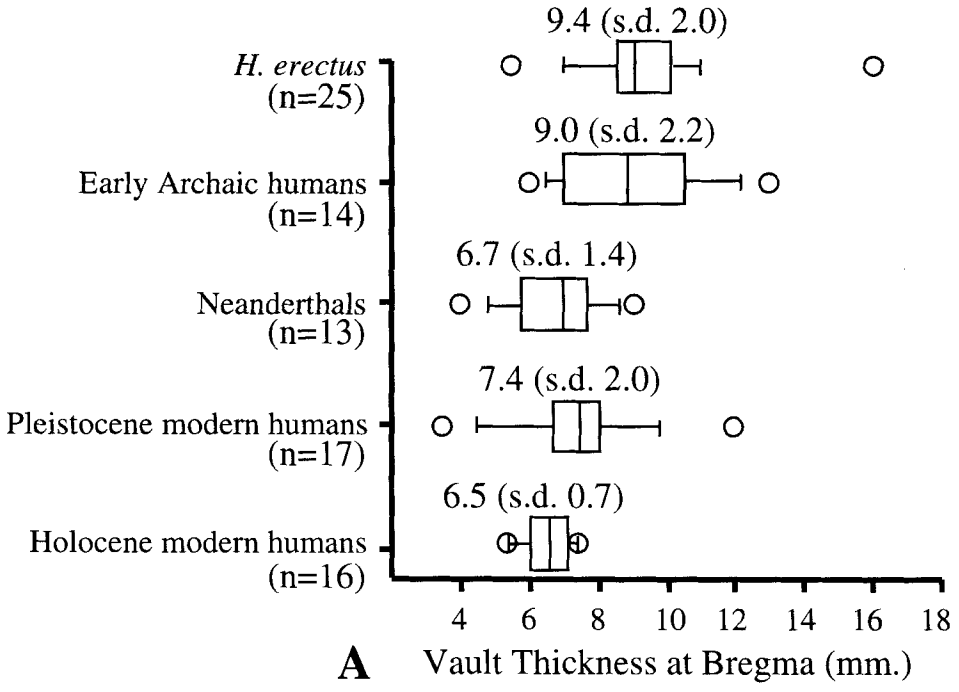
DISCUSSION

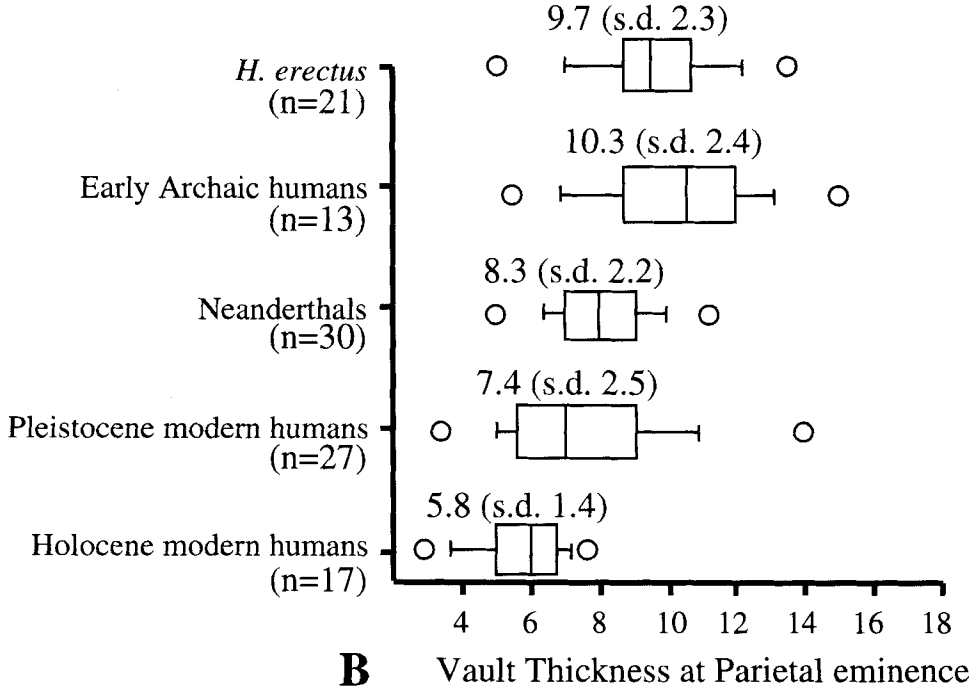
The fact that genetically identical armadillos and sibling pigs can develop differences in vault thickness equivalent to those between recent and Pleistocene humans (20–30% in most regions of the vault) suggests that CVT in these species is probably not a very genetically heritable character. The hypothesis that recent humans have thin cranial vaults because of a relaxation of selection to maintain thick vaults is, therefore, unlikely. In addition, the fossil record provides further evidence against the adaptation hypothesis. As discussed above, there is no apparent reduction in CVT associated with the transition from Middle to Upper Palaeolithic technologies, nor are early anatomically modern humans from the Pleistocene consistently more gracile in terms of vault thickness than contemporary or earlier archaic human populations such as the Neanderthals.

The hypothesis that differences in vault thickness among hominid taxa are attributable to local responses to loading from either running or chewing is neither rejected nor strongly supported. The neurocranium must experience some strain from the contractions of the *m. temporalis* that attaches along much of its surface, presumably generating inferiorly and laterally directed tensile forces in the bones and sutures of the vault. However, the strain levels recorded in the pig vault in this experiment—less than 150 με of shear—are low in comparison with strains recorded elsewhere in their postcranium (Lieberman and Crompton, in press). If the differences in CVT within taxa noted above are a consequence of strain-induced osteogenesis, then one must conclude that lower amounts of force are necessary to generate bone growth in the pericranium and endocranium. One might predict the cranial vault to have a much higher safety factor than other parts of the skull or postcranium because of the high cost of breaking a bone in this region (Hylander and Johnson, 1992; Hylander et al., 1992; Lieberman and Crompton, in press).

This safety factor hypothesis deserves further investigation but must remain tentative in the absence of stronger support and/

Fig. 2. Differences in vault thickness at bregma **(A)** and the parietal eminences **(B)** for taxa within the genus *Homo*. Boxes show the standard error, with a vertical line at the mean; the tails show the standard deviation from the mean, and open circles show the range. According to a single factor ANOVA, Pleistocene modern humans are not significantly thinner than Neanderthals at bregma or the parietal eminences. Holocene modern humans, however, are significantly ($P < 0.05$) thinner at the parietal eminences than all earlier taxa, including Pleistocene modern humans. At bregma, Holocene modern humans are significantly ($P < 0.05$) thinner than *H. erectus* and non-Neanderthal archaic humans but are not significantly thinner than either the Neanderthals or Pleistocene modern humans. See text for discussion of measurements and Table 2 for the fossils included in each taxon.


9.4 (s.d. 2.0)
H. erectus
(n=25)
9.0 (s.d. 2.2)
Early Archaic humans
(n=14)
6.7 (s.d. 1.4)
Neanderthals
(n=13)
7.4 (s.d. 2.0)
Pleistocene modern humans
(n=17)
6.5 (s.d. 0.7)
Holocene modern humans
(n=16)
4 6 8 10 12 14 16 18
A Vault Thickness at Bregma (mm.)


9.7 (s.d. 2.3)
H. erectus
(n=21)
10.3 (s.d. 2.4)
Early Archaic humans
(n=13)
8.3 (s.d. 2.2)
Neanderthals
(n=30)
7.4 (s.d. 2.5)
Pleistocene modern humans
(n=27)
5.8 (s.d. 1.4)
Holocene modern humans
(n=17)
4 6 8 10 12 14 16 18
B Vault Thickness at Parietal eminence (mm.)

or more rigorous testing. For instance, the osteoblasts in different regions of the skeleton may be activated by different strain threshold levels. Preliminary studies, however, indicate that neurocranial osteoblasts appear to be *less* sensitive to strain than in the postcranial osteoblasts. Rawlinson et al. (1995), for example, found that in vitro strains between 100 με and 1,000 με fail to stimulate osteoblasts from rat calvarium but do stimulate cells from ulnae. Moreover, other recent studies in several mammal species, including primates, have reported similarly low strain levels in the sutures and bones of the neurocranium. Behrents et al.'s (1978) in vivo study of strain around the sagittal suture in macaques during maximum, bilateral contraction of the temporalis muscles recorded maximum tensions of approximately 180 με across the suture and 100 με just lateral to the suture in the parietal bone. Sugimura et al. (1984) recorded on average 59 με of tension along the sagittal suture in dogs. Iwasaki (1989) consistently recorded peak shearing strain of less than 70 με in the temporal and parietal regions of the cranial vault in adult and infant macaques during chewing. In addition, it appears that several regions of the cranium other than the vault do not experience the high strains that are common within the face, mandible, and most of the postcranium. The low strain levels reported above in the pig occipital are consistent with those recorded by Hylander and colleagues in the supraorbital torus in macaques and baboons (Hylander et al., 1991; Hylander and Johnson, 1992). The browridge is, thus, more likely to be a developmental consequence of the spatial separation of the splanchnocranium and neurocranium (Shea, 1985; Picq and Hylander, 1989; Ravosa, 1988, 1991) than a beam to provide resistance against twisting or bending forces (e.g., Endo, 1966; Greaves, 1985; Russell, 1985).

Finally, the hypothesis that systemic hormones are the primary cause of variation in CVT is not rejected but is instead partially supported by this study. As demonstrated above, the pigs and armadillos who exercised daily experienced more systemic cortical growth than control animals throughout the skeleton. Since all bone growth is mediated by circulating hormones, it should not be surprising that exercise can induce systemic osteogenic activity. The hormone most likely to mediate this phenomenon is GH, which the anterior pituitary synthesizes in response to thyroid hormone as well as to corticosteroids. In most mammals, the anterior pituitary secretes GH every 3–4 h in a pulsatile fashion, with the largest peaks occurring during sleep. GH, which has numerous functions, is critical for inducing systemic bone growth by stimulating the synthesis of IGF-I and IGF-II (the somatomedins) that mediate many of its effects on cells, as well as by directly activating DNA synthesis in a variety of related skeletal cell types including fibroblasts, chondroblasts, and myoblasts (see Daughaday, 1989).

GH, moreover, is strongly linked to exercise and may, therefore, account for the overall differences in bone thickness between the exercised and control animals. Even moderate levels of exercise significantly increase secretions of GH secretion (Borer, 1980; Poehlman and Copeland, 1990). The magnitude of the GH response is related to work intensity, so that subjects who exercise regularly and strenuously have higher circulating GH levels than more sedentary individuals (Lasarre et al., 1974; Naveri, 1985; Van Helder et al., 1986; Felsing et al., 1992). The effects of higher levels of GH on systemic bone growth, including the cranial vault, are well established in mammals. For example, exogenous GH injected in mice causes them to develop thicker, longer crania and postcrania, particularly at the site of muscle insertions (Vogl et al., 1993). Humans with deficient levels of growth hormone prior to skeletal maturity (e.g., hypopituitarism) develop dwarfism unless they are treated with regular GH injections (Brook, 1989). Similarly, individuals with abnormally high GH levels develop gigantism (e.g., acromegaly). Acromegalics are not only taller than individuals with normal GH levels, but they also develop extreme cortical thickening throughout the skeleton, including the cranial vault; in contrast, individuals with GH deficiencies have abnormally thin cortical bone development in the skull and postcranium (Brasel et al., 1965; Randall, 1989; Pirinen et al., 1994).

It is, therefore, reasonable to suggest that higher GH levels induced by physical activity could cause the differences in CVT between the exercised and nonexercised animals reported above and that similar differences in activity levels in humans also produce variation in CVT. As demonstrated above, the most important factor that influences CVT in human taxa appears to be subsistence strategy since agriculturalists have thinner vaults than hunter-gatherers (although it is difficult to factor time out of this comparison) and postindustrial populations have significantly thinner vaults than farming populations. As one would predict, Ruff and coworkers (e.g., Ruff and Hayes, 1983a,b; Ruff, 1992; Ruff et al., 1993, 1994) have documented a similar relationship between subsistence strategy and limb bone cortical bone robusticity that appears to be relatively independent of taxonomy. Ruff et al. (1993:21) note that "early modern *H. sapiens* are closer in shaft robusticity to archaic *H. sapiens* than they are to recent humans." In other words, human populations who get less habitual exercise because of technological advances not only have thinner weight-bearing limb bones but also have less cortical robusticity throughout the skeleton. While nutritional and/or general health factors associated with these subsistence shifts undoubtedly occurred that must also be considered[3], these would probably have competing, opposite effects on CVT since better nutrition leads to increased rather than decreased rates of bone growth in the postcranium and cranium (Israel, 1978).

The hypothesis that systemic cortical robusticity is primarily a consequence of the effects of exercise suggests several predictions that can be tested using the fossil record. First, if bone thickness is a character with low heritability that is not subject to strong selective pressures, then neonatal and young *H. erectus* and archaic humans should have cranial vault and postcranial bones that are as thin as those of recent humans. Measurements of vault thickness on approximately neonatal archaic humans are available for La Ferrassie 4b (Heim, 1982) and for Hortus 1 and Hortus 1b (de Lumley, 1973)—all of which fall within the range for modern European values of CVT at birth, with the one exception of the maximum thickness of La Ferrassie 4b, which is 0.5 mm thicker (Minugh-Purvis, 1988). There are no fossils of *H. erectus* neonates, but the only known skull of an *H. erectus* infant, the Modjokerto fossil, has cranial walls that are very thin, "in the parietal region up to 3 mm., and elsewhere even less" (LeGros Clark 1978:99). The Modjokerto fossil thus falls within the range of modern values for infants between 2 and 3 years, which is likely to be a reasonable estimate of its age.

If, as these limited data suggest, CVT at birth is similar for all taxa of the genus *Homo,* then most of the variance in robusticity must develop later during childhood. In particular, one might expect the pattern of systemic growth differences in cortical bone thickness to occur in populations with high levels of exercise prior to skeletal maturity when the systemic effects of GH on growth are most profound. After adolescence, GH receptors at many sites of bone growth are blocked, leading to growth plate fusion and to a general deceleration of overall growth levels (Isaakson et al., 1982; Armstrong, 1988). This age-effect hypothesis remains to be tested, but there are several lines of evidence which provide some support. Brown et al. (1979) demonstrated that adult Australian aborigines tend to have thicker vaults than adult Americans of European descent because their vaults grow at a faster rate during adolescence. For example, the rate of growth of CVT at vertex (Fig. 3A) is about the same in Australian aborigines and Americans until about the age of 12, when there is a substantial decrease in growth rate in Americans but not Aborigines. Similar differences in growth rate after childhood but prior to adulthood also appear to account for the thicker skulls of Neanderthals and perhaps *H. erectus,* perhaps beginning as early as 3–4 years of age. Minugh-Purvis (1988) compared parietal thickness at bregma and the parietal eminences in Neanderthals and recent humans divided into

[3]Early farmers may have had decreased levels of nutrition compared with contemporary hunter-gatherers, but these populations are not considered here.

broad age classes (Fig. 3B). Although the sample sizes are unavoidably small, they clearly indicate that the differences in CVT between the two groups are the result of a continued rapid growth rate after infancy in Neanderthals when recent humans begin to experience a slower growth rate. Zollikofer et al. (1995) reached similar conclusions based on their computerized reconstruction of the Devil's Tower Neanderthal infant. It is significant to note that Pleistocene modern humans from Europe, like the Neanderthals, also had rates of cortical thickening more rapid than recent Europeans (Minugh-Purvis, 1988). In recent populations, vault thickness increases very slowly after the age of roughly 20 in both sexes until approximately 50 or 60 years of age (Todd, 1924; Young, 1957; Israel, 1973; Adeloye et al., 1975).

The development of cortical robusticity for the rest of the postcranium in archaic humans appears to mirror the apparent pattern in the vault. Ruff et al. (1994) analyzed cortical bone robusticity in two juvenile Neanderthal postcranial skeletons for which there is reasonable age data, Teshik Tash and La Ferrassie 6. While both have thick cortices, the ratio of their femoral cortex area standardized to femoral length is only slightly above that of recent humans. Some linear measurements of neonatal postcrania from La Ferrassie, however, are greater than those of recent Europeans (Heim, 1982). Since young archaic humans appear to be only slightly more robust than young anatomically modern humans, one cannot reject the hypothesis that there may be some genetic component to intertaxon variations in systemic robusticity, but the above data suggest that the source of the variation appears to be mostly nongenetic.

The hypothesis that CVT is primarily a consequence of systemic bone growth is also supported by the allometric relationship between CVT and body mass. Gauld (1992) and Nelson and Gauld (1994) have shown that CVT tends to scale positively with body mass in anthropoid primates, in spite of the fact that body mass clearly does not transmit through the skull. Gauld (1992, 1993), moreover, has shown that while recent, thin-skulled humans fit this interspecific regression well, postcranially based body mass estimates give *H. erectus* and archaic humans significantly thicker vaults relative to body mass than those predicted by the best-fit line for all anthropoids. Although Gauld (1993) has suggested that *H. erectus* and archaic humans may have had heavier body masses than their postcranial dimensions predict, such an argument clearly cannot apply to recent Australian aborigines and probably not to early anatomically modern humans whose body masses were almost certainly within modern human ranges. Perhaps we should not ask why recent humans tend to have thin skulls but why *H. erectus* and Pleistocene humans have such thick skulls. The answer may be that hunter-gatherers, from *H. erectus* until recent times, experienced relatively longer durations of sustained exercise relative to body mass than other anthropoids or recent humans. Alternatively or additionally, robusticity in non-stressed bones such as the vault might be a consequence of the longer duration of skeletal immaturity in the genus *Homo,* which would tend to increase the effects of exercised-induced systemic growth prior to adulthood.

In order to test the hypothesis that overall differences in robusticity are a consequence of GH-mediated epigenetic responses to exercise, particularly exercise that occurs prior to skeletal maturity, it will be necessary to integrate controlled developmental studies with measurements of in vivo levels of GH and other osteogenic hormones. In addition, it is not known to what extent systemic bone growth can occur during adulthood. Most studies on the effects of exercise on adult bone modeling and remodeling have focused on Haversian remodeling, calcium exchange, and changes in limb bone cortex in diaphyses and trabecular architecture in epiphyses (see Currey, 1984; Martin and Burr, 1989). Finally, we do not know whether or how different regions of the skeleton respond to disimilar strain levels.

The phenomenon of systemic bone growth in response to exercise merits further consideration for several reasons. From a clinical perspective, such research may help us to evaluate approaches to preventing or treating osteoporosis in humans. While there is consensus that weight-bearing exercise has important local effects on bone growth be-

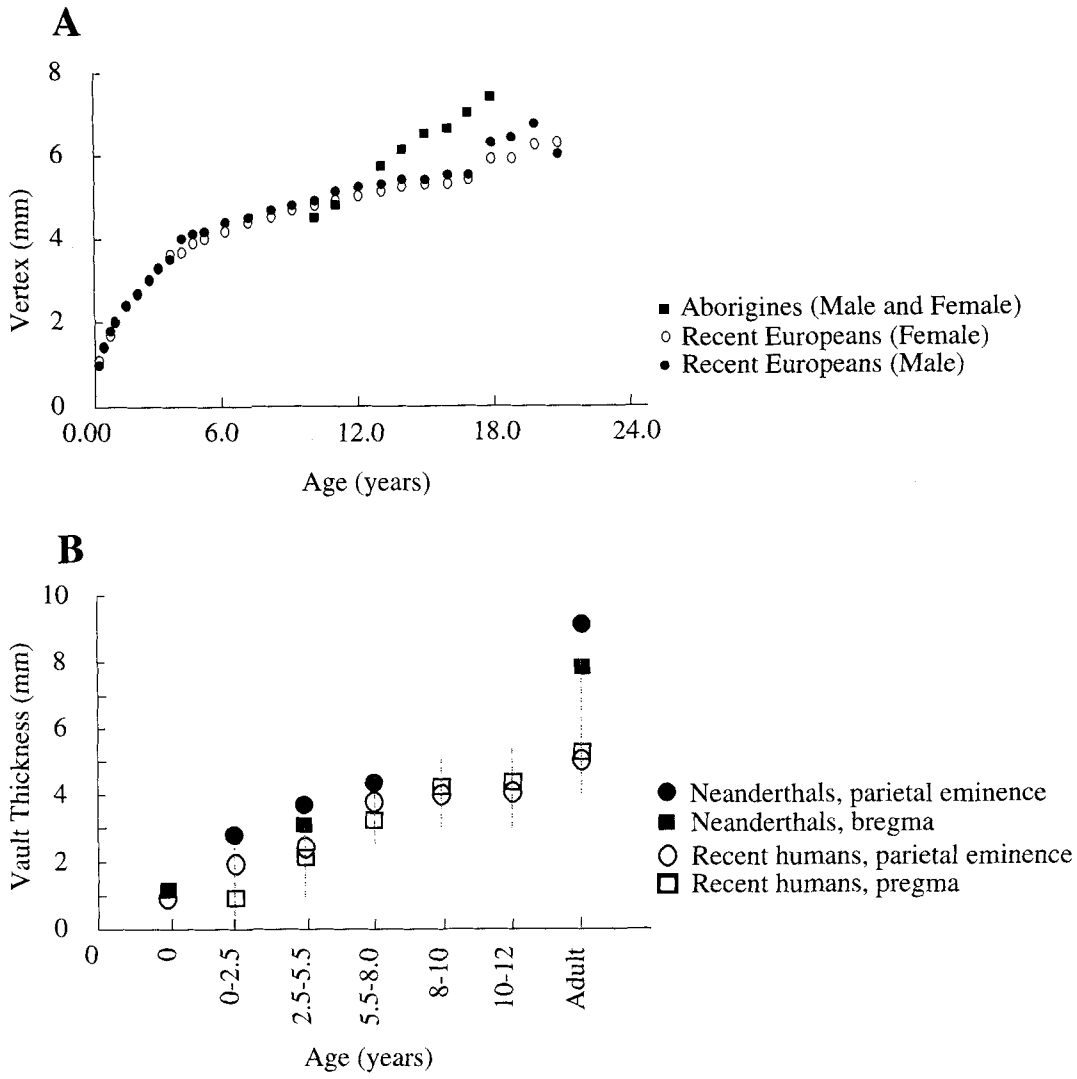


Fig. 3. **A:** Longitudinal increases in vault thickness at vertex in Australian Aborigines and Europeans. Data from Roche (1953) and Brown et al. (1979). **B:** Cross-sectional data on increases in vault thickness at bregma and the parietal eminence for Neanderthals and recent humans. Data from Minugh-Purvis (1988).

cause of strain, its importance for systemic growth has not been widely appreciated. The high rates of osteoporosis among old people in industrial populations may result from a sedentary lifestyle not only during adulthood but also during childhood and adolescence, with lasting consequences on cortical bone thickness. Exercise-related systemic cortical robusticity may, therefore, help explain why the single best predictor for a subject's likelihood to develop severe osteoporosis is how active she/he was is early in life (Lane et al., 1986). In addition, the phenomenon of exercise-induced systemic bone growth is important for interpreting certain aspects of the hominid fossil record. For one, it is clear that CVT is an inappropriate character to use for phylogenetic studies of the relationships of recent humans because it is neither a derived character of anatomically modern humans nor highly heritable (Lieberman, 1995). The above data suggest that early modern and archaic humans, despite their anatomical contrasts, may not have

been as different in terms of overall exercise as other studies have concluded (e.g., Lieberman, 1993; Lieberman and Shea, 1994). The thickness of the cranial vault may be similar in archaic and modern hunter-gatherers because, as a subsistence strategy, it demands frequent and regular exercise from a relatively early age. In other words, it appears that young hunter-gatherers, regardless of their anatomical modernity, obtained lots of exercise.

ACKNOWLEGMENTS

I am especially grateful to A.W. Crompton and F.A. Jenkins, Jr., for their support and help with the experiments and to S. Nawrocki for generously sharing data from his 1991 dissertation and for his detailed comments on an earlier draft of this paper. Additional thanks go to A. Glazer and T. Owerkowicz for running the animals and to D. Pilbeam, R. Trivers, B. Wood, and two anonymous reviewers for their suggestions. Funding was made possible by grants from the Milton Fund (Harvard Medical School) and the American School of Prehistoric Research.

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