Evolutionary emergence of a psychozooic, an animal relying for survival and reproduction on its intellect rather than on its sheer physical attributes, is of great interest to us humans, who are the only psychozooic known to science. There is little doubt that the human mind is more efficient in providing a range of behavioural adaptations than that of any other mammal. It is, however, still unclear how this better function is achieved. Anatomical, cellular and physiological details of human brains are very similar to those of other mammals, in particular the apes. The amount of cortex in the human brain in proportion to its overall size is not much different from that of apes and many other mammals; the same is true with respect to the proportion between the size of the cerebellum and the cerebrum.\(^1,2\) The main difference between the human and ape brain is its size. Evidence for the widely accepted assumption that hominid brain size is related to its functional abilities is critically examined in the present paper.

### COMPARATIVE ANATOMY OF HUMAN BRAIN SIZE

Brain size of an animal, obviously, must be considered in the context of its body size.

The relationship between brain and body size of vertebrates is allometric. Extensive studies\(^3\)\(^\rightarrow\)^\(^5\) have shown that the phyletic increase of vertebrate brain size is slower than the increase in body size. According to Jerison,\(^4\) a general relationship between mammalian brain mass (E) and body mass (P) is described by the formula:

\[
E = 0.12P^{0.67}
\]

Martin\(^6\) argues that the scaling parameter (exponent) of 0.75 is more appropriate, as it reflects the relationship between the metabolic rates of mammals and their brain size.

When a generalized allometric formula is applied to humans, their brain size predicted from body mass is much smaller than the one actually observed, thus showing our excessive ‘encephalization’. Allometric relationships between mammalian brain and body size differ between taxa\(^8\) and, thus, one can doubt whether one generalized formula should be applied to all mammals. Allometric relationships are dependent on specific proportions between various body parts of animals that develop as a mixture of their phyletic histories and adaptations to particular environments. Brain:body size indices, which are not based on generalized allometric formulae, do

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**Keywords**: Australopithecus, body size, body weight, encephalization, gut, Holocene, hominids, intelligence, Pleistocene.
not give us pride of place among animals. The simple brain
weight:bodyweight ratio of humans is 1:45, while it is 1:30 for a
New World monkey (Hapale rosalia) and even higher (1:25) for
common mice. Absolute size of elephant and whale brains exceeds
by several-fold that of the human brain.\textsuperscript{7,8}

The relationship between brain size and 'intelligence', as meas-
ured by IQ tests or by socio-economic performance, within present-
day humans is practically non-existent. Most studies find that brain
size explains approximately 1\% of the variance in variously meas-
ured 'intelligence' or mental aptitude.\textsuperscript{9-13} Recent studies using mag-
netic resonance imaging of the brain in individuals tested for IQ also
find modest correlations between the size of cerebral structures and
measures of intelligence.\textsuperscript{14,15}

**FOSSIL RECORD OF HOMINID BRAIN
EVOLUTION**

**Endocasts and cranial capacity**

The ape–human comparison sets the limits for what comparative
physiology and anatomy can reveal about our brain evolution.
Between the ape and ourselves there are no living intermediate
forms; the only possibility of revealing the specificity of human brain
evolution is to study fossil material. Alas, brains, being very deli-
cate, soft organs, do not fossilize. What, however, fossilizes well is
the braincase, the bones of the skull. Living brain impresses itself
onto the inner surface of the braincase due to intracranial bone re-
modelling. Therefore, the inner surface of the cranium bears impres-
sions of cortical sulci, gyri and meningeal vessels. During the process
of fossilization, some hominid skulls were filled, to varying levels,
with minerals from the surrounding soil, producing natural end-
ocasts. Those braincases that are found empty can be easily filled
with latex to produce artificial endocasts. The first *Australopithecus*
ever found, the Taung child, had a perfectly preserved natural endocast,
including the entire right hemisphere and parts of the left hemi-
sphere.\textsuperscript{16} Even as the impressions of sulci and gyri on the endocasts
seem to be accurate, there are difficulties with interpretation of de-
tails; just one detail of the Taung’s child brain endocast surface, the
position of the lunate sulcus, has become the subject of a series of
papers presenting competing views that the sulcus is either po-
ositioned in a human or in an ape’s way.\textsuperscript{17-19} Many hominid cranial
finds are fragmentary, thus preventing analysis of the details of the
brain surface. It is, however, relatively easy to reconstruct from the
size and shape of the fragments the total size of the braincase. Hence,
the feature that can be most consistently and uniformly studied for
a large number of hominid specimens is the total size of the brain
(cranial capacity). Although the volume of the braincase is some-
what larger than that of the actual brain, with the specific gravity of
the brain tissue being slightly above 1.0 g/mL,\textsuperscript{7} the volume of the
endocast becomes an acceptable approximation of the actual size
of the brain.

Avid searches of the fossil record of human ancestry over the past
century have produced over 200 variously preserved hominid pre-
Holocene crania whose capacity can be reconstructed. This fossil
record shows a striking and rather gradual, three-fold increase in
brain size over the past 4 million years from approximately 450 mL
in the *Australopithecus*\textsuperscript{20} to the modern human average of
1350 mL.\textsuperscript{21} This increase coincided with intellectual progress, as
revealed by increasing complexity of the material remnants of
culture: tools, weapons, hearths, shelters, burials and rock art. This
coincidence corroborates the hypothesis that mental capacity is
related to brain size. The fact that brain size of equids increased
3.2-fold over the same period of time is often overlooked, although
there are no known indicators of the change in equid intelligence.\textsuperscript{22}

**Cranial capacity and body size**

Numerous reconstructions of cranial capacities and body sizes are
available in the literature. In the present paper, an updated version
of the cranial capacity file compiled by Beals et al.\textsuperscript{23} and the body
size file compiled by Mathers and Henneberg\textsuperscript{24} has been used. The
file contains all estimates published until mid-1997. There are 276
estimates of cranial capacity, 297 estimates of body height and 626
estimates of bodyweight, covering the period from 5100 to 10 kaBP
(thousands of years before present). Descriptions of exact methods
used to produce various estimates included in the file are given else-
where.\textsuperscript{25-44} Averages of brain size and body size of modern humans,
based on some 10 000 individuals representing 122 populations
worldwide,\textsuperscript{21} were also used.

Statistical analyses consisted of calculation of regressions and
correlations between dates of fossils and their brain and body size
estimates. Linear and exponential regression models were used.
Significance of correlation coefficients was assessed by means of a
t-test at the 0.01 probability level. The analysis was limited to cranial
capacity and bodyweight because in all higher primates there is
a strong and uniform relationship between bodyweight and
height\textsuperscript{45} and, thus, analyses using body height as a body size in-
dicator yield results similar to those obtained using weight.

When the entire period of the past 5 million years of hominid evo-
lution is considered, it is apparent that the increase in cranial capacity
is accompanied by an increase in bodyweight (Fig. 1). The strength
of correlation with date is larger for cranial capacity, which has
a lower error of estimate than bodyweight. Both correlation co-
efficients are highly significant, indicating concurrence of brain and
body size increase.

Despite the large number of cranial capacity and body size esti-
mates for hominid fossils, we were able to find only 45 individuals

![Fig. 1](image-url)  Regression of fossil hominid cranial capacity (CC, dashes) and es-
timated body weight (open triangles) with date in thousands of years before
present. Scales of CC and weight are logarithmic, exponential regressions
were fitted to the data. Both correlation coefficients ($r = 0.91$ and 0.48,
respectively) are statistically significant ($P < 0.01$; d.f. > 200). Linear, log-
arithmic and power regressions all yield lower correlation coefficients for
both variables than the exponential regressions shown.
for whom both bodyweight and cranial capacity are available. These include Al-288, Oh5, TM1517 and WT15000 hominids dated at between 3300 and 1500 kaBP plus a number of Late Pleistocene (90–10 kaBP) specimens listed in the Ruff et al. file. A plot of cranial capacities of these hominids against their bodyweights yields an exponent of the allometric power curve practically equal to 1.0 (Fig. 2). The 95% confidence interval of the exponent is 0.889, 1.305. Therefore, the relationship between bodyweight and cranial capacity in hominids seems to be linear; that is, isometric rather than curvilinear, allometric. An isometric relationship is also obtained when average cranial capacities and bodyweights or heights of various hominid species are compared. In a large sample of brain size and bodyweight averages of modern human populations, a linear relationship with $r = 0.63$ was observed. This isometric relationship in hominids differs from negatively allometric relationships with exponents 0.67–0.75 recommended for calculation of mammalian encephalization quotients. When the standard allometric coefficient of 0.75 is applied to the data in Fig. 2, the squared correlation coefficient of 0.6604 is lower than that for the depicted isometric relationship (0.7299), while the confidence interval of the isometric exponent does not include 0.75, indicating a significant difference.

The decrease of human cranial capacity by approximately 10% of its average value (i.e. one standard deviation or approximately 100–150 mL) since the Late Pleistocene until the early 20th century has been documented on large samples from Europe and the Near East, Africa, Japan and Australia. This phenomenon of microcranialization has been accompanied by a decrease in body size (Fig. 3). The averages depicted in Fig. 3 seem to suggest that the decline in brain size was inversely exponential while body size declined in a rather linear fashion. Detailed analysis of this disparity must await accumulation of more data on body size; at this stage, it is sufficient to point out that correlation coefficients of both body and brain size on time, as presented in Fig. 3, are -0.99 and -0.95, respectively, and are both significant. It is worth noting that the reduction of human brain size during the past 10 kaBP coincides with the invention of agriculture, metal-based technologies, mass transport, urbanization, complex social and political systems and intellectual culture based on writing, mathematics and science. It can be argued that the recent decrease in average brain size is a result of the support provided by complex cultural systems for less intelligent and, thus, smaller-brained individuals. This would, however, produce a greater range of variation in modern human brain size in response to the postulated relaxation of selection. This is not the case as the variability of the modern human brain size is actually the same or smaller than that observed among fossil hominids.

Therefore, it seems that the hominid brain size tracks in its increase and decrease as well as in the individual variation the size of the body rather than the level of intellectual abilities. In samples of modern humans, correlation between brain size and bodyweight is weaker than that between brain size and body height, probably due to large individual variation in the amounts of body fat. Brain size is most probably related to the lean body mass consisting of the musculoskeletal apparatus and the highly metabolically active tissues of the viscera, rather than to the overall bodyweight, which may incorporate a substantial proportion of inert adipose tissue.

**Reduction of body size caused human encephalization**

Irrespective of its close relationship to body size, the hominid brain constitutes a larger proportion of total bodyweight than the brains of apes. Several authors have attempted to explain this greater encephalization of humans in terms of physiological factors unrelated to intelligence. Falk proposed that the prime physiological ‘releaser’ of brain size in the genus Homo was an evolution of a network of cranial veins that allow cooling of the enlarged brain under conditions of hyperthermia, which affected hominids during foraging in Africa (‘radiator theory’). Working from the similar premise of the need for thermohomeostasis in hominids hunting under the African sun, Fialkowski argued that the enlarged hominid brain was a result of the application of von Neumann’s rule, which states that a reliable system for information processing can consist of unreliable elements (neurons), provided the number of these...
elements is increased. This would produce structural redundancy, resulting in physical enlargement of the human brain. Sacher argued that the increased human brain size is related to our greater longevity as mammalian brain size is correlated with the length of life and the reproduction. Brain size of mammals seems to be scaling in proportion to their metabolic rates. This led Aiello and Wheeler to ask how, in terms of energy supply, can humans afford to have large brains. They proposed 'the expensive tissue hypothesis' stating that the reduction in the size of the hominid gut offset the increased metabolic requirements of larger brains. Although interesting, this hypothesis is untestable because energy balances of hominids may have changed in numerous ways other than the trade-off between gut and brain.

The observation that, during hominid evolution, the relative size of the gastrointestinal tract decreased in comparison with apes can be used to interpret human encephalization without speculation about the trade-off in metabolically expensive tissues. Since the Pliocene, the human gastrointestinal tract has evolved towards smaller relative size due to the ingestion of higher quality, partly extra-orally processed foods. This is a result of a combination of hominids turning to an increasing proportion of meat in their diets and to the use of tools and, later, fire to soften and chemically breakdown raw foods. These led to a reduction in the size of the teeth and masticatory skeleton as well as the muscles and size of stomach and the intestines. The basic cultural developments allowing this reduction to occur, use of weapons, tools and fire related to habitual consumption of meat, occurred well before 1 million years ago, at the time when hominid brain size was approximately one-half of its modern value. Hence, these cultural developments can hardly be considered a result of hominid brain expansion.

The change in hominid bodyweight during the Pliocene and the Pleistocene is a combination of two processes: (i) an overall increase resulting, like in many other mammals, from adaptive gains related to increased body size ('Cope's law'); and (ii) a decrease in the masticatory apparatus and gut size with a concomitant decrease in supporting musculoskeletal structures. It can be hypothesized that the variation in the size of the masticatory apparatus and gut is responsible for a sizeable portion of the variation in total body size, as this factor influences bodyweight directly and indirectly through the size of the locomotor apparatus required to carry around the gastrointestinal tract with its contents. Taking into account the three-fold increase in hominid brain size, hominid body size should increase from 35 kg in the Pliocene to 105 kg in modern humans. At the same time, however, the gut and the masticatory complex decreased to approximately 60% of their expected size. Loss of approximately 40% of the gastrointestinal and masticatory complex size could be hypothesized to have caused an overall reduction of the body size by approximately one-third (a conservative estimate). This reduction would result from the direct loss of the mass of the gastrointestinal and masticatory structures, a related decrease in the size of the trunk and a reduction in the size of the musculoskeletal apparatus required to support a relatively smaller face and trunk. The reduction of modern human body mass predicted by the three-fold increase in brain size (105 kg) by one-third produces the figure of 70 kg, which was the actual Late Pleistocene estimated human bodyweight and which lies close to the bodyweight of many modern humans. With a full 40% reduction in body mass, the estimate for modern humans is 63 kg. Pliocene hominid brain size (450 mL) and bodyweight (35 kg) yield a brain size/body size ratio of 0.013.

Applying this ratio to the hominid body size that is expected without gut reduction (105 kg), one obtains a brain size of the late hominid of 1365 mL, which is similar to the average for modern humans (1350 mL).

CONCLUSIONS

The macro-evolutionary enlargement of the hominid brain in parallel with that of other mammals, its co-evolution with body size, the micro-evolutionary decrease in human brain size during the period of major intellectual and cultural achievements and the virtual lack of intraspecific correlation between brain size and variously measured human 'intelligence' lead to the conclusion that the special qualities of the human brain are not the result of its size or, probably, also not of its gross anatomical structure. The unusually high human encephalization may be more a result of the reduction in the relative body size than the increase in brain size.

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REFERENCES

Evolution of the human brain