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HUMAN EVOLUTION EXPANDED BRAINS TO INCREASE EXPERTISE CAPACITY, NOT IQ
Target Article on Brain-Expertise

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Abstract

Why do modern humans have larger brains than earlier people such as Homo erectus? As large brains cause problems in childbirth, infancy and locomotion, the advantage they offer must be substantial. This advantage might be associated with increased IQ, but there is a problem: evidence from MRI volumetric surveys, microcephaly and hemispherectomy shows that there exist individuals with psychometrically normal IQ but Homo-erectus-sized brains. Why did evolution increase brain size (with its associated costs) when humans (as these individuals demonstrate) can have normal IQ without bigger brains? I propose that the advantage may be related to increased capacity for an aspect of intelligent behaviour not measured by IQ tests but critical to the survival of our simple hunter-gatherers ancestors: the capacity to develop expertise.

Keywords

brain size, brain imaging, evolution, expertise, hemispherectomy, Homo erectus, individual differences, intelligence, IQ, language, microcephaly, MRI volumetrics, psychometrics.

I. THE COGNITIVE PUZZLE OF OUR BIG BRAINS

1. Human brains expanded roughly by half between Homo erectus and modern Homo sapiens sapiens. The brains of modern people are roughly 1371 cc (male), and 1216 cc (female). In contrast, those of Homo erectus were roughly 930 cc (SD 130 cc, range 736 cc to 1172 cc, based upon the 28 cranial remains of Homo erectus intact enough to allow estimates of brain volume [Stanyon, Consigliere & Morescalchi, 1993; cranial to brain volume adjusted with equation 4 from Aiello & Dunbar, 1993] -- see also note 1). What aspect of early cognition drove this increase in size?

2. First, we should note that brain expansion beyond that of Homo erectus size causes neonatal, obstetric and female locomotor handicaps (reviewed below). Thus, whatever selected for increased brain size must have offered a very strong compensating benefit. Second, clinical evidence indicates that modern people can have brains no larger than Homo erectus yet exhibit normal IQ scores. Thus, the compensating benefit offered by large brains is unlikely to be intelligence as measured by IQ: Why should evolution have increased brain size with all its associated problems for something that Homo erectus sized brains could have without expansion?

3. Does this represent an anomaly, or are these reports of individuals with small brains with normal intelligence incorrect upon closer examination? I shall argue that neither of these is the case: Rather, the IQ/size puzzle may provide insight into the kind of the cognition for which evolution increased early human brain size. This is because psychometrically measured IQ leaves out many cognitions relevant to intelligent behaviour. In particular, IQ tests by design ignore one well studied area of intelligence, known to be independent of IQ scores: expertise (Ackerman, 1996; Ericsson & Lehmann, 1996; Ceci & Liker, 1986). I will argue the following:

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(i) The capacity for expertise correlates absolutely with brain
size: to have more capacity for expertise, a brain must be bigger.
The capacity reflects the number of "information chunks" that can
be created and processed, which may in turn be related to the
number of the cortical columns (Jerison 1991).
(ii) Expertise plays a critical role in the survival of simple
hunter-gatherers (Lee 1979); early humans would have been under
evolutionary pressure to increase their capacity for expertise.
Hence, empirical data could be brought to bear on whether it was
expertise capacity (rather than IQ) that selected for increased
brain size.
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4. This possibility may have been overlooked because it cuts across three different (and largely noncommunicating) areas of science. (1) Paleobiologists study the problems posed by the enlargement of the Homo brain. (2) Brain Imaging shows that contemporary individuals with brain size as small as that of Homo erectus can exist with normal IQ and can live normal, nonretarded lives (a finding that many paleoanthropolgists might doubt, in view of the presumed link between brain size and IQ). (3) Anthropologists report that expertise is a component of intelligent behaviour that is independent of what is measured by IQ tests, may be related to brain size, and plays a key adaptive role in the lives of hunter-gatherers. The primary objective of this target article is to review and bring together in one place these three separate areas of evidence. One hopes that PSYCOLOQUY's electronic medium will bring scholars in these various areas together.

II. LARGE BRAINS, LARGE PROBLEMS

5. The size of most but not all body parts can be increased without causing problems. For example, if it had advantaged earlier hominids that their legs or arms should increase or decrease 50% in length, no strong handicap (other than the changed nutrition needs for their physiological development and maintenance) would impede the natural selection of such different body proportions. This is not the case with hominid brain size, however. The expansion of the brain to modern dimensions since Homo erectus is known to have had severely disadvantageous effects on infancy, birth and female locomotion.

6. (a) To enlarge Homo erectus brains required developmentally extending brain growth into the first postnatal year. As a result, for its first year of life modern human infant is like a foetus outside the womb. This period of extreme immaturity would have substantially increased the burden and complexity of rearing infants (Martin, 1982).

7. (b) Not all brain expansion can be delayed into the postnatal period. To achieve its later size, the human brain is already highly enlarged before birth compared to other primate brains. In consequence, the human infant's head at birth is a tight fit in the birth canal. This creates considerable obstetric complications (Rosenberg, 1992), which became particularly significant when brain size increased with Homo erectus beyond 801 cc (Martin, 1982; his 850 cc figure for cranial volume is converted here to brain volume for comparability; Aiello and Dunbar, 1993, equation 4 [FOOTNOTE 2]).

8. (c) To minimise these problems, the female pelvis has increased its dimensions to accommodate the birth canal. Such anatomical adaptations have been achieved at the cost of a pelvis that is nonoptimal (though still functional) for efficient bipedal locomotion in women. (This is responsible for performance differences between men and women in sports depending on lower limbs; Day, 1992).

9. These disadvantages of increasing brain size suggest that some component of cognition increased by brain size must have outweighed them. Given that intelligence is central to the behaviour of our species, and that it is traditionally linked to its measurement by psychometric IQ tests, we would expect brain size to be related to normal IQ.

10. Moderate correlations between IQ and brain size do indeed exist (Wickett, Vernon, & Lee, 1994). However, outliers in the clinical and MRI volumetric literature cause theoretical problems for this correlation, for if small brains can support modern levels of intelligence today, why not a million years ago? Would not such small but bright brains have been selected in preference to large bright ones to avoid the extra problems associated with big brains? This anomaly only arises, however, if we assume that IQ tests measure the cognitions that favoured the increase of brain size in early hominids. As we shall see, an overlooked aspect of intelligent cognition, "expertise capacity," is a much better candidate. It turns out that this capacity is (i) not measured by IQ tests (indeed it is independent of IQ scores), (ii) central to early human survival, and (iii) directly linked to brain size. Thus, instead of an anomaly, we have a new way of empirically investigating the cognition central to human evolution. First, the MRI volumetric and clinical evidence for people with normal IQ and very small brain size will be reviewed and then the literature on expertise capacity and its importance for the survival of early humans.

III. SMALL BRAINED BUT NONRETARDED

11. Research of three kinds suggests that small brained people can have normal IQs: (i) a recent MRI survey on brain size (Giedd et al. 1996), (ii) data on individuals born with microcephaly (head circumference 2 SD below the mean; Dorman, 1991); and (iii) data on early hemispherectomy (the removal of a dysfunctional cerebral hemisphere; Smith & Sugar, 1975; Griffith & Davidson, 1966; Vining et al., 1993).

III.1. VOLUMETRIC SURVEYS UPON BRAIN SIZE

12. Jay Giedd and colleagues of the National Institute of Mental Health, Child Psychiatry Branch received 624 responses to a newspaper advertisement for a MRI brain scanning study of 4-18 year-olds (1996). This group was carefully screened with psychometric tests and a psychiatric interview. Those with a learning disorder (or family members with one) were excluded. Of the 624 responses, only 112 met their stringent criteria for "normality." After MRI scans, volumes for various brain areas were measured. Striking variance was found. Of the 104 individuals who successfully completed their scans, volume for the cerebral hemispheres ranged from 735 cc (a 10-year-old male) to 1470 cc (a 14-year-old male) (taken from scatter diagram, Fig. 4). Unfortunately, Giedd did not report total brain volumes, but these can be inferred. The cerebral cortex makes up only 86.4% of brain volume when measured by MRI (Filipek, Richelme, Kennedy & Caviness, 1994), so the total brain volume of the 10-year-old would be larger at 850.7 cc. Brains at 10 years are about 4.4% smaller than adult size (Dekaban & Sadowsky, 1978), suggesting that that brain would grow to an adult size of 888 cc. Even using the lower figure of 80% cerebrum to brain ratio derived from anatomical studies suggests a figure of only 960 cc.

13. The finding of normal people with small brains is not without precedent in earlier cranial circumference surveys. In a group of 1,006 school aged children, Sells (1977) found 19 (nearly 2%) to be microcephalics. On tests of Academic Achievement (measured by the Comprehensive Test of Basic Skills), nine performed above 50% (one individual scored at 81%). Of the 19, 12 had also been measured on standardised IQ tests (seven students were in school districts that did not do intelligence testing); of these 12, seven had average IQ or higher (one had an IQ of 129).

14. Of 188 children with microcephaly (of mixed origins, including Down syndrome) studied by Sassaman and Zartler (1982), 60 (39.1%) were not retarded and 13 (7%) were of average IQ. In two subgroups, there were more nonretarded individuals: amongst those with normal body growth, 48%, and amongst those with growth failure and head breadth deficiency, 44.4%, were nonretarded. The breakdown of the last group of 18 individuals is interesting, because the Stanford-Binet Intelligence Scale, Wechsler Intelligence Scale for Children-Revised and the Bayley Scales of Infant Development (Mental Scale) showed that four had normal intelligence (22%), two had below average intelligence, two were borderline, and ten were retarded (five mild, three moderate, none severe or profound, plus two "untestable"). Thus, while microcephaly is strongly associated with retardation and low intelligence, a small but significant percentage -- 7% overall, and 22% in one subgroup -- show average intelligence despite their small brains.

III.2. MICROCEPHALIC INDIVIDUALS

15. In the late 1960s, several paleoanthropologists (Holloway, 1968; Lenneberg, 1967) noted that microcephalic individuals could speak despite having very small brains. All such cases, however, were mentally retarded. More recent clinical reports have shown that microcephalics need not be retarded and often have normal IQs.

16. Livia Rossi and colleagues (1987) reported a genetic study covering 21 autosomal dominant microcephalic adults and children of six families. Psychometric tests were given to 13 of them and only one was found to be retarded. (Several microcephalic individuals, it should be noted, refused to do IQ tests, as the researchers observed, "because they perceived themselves as perfectly normal" and resented the implication that they were not (p. 656)!) Of the 13 who allowed their IQ to be measured, a 29 year old mother, referred to as C2, is notable for the extreme smallness of her brain (4.7 SD below a control group) given her above average mental abilities.

17. C2 had the smallest brain amongst the 21 microcephalics. Nevertheless, she had a Wechsler IQ of 112 and a performance on Raven's matrix task described as "good." Her school record notes she was good in mathematics though inadequate in "Italian literature." At present her employment is described as semi-skilled, but this is typical for people in her area.

18. Unfortunately, though C2 has a head 4.7 SD smaller than average, the exact size of her brain is unknown. Only her cranial volume and head circumference were measured, together with those of a control group of 15 women. This found her to have a head circumference of 48.8 cm, 4.7 SDs below that of a control group range of 53.3 and 56.2 cm (with deviation from the mean between -1 and +1.4 SD). For comparison, reference data for US children indicate that the average female child has a head circumference of 48.6 cm at two years and 54.4 cc at 18 (Roche, Mukherjee, Guo & Moore, 1987). C2's cranial volume was estimated by Moesch's procedure (displaced water with head immersed to the upper rim of the orbit and occipital protuberance [which hence includes the volume of a person's hair]). The volume of the heads of the 15 control women by this measure was 2,118+/-158 cc; C2's was 61% of this, at 1,300 cc. On the surface this may seem an inadequate guide to brain volume given that the average female brain has a volume of only about 1216 cc. But head size includes the skull and the meninges surrounding the brain; these are usually described as filling up roughly one centimetre around the brain (as can be seen in any brain scan which includes the surrounding skull); and, of course, this volume also includes hair volume. This would account for apparent discrepancies: for example, the volume of a sphere one centimetre smaller in radius than one which would give a volume of 2118 cc is 1416 cc; if 1.345 centimetres smaller, it would be 1216 cc (the average volume of a female brain). Comparison with the control group (assuming they have average brain volume, and that the measure of head volume parallels brain volume) would suggest that C2 has a brain volume somewhere near 741 cc. An alternative approach would be to note that the average volume of a female brain is 1216 cc with 194 cc at 2 SD, which would suggest a brain at 4.7 SD would be 760 cc. It would thus seem unlikely that her brain approached anywhere near normal size and was possibly on the low side for Homo erectus.

19. Medline searches under microcephaly and normal intelligence (or normal IQ) yielded 21 other reports of microcephaly and normal intelligence, though unfortunately most papers do not report psychometric or volumetric data.

III.2.2 DANIEL LYON

20. One report of normal intelligence exists for a brain smaller than Homo erectus. According to Wilder (1911), Daniel Lyon was a nonretarded white watchman who worked for 20 years at the end of the nineteenth century in New York at the Pennsylvania Railway Terminal. He could read, write, and according to legal representatives of the company that employed him "there was nothing defective or peculiar about him, either mentally or physically." He was of average weight 65.8 kg, though of a below average height of 1.55 m. After he died at age 46 in 1907 from bronchitis, his brain was removed and subject to a professional autopsy with "accurate scales." It weighed just 680 grams (624 cc assuming a specific gravity of 1.09 for fresh brain).

21. Upon examination, Wilder could not attribute the small size of Lyon's brain to either pathology or atrophy. Indeed, the only unusual feature he noted was that the cerebellum was near normal size. This suggests that the volume of Lyon's cerebral hemispheres might have been small even for his already small brain. Indeed, the total size of his cerebral hemispheres, 371 cc is 128 cc less than the 499 cc (80%) which would be expected of a normally proportioned brain of 624 cc.

III.2.2 ANATOLE FRANCE

22. All these cases have been average or only slightly above average in intelligence. Perhaps small brains prevent extremely high levels of intelligence. But distinguished modern people have had brains within the size range of Homo erectus. For example, the brain of the Noble Prize winning novelist Anatole France (1844-1924) weighed 1017 grams (933 cc) post mortem (Gould, 1981, p. 92). One qualification to this figure is that brains shrink slightly with age and Alzheimer's disease. Although 80 years old, he was nondemented (he had married one Mademoiselle Emma Laprevotte only a few months before he died). Estimates for brain shrinkage over the 20 to 80 year age range for men vary in six studies between 3.9% and 8.6% (Dekaben & Sadowsky, 1978), suggesting France's brain when young could have been as big as 1013 cc, yet still well within the SD range of Homo erectus, 930 cc - 130 cc.

III.3. HEMISPHERECTOMY

23. One rare treatment for brain pathology is hemispherectomy: removal of one of the two cerebral hemispheres. Only those with severely diseased brains have such operations; thus (as might be expected) while the surgery does not make them any worse, it leaves most in a poor state. A few, however, recover to lead surprisingly normal lives and show psychometrically normal or above normal IQs.

24. Smith and Sugar (1975) report the case of a male who started to become paralysed on the right side at five months; he had seizures at three and at five and half and consequently had his left hemisphere removed. In spite of this, he went to a normal school, learned to play the baritone horn, and even became a member of his high school band. At 26, he was working as an "industrial executive (traffic controller)" having completed "his senior year at a prominent Midwestern university with a dual major in sociology and business administration." His full IQ at that time was 116 (WAIS verbal IQ, 126; performance IQ, 102).

25. Griffith and Davidson (1966) report the case of P.G. who at the age of 10 started having seizures followed a year later by paralysis on the left side of his body. At the age of 19 he had his right cerebral hemisphere removed. Postoperatively, his IQ according to the revised Stanford Binet was 142 points; Wechsler verbal, 118, and performance, 94. 15 years later, at

34, he was retested; the Wechsler verbal had increased to 121 and the Wechsler performance had remained relatively unchanged at 91. Since his operation, according to Griffith and Davidson,"having obtained a university diploma after [the] operation [he] has [now] a responsible administrative position with a local authority."

26. Vining and colleagues (1993) report the outcomes for 12 hemispherectomized children at an average of 9 years follow up. They give extended details on five of them. One case, "13," a female, is of interest. She started having seizures at five; by seven she was having up to 20 a day. At seven and half, she had a left hemispherectomy, remaining in coma for six weeks. Two years later she had a full scale IQ of 98. Three years afterwards, though she needed some help in mathematics, she was in seventh grade gaining grades of A and B.

27. The brain mass following hemispherectomy in these three individuals can only be estimated. The human cerebral cortex makes up 80% of the total brain (using the percentage found by post mortem rather than MRI); as a result, hemispherectomy will reduce it by around 40%. Assuming that their initial brains were average, their brain mass would have been 1371 cc, of which 1097 cc would be cerebral cortex and associated white matter. Thus, they would have lost around 548 cc of cortical tissue, leaving them with a brain of around 823 cc. Similar calculations for the average volume of a female brain would suggest a brain after hemispherectomy of 730 cc.

28. As a group, the above cases provide evidence that some brains can have normal cognition according to psychometric tests despite being within the range of the average Homo erectus or smaller.

IV. OBJECTIONS

IV.1. SMALL BRAIN SIZE NORMALLY LINKS TO RETARDATION

29. The above individuals are exceptions: the presence of a small brain in the overwhelming number of individuals (whether due to early brain removal or microcephaly) is associated with retardation. However, this would be expected. Even if microcephalic brains were capable of normal levels of intelligence, the pathological factors responsible for their abnormal brains not only reduce their size but will usually have other effects (independent of this) on their neural integrity. In the case of hemispherectomy, the prior pathology in the original brain might already have effected the remaining normal brain. Thus, it will be relatively uncommon that brain mass is reduced without a parallel but separate impairment of cognition.

IV.2. BRAIN INJURIES DESTROY COGNITION

30. Following accidents and strokes, people show dramatic loss of cognitive abilities. This might be taken to suggest that the brain cannot work with reduced brain mass. However, the damage in these cases is connected with its suddenness. The brain can easily recover from injuries incurred in small stages, but not when they occur all at once (Feeney & Baron, 1986). This is in part because sudden brain injuries are followed by the release of excitotoxins which cause further neuronal loss. In contrast, the brain loss which occurs slowly can pass without notice. For example, asymptomatic meningioma can grow (at an average of 2.4 millimetres a year) into the size of plums -- five in centimetres diameter -- without noticeable effects (Olivero, Lister & Elwood, 1995). Interestingly, even when brain damage is sudden, as with

post-traumatic atrophy or focal damage, it can happen with minimal change in measured IQ (Bigler, 1995).

IV.3. IQ CORRELATES WITH BRAIN SIZE

31. Although IQ correlates with brain-size, the correlation is modest, the best recent estimate being around 0.40 (Wickett, Vernon & Lee, 1994). The percentage contribution of a 0.40 correlation is 16%, leaving 84% of intelligence to be explained by things other than brain size. Even higher reported correlations of up to 0.51 (Andreason, Flaum, Swayze et al., 1993; Willerman, Schultz, Rutledge & Bigler, 1991) would still leave 74% of the variance unexplained. Moreover, such IQ/brain-size correlations derive from studies on educated people with a restricted range of IQ and brain size, raising methodological problems about their generality (Peters, 1993). It is not known whether the 0.40 correlation found between IQ and brain size likewise holds in extreme cases outside the range tested; indeed, the evidence reviewed above suggests that it does not. Moreover, size would not be expected to increase cognitive competence more than modestly because larger brains have larger neurons and more myelinated axons connecting them (Deacon, 1990). It is perhaps because for this reason that people with larger than normal brains are not necessarily brighter (DeMyer, 1986); indeed, there appears to be a plateau and perhaps a decrease in IQ in the largest brains (Reiss, Abrams, Singer, Ross, & Denckla, 1996).

32. The 0.40 correlation, moreover, does not by itself rule out the existence of outliers. A statistical correlation is, after all, only a mathematical means of describing a data set. Thus, the 0.40 correlation between IQ and brain size is in itself not evidence against the existence of the cases reviewed above.

V. EXPERTISE, IQ AND EVOLUTIONARY COGNITION

V.1. PSYCHOMETRIC IQ

33. Perhaps surprisingly, given its status, psychometric measures of intelligence deliberately leave out some aspects of cognition known to be linked to intelligent behaviour. First, Binet and Simon, the founders of IQ testing, wished to separate "natural intelligence from instruction" by "disregarding, in so far as possible, the degree of instruction which the subject possesses" (Binet & Simon, 1908/1961, p. 93). As a result, from its advent, IQ testing has excluded that important aspect of intelligence that concerns a person's capacity to learn a skill in depth over a prolonged period (which would require measuring skills that might have depended upon "instruction"). Second, IQ tests are for pragmatic reasons restricted to measuring skills that can be tested with easily administered and standardised tasks. The result is that IQ tests are biased toward measuring those skills which can measured in terms of performance against time (it is easy to time performance) while ignoring a person's capacity to know a specialised domain in depth (it is difficult to create standardised measurements for this). Reflecting these factors, although IQ tests show high correlations with tasks that measure reaction times, such as the time taken to judge whether two lines are different lengths (Deary & Stough, 1996; Kranzler & Jensen, 1989), they show very moderate to zero correlations with people's ability to acquire expertise (Ackerman, 1996; Ceci & Liker, 1986; Doll & Mayr, 1987; Ericsson & Lehmann, 1996; Shuter-Dyson & Gabriel, 1981).

V.2. EXPERTISE CAPACITY

34. Experts bring to a problem a store of knowledge acquired over a long period that shapes how they analyse and approach its solution. Generally, novices view a problem situation in terms of its salient features (they lack knowledge of how to analyse it better), whereas experts (with their extensive knowledge) retrieve part of the solution as they comprehend it (Ericsson & Lehmann, 1996). Hence, whereas nonexpert players see only chess pieces, chess masters see possible future moves and potential strategies. Such in depth perception arises from acquiring and being able to actively use a larger numbers of informational "chunks" in analyzing a problem. The number of such chunks in chess masters has been estimated at 50,000 (Gobet & Simon, 1996). Such information processing chunks take many years to acquire. After reviewing performance in sport, medicine, chess and music, Ericsson and Lehmann (1996) propose that before people can show expertise in any domain they must have performed several hours of practice a day for a minimum of 10-years.

V.3 EXPERTISE AND BEHAVIOURAL INTELLIGENCE

35. In the modern world, in depth knowledge is not required for nonretarded and successful existence nor for being measured with a normal IQ. In general, skills depending on in depth knowledge are limited to a few occupations or task domains which require a person to process a large variety of possibilities, variables or options (Ericsson & Lehmann, 1996). One example which has been studied in the context of IQ is the ability of those with many years of daily experience in studying racing statistics to predict the odds in races (Ceci & Liker, 1986). This requires making complex inferences and trade-offs between statistics concerning horses, jockeys and the physical state of different race tracks. Reasoning among experts can be as complex as considering "the need of horse A to avoid challenging horse B at the first quarter mile mark, if horse C is to have any change of beating horse D." Ceci and Liker (1986) measured the IQs (Wechsler Adult Intelligence Scale) of experts in predicting form. For 12 experts, IQs ranged between 81 and 128 (four were between 80 and 90, three between 90 and 100, two between 100 and 110 and only three above 120 Table 6). Ceci and Liker (p. 265) comment "whatever it is that an IQ test measures, it is not the ability to engage in cognitively complex forms of multivariate reasoning." The expert performance in other domains such as chess (Doll & Mayr, 1987) and music (Shuter-Dyson & Gabriel, 1981) likewise show expertise that correlates poorly, or not at all, with IQ.

V.4. EXPERTISE AND EARLY HOMINID FITNESS

36. Although the capacity to develop expertise is not necessary for normal life in a modern industrial society, such skills would have been critical for the survival of early hunter-gatherers. Lee (1979) noted that in hunting the !Kung use in depth expert knowledge and reasoning. For example, hunters can spot from a particular track the animal which made it, its sex, age, whether alone or ill, what it was eating, and how long ago (to within 15 minutes) since the animal made the track. They can do this by reading the shape, depth and condition of tracks, whether they are alone, and how they are spaced and located. Tracks found to the east side of a tree might suggest that the animal rested there in the morning shade (Lee 1979, pp. 212-213). Such knowledge, like other forms of expertise, takes many years, indeed decades, to learn. Moreover, it is known to be more important than physical skill to hunting success: the individuals most successful at hunting are those in the over 39 age group (with decades of experience tracking), not the more physical able (but less experienced) individuals under this

age (Lee 1979, pp. 242-244). Indeed, an old man in his fifties or sixties might go with a young man (usually his son), interpreting the tracks while the young man does the hunting.

37. This example suggests that among early humans the individuals with the brains that had the greatest capacity to acquire expertise would survive more successfully than those without their extensive knowledge. The reasons for this would not only include expertise in hunting but expertise in many other activities such as gathering, tool manufacture and social communication. Over time, the advantages conferred by success in these activities would result in the natural selection of brains with increased capacity for expertise.

38. One factor increasing a person's expertise capacity is likely to have been brain size. Expertise, as noted, is linked to the number of chunks a person can hold and actively process. Capacity for expertise may be related to the number of cortical columns able to specialise neural networks in representing and processing them, and through this to cerebral mass (Jerison (1991). There is also some recent evidence that the increased information processing requirements of expertise lead to skill expansion over large areas of the cortex. Expertise in violin playing depends upon fine coordination of the left hand fingers and accurate coordination between the two hands. If expertise is related to increased cortical area devoted to finger coordination, we would expect expert violinists to devote more of their brain to finger coordination. This is indeed the case. Expert violinists have two to three times as much area cortical area devoted to their left fingers as nonviolinists (Elbert, Pantev, Wienbruch, Rochstroh & Taub, 1995). Moreover, the need of expert violinists to coordinate their two hands leads them to develop a larger connection between the two sides of the brain dealing with motor coordination compared to nonviolinists (Schlaug, Jaencke, Huang, Staiger & Steinmetz, 1995). Thus, there is not only theoretical but empirical evidence that expertise needs large amounts of brain to store and actively process its informational chunks. This suggests that a strong connection should exist between the capacity for acquiring expertise skills and brain mass.

39. In conclusion, the puzzle of individuals with Homo-erectus-sized brains but normal IQ may be explicable. Intelligence may be related to IQ tests, but the intelligence which was central to the evolution of our brains could be associated with something IQ tests do not measure: expertise capacity. Although the example given above concerns hunting, no reason exists why expertise in this should have been the sole advantage of larger brains. Expertise in gathering, scavenging, social relationships, language, tool making and passing on acquired skills and knowledge could likewise have been critical.

VI. FUTURE RESEARCH

40. If expertise is the missing link between brain size and human intelligence, then opportunities exist for cognitive scientists and clinicians to contribute directly to understanding human evolution. The evidence of small brains and normal IQ needs to be investigated in much more detail. Do individuals with normal IQs but small brains show limited expertise, as might be predicted? As noted, expertise would have been important not only in hunting (the only case discussed here, owing to lack of both space and evidence), but also in social skills and the motor control needed in tool making. The role of expertise in these areas still needs detailed study by social psychologists and motor control scientists.

41. Recent volumetric studies of the brain have found considerable variation in the size of brain areas. Raz and colleagues (1997), for example, have found great volumetric variation in the inferior parietal cortex and even more in the primary visual cortex (1997: diagram 5B). Does one's capacity to develop a form of expertise depending upon the abilities of circuits in a particular area vary with that area's size?

42. Psychologically oriented anthropologists need to provide us with observational data about the role of expertise in simple hunter-gather bands, especially in nonhunting activities such as gathering. One of the PSYCOLOQUY referees for this papers questioned whether tracking as done by the !Kung actually required expertise. There is no anthropology of the expertise of such activities with which to answer him. By engaging in an interdisciplinary "colloquy" over expertise, palaeoanthropology and many areas of psychology could do much to advance the science of our origins.

NOTES

[1] Estimates of the capacities of some early hominids have recently been called into question (Conroy et al., 1998), but concerns are about an estimate of an Australopithecus africanus cranium that was published in a nonrefereed source and out of line with other estimates for A. Africanus.

[2] The formula derived by Aiello and Dunbar (1993) for linking hominid skull volume to brain volume is Log10(B) = 3.015 + 0.986 Log10(C), where B is the total brain size in mm3, and C is the internal cranial capacity measured in cc.

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