Brain Size and Intelligence in Man

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ABSTRACT Although estimates of brain weight are useless in prediction of individual intelligence in man, the available data (none of them entirely adequate) suggest that the real correlation may be as high as 0.3. Evaluation of causes suggests the participation of a direct effect. Natural selection on intelligence at a current estimated intensity suffices to explain the rapid rate of increase of brain size in human evolution. Selection on birth weight may also suffice for this. It does not seem overly difficult to estimate directly the relationships among brain weight, intelligence, and fitness.

It is commonly and often vehemently stated that there is no relationship between brain size and intelligence in modern man, although a causal relationship when different species are compared is usually granted. Rensch ('58) and Hemmer ('71) investigated the latter point at length, and Tobias ('70, '71) has objectively reviewed many anatomical and anthropological aspects.

The evidence I know suggests a relationship in man strong enough to be of major evolutionary importance. I will review this evidence briefly, reanalyze some of it, and quantify the selective pressure implied. I do not claim to prove a relationship, but rather to show that it is a real possibility which deserves unbiased attention. I do not mention diverse related topics which, however interesting they may be, are beyond the scope of this paper.

CORRELATIONS

I know of no study that directly correlates brain size (or even cranial capacity) and intelligence. Between 1900 and 1930, however, a number of people studied the relation between intelligence and external measurements of the head. Paterson ('30) reviewed these studies. I have found almost no suitable papers after 1930, although there are a few medical reports (e.g., Nelson and Deutschberger, '70) on young children or mental defectives. Clark, Vandenberg, and Proctor ('61) studied intelligence and head measurements of a small sample of like-sexed adolescent twins, using con-

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cordance or discordance of direction of the difference of the measurements as the variable tested. They found a stronger relationship than in the earlier studies, as their better control of extraneous variables makes reasonable, but their method of analysis precludes an unbiased estimate of the correlations (see APPENDIX). Schreider ('56, '68) studied peasants and Mexican Indians, but his samples were so small that his estimates of correlation have large standard errors and differ significantly neither from zero nor from the largest estimate made in other studies.

Probably the best of the earlier studies are those of Pearson ('06 and earlier work cited there), Pearl ('06), Murdoch and Sullivan ('23), Reed and Mulligan ('23), and Sommerville ('24). Using crude measures of intelligence in most cases, all found correlations of 0.1 or somewhat higher with external linear measurements of cranial size. Use of head circumference or an index based on the product of linear measurements did not appreciably raise the correlations. Both Pearson and Reed and Mulligan removed the effect of body size by partial correlation; again the correlations were unchanged. The same treatment of Sommerville's results halves the ostensible correlation, but the standard error is so large that this study has little value. Schreider's samples give similar results. Murdoch and Sullivan did not calculate the correlation between head length and stature, but assuming a value of 0.30 [as found by Reed and Mulligan ('23) and Lee, Lewenz,

and Pearson (02) the partial correlation between intelligence and head length is 0.19. If we weight various estimates of the normalized correlation z (Cohen, '38, '41; Hammond, '42; Howells, '51, Moore and Hsü, '46; Rees and Eysenck, '45; and the above studies) by the reciprocal of the variances of these estimates, we get a value of the estimated correlation r = 0.27, which results in the same partial correlation of 0.19. The correlation between stature and brain weight is the same as that between stature and external head dimensions (Schreider, '66; linearity of the relationship was not tested and is suspect because of the different dimensionality of the variables, but see APPENDIX). The data (Eyerich and Loewenfeld, '05) used by Pearl ('06) do not permit correction for stature. There seems to be no correlation of brain weight and body weight except for the effect of stature (Paterson, '30; Schreider, '66; Pakkenberg and Voight, '64; Spann and Dustmann, '65). All the studies controlled age and sex. Table 1 compares the studies. It is interesting and possibly a real effect that the highest correlation comes from the only study to use a reasonably good measure of intelligence on a large and nearly random sample. Exclusion of individuals with high or low intelligence reduces the correlation by the statistical artifact of changing the shape of the distribution; Murdoch and Sullivan ('23) halved their correlation by excluding individuals with IQ's above (or, in another comparison, below) 100. Their correlation of 0.22 between estimates of head size and intelligence is the same as the unweighted mean of 11 independent estimates of correlations between various mental test scores and stature (Schreider, '67, '68; Murdoch and Sullivan, '23; Sommerville, '24), most of which lack published details.

A population correlation (ρ) of 0.1 means that 0.01 of the variance of either variable is geometrically, if not causally, determined by the other. This lack of predictive power for individuals is what has been emphasized, perhaps first by Pearson and Pearl.

However, natural selection does not care about individuals and is sensitive to small average effects. The common extrapolation of the conclusion about individual prediction to a conclusion about natural selection therefore does not follow, as Pearson ('25) noted.

We can go further. The observed correlation of 0.1 is between poor measures of intelligence and poor measures of brain size. Any real relation between intelligence and brain size will be diluted by the random noise introduced by inadequate measurement. This loss of information can be quantified.

Let i denote intelligence, b brain size, and c external cranial size. Assume that cis correlated with i only through its relationship with b. Then, as proved in the

APPENDIX,
$$\rho_{ic} = \rho_{ib}\rho_{bc}$$
 (1)

For example, we can take $\rho_{ic} = 0.1$ and $\rho_{bc} = 0.5$ (see APPENDIX). Then $\rho_{ib} = 0.2$. The difference of ρ_{ib} from 0.1 would be less if part of ρ_{ic} has some other cause. We can apply the same equation to loss of information because of poor measures of intelligence. If the loss here $(1 - \rho^2)$ is 0.5, ρ_{ib} rises to about 0.3.

The loss of information due to poor measures of intelligence can only be guessed at, although table 1 is consistent with the value 0.5, and the inadequacy of the measures may itself introduce a correlation

| TABLE 1 |
|---|
| Comparison of eight studies on head size and intelligence |

| Author | Year | Sample | Intelligence measure | Sample size | Correlation ¹ |
|----------------------|------|------------|-------------------------|----------------|--------------------------|
| Pearson | 1906 | random | subjective | 4486 | 0.11 ± 0.015 |
| Pearson | 1906 | university | grades | 1011 | 0.11 ± 0.031 |
| Pearl | 1906 | soldiers | subjective | 935 | 0.14 ± 0.033 |
| Murdoch and Sullivan | 1923 | random | IQ tests | 595 | 0.22 ± 0.041 |
| Reed and Mulligan | 1923 | university | grades | 449 | 0.08 ± 0.047 |
| Sommerville | 1924 | university | IQ tests | 105 | 0.10 ± 0.099 |
| Schreider | 1968 | random? | IO tests | 80 | 0.08 ± 0.114 |
| Schreider | 1968 | random? | IQ tests | 71 | 0.12 ± 0.121 |

¹ For these values, z = r to 2 significant figures. The standard error of z is also given.

with brain size, but it would seem that 0.3 is the best estimate we have now for the correlation between brain size and intelligence in man.

The value of ρ_{bc} used above is inaccurate for some purposes because much of the volume within the brain has functions other than what we could reasonably call intelligence.

The correlation between external cranial volume and brain volume seems larger than that between cranial circumference and brain volume, as might be expected. I did not calculate the former correlation, but figure 1 of Jørgensen, Paridon, and Quaade ('61) shows the relationship. It is, however, the relation between internal cranial volume and brain size in which we are usually more interested, and I have found no study of this correlation.

NATURAL SELECTION

In order to see the evolutionary effect of a correlation between brain size and intelligence, we must relate one or both of these parameters to natural selection. This is again not yet possible to do accurately, but I will use the available data to indicate their ostensible consequences.

Although Bielicki and Welon ('64) and Huizinga and Slob ('65) found a fascinating relationship between sib number (in this case probably a reasonably good measure of fitness) and cephalic index, I know of no such estimates for head measurements, much less brain size. Clark and Spuhler ('59) found a relationship of head length to fertility in men but a nonsignificant opposite effect in women. Their method of analysis did not permit an estimate of the strength of any effect found. I will assume for the calculation that there is no effect of brain size itself on fitness. This is undoubtedly false, at least for brain size at birth in relation to the size of the birth canal, but some value must be taken and it is useful to see how two components of selection oppose each other.

There are three studies which relate intelligence to an appropriate measure of fitness. One of these (Higgins, Reed, and Reed, '62; with a book-length report of related work by Reed and Reed, '65) did not give results in a form suitable for the present analysis, and also did not include childless individuals who had no surviving sibs.

The first study by Bajema ('63, '66) is one of the best on natural selection in any organism. If we take reasonable values (75, 90, 100, 110, 125) for the means of Bajema's five IQ groups and an additive heritability of 0.5 (Cavalli-Sforza and Bodmer. '71), it is easy to calculate that the expected change in IQ in one generation, excluding sampling error, is an increase of 0.14 point, or an eightieth of a standard deviation. Falconer ('66) obtained a similar value by a slightly different method. If we take the genetic correlation between intelligence and brain size to be 0.3, brain size would increase by one standard deviation (about 150 gm) in 800 generations (say 15,000 years) in the absence of other effects. If the genetic correlation is 0.1, 8,000 generations would be needed.

A second study by Bajema ('71), not yet fully published, finds a similar relationship between fitness and IQ.

The point of the above calculation is that an explanation of the evolution of human brain size by selection for intelligence is quantitatively reasonable. It does not show that this was actually the major cause.

DISCUSSION

I must emphasize again that the quantitative estimates given are inaccurate in detail and that I have merely used the best data available.

There are three sorts of interpretations that we can give to a real correlation between brain size and intelligence. One is gametic disequilibrium or some other kind of artifact of a heterogeneous population. (A correlation between skin color and nose width in the population of Mississippi would obviously have only this significance, but the effect can be subtler.) Presumably for this reason Pearson ('06) found correlations of "intelligence" with hair and eye color almost as large as those with cranial dimensions. Because cranial dimensions (as distinct from cranial indices) show much more overlap among groups than do hair and eye color, it seems unlikely that this effect is important. The results of Clark et al. ('61), which consider only betweencotwin comparisons, in fact disprove it as being generally applicable.

A second interpretation is that some other factor has similar effects on both intelligence and brain size. Pearl ('06) suggested that nutrition might have this effect, and Pearson (25) noted without advocating it that even a causal effect of intelligence on brain size was possible. This class of interpretations cannot be ruled out, and the fact that measurements of stature, cranial size, and intelligence are usually all correlated positively, suggests that it is probably to some extent true. Starvation of course has both appropriate effects, but it is normal variation that generated the available data. Moreover, we can't now exclude the possibility that any effect of nutrition acts on intelligence via brain size as well as by other and undefined mechanisms. Pearson ('06) found a correlation of 0.18 between measures of intelligence and health but did not relate health to other variables, and Schreider ('68) found correlations of 0.23 and 0.29 between intelligence and undefined "vital capacity." However, the slight effect of controlling stature and body weight suggests, but by no means proves, that the second class of interpretations is relatively minor.

The third class postulates a direct effect of the size of the brain or some part of it on intelligence. As Tobias ('70) and others have noted, most of the material inside the human cranium is not directly concerned with thought, although the amount of this material is to some extent related to intellectual function and its preservation. Further, the well known but widely ignored work of Lashley ('29; Beach, Hebb, Morgan and Nisson, '60), and the recent extraordinary set of experiments by Pietsch ('72), if the latter can be replicated, show that most of the brain of at least some vertebrates is redundant in terms of basic information carried. This is not to say that an increase in size or an improvement in construction of a brain might not cause more effective thought, but it removes one simple-minded explanation. The relation between brain size and intelligence among widely different species (compare an earthworm, a bird, dog, man) is difficult to explain except by a rather direct causal chain. If such causation exists, it is implausible that the mechanism for it would not also apply within species even if largely obscured by other influences. Lashley ('49) himself noted that "the severity of deterioration (of behavior) is proportional to the quantity of cerebral tissue destroyed." To know the mechanism will be to know much about the nature of thought.

The third class of explanations and some of the second class have evolutionary consequences. What is almost necessary (on the "almost" see an important paper by Braestrup, '71) is a genetic correlation between brain size and intelligence, i.e., that some genes or equivalents of genes affect both characters. This can be indirect as well as direct; a gene influencing the rate or timing of release of growth hormone could affect general vigor as well as brain size, thereby improving nutrition for the individual and his relatives (who may have similar genotypes) at least in bad years.

For it is not to modern civilizations that we must look for the main importance of a relationship between intelligence and brain size, whatever may be the effects of advances in obstetrical practices. Brain size may have stopped increasing by Neandertal time (there are not enough good endocranial volumes to say more than this, and I have seen no consideration here of the effect of body size although the short Neandertal stature suggests that the ostensible decrease in brain size later is real). But brain size has increased dramatically and at an unusually high rate in human evolution. This must have an explanation.

One explanation is the effect of intelligence. As Bajema ('63) noted, the relationship of intelligence to fitness now probably changes importantly even over decades. It is, however, likely that in hunter-gatherer populations whose density is ultimately or proximally regulated by the availability of food or possibly shelter, intelligence has had some importance to fitness. The very small directional relationship that Bajema found in twentiethcentury Michigan more than suffices to account for the rapid observed evolution of brain size, in the absence of other factors, if available data are adequate. It provides a selective vector for contemporary evolution as well.

There is another explanation which has some evidence. In addition to natural selection against large (and large-headed) babies, there is also selection against small ones. Much but not all of this is due to prematurity; heritability of birth weight is about 0.2 (Penrose, '54). In both London

and New York the intensity of directional selection, which is always towards higher birth weight, is about 0.02 (Van Valen and Mellin, '67). Although all studies of the phenomenon come from large cities, the intensity of selection is positively related to the total amount of perinatal mortality (Van Valen and Mellin, '67). Therefore we may assume the selection is at least as strong in more primitive conditions. There is then a step in the argument on which we (or at least I) have no quantitative evidence: the correlation between brain size at maturity and birth weight, as well as any possible interactions. If we assume this correlation is 0.1, the expected increase in brain size is one standard deviation in about 7,500 generations, effectively the same rate as found from intelligence, with large inaccuracy in both cases. Because of the physical limitations of birth, however, it is entirely possible that interactions are such as to eliminate or reverse the inferred selection for larger brain size. Intelligence is also positively correlated with birth weight at least in heterogeneous populations (Weiner, '62; Weiner, Rider, Oppel, '65; Barker, Fischer, and Harper, ²66: Record, McKeown, and Edwards, '69).

Experiments on animals more amenable than man to experimentation could help in understanding intraspecific relations between components of intelligence and the size of the brain and its components. Wildcaught animals (from single populations) would be preferable to the ubiquitous White Rat, and measures of intelligence should be scrutinized to avoid what may be even a negative relationship (Michie, '62) between standard measures and adaptive intelligence.

It should not be difficult to estimate the present relationships among brain size, intelligence, and fitness in man directly. The history of cadavers dissected in medical schools is usually known, and intelligence scores can often be obtained from school records. Amount and times of reproduction may also be available. The sample is biased in various ways. Such a study would need to control, in one way or another, several variables known to affect brain size in relevant or irrelevant ways (Appel and Appel, '42; Tobias, '70), and would have the usual difficulties associated with IQ tests. But the problems are probably less serious than in most comparative studies of intelligence, and use of cadavers would also permit estimation of the size of individual parts of the brain which may be considered potentially important. Schreider ('66) found rather low correlations among the sizes of different parts of the human brain, which may reflect a constraint by total cranial capacity. Estimation of cranial capacity from x-rays of living persons is also possible (Weinmeister and Inke, '68) but for several reasons is clearly a second choice.

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APPENDIX

A. Proof of equation (1): Consider the causal chain $c \rightarrow b \rightarrow i$. Then the proportion of the variance of *i* that is due to *c* is the product of the proportion of the variance of *i* that is due to *b*, with the proportion of the variance of *b* that is due to *c*. Statistically, $\rho_{ic}^{\ 2} = \rho_{ib}^{\ 2} \rho_{bc}^{\ 2}$, from which only the positive square root is meaningful. Alternatively consider $|\mathbf{R}|$, the determinant of the correlation matrix, and $(1 - |\mathbf{R}|)$, the square of the collective correlation coefficient of Frisch ('29). Solving the identity

 $\begin{aligned} |\mathbf{R}| &= 1 - \rho_{ic}^{2} - \rho_{ib}^{2} - \rho_{bc}^{2} + 2\rho_{ic}\rho_{ib}\rho_{bc}, \\ \rho_{ic} &= \rho_{ib}\rho_{bc} \pm (\rho_{ib}^{2}\rho_{bc}^{2} - \rho_{ib}^{2} - \rho_{bc}^{2} + 1 - |\mathbf{R}|)^{1/2}. \\ \text{Equation (1) follows if and only if} \\ (1 - |\mathbf{R}|) &= \rho_{ib}^{2} + \rho_{bc}^{2} - \rho_{ib}^{2}\rho_{bc}^{2} \end{aligned}$

B. Correlation of head size and brain size: Jørgensen et al. ('61) give a scatter diagram of brain volume and head circumference of 105 individuals. Children are included and not identified. If we follow their procedure of determining adults and eliminate the smallest 15 individuals (of either variable), the correlation of the remainder is 0.57 ($z = 0.65 \pm 0.11$; data read from the figure). If we eliminate the smallest of the 90 remaining individuals, who is isolated from the rest, the correlation is 0.50 ($z = 0.56 \pm 0.11$). On somewhat larger samples Pearl ('05) found values of $0.55 (z = 0.62 \pm 0.05)$ and 0.36 (z = 0.38 ± 0.07). Data of Jørgensen and Quaade ('56) and Dekaban and Lieberman ('64) indicate, predictably, a higher correlation than this between cranial capacity and linear measures of the external size of the cranium; the relationship is not far from linearity in adults. Macdonnell ('04) calculated some correlations for the latter relationship. Normalizing his eight estimates and weighting them by the reciprocal of their variances, the mean r is 0.66 $(z = 0.78 \pm 0.04).$

C. Clark et al. ('61) did not give estimates of correlations comparable to previous ones because they made comparisons only within pairs of like-sexed twins and tested significance of associations by a method that considers only the sign, not the magnitude, of differences. The use of comparisons only between co-twins provides a much more homogeneous population than is otherwise possible, but it has the important defect that most of the variance of the total population is lost. We can nevertheless make estimates of correlations on the within-twin data, but these will be biased toward low values because the extremes of an elongate distribution largely determine the correlation. These extremes, if the distribution is really elongate, are absent for twin comparisons with characters of even moderate heritability. The proportion of the total variance (mean withinsex) that is due to within-twin comparisons is 0.039 for monozygotics and 0.081 for dizygotics for total test score ("intelligence," excluding twin pairs lacking one or more scores), 0.035 and 0.129 respectively for head circumference, and 0.067 and 0.125 respectively for an index of head cross-sectional area (correcting an obvious misprint for individual 16629 for this derived character). Some unknown proportion of each total variance is due to age; the twins ranged from 12 to 20 years old and individual ages were not given. The between-cotwin correlations between test score and head circumference are -0.09 \pm 0.16 for monozygotics and 0.20 \pm 0.17 for dizygotics, and between test score and cross-section they are 0.21 ± 0.16 and 0.09 ± 0.17 respectively. These correlations (r) are derived from the mean of the values for the sexes using the normalizing z-transformation. The standard errors are of z, which equals r to two significant figures at values of 0 to 0.23. The joint mean happens to be 0.10, as with the more extensive data of Pearson and others, but the agreement is presumably fortuitous. Removal of stature by partial correlation gives mean correlations of -0.11, 0.21, 0.24, and 0.11 in the same order. These, again, are likely to be underestimates.