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GALTON LECTURE

BEHAVIOUR GENETIC STUDIES OF INTELLIGENCE, YESTERDAY AND TODAY: THE LONG JOURNEY FROM PLAUSIBILITY TO PROOF

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Introduction

When asked whether he would discuss man in the *Origins of the Species*, Darwin replied, 'I think I shall avoid the subject, as so surrounded with prejudices, though I fully admit it is the highest and most interesting problem for the naturalist'. Galton on the other hand replied to the same question, 'I shall treat man and see what the theory of heredity of variations and the principles of natural selection mean when applied to man' (Pearson, 1914–30, Vol. II, p. 86).

Galton grappled with this task in his book *Hereditary Genius* (Galton, 1869/1914). The title of that book is misleading and Galton later asserted he would have called it *Hereditary Ability* if he could have retitled it. His intent was to show 'that a man's natural abilities are derived by inheritance, under exactly the same limitations as are the form and physical features of the whole organic world' (Galton, 1869/1914, p. 1).

Galton's views on these matters were immediately challenged. A reviewer of *Hereditary Genius* wrote:

> 'Mr. Francis Galton has bestowed immense pains upon the empirical proof of a thesis which from its intrinsic nature can never be proved empirically. In the philosophy of the intellect, as in the philosophy of mechanics, there are problems which are capable at best of but a partial and approximate solution. The elements of analysis and proof are too multiform and variable, and the only available method of investigation is too complex and subtle, for any results of a decisive and satisfactory kind' (The Saturday Review, December 25, 1869, p. 832).

Of the same book Charles Darwin wrote in a letter to Galton:

> '. . . I do not think I ever in all my life read anything more interesting and original. And how well and clearly you put every point! . . . You have made a convert of an opponent in one sense, for I have always maintained that, excepting fools, men did not differ much in intellect, only in zeal and hard work; and I still think there is an eminently important

> difference, I congratulate you on producing what I am convinced will prove a memorable work' (Pearson, 1914–30, Vol. 1, p. 6).

In *The Descent of Man* published two years later Darwin's views on the inheritance of mental characteristics were made public.

> 'So in regard to mental qualities, their transmission is manifest in our dogs, horses and other domestic animals. Besides special tastes and habits, general intelligence, courage, bad and good tempers, &c., are certainly transmitted. With man we see similar facts in almost every family; and we now know, through the admirable labours of Mr Galton, that genius which implies a wonderfully complex combination of high faculties, tends to be inherited; and, on the other hand, it is certain that insanity and deteriorated mental powers likewise run in the same families' (Darwin, 1871, pp. 101–111).

Within two years Darwin had incorporated Galton's ideas into his paradigm and acknowledged him as the founder of what is now called 'behaviour genetics'.

Paradoxical as it may seem both commentaries on Galton's book were prophetic. The idea that genetic factors importantly influence behavioural traits such as IQ, personality, mental illness, creativity, etc, continues to be highly controversial and arguments similar to those found in the review of *Hereditary Genius* continue to be put forward (Horgan, 1993; Kamin, 1974; Lewontin, Rose & Kamin, 1984). On the other hand, over the last 20 years the enterprise of behaviour genetics has literally exploded. There are numerous speciality journals, and virtually all the standard journals in the behavioural sciences now publish human behaviour genetic studies based on the twin and adoption designs inspired by Galton's insights (Plomin, Owen & McGuffin, 1994).

The most recent round in this long debate was launched by Jensen in his now famous article entitled: 'How much can we boost IQ and scholastic achievement?' (Jensen, 1969), which outlined most of the Galtonian research programme and initiated a storm of controversy. Shortly after Jensen's article appeared Herrnstein published an article in the *Atlantic Monthly* which eventuated in a book entitled *IQ in the Meritocracy* (1973). Hernstein drew heavily on Jensen's work and argued that the message regarding the 'significance of intelligence testing lies in what it says about a society built around human inequalities' (p. 197). The conclusion of that book was that social standing (which reflects earnings and prestige) is based to some extent on inherited differences among people.

The work of Herrnstein and Jensen prompted Kamin to write *The Science and Politics of IQ* (1974). That book became highly influential in psychology at large in spite of severely critical reviews in the professional literature (Fulker, 1975; Jackson, 1975; Scarr, 1976). One reason for its widespread popularity is that it documented in considerable detail the case against Burt (the Burt controversy has continued to generate a contentious literature: Fletcher, 1991, 1993; Hernshaw, 1979; Joynson, 1990; Mackintosh, 1995) put forth in earlier talks and a widely circulated but unpublished paper (Kamin, undated). After reviewing the literature regarding genetic influence on IQ test scores Kamin asserted:

> 'This book has attempted . . . to review the major sources of evidence that have been asserted to support the view that IQ is heritable. The data have repeatedly demonstrated profound environmental effects on IQ scores in circumstances where the genes cannot be implicated. The apparent genetic effects, upon analysis, have invariably been confounded with environmental factors that have been slighted or ignored. The studies of separated

> MZ twins have ignored the correlated environments of the twins, as well as artifacts produced by the confounding of age with IQ and by unconscious experimenter bias . . .
>
> . . . There should be no mistake here. The burden of proof falls upon those who wish to assert the implausible proposition that the way in which a child answers questions devised by a mental test is determined by an unseen genotype . . . There are no data sufficient for us to reject the hypothesis that differences in the way in which people answer the questions asked by testers are determined by their palpably different life experiences' (Kamin, 1974, pp. 175–176).

Kamin did not convince Herrnstein that IQ is not heritable and unimportant to the organisation of complex societies as demonstrated by the recent publication of *The Bell Curve* (Herrnstein & Murray, 1994). This is a continuation and extension of precisely the same arguments made in Herrnstein's earlier book but drawing on the larger number of studies published since 1973 and exploiting the rich data base of the National Longitudinal Study of Youth. Anyone who has read the recent reviews (Bouchard, 1995a; Dorfman, 1995; Gould, 1995; Kamin, 1995; Miller, 1995; Scarr, 1995; Taylor, 1995) and exchanges regarding this book and participated in the debates of the 1970s and 1980s can be excused for experiencing deja vu and concluding that nothing has changed.

Hunt (1996) in a summary to a recent book of specially prepared chapters on the topic of genetic and environmental influences on IQ concludes:

> 'Genetics counts. If we insist on treating genetic and cultural explanations of intelligence as a stomping match, then the behavioral geneticists are the stompers and the proponents of cultural effects are the stompees. Twin, kinship, and adoption studies have more than proven the point that genetic variance in intelligence is substantial. It is not clear why we need to tie down the numbers to the second or third decimal point.'

The debate, initiated by Galton, over the nature of mental abilities, the influence of heredity on such abilities, and the consequences of these facts for the organisation of society appears interminable (Bouchard, 1995a; Brand, 1993; Dorfman, 1995; Fancher, 1985; Kamin, 1974). Why does this argument appear interminable? There are many reasons but just one will be briefly discussed. The everyday world is a non-scientific world. Science is an enterprise carried out only in some societies and always by a small sub-set of individuals. The results of scientific activity therefore inform societies and/or cultures with a different perspective than that of science itself. In addition, much as scientists may hate to admit it, science never provides all the answers to any question. All decisions by human beings are made on the basis of information that satisfices rather than being conclusive. A natural consequence of this fact is that it will always be possible to argue that there is not sufficient scientific knowledge about a topic to make an unalterable decision.

In the United States opposition to the fluoridation of water has been a classic example of how non-scientific belief systems have delayed the implementation of an important scientifically based public health practice. This example illustrates both facets of the argument rather clearly. The resistance to fluoridation is generated by individuals with a world view that is fundamentalist, some would argue authoritarian, and which is largely anti-scientific. On the other hand, scientists who specialise in this domain would not argue that everything is known about how fluoridated water influences human beings but that enough is known to argue that there are clear dramatic benefits for some individuals and little evidence of harm.

The same kind of motivation that underlies the reasoning of the critics of fluoridation underlies the reasoning of the critics of Galton's ideas (that a man's natural abilities are derived by inheritance, under exactly the same limitations as are the form and physical features of the whole organic world). This argument may appear unlikely. However, one must keep in mind that Galton's ideas are really just an extension of what Dennett has called *Darwin's Dangerous Idea* (Dennett, 1995). This book is a formidable defence of the adaptationist paradigm and it includes a devastating critique of the broad frame of reference that underlies the reasoning of some of the major critics of behaviour genetics including Gould, Kamin, Lewontin and Rose. Dennett uses the analogy of skyhooks and cranes to make his point. He argues as follows:

> 'Now imagine all the "lifting" that has to get done in Design Space to create the magnificent organisms and (other) artifacts we encounter in our world. Vast distances must have been traversed since the dawn of life with the earliest, simplest self-replicating entities, spreading outward (diversity) and upward (excellence). (This evaluative term is used here to mean complexity or higher in the sense of built on previously evolved forms; Darwin used the term higher organisms in this sense (Rushton, 1989).) Darwin has offered us an account of the crudest, most rudimentary, stupidest imaginable lifting process—the wedge of natural selection. By taking tiny—the tiniest possible—steps, this process can gradually, over eons, traverse, these huge distances ... At no point would anything miraculous—from on high—be needed. Each step has been accomplished by brute, mechanical, algorithmic climbing, from the base already built by the effort of earlier climbing' (p. 75).
>
> 'Cranes are obviously mechanisms built by genes via natural selection. A skyhook on the other hand "is a mind first" force or power or process, an exception to the principle that all design, and apparent design, is ultimately the result of mindless, motiveless mechanicity' (p. 76).

In other words a skyhook is a deus ex machina, an élan vital or a miracle: the non-miraculous power of selection to shape the non-biological world has been well described by Cziko (1995).

As Dennett points out 'those who yearn for skyhooks call those who eagerly settle for cranes "reductionists" ...' (p. 80). He clearly demonstrates that the largely anti-reductionist arguments of Gould, Kamin, Lewontin, Rose and many others are largely a paean for skyhooks.

Demonstrating genetic influence on intelligence is a problem in construct validity. This means that it involves the use of both theory and multiple lines of evidence, not all of which are necessarily directly related to intelligence. In this paper, this problem will be approached from two different directions. The first involves direct evidence and the demonstration that, contrary to widespread belief, the quality and meaningfulness of the kinship data used for estimating the degree and types of genetic and environmental influences on intelligence have increased dramatically over the years. This has occurred due to the constant accumulation of more and better data, the recent development of meta-analysis as a method of evaluating and cumulating data and the application of modern mathematical genetic methodology. The second approach involves indirect evidence, that provides a context of plausibility for the direct evidence.

These findings, also often generated via twin and adoption studies, involve the demonstration that other interesting and behaviourally important traits are significantly influenced by genetic factors. These include fundamental brain and sensory processes—average evoked potentials, EEG spectral profiles and spontaneous otoacoustic emissions. These latter demonstrations are possible because of the availability of new technologies that allow the measurement of variables of which Galton was not even remotely aware. It is unquestionably the case that had these tools and measures been available to Galton he would have predicted both individual differences and genetic influence on all of them.

From anecdotes to evidence: incremental progress

The observations Galton brought to bear on the question of genetic influence on human behaviour were extremely crude by today's standards. Although he integrated many lines of evidence, including evidence from twins and from outstanding families, none of it was dispositive. The findings regarding twins were anecdotal and gathered by mail from respondents to a questionnaire about twins whom they knew. (This was one of the first uses of a printed questionnaire to gather data; while Galton did not report how he located his respondents, a letter in the Galton archives indicates that he obtained a systematic list of twin births from a correspondent who worked for an insurance company. The correspondent requested that his role remain confidential.) Recognising that his twin and family data were equivocal, as heredity and environment were confounded, he invented the adoption design. The plausibility of his case thus depended on the integration of multiple lines of evidence and a willingness to accept the larger Darwinian theoretical framework within which the questions were formulated. His numerous hypotheses regarding genetic influences on the structure of society, that is the role of assortative mating, the causes of familial mental retardation, etc, were all, however, in principle empirically testable. The tools necessary to carry out these tests rigorously (the IQ test, statistical theory, the correlation coefficient, the theory of genes) simply needed to be invented and, of course, Galton set about inventing them, sometimes successfully (the statistics), sometimes not (the measures of intellectual ability).

It is not intended to suggest that Galton's data were worthless. Johnson *et al.* (1985) re-analysed some of Galton's data and concluded:

> 'The analyses we have described using the data that Galton did manage to acquire point out the value inherent in Galton's ideal and suggest that such a continuously maintained data bank and the historical perspectives it would provide may still be of considerable worth in contemporary psychology. The fact that his data acquired a century ago are the best and sometimes the only data available regarding some domains of individual differences is indicative of the uneven growth of different areas of psychology' (p. 892).

The earliest data: 1900–1920

Early studies that made use of the new IQ tests and statistical methods all tended to support the idea that there was some form of genetic transmission for intelligence. The measurement instruments were rough and ready and could easily be criticised on a variety of grounds. The selection of participants was also idiosyncratic and hardly ideal from a statistical sampling point of view. Some of the early twin studies using these new tools did not even distinguish between monozygotic and dizygotic twins because this important conceptual distinction remained to be solidly established as a biological fact (Bouchard, 1993b; Rende, Plomin & Vandenberg, 1990). According to Darlington (1962, p. 14), Darwin had considered the problem of twins and concluded that they were more alike than ordinary brothers and sisters for environmental reasons (i.e., they lived in the same womb and were reared together during their formative years). Galton, on the other hand, adopted the new cellular view and Weisman's theories, and argued that some twins came from two cells, like ordinary brothers and sisters, while others were from one cell and shared the same heredity. As is now known, Darwin was wrong and Galton was right. It is often thought that views on scientific matters are based entirely on the empirical facts and it may well be that Galton also felt that way. This particular episode, however, makes it clear that betting on the right theory makes all the difference in the world. Had it eventually been shown that twins originated from a different set of processes Galton's arguments would now be part of the dust bin of history. Galton, however, believed incorrectly that dichorionic placentation always meant dizygosity and of course it does not (Corney, 1984).

Better data: 1920 to 1960

As more numerous studies of a wide variety of kinships were carried out, it became necessary to organise all the data in a meaningful manner. This was accomplished by Erlenmeyer-Kimling & Jarvick (1963) who published what would today be considered an elementary meta-analysis of all the kinship data to that date (Fig. 1) in only ten informative kinship categories.

The authors concluded that,

> 'Taken individually, many of the 52 studies reviewed here are subject to various types of criticisms (for example methodological). Nevertheless, the overall orderliness of the results is particularly impressive if one considers that the investigators had different backgrounds and contrasting views regarding the importance of heredity. Not all of them used the same measures of intelligence, and they derived their data from samples which were unequal in size, age structure, ethnic composition, and socio-economic stratification; the data were collected in eight countries on four continents during a time span covering more than two generations of individuals. Against this pronounced heterogeneity, which should have clouded the picture, and is reflected by the wide range of correlations, a clearly definitive consistency emerges from the data' (p. 1478).

Erlenmeyer-Kimling & Jarvick also emphasised the contingent nature of their conclusions: 'We do not imply that environment is without effect upon intellectual functioning; the intellectual level is not unalterably fixed by the genetic constitution. Rather, its expression in the phenotype results from the patterns laid down by the genotype under given environmental conditions' (p. 1478).

They concluded that the polygenic hypothesis of inheritance was supported by the data and that the hypothesis of sex-linkage was not supported.

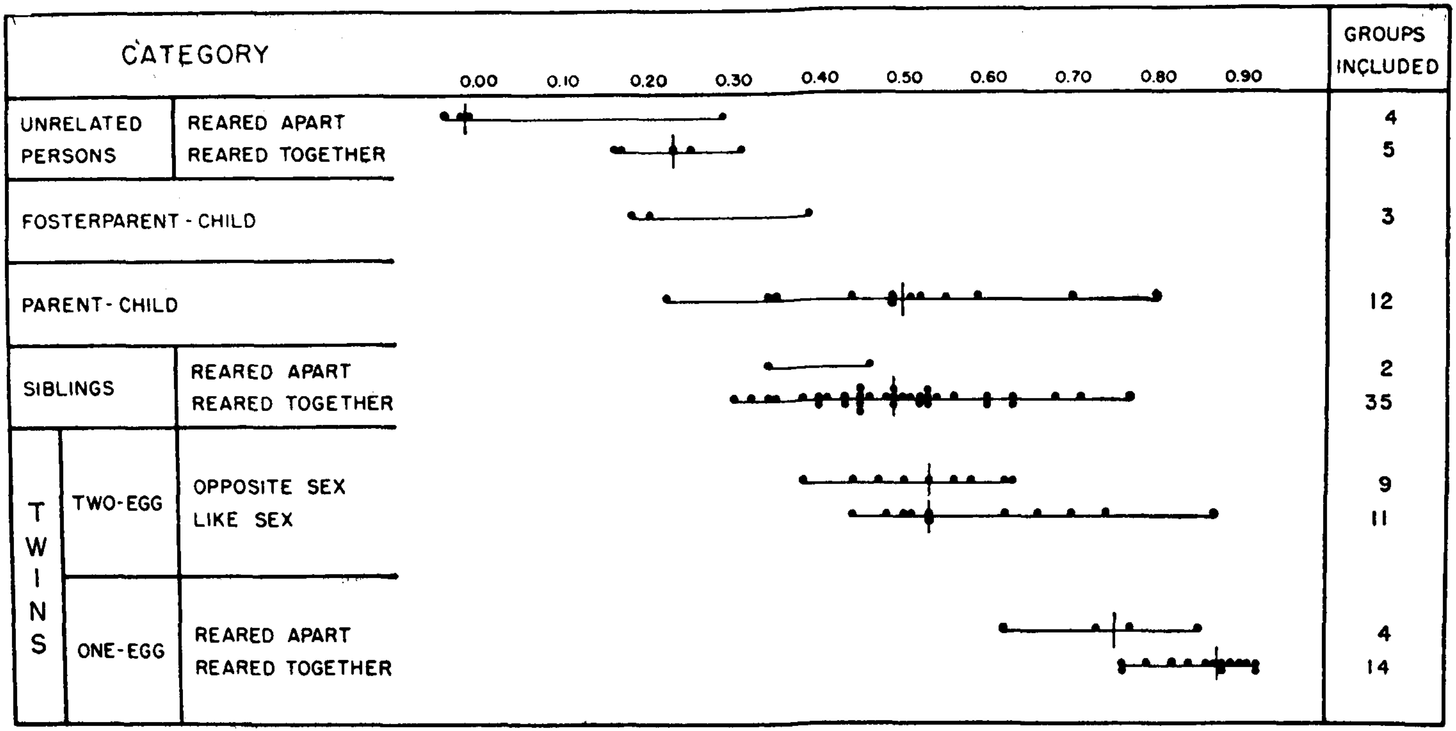
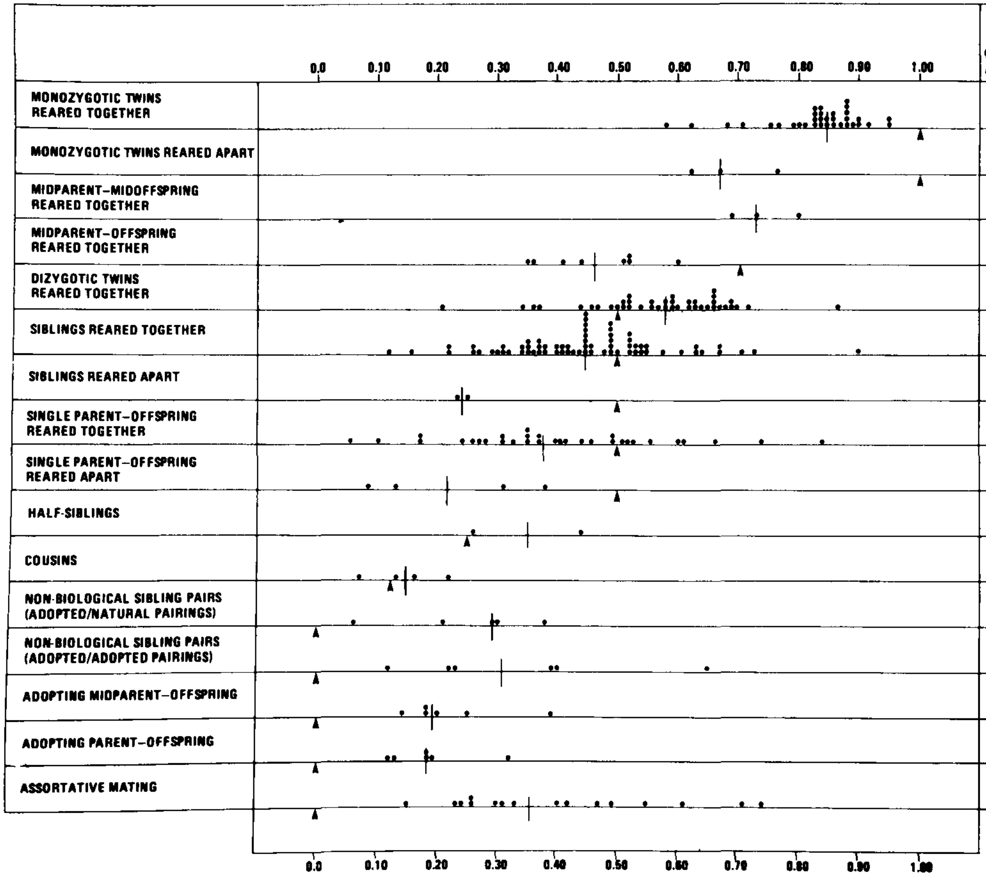


Fig. 1. Correlation coefficients for ‘intelligence’ test scores from 52 studies. Some studies reported data for more than one relationship category; some included more than one sample per category, giving a total of 99 groups. Over two-thirds of the correlation coefficients were derived from IQs, the remainder from special tests (e.g. Primary Mental Abilities). Mid-parent–child correlation was used when available, otherwise mother–child correlation. Correlation coefficients obtained in each study are indicated by dark circles; medians are shown by vertical lines intersecting the horizontal lines which represent the ranges. From Erlenmeyer-Kimling & Jarvick (1963).



	NO. OF CORREL-ATIONS	NO. OF PAIRINGS	MEDIAN CORREL-ATION	WEIGHT-ED AVER-AGE	χ^2 (d.f.)	$\chi^2 \div$ d.f.
MONOZYGOTIC TWINS REARED TOGETHER	34	4672	.85	.86	81.29 (33)	2.46
MONOZYGOTIC TWINS REARED APART	3	65	.67	.72	0.92 (2)	0.46
MIDPARENT–MIDOFFSPRING REARED TOGETHER	3	410	.73	.72	2.66 (2)	1.33
MIDPARENT–OFFSPRING REARED TOGETHER	8	992	.475	.50	8.11 (7)	1.16
DIZYGOTIC TWINS REARED TOGETHER	41	5546	.58	.60	94.5 (40)	2.36
SIBLINGS REARED TOGETHER	69	26,473	.45	.47	403.6 (64)	6.31
SIBLINGS REARED APART	2	203	.24	.24	.02 (1)	.02
SINGLE PARENT–OFFSPRING REARED TOGETHER	32	8433	.385	.42	211.0 (31)	6.81
SINGLE PARENT–OFFSPRING REARED APART	4	814	.22	.22	9.61 (3)	3.20
HALF-SIBLINGS	2	200	.35	.31	1.55 (1)	1.55
COUSINS	4	1,176	.145	.15	1.02 (2)	0.51
NON-BIOLOGICAL SIBLING PAIRS (ADOPTED/NATURAL PAIRINGS)	5	345	.29	.29	1.93 (4)	0.48
NON-BIOLOGICAL SIBLING PAIRS (ADOPTED/ADOPTED PAIRINGS)	6	369	.31	.34	10.5 (5)	2.10
ADOPTING MIDPARENT–OFFSPRING	6	758	.19	.24	6.8 (5)	1.36
ADOPTING PARENT–OFFSPRING	6	1397	.18	.19	6.64 (5)	1.33
ASSORTATIVE MATING	16	3817	.365	.33	96.1 (15)	6.41

Fig. 2. Familial correlations for IQ. The vertical bar in each distribution indicates the median correlation; the arrow, the correlation predicted by a simple polygenic model. From Bouchard & McGue (1981).

The 1981 update

By 1980 the number of studies had increased enormously. Bouchard & McGue (1981) reviewed the literature, and reported on 111 studies that yielded 526 correlations based on 113,942 pairings, and were able to present far more comparisons and carry out a slightly more sophisticated analysis than Erlenmeyer-Kimling & Jarvick.

Figure 2 shows the familial correlations as well as the correlations for assortative mating. One striking feature is the great heterogeneity of some of the correlations, particularly the sibling and parent–offspring correlations. At first glance such heterogeneity strongly suggests that the degree of similarity for these kinships is moderated by some other factors. This point will be considered later.

In 1981, there were 41 informative kinship categories and it was possible to plot the twin data by opposite-sex and same-sex pairings as a method of exploring the observed heterogeneity. It was also possible to plot many of the other kin data by male and female pairings. Virtually no influence of sex on the data was found and the heterogeneity remained very large. As with the Erlenmeyer-Kimling & Jarvick analysis, it was concluded that sex-linkage was not supported. It was also suggested that sex role effects on general cognitive development did not seem to be supported either.

> 'That the data support the inference of partial genetic determination for IQ is indisputable; that they are informative about the precise strength of this effect is dubious. Certainly the large amount of unexplained variability within degrees of relationship, while not precluding attempts to model the data, suggest that such models should be interpreted with caution' (p. 1058).

However, there was some naivete about both sampling error and the multiple artifacts that can influence correlations.

Development of meta-analysis and analysis of the unexplained heterogeneity

In the same year that Bouchard & McGue (1981) published their review, Glass, McGraw & Smith (1981) published their classic book *Meta-Analysis in Social Research.* The following year Hunter, Schmidt & Jackson (1982) published a development of their earlier work on validity generalisation entitled *Meta-analysis: Cumulating Research Findings Across Studies.* The procedures described in these books led Caruso (1983) to examine the heterogeneity in the parent–offspring and sibling correlations discussed previously. Caruso was able to show that the heterogeneity in the parent–offspring correlations could be entirely accounted for by the differences in sample sizes, test reliability, and range restriction. The corrected parent–offspring correlation was 0·57 with a variance of 0. Corrections for sampling error (a primary cause of heterogeneity in most data summaries) reduced the heterogeneity of the sibling correlations but did not explain all the variance. The final corrected correlation was 0·51 with a standard deviation of 0·11.

The methodology of meta-analysis has advanced a great deal since 1983 (Cook *et al.*, 1992; Cooper & Hedges, 1994; Hunter & Schmidt, 1990; Schmidt, 1992) and a new analysis of this data base would be very informative.

The discovery that genetic influence on IQ increases with age

Caruso (1983) raised the question as to whether age effects might be important in this data base but he could find no patterns in the data. Plomin, in his book entitled

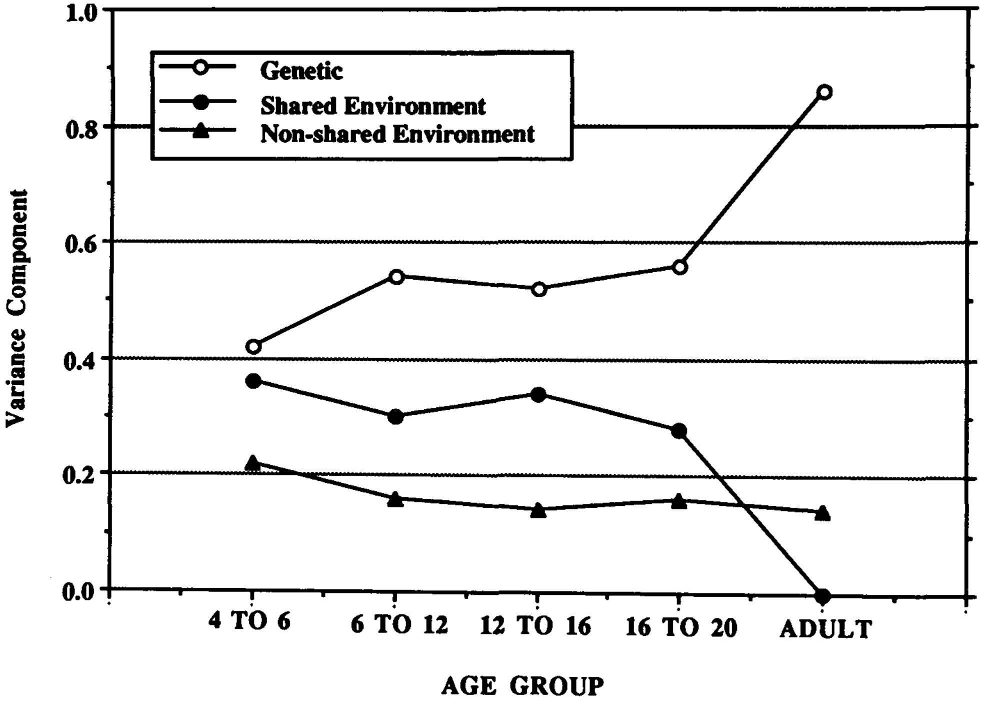


Fig. 3. IQ variance component estimates derived from published IQ correlations. Estimates are based on the standard assumptions used with the Falconer heritability formula. From McGue *et al.* (1993).

Development, Genetics, and Psychology (1986) argued that, contrary to the widely held belief that environmental influences accumulated with age and therefore the heritability of cognitive ability decreases with age, the facts seemed to indicate the opposite. McGue *et al.* (1993) organised all the twin IQ data by age and incorporated the more recent twin studies. It became clear very quickly that the vast majority of kinship studies had been carried out on young people and that when older samples were added the picture changed. The plot of the estimates of genetic, shared environmental and non-shared environmental variance based on the twin data is shown in Fig. 3. The estimate of a shared environmental influence of near zero is striking and consistent with data and arguments put forward by others (Plomin & Daniels, 1987).

These findings were checked against a growing data set from a number of twin studies being carried out at the University of Minnesota. Figure 4 shows the estimated heritability and shared environmental component of variance of IQ (Wechsler tests) for twins in the age periods 11–12 and 60–88. The trends for almost all subtests confirm this important age effect. A recent more detailed analysis of heritability of cognitive ability in adulthood comparing Minnesota twins reared together and Swedish twins reared together confirms these general findings but suggests that the heritability of cognitive abilities may be lower after age 70 (Finkel *et al.*, 1995).

This age effect is also demonstrated in an important non-twin kinship, namely

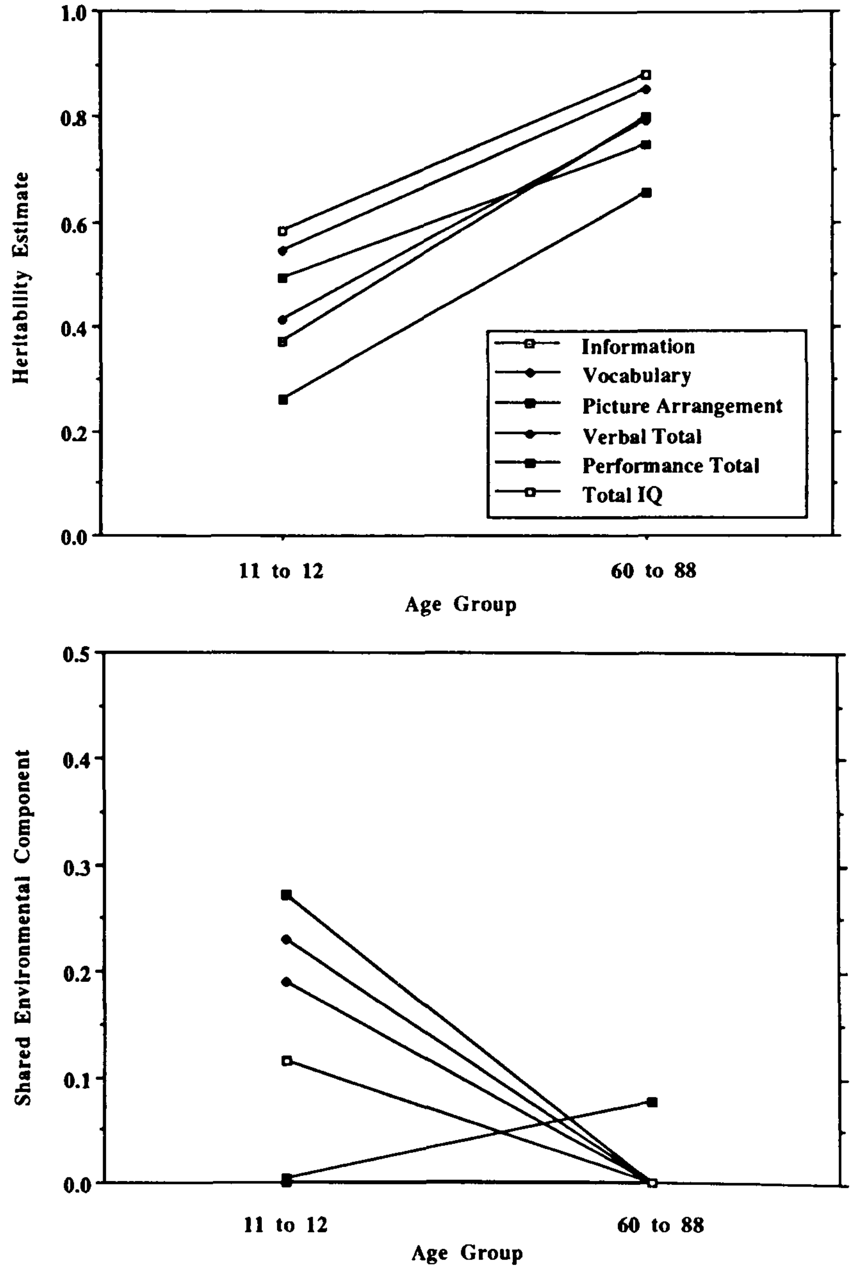


Fig. 4. Proportion of Wechsler test performance associated with heritability estimates (top panel) and shared environmental components (bottom panel) derived from the ongoing University of Minnesota cross-sectional study of reared-together twins. From McGue *et al.* (1993).

Table 1. Intraclass correlations, confidence intervals, samples sizes, and test utilised for IQ measurement in five studies of MZA twins reared apart

Study and test used (primary/secondary /tertiary)	N for each test	Primary test	Secondary test	Tertiary test	Mean of mutliple tests
Newman *et al.* (1937) (Stanford-Binet/Otis)	19/19	0·68 ± 0·12	0·74 ± 0·10		0·71
Juel-Nielsen (1980) (Wechsler-Bellevue/Raven)	12/12	0·64 ± 0·17	0·73 ± 0·13		0·69
Shields (1962) (Mill-Hill/Dominoes)	38/37	0·74 ± 0·07	0·76 ± 0·07		0·75
Bouchard *et al.* (1990) WAIS/Raven-Mill-Hill First Principal Component	48/42/43	0·69 ± 0·07	0·78 ± 0·07	0·78 ± 0·07	0·75
Pedersen *et al.* (1992) First principal component	45	0·78 ± 0·06			0·78
Weighted average					0·75

From (Bouchard, in press).

unrelated individuals reared together, where the correlation estimates the influence of shared family environment. The weighted average correlation between such individuals when they are assessed in childhood is 0·29 ($N = 1882$) (Bouchard & McGue, 1981). When assessed in adolescence/adulthood five samples yielded a weighted average correlation of 0·04 ($N = 398$) (Loehlin, Horn & Willerman, in press; Scarr & Weinberg, 1978; Scarr, Weinberg & Waldman, 1993; Teasdale & Owen, 1984). There is a paucity of studies of unrelated individuals reared together; such studies should be an important scientific tool for research psychologists interested in family environmental influences on psychological traits.

The age effect findings nicely account for the discrepancy between the results of model fitting of the entire kinship data base—a heritability of about 0·50 (Chipuer, Rovine & Plomin, 1990)—and the results from studies of monozygotic twins reared apart (to be discussed below) which suggested heritabilities in the 0·60–0·75 range.

Monozygotic twins reared apart

It is remarkable that, in spite of having accurately conceptualised the origin of twins, initiating the development of the statistical methods by which twin data would eventually be analysed, and proposing the adoption method to control for family environmental influence, Galton failed to propose the twins reared apart method, which is surprising, given that Townsend (1874–75) wrote to him about one such pair of twins.

If the appropriate assumptions are met, monozygotic twins reared apart (MZAs) can provide a direct estimate of genetic influence on a trait. The various assumptions necessary to justify this interpretation have been discussed in detail elsewhere (Bouchard, 1993a; Bouchard, 1996). Here the findings from the relevant studies will be presented, with comments. There have now been five MZA studies (Bouchard *et al.*, 1990; Juel-Nielsen, 1980; Newman, Freeman & Holzinger, 1937; Pedersen *et al.*, 1992; Shields, 1962) and the results are shown in Table 1.

Kamin (1974) reviewed the earlier studies and concluded that the results can be explained by contact between the twins. Both studies conducted since Kamin made his claims measured degree of contact between the twins directly and demonstrated that contact could not explain the similarity. A second major complaint about the previous studies was that placement of the twins in similar homes could explain much of the similarity in IQ. Again in neither of the newer studies could this factor explain a significant amount of the IQ similarity. The near zero correlation for genetically unrelated individuals reared in the same home and the correlation of 0·15 for cousins reared in the homes of brothers (predicted correlation based on additive genetic effect is 0·125) makes placement or rearing by relatives an unlikely explanation of the similarity of the MZAs. Also, Bouchard (1983) demonstrated the incorrectness of claims that in the previous studies of MZAs, placement, rearing by relatives and contact were major causes of IQ similarity.

Comprehensiveness and quality of key contemporary studies

While it probably will always be necessary to make use of samples of opportunity in behaviour genetics it should be clear that a number of key studies have used population-based samples. The Swedish Adoption/Twin Study of Aging (SATSA), which provided one set of MZA data in Table 1, is particularly notable. This is a longitudinal study of twin pairs (MZ and DZ) in the population-based Swedish Twin Registry who indicated that they had been separated before the age of 10 and reared apart, and a control sample of conventionally reared twins (MZ and DZ), matched on the basis of sex, county of birth and date of birth. The SATSA twins represent a well-enumerated sample. The twins were administered a comprehensive battery of special mental abilities (13 tests) and the first principal component was treated as a measure of general cognitive ability. The correlations are MZA$=0{\cdot}78$ ($n=45$), MZT$=0{\cdot}80$ ($n=63$), DZA$=0{\cdot}32$ ($n=88$) and DZT$=0{\cdot}22$ ($n=79$). Model fitting this data yields a heritability of about 0·80 and evidence for non-additive genetic variance (due to the modest DZ correlations). These data are quite consistent with the findings reported in Fig. 4. The adult DZ correlation on which Fig. 4 was computed was slightly below 0·40. This estimate is based on only 178 pairs highlighting the dearth of data on adult twins. One of the remarkable discoveries made by behaviour geneticists in recent decades is the absence of much common family environmental influence on many psychological traits when the data are gathered on adults. The IQ correlations for unrelated individuals reared together and measured as adults illustrate that point nicely, and those findings are fully confirmed by the SATSA data as twins reared together are no more similar than the twins reared apart. The URT data might have properly been reported in this section as most of the data come from comprehensive adoption studies rather than volunteer samples (two data points come from the Texas Adoption Study discussed below). Twins reared together, twins reared apart and unrelated individuals reared together provide three independent lines of evidence converging on a single conclusion. In addition one of the lines of evidence does not involve twin data, thus removing claims that perhaps the method itself is in some way contaminated.

A recent comprehensive analysis of fourteen kinships (no twins are included) from the Texas Adoption Study (Loehlin *et al.*, 1996) confirms the SATSA findings. The Texas Adoption Study also makes use of a sample of participants who were sought out by the investigators rather than recruited as volunteers. While there are probably recruitment biases in such a sample, they are likely to be different from those that influence volunteer samples of the sort that are usually used in twin studies. The authors conclude, 'The genetic effects on IQ increase with age. We estimated the heritability (for true scores in the population) to be about 0·78 for the Revised Beta test at the time of the second study, when the children average about 17 years old. This is a figure consistent with results of adult studies of identical and fraternal twins and of separated identical twins'. This estimate is for the true scores and estimates narrow heritability as opposed to the broad heritability estimated by the MZA correlations and twin studies.

These studies do not, of course, answer every question. The heritability of IQ is not a physical constant which should turn up in any study so long as the study is conducted properly. Sundet *et al.* (1988) retrieved intelligence test data from the files of the Norwegian Armed forces for twins born in the period 1931–60. These twins were tested in the late teens or early twenties. The correlations for the entire sample are $MZ = 0{\cdot}83$ ($n = 757$ pairs) and $DZ = 0{\cdot}51$ ($n = 1093$ pairs). When plotted by year of birth the heritabilities yield quite conspicuous non-linear trends. The authors attempted to interpret the data in relation to known social trends but could not do so in a satisfactory manner and therefore chose to leave the issue open.

What causes change over time in normal samples?

One of the most common criticisms of the claim that genetic factors importantly influence the expression and transmission of IQ is that many children show considerable change in IQ during the course of development. It is now possible to bring some important findings to bear on this question. The ideal design to address this question is a longitudinal study of twins and adoptees. The Colorado Adoption Project is such a study, and attempts to assess the expression of both genetic and environmental influences on cognitive ability over time. The project (Fulker & Cardon, 1993; Fulker, Cherny & Cardon, 1993) illustrates the enormous gain in conceptual power that occurs when twins and adoptees are added to a longitudinal design. The study is a multivariate one, and powerful modelling techniques are utilised.

The analysis of one example (Fig. 5) makes use of twin (201 MZ, 175 same-sex DZ pairs) and sibling (102 biological, 87 adopted pairs) data (with the sample size dropping to about half at the last data point) gathered at ages 1, 2, 3, 4, 7 and 9 years of age (Bayley Mental Development Index at 1 and 2, Stanford-Binet at 3 and 4, WISC-R at 7). Figure 5 shows the results of fitting a Cholesky decomposition model (often referred to as a triangular factorisation) to the IQ data for years 1 to 9. The boxes indicate the IQ phenotype at each age. Sources of environmental variance are shown at the bottom and sources of genetic variance are shown at the top. The loadings are factor loadings

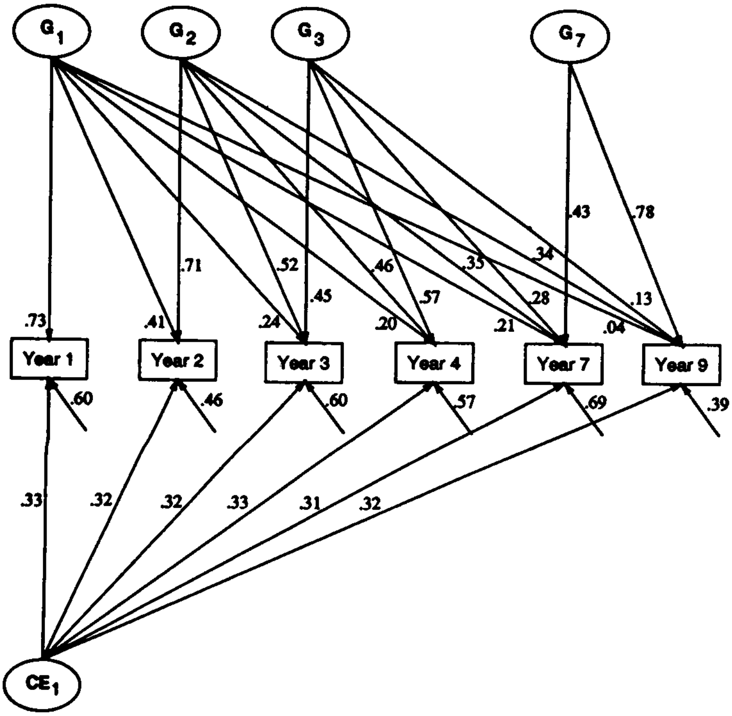


Fig. 5. Final reduced model of cognitive development for years 1, 2, 3, 4, 7, and 9. The boxes represent phenotypic measures, the circles represent latent influences, G = genetic influence, CE = shared environmental influences. The unlabelled factors are unique environmental time-specific influences. From Fulker *et al.* (1993).

for common environmental (CE) influences, genetic (G) influences and unique environmental influences (unlabelled).

The following conclusions flow from the analysis and figure.

1. There is one continuous source of common family environmental influence across all ages. The remaining environmental influence is unique and transitory to each age. At no point does it persist across even a single pair of years. Most of this influence is measurement error and state fluctuation. This unique environmental variance will be discussed with the Dunedin longitudinal study below.

2. A common genetic factor existing at year 1 continues to influence IQ, but with diminishing impact through year 9.

3. New genetic factors come into play, with continuing but diminishing influence, at years 2 and 3 but not at year 4.

4. New genetic influence arises at year 7 and persists to age 9.

Clearly there is a dynamic process at work. Fulker *et al.* (1993) speculate that the new genetic variance which expresses itself at age 7 may be in response to the 'novel environmental challenge' of schooling. While this is possible, the observation of fundamental cognitive change coming into play at about this age has been recognised for a long time and one can ask why is it that most societies send their children to school at about this age? In any event it is clear that genetic factors are implicated in developmental change. None of these findings can be inferred from the phenotypic correlations alone. Only a behaviour genetic longitudinal design can bring them out.

The recent analysis of IQ from the Dunedin Longitudinal Study deserves mention at this point even though it is not a behaviour genetic design. This report makes use of the IQ data gathered from middle childhood to adolescence (ages 7, 9, 11 and 13) for a representative sample of children from the city of Dunedin (Moffitt *et al.*, 1993). The analysis of the data is exemplary, and the authors summarise their findings thus: 'The findings suggest that, in the majority of children, IQ change is either negligible in amount, unreliably measured or both. In a non-trivial minority of children, naturalistic IQ change is marked and real, but this change is variable in its timing, idiosyncratic in its source and transient in its course' (p. 455). These conclusions are remarkably similar to those of the Colorado Adoption Project investigators. The Dunedin researchers explicitly tested and rejected the hypothesis that IQ change in the sample was systematically associated with environmental change (i.e. family change in socioeconomic status, etc). They also recognise that at a minimum a longitudinal twin design would be necessary to assess the important developmental influences driving the development in these children's IQ. They draw heavily on Scarr's developmental theory of genotype-environment effects (Scarr, in press; Scarr & McCartney, 1983) in order to put their findings in a meaningful theoretical context and they explicitly argue that the patterns of IQ change they observed 'appear to conform to recovery curves and seem to reflect level-maintaining or even level-seeking phenomena. Intellectual performance that was reliably deflected across time was characterized by a self-righting tendency. IQ appeared to be elastic, rather than plastic' (p. 496). Wilson (1983) formulated a remarkably similar argument on the basis of his well known longitudinal twin study.

The analyses carried out on the SATSA data, the Texas Adoption Study and the Colorado Adoption Project data were all possible because of the very recent development of powerful statistical modelling tools. This important topic does deserve a few words. Figure 6, from Neale & Cardon (1992), attempts to trace the intellectual roots of modern mathematical genetic methodology. Galton, deservedly, is found at the head of the list.

In his classic book *A History of Genetics*, Sturtevant (1965) speculated on an interesting question:

> 'The question has often been raised: would any biologist have appreciated Mendel's work if he has seen the paper before 1900? My own candidate for the most likely person to have understood it is Galton, because of his interest in discontinuous variation, his mathematical turn of mind, and his acceptance of Weisman's view that the hereditary potentialities of an individual must be halved in each germ cell' (p. 22).

On the same grounds, had Galton lived at the appropriate time he would not necessarily have invented each of the techniques listed, but it is very likely that he would have encouraged a capable colleague to do so, just as he did with the problem of correlation (Stigler, 1989).

All of the advances discussed so far are based on what most people would characterise as 'normal science', or puzzle solving. This involves the devising of new ideas, qualitative and quantitative techniques, new technologies and a great deal of

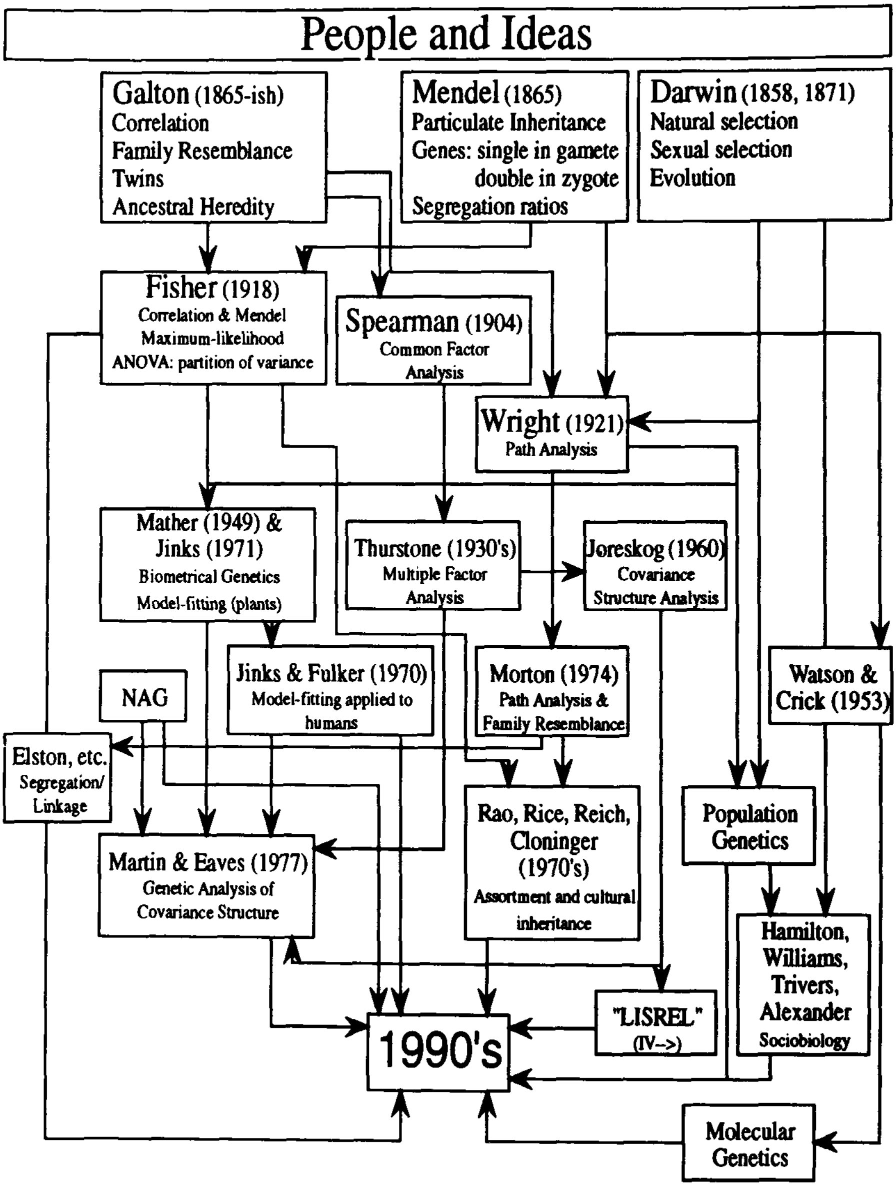


Fig. 6. Diagram of the intellectual traditions leading to modern mathematical genetic methodology. From Neale & Cardon (1992).

data gathering designed to test and refine the fundamental ideas (theories) that drive the enterprise. Galton was a master of all these activities, and he would have loved the various tools and designs that have been created in pursuit of knowledge regarding the origins of human individual differences.

Genetic influence on conceptually related non-intellective traits

Zeal and hard work: personality and creativity

Darwin in commenting on *Hereditary Genius* noted that zeal and hard work were probably important determinants of success. Measures of achievement motivation are typically designed to assess these facets of personality. Three measures of achievement motivation are used in the Minnesota Study of Twins Reared Apart. They are assessed by the Multidimensional Personality Questionnaire (MPQ) and the California Psychological Inventory (CPI) and have heritabilities of 0·39, 0·41 and 0·67 (Bouchard & McGue, 1990; Tellegren *et al.*, 1988). Zeal is also captured in two scales developed by Gough to characterise specifically the creative individual. The Creative Temperament scale (Gough, 1990) is scored from the CPI and the Creative Personality Scale is scored from the Adjective Checklist (Gough, 1979). The MZA ($n=59$) correlations for these scales are 0·51 and 0·54 respectively. The DZA ($n=46$) correlations are 0·18 and 0·06 (Bouchard & Lykken, in press; Waller *et al.*, 1993). Comparable data on ordinary twins samples are being gathered before fitting models to these data, but it is clear that there is a very significant genetic influence on these traits.

Psychological interests

Zeal can also be reflected in patterns of psychological interest and a number of behaviour genetic studies of interests have been published. One is based on twins reared apart (Moloney, Bouchard & Segal, 1991), another is based on a large registry sample of twins reared together (Lykken *et al.*, 1993), and a third is based on eight different kinship groups (Betsworth *et al.*, 1993). All demonstrate significant genetic influence on traits in this domain.

Genetic influence on sensory and central processes

It was Galton's belief that individual differences in mental ability were mediated by individual differences in sensory and central processes, which he believed were under the influence of heredity. He had no idea what these processes might be, nor did he have access to the measurement devices necessary to explore these questions, so he was unable to test his ideas. Work in this domain is of interest in its own right, but it is of particular interest to students of higher mental processes because of the seldom stated but widely held belief that there are no significant genetically based individual differences in important central or sensory processes. Thus even if the processes discussed below are eventually shown not to have any relationship to higher order processes, the demonstration of genetic influence would counter an important assumption underlying one class of criticism of behaviour genetic findings in the domain of intelligence, a trait which is unquestionably mediated by central processes.

Event-related potentials

Discriminatory abilities were of particular interest to Galton and the psychologists of subsequent generations. Indeed, Spearman's (1904) classic study of intelligence made

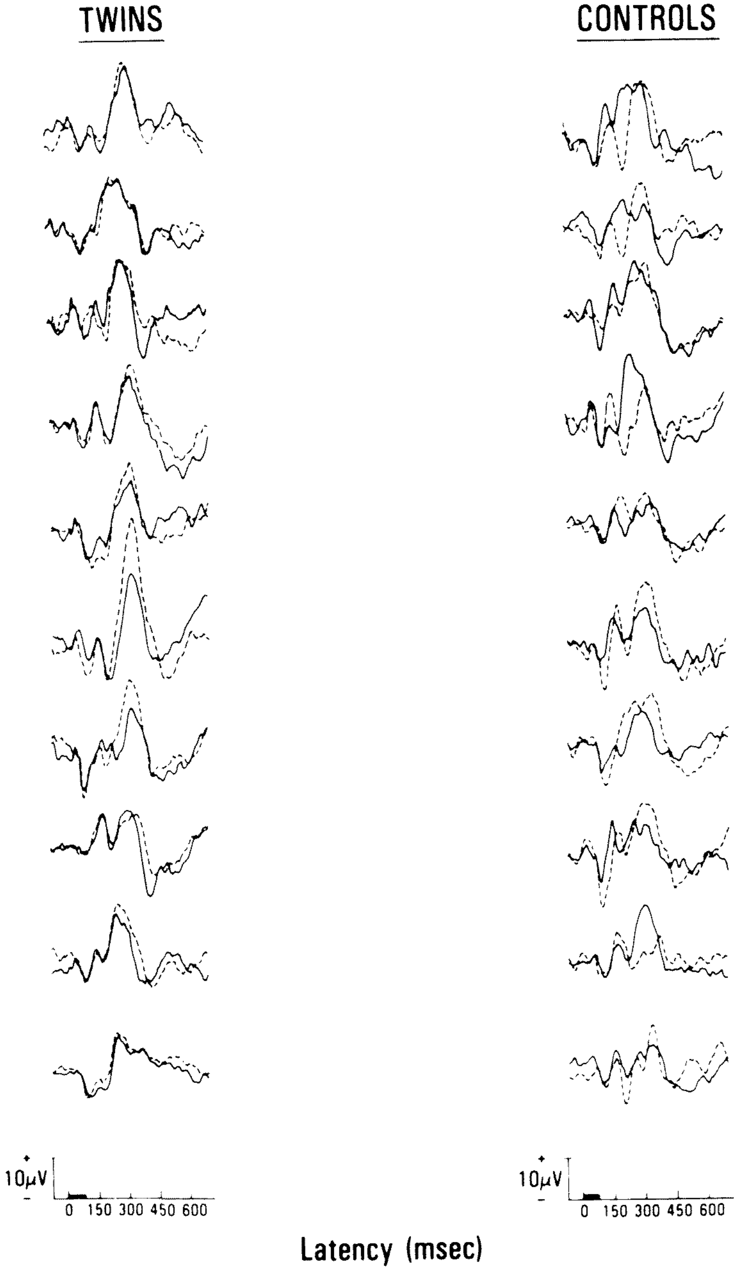


Fig. 7. Event-related potential from ten twin and control pair subjects. The solid and broken lines represent one individual from each pair type. From Polich & Burns (1987).

use of a number of sensory discrimination measures. Whenever a person discriminates a stimulus, a large (10–20 μV) positive-going wave form is elicited. This event-related brain potential (ERP) has a peak at 300 milliseconds. Like many experimental measures there is a tendency to think of this phenomenon as invariant across individuals. But like virtually any measure that can be taken on biological organisms it varies from individual to individual and is remarkably similar in monozygotic twins. Polich & Burns (1987) gathered ERPs on ten pairs of MZ twins and ten control pairs matched to the twins on sex, age, educational level, race and alcohol consumption. They ranged in age from 18 to 30 years. The ERPs for these 40 individuals are shown in Fig. 7. There is little doubt that these wave forms are unique and that the twins are dramatically alike.

Spontaneous otoacoustic emissions

Surprisingly the normal human cochlea can not only analyse sounds it can also produce them. These sounds can be recorded and their characteristics analysed. One type of such emissions, called spontaneous otoacoustic emissions, have a very high prevalence, are similar in infants and adults and appear to be highly stable. The number of such emissions appears to be related in some manner to acoustic sensitivity. Interestingly these emissions show both striking sex and race differences.

McFadden & Loehlin (1995) have shown, using a twin design, that the number of spontaneous otoacoustic emissions, but not their frequencies, has a quite significant heritability. Their findings replicated those of an independent study carried out concurrently (Russell, 1992; Russell & Bilger, 1992). The heritabilities in the two studies were 0·71 and 0·78. The correlations for number of emissions between the two ears of the same person for the four groups used in these two studies were 0·81, 0·69, 0·78 and 0·78. The twins are as similar to each other as are their two ears.

Electroencephalograms

Similar effects have been demonstrated for the entire resting electroencephalogram (EEG). Human EEGs demonstrate considerable individuality. The EEGs gathered from Bouchard and colleagues' study of monozygotic and dizygotic twins reared apart have been analysed in conjunction with comparable data from twins reared together gathered in Zurich (Stassen, Lykken & Bomben, 1988a; Stassen *et al.*, 1988b). Two sample EEG spectral profiles from pairs of MZAs are shown in Figs 8 and 9.

The spectral profiles within twin pairs are remarkably alike and the two pairs differ dramatically from each other. The authors of this report conclude:

> 'Our results provide ample evidence that the individual characteristics of the resting EEG are primarily determined by genetic factors . . . the EEGs of MZ twins reared apart turned out to be as similar to each other as are the EEGs of the same person over time, and there is no significant difference in the resting EEG between the two populations of MZ twins brought up together and MZ twins reared apart' (Stassen *et al.*, 1988b, p. 175).

To summarise, it has now been demonstrated that traits which span the range of complexity from whole brain EEGs through event-related potentials to narrow sensory

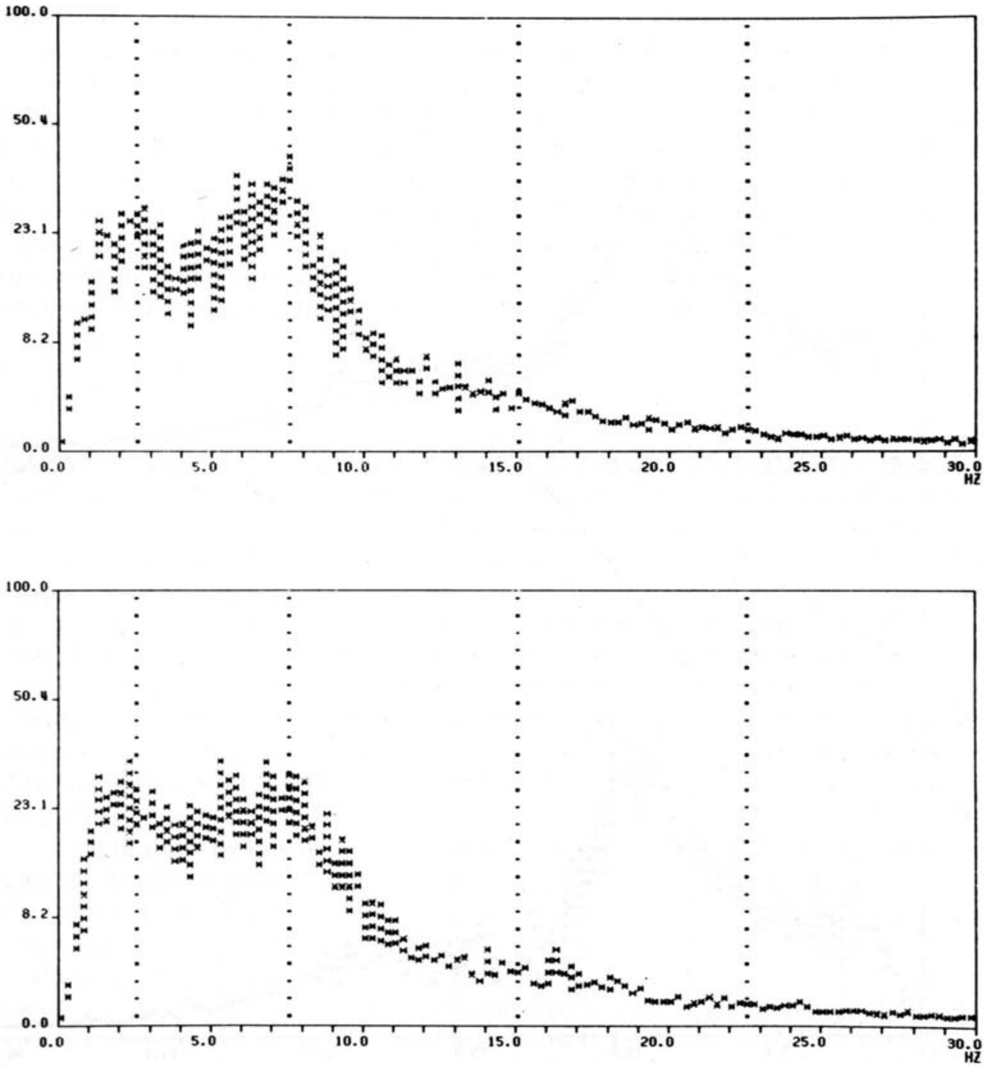


Fig. 8. Pair of MZ female twins reared apart, 41 years old. The spectral intensities are plotted as a log-proportional scale along the vertical axis. From Stassen *et al.* (1988a).

system features such as otoacoustic emissions show considerable uniqueness and sizeable genetic variance.

Galton would not have been surprised by any of these results. He would also have pointed out that genetic influences are not inevitable but are contingent on an adequate environment. Damage to the brain of one twin would, for example, clearly influence the results and, depending on the age at which it occurred and its extent, it might have profound consequences for the development and expression of ability and other traits in the damaged individual.

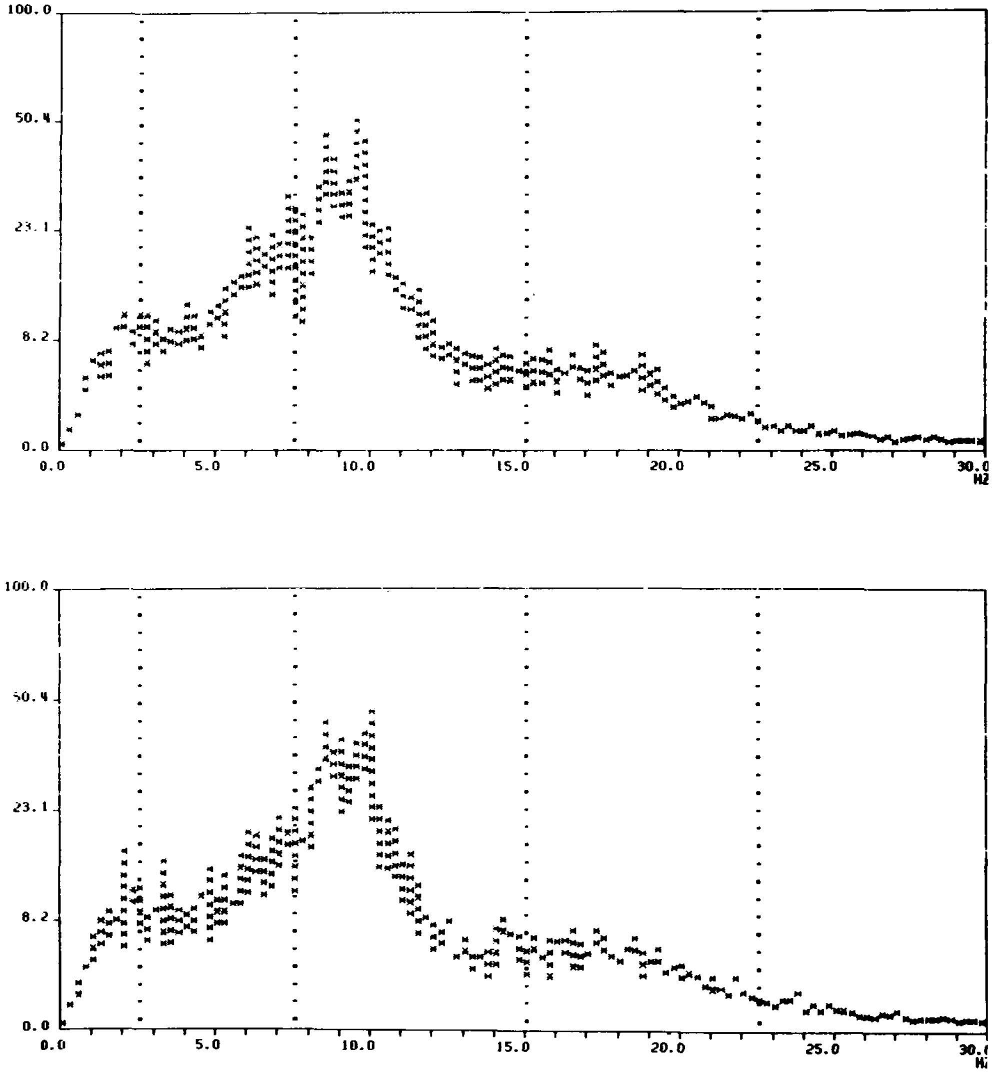


Fig. 9. Pair of MZ male twins reared apart, 38 years old. The spectral intensities are plotted as a log-proportional scale along the vertical axis. From Stassen *et al.* (1988a).

The evolution of intelligence and the human brain

Rushton & Osborne (1995) have recently demonstrated that cranial size is a significantly heritable trait with values ranging from 38% to 52% depending on a variety of factors, including race. This finding is of considerable interest given the now well established correlation between brain size and IQ (Jensen, 1994; Jensen & Sinha, 1993). This raises some interesting questions regarding the evolution of intelligence.

In recent years the emerging discipline of evolutionary psychology has shown the markings of a major scientific advance. Developments in this area are well represented by the work of Barkow (1989), Buss (1994), Daly & Wilson (1988), Pinker (1994), Tooby & Cosmides (1990), Barkow, Cosmides & Tooby (1992), Cosmides, Tooby & Barkow (1992) and Symons (1979). Virtually all theorising in this domain suggests that nature designs specific mechanisms for specific purposes—that is, the brain is modular in construction. Fodor (1980) has put the argument very explicitly with regard to language. According to his argument human language simply cannot reflect the general capacity of the human brain to learn; '. . . in all other species cognitive capacities are moulded by selection pressures as Darwin taught us to expect. A truly general intelligence (a cognitive capacity fit to discover just any truths there are) would be a biological anomaly and an evolutionary enigma.' (p. 333). Pinker has put forward precisely the same argument in great detail in his recent book *The Language Instinct* (1994). The logic underlying the argument of evolutionary psychologists appears compelling and when applied to mental abilities it strongly favours the view that human cognitive ability should be conceived of as a set of specialised skills each having evolved to solve a specific adaptive problem. The idea of a domain general cognitive capacity, *g*, is simply unacceptable to these theorists. A related argument put forward by evolutionary psychologists is that traits with high heritability are *de facto* not adaptations because, according to genetic theory, directional selection will reduce the narrow-sense heritability to zero. This latter problem is not thought to be serious (Bouchard *et al.*, in press; Wilson, 1994). As Wilson put it, 'Whenever genes are maintained in a balanced polymorphism, either by frequency-dependent forces within a population or by frequency-independent forces operating in different directions over time and space, heritable variation exists for the traits in question. There is simply no consistent relationship between the heritability of a trait and its status as an adaptation' (p. 225).

A recent study by Finlay & Darlington (1995) asked a very interesting question that touches directly on these matters: 'If a species undergoes strong selection pressure for the optimization of a behavioral ability that depends on the size of a localized functional system in the brain, what changes take place in the organization of the brain as a whole?' (p. 1578). Because the human brain is such a metabolically expensive organ consuming 20–25% of resting metabolism compared to about 8% for anthropoid primates and 3–4% for most mammals (Leonard & Robertson, 1994) standard Darwinian theory on this matter would argue in favour of highly localised functions—expansion of only those areas necessary. Gould (1977) and others have alternatively argued that for a variety of reasons (e.g. maturational clocks, tropic relations between developing structures, etc) there may be constraints on what is possible under such selection pressures. The question is an empirical one and to explore it Finlay & Darlington carried out an analysis of brain size across 131 species of mammals. They found that the absolute size of the brain predicted the sizes of all the components (excluding the olfactory component) in a non-linear way with an 'explosive' change in the size of the neocortex in the largest-brained primates. They conclude that, 'the most likely brain alteration resulting from selection for any behavioral ability may be a coordinated enlargement of the entire nonolfactory brain' (p. 1578).

These findings appear to override the major theoretical objection—that of selection for specialisation of function—to the idea of *g* put forward by evolutionary psychologists. These facts also take on additional meaning when considering how rapidly brain size could change. As Williams (1992) has put it:

> 'Some widely recognized examples of rapid evolution are really extremely slow. Data on Pleistocene human evolution are interpretable in various ways, but it is possible that the cerebrum doubled in size in as little as 100,000 years, or perhaps 3000 generations (Rightmire, 1985). This, according Whiten and Byrne (1988) is "a unique and staggering acceleration in brain size". How rapid a change was it really? Even with conservative assumptions on coefficient of variation (e.g. 10 per cent) and heritability (30 per cent) in this character, it would take only rather weak selection ($s = 0{\cdot}03$) to give a 1 per cent change in a generation. This would permit a doubling in 70 generations. An early hominid brain could have increased to the modern size, and back again, about 21 times while the actual evolution took place. Indeed, it is plausible that a random walk of 1 per cent increases and decreases could double a quantitative character in less than 3000 generations' (p. 132).

The large human brain is without doubt the outcome of the process of natural selection as is intelligence, one of its concomitant qualities, just as Darwin and Galton always thought it was.

Conclusions

Have any advances been made since Galton? The answer is yes, a great deal of progress has been made. Considerably more is now known about genetic and environmental influences on intelligence than even a few years ago. None of the advances has been dramatic. Rather they have been incremental across a wide variety of domains of scholarship. Slowly but surely these advances have helped to fill in the rough picture derived from Darwin's theory and brilliantly sketched out by Galton over a century ago.

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