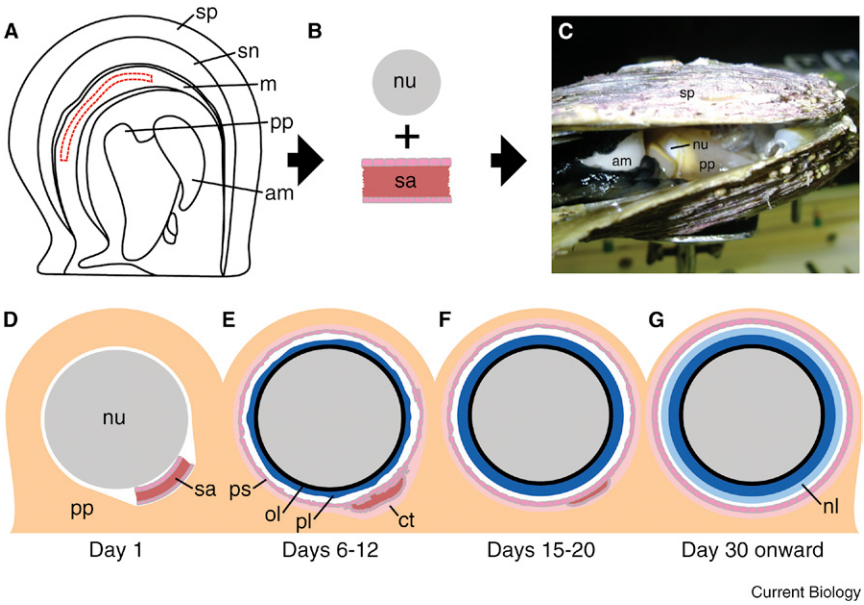

Figure 2. Pearl culture.
(A) Schematic of the internal anatomy of the pearl oyster. The region from which donor tissue (saibo) is extracted is indicated by the red dotted line. (B) A marble-shaped nucleus and small piece of saibo are implanted into the host oyster. (C) Host oyster after harvest of first pearl and insertion of second nucleus. (D–G) Schematic of pearl sac development. On day 1, nucleus and saibo are inserted into the pearl pocket (D). After approximately 6–12 days, the incision has healed and epithelial cells from the saibo have migrated around the nucleus to form the pearl sac. Organic material has been deposited onto the nucleus, followed by an irregular prismatic layer (E). On days 15–20, the prismatic layer now has a regular appearance (F). After approximately 30 days, the pearl sac has a homogeneous appearance and no trace of the saibo graft remains. The nacreous layer of the pearl has begun to form (G). (am: adductor muscle; ct: connective tissue; m: mantle; nl: nacreous layer; nu: nucleus; ol: organic layer; pl: prismatic layer; pp: pearl pocket; ps: pearl sac; sa: saibo; sn: nacreous layer of shell; sp: prismatic layer of shell.)

increase in the amount of genetic data available for pearl molluscs, including the sequencing of the *Pinctada fucata* genome last year. Transcriptome sequencing of both the mantle and pearl sacs and proteomics of shells and pearls has shown that the same genes and proteins are involved in their synthesis — to date, no unique 'pearl' genes have been found. There are, however, indications that genes that are highly expressed in the nacreous region of the mantle are not necessarily also highly expressed in the pearl sac, and that pearl formation may be more complex than originally supposed.

Where can I find out more?

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Primer

Intelligence

Ian J. Deary

Some people are cleverer than others. I think it would be a good thing if more biologists began with that observation as the starting point for their research. Why? Because it is a prominent and consistent way in which people differ from each other; because the measurements we make of people's cleverness produce scores that are correlated with important life outcomes; because it is interesting to discover the mechanisms that produce these individual differences; and because understanding these mechanisms might help to ameliorate those states in which cognitive function is low or declining.

Psychologists study intelligence in two different ways. First, cognitive psychologists mostly focus on trying to find out how the normal mind works. They try to enumerate the mental functions that we share. They try to discover how those functions fit into a mental system. Second, differential psychologists mostly focus on how people differ in the workings of their minds. They try to enumerate the major domains of function in which people differ. They try to discover the causes and consequences of these differences. The two types of psychologist studying intelligence don't communicate very well. For example, if you look at texts on cognitive psychology, you will find few mentions of individual differences. This primer is about the differential psychology of intelligence.

Most academics who do not work in intelligence differences are skeptical when the field is mentioned. This might be for a number of reasons. First, the word 'intelligence' can appear to be too general; surely, it is argued, that there are so many distinct cognitive capabilities that we are all good at some mental skills. Second, there are some events in the history of intelligence research that have appeared to discredit the field; some people will recall divisive 11-plus tests of the old UK school system, or have heard about the Cyril Burt affair (there is debate about whether

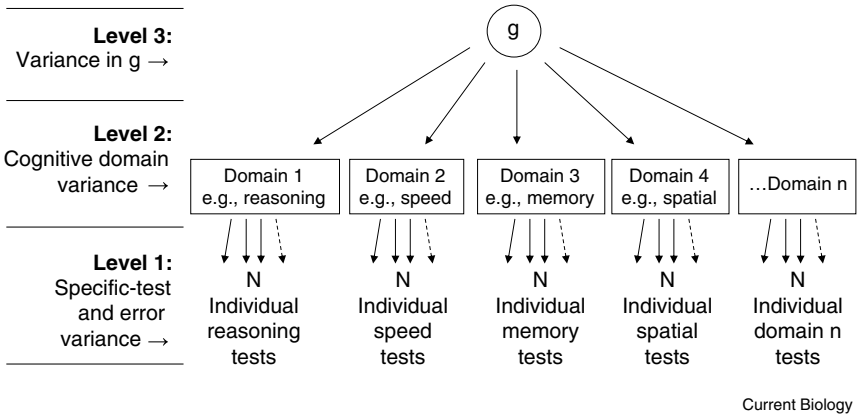

Figure 1. The hierarchical model of intelligence variance.
At level 1 people differ in specific tests that assess the various cognitive domains. Scores on all the tests correlate positively. It is found that there are especially strong correlations among the tests of the same domain, so a latent trait at the domain level can be extracted to represent this common variance. It is then found that people who do well in one domain also tend to do well in the other domains, so a general cognitive latent trait called *g* can be extracted. This model allows researchers to partition cognitive performance variance into these different levels. They can then explore the causes and consequences of variance at different levels of cognitive specificity-generality. For example, there are genetic and ageing effects on g and on some specific domains, such as memory and speed of processing. Note that the specific-test-level variance contains variation in the performance of skills that are specific to the individual test and also contains error variance.

he was fraudulent or careless with his twins' data on intelligence), or be aware of the over-application of IQ tests at Ellis island, or have read about controversies concerning studies of intelligence differences between ethnic groups, or think that the IQ-type test has been replaced with the idea of 'multiple' intelligences, and so on. Third, it is possible that clever people develop a kind of cognitive *noblesse oblige*; they kind of know they have won the lottery on a valuable trait, but they think it is bad form to acknowledge it. Fourth, it is possible that they have not been exposed to the research which has accumulated on the topic; if they have the opportunity to study the research, they can make up their own mind.

Intelligence as phenotype

"Define intelligence," is the common skeptical imperative. The researcher Linda Gottfredson's definition of intelligence is often repeated: "Intelligence is a very general mental capability that, among other things, involves the ability to reason, plan, solve problems, think abstractly, comprehend complex ideas, learn quickly and learn from experience. It is not merely book learning, a narrow academic skill, or test-taking smarts. Rather, it reflects a broader and deeper capability for comprehending our surroundings — 'catching on,' 'making sense' of things, or 'figuring out' what to do."

I prefer to begin the consideration of the intelligence phenotype from an empirical regularity that was discovered in 1904 by the British psychologist Charles Spearman. He found that people who perform well on one type of cognitive test tend to perform well on others. That is, if cognitive test scores are ordered so that better performance equals a higher score, the correlations between them are all positive. There is shared variation among all types of cognitive performance. Spearman called this shared/common variance *g*: an abbreviation for general intelligence. In the 100+ years since then, every study that has applied a diverse battery of cognitive tests to a decent-sized group of people with a mix of ability levels has re-discovered the same thing: there is some cognitive variance shared by all cognitive tests. Typically, if one applies principal components analysis, just under half of the total test score variance is accounted for by the first unrotated principal component. This applies: whether the tests are paper-and-pencil-based, or one-to-one tests; whether the content is verbal, numerical, or spatial; or whether the functions being tested are to do with reasoning, memory, speed of thinking, vocabulary, or even simpler tasks like reaction time, and so on. Therefore, from a cognitive test battery, people can be given a score to represent their relative *g* levels. These are not idiosyncratic to the particular tests they were given; as long as a decent-sized battery of tests is given, any group of tests will produce a *g* score that will rank people almost identically.

Therefore, part of the reason why some people do better on any one mental test is because they have a higher *g* level. The parameter *g* is not the whole story, however; there is some variance in cognitive performance that is not explained by *g*. Intelligence researchers have reached a consensus that there are three levels of variance in cognitive performance (Figure 1). So, if we ask why, for example, 100 people obtain different scores in a test that requires them to find the next number in a series of numbers, the answers are that: some of them are generally better at all cognitive tests, some are better at reasoning tasks as a whole, and some are better at a narrow skill that is specific to numerical reasoning tasks. Of course, we should not omit that there is error and idiosyncratic variance; some of them just felt better on the day.

There is an industry of cognitive test development. Some tests are devised for researchers, and some for applications in child development, education, occupational selection, and health and dementia. Tests range hugely in forms and contents: some are self-completed, and some require one-to-one examination. There is growing on-line testing. Alongside the tests, the statistical field of psychometrics has grown in parallel, with statistical procedures such as factor analysis, item response theory, and structural equation modeling. These are concerned with the reliability and validity of cognitive tests. IQ-type test scores are highly reliable, and validity is dealt with later. The test scores are also highly stable. For example, when the same intelligence test is taken at age 11 years and repeated at almost 80, about half of the variance is stable.

Causes of intelligence differences

Genetics and environment

Twin and adoption studies provide evidence that differences in intelligence are heritable. The percentage of the variation in intelligence accounted for by genetic causes is usually given at about 50%. Heritability estimates

for young children are typically lower, whereas estimates for adults are higher (up to 70–80%). There might be some small decline in heritability in old age, but it remains high. Some studies that include many diverse tests of mental abilities have computed the heritabilities of *g* and the more specific domains of intelligence. They find that *g* is highly heritable and that there is less genetic influence that is specific to each domain. There is some evidence, though mixed, that the heritability of intelligence is higher among more affluent people when compared with more deprived individuals.

Within the range of normal cognitive abilities — that is, apart from studies of learning difficulties — the molecular genetic study of intelligence is still quite new. There have been almost no well-replicated associations between candidate genetic variants and intelligence. An exception is the *APOE* gene: people with one or two *e4* alleles of this gene tend to have lower cognitive ability in old age, and tend to decline more in cognition across their lifetimes, than those who lack *e4*. Genome-wide association studies (GWAS) of intelligence have not yet revealed any additional variants with genome-wide significance.

There is, though, molecular genetic evidence that some variance in intelligence differences is detected by common single nucleotide polymorphisms (SNPs). The application of the genetic complex trait analysis (GCTA) method to intelligence differences in childhood and older age found that between a quarter and a half of the variance could be accounted for by variants in linkage disequilibrium with common SNPs. GCTA creates a genetic relationship matrix among unrelated individuals and calculates the association between this genetic similarity and phenotypic similarity. This analysis did not identify the causal variants; it suggested that intelligence is highly polygenic, with large numbers of variants of small effect sizes. Bivariate GCTA analysis has shown that the genetic correlation between intelligence measured in childhood and old age in the same individual is high; to a substantial extent, the same genes cause higher intelligence in childhood and older age.

Current research is accumulating larger sample sizes for larger GWAS of intelligence; for the complex traits of height and obesity, for example, increasing the sample sizes has brought substantially more genome-wide significant hits, and these are accounting for ever-higher proportions of the phenotypic variance. Also being pursued are strategies whereby the GWAS of phenotypes linked with intelligence are being used to create, in separate samples, polygenic risk scores for the phenotype. These polygenic risk scores are then tested for association with intelligence. For example, using GWAS data from the Psychiatric GWAS Consortium, a polygenic risk score was created for schizophrenia in separate samples of older people with intelligence data, none of whom had suffered from schizophrenia. Those with higher polygenic risk for schizophrenia tended to have lower cognitive ability in old age and also had larger relative declines in cognitive ability between childhood and old age. Further studies will extend such analyses to other phenotypes with which intelligence is associated, to establish the extent of their genetic correlations.

With regard to the environment, twin studies suggest that the contribution of shared environment to intelligence differences is small, even negligible, by adulthood, and that that which is non-genetic is largely due to non-shared environment and measurement error.

Brain correlates of intelligence differences

Beyond the general finding that there is some genetic variation in intelligence, there is a modest (~0.30) correlation between intelligence test scores and overall brain size. As yet, it is not understood what it is about bigger brains that is associated with being brighter. There is a similar-sized correlation between general intelligence and the general integrity of the brain's white matter, as measured using diffusion tensor magnetic resonance brain imaging. This correlation is largely accounted for by people's differences in speed of processing. There is some support from brain imaging and electroencephalographic research that cleverer brains are more efficient.

Consequences of intelligence differences

A reason to take intelligence differences seriously is that scores on intelligence tests are associated with a number of important life outcomes.

Education

People who score better on intelligence tests tend to stay longer in education, to gain higher-level qualifications, and to perform better on assessments of academic achievement. Some of the correlations between intelligence scores at the end of primary school and academic results some years later are high, suggesting that it is not just a matter of education boosting intelligence. Also, educational attainment has a moderately high heritability, and a strong genetic correlation with intelligence. On the other hand, there is also evidence that education can provide a boost to scores on tests of complex thinking, and some of these increments last into old age. Therefore, there is probably a bidirectional causal association between intelligence and education.

Social status and social mobility

People who score better on intelligence tests tend to go into more professional occupations (typically those with higher status) and to perform better in the workplace. There is a positive association between intelligence test scores in childhood and social position later in life: people who score higher tend to be in more professional jobs, to live in less deprived areas, and to have higher incomes. The association is not perfect. Results show that, when it comes to attained social position in maturity, intelligence, education and parental background all count to some extent. That is, there is some meritocracy and intelligence-driven social mobility, and there is also some social inertia. There is some evidence for a so-called gravitational hypothesis: that intelligence in youth relates more strongly to occupational and social position later rather than earlier in adulthood.

Health, illness, and death

People who score better on intelligence tests tend to make healthier lifestyle and dietary choices, to have better health, to be less likely to have chronic illnesses like cardiovascular disease, and to live longer. These findings have been the result of the field of cognitive epidemiology, which is little more than a decade old. Some of the studies in this field have been heroic in size and duration: some are of sample sizes of over 1,000,000 people, and some have intelligence test data in childhood and then data on health information up to

more than 60 years later. Just focusing on the intelligence–death associations, this applies to mortality from all causes, to cardiovascular deaths, to suicides and homicides, and to accidental deaths, but probably not to deaths from cancer. The associations between intelligence in youth and health and survival into old age are not explained by parental social class. There is some statistical mediation of the association by education and the person's own social class in mid-life, though it is not clear whether this is informative about the mechanistic pathways involved or whether education and occupational social class are, in part, acting as proxies for intelligence.

Currently, there are four possible accounts of the intelligence versus health/death associations: that they are associated because, even in youth, intelligence is capable of indexing some general, underlying bodily system integrity; that the intelligence test scores detected some pathology even in youth; that intelligence is associated with later health choices and lifestyles; and that intelligence acts as a selection variable into safer occupational and social environments. These are being tested at present.

The ageing of intelligence

Intelligence has an important place in the world's changing demographic structure. Especially in so-called developed countries, populations have a growing proportion of older people, greater absolute numbers of them, and people are living longer. As well as bodily changes with age, cognitive capabilities decline too. There are declines in cognitive function even among people who do not develop dementia. Not all cognitive functions decline at the same rate. Some cognitive functions — often referred to as markers of crystallized intelligence — hold up well with age. These include vocabulary and general and specific knowledge. The cognitive functions that tend to decline are called fluid intelligence. These tend to involve on-the-spot thinking with novel materials, and in situations in which past knowledge is of limited help. This includes abstract reasoning, spatial abilities, processing speed, and working and other types of memory. The empirical data show that, when the various fluid-type cognitive functions are studied, we find the hierarchy again. That is, age has a negative effect on the variance shared by all tests, and also some specific effects in addition to that, principally on the domains of processing speed and memory.

Not everyone experiences the same rate of cognitive decline, and there is a growing interest in the genetic and environmental (biological and social) determinants of people's differences in age-related cognitive changes. Not many of these determinants are well replicated. Some of the more solid evidence exists for the following being cognitively protective: not having the *APOE* e4 allele, being physically more active and fit, and not smoking.

For biologists, apart from helping psychologists to seek more determinants of healthy cognitive ageing, there are two theoretical ideas that might be attractive in the study of the ageing of intelligence. The first is the idea that some people have cognitive reserve such that their brains are better able to withstand the insults of age and illness. Researchers in this area write about the possibility of there being passive brain reserve and active reserve. Passive reserve refers to the possibility of there being some aspects of brain structure — maybe even as prosaic as just having a bigger brain — that provides the reserve. Active reserve refers to the possibility that, in response to an insult, some people's brains are more flexible in reorganizing networks to regain or retain cognitive functions. The other idea in research on the ageing of intelligence is the common cause hypothesis. This is built upon some empirical findings which suggest that the age-related decline of different bodily systems is correlated; that is, people who are experiencing faster cognitive declines might also be experiencing faster declines in sensory and some physical functions. In so far as this occurs, researchers have sought possible common causes that might provide the mechanisms or at least indicators of them. They have, for example, considered inflammation, oxidative stress, telomere length, and the hypothalamic-pituitary-adrenal axis.

Other issues in intelligence research

There are still findings and controversies about sex and race differences in research. With respect to the former, the better data come from massive samples of children tested in school settings, where there has been either full-population testing or the testing of representative samples. These tend to show that boys and girls have about the same mean level of intelligence. They also show that, for *g*, the boys have greater variance: there is an excess of boys at the lower and upper ends of the intelligence scale.

There continues to be discussion about the so-named Flynn effect, whereby the absolute scores on intelligence tests have been rising since testing started in the early-to-mid 20th century. The extent of the rise, its geographical distribution in the world, and especially its causes are all still being studied. Some hypothesise that better nutrition might explain some of the increase, and others put it down to society's making more accessible and emphasizing the skills tested by intelligence tests.

There is interest in finding interventions that might boost intelligence. On the biological side there is research showing that breast feeding is associated with a sizeable advantage in intelligence later in childhood. However, there is also some evidence that this is explained by the higher intelligence scores of the mothers who tend to breastfeed. There is still unresolved researching and discussion of the possible social boosters of intelligence. For example, adoption from a deprived to a more affluent setting is reported to be associated with an intelligence advantage. There is still debate about the effectiveness of intensive intervention programmes early in life, and whether any cognitive advantages last or whether advantage accrues to social rather than cognitive skills.

Human intelligence is important; it matters in our lives. Understanding the biology of intelligence differences could help to ameliorate declines in cognitive function.

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