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ORIGINAL RESEARCH

# Genes, Evolution and Intelligence

**Thomas J. Bouchard Jr.**

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**Abstract** I argue that the *g* factor meets the fundamental criteria of a scientific construct more fully than any other conception of intelligence. I briefly discuss the evidence regarding the relationship of brain size to intelligence. A review of a large body of evidence demonstrates that there is a *g* factor in a wide range of species and that, in the species studied, it relates to brain size and is heritable. These findings suggest that many species have evolved a general-purpose mechanism (a general biological intelligence) for dealing with the environments in which they evolved. In spite of numerous studies with considerable statistical power, we know of very few genes that influence *g* and the effects are very small. Nevertheless, *g* appears to be highly polygenic. Given the complexity of the human brain, it is not surprising that that one of its primary faculties—intelligence—is best explained by the near infinitesimal model of quantitative genetics.

**Keywords** Intelligence · Heritability · Evolution · *g* Factor · Brain

## Introduction

It is a delight and an honor to participate in the celebration of the career of such a distinguished colleague as John Loehlin. John should recognize the title of this paper as we jointly published a paper with a similar title—Genes, Evolution and Personality—in this journal a number of years ago (Bouchard and Loehlin 2001). That paper was commissioned by Norman Henderson the editor of Behavior Genetics who instructed us to write at the level of a beginning graduate student unfamiliar with the domain. I have followed those instructions here. When I began this paper I expected it to mimic the structure of our joint paper. As I should have expected that did not happen.

A very large body of evidence now strongly supports the view that a hierarchical model with a *g* factor at the top "explains" the core empirical findings that underlie most conceptions of human intelligence better than any other theory. In addition the *g* factor meets the fundamental criteria of a scientific construct more fully than any alternative conceptualization. More specifically it meets the criteria of mensuration (there are adequate measuring instruments), it is replicable/generalizable, it is parsimonious, it is refutable, and it continues to be generative. Any competing or newly proposed theory of intelligence must specify its domain of application and, if its domain of application is the same as or overlaps significantly with that of *g* theory it must demonstrate that it is superior to *g* theory as a scientific explanatory construct (Bouchard 2009a, b). This paper explicates human *g* as a psychological construct and demonstrates that its roots can be found deep in the evolutionary history of complex biological organisms.

## Intelligence: psychometric considerations

### The *g* factor

What is the domain of application? The idea of a *g* factor flows from the consistent empirical finding that virtually all the correlations between mental abilities are positive. Such

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T. J. Bouchard Jr. (✉)
University of Minnesota, Minneapolis, MN, USA
e-mail: bouch001@umn.edu

T. J. Bouchard Jr.
280 Storm Peak Court, Steamboat Springs, CO 80487, USA

a matrix is called a positive manifold. Guttman and Levey (1991) has appropriately called this the first Law of Intelligence Testing. What do we use to generate this manifold? We use tests, very broadly defined. Following Guttman, the domain of application is the universe of intelligence test items defined as questions/puzzles having an objectively correct or incorrect answer (defined by logic, by empirical science or by very broad convention as for example word meaning). Charles Spearman invented a simple form of what is now called factor analysis to explain this phenomenon and argued in favor of a general factor, now called the *g* factor or Spearman's *g*, as a parsimonious theoretical explanation of this observation (Bartholomew 2004; Blinkhorn 1995; Jensen 1998; Nyborg 2003). Note that speed of response, as in a reaction time test (Jensen 2006), addresses a process that may well underlie *g*, but is not by this definition a test of intelligence. The density of dendritic spines in brain cells would have the same status. *g* by this definition is a purely psychological construct and a *g* score is our best measure of this dominant and pervasive factor.

Let's be clear what this definition of the domain of application entails. First, we can, as noted by Guttman as well as many others, ask questions, present puzzles or observe their analog in any species. The items must come from the organism's universe of experience (ecological relevance). The correct answer is defined by the logic of the species, which may be partly wired, shared knowledge within the species (its rudimentary science), or conventions. Being able to find food behind a complex but ecologically relevant set of barriers (which can vary in difficulty) would be an example of an answer to the question; Can this individual find food under these circumstances? Novel responses that succeed would gain points, just as they do in human IQ tests, as they are objectively correct. With a variety of different kinds of questions we can ask, Does a population of individuals studied within this species generate a *g* factor? What is the structure of its mental abilities? Second, there is nothing in the definition that says the absolute level of performance of the population cannot rise or fall on one or more tests over time. An accumulation of shared knowledge, in the sense that there is a body of knowledge that some members have more of and others have less of, means those members of a later generation with more knowledge score higher than members of an earlier generation with less knowledge. Third, the previous reference to sampling of items raised the question, What domains should be sampled? How many items should be used? What level of reliability is necessary for proper inferences? How many participants should be included?, etc. These are practical questions of considerable importance, and they have to be worked out in each setting (birds, chimpanzees, mice, humans, etc.). These are questions of sampling theory, test bias, measurement quality (reliability, validity), etc. They need to be dealt with properly if we are to obtain a *g* score that reasonably approximates the construct of *g* at a particular time and for a particular population of organisms. How long it took to work out these problems in the domain of human intelligence testing is not widely recognized (Jenkins and Patterson 1961). They still bedevil most animal testing (Sauce and Matzel 2013; Thornton and Lukas 2012).

The amount of variance accounted for by the *g* factor in a human study of mental abilities varies as a function of the same factors that limit any scientific study: sampling adequacy of both the population of participants and the breath of mental ability measures, reliability of the measures, care with which the mental ability measures are administered, etc. Typically the *g* factor accounts for 45–50 % of the variance in a correlation matrix of representative human mental abilities (Austin et al. 2002; Floyd et al. 2009). The total score of such a battery (e.g. the IQ score) is so highly loaded with *g* it is often not necessary to calculate a *g* as the IQ scores will often give the same results. Nevertheless for both scientific and applied reasons it is always preferable to calculate a *g* score (Bartholomew 2004; Major et al. 2011; Reeve and Lam 2005).

Historically there has been considerable controversy over the specific structure of human mental abilities, particularly regarding the existence of a general factor. The arguments fall into two classes. The first is a general argument against factor analysis as a scientific tool. The second involves a mixture of theory and methodology, but boils down to competition between lumpers and splitters.

## Arguments against *g* because factor analysis is seen an inadequate scientific tool

Perhaps the strongest version of this argument was advanced by Steven J. Gould in his book *The Mismeasure of Man* (1981, 1996). Gould argued;

(a) "The fact of pervasive positive correlation between mental tests must be among the most unsurprising major discoveries in the history of science". (p. 315),
(b) "Spearman's *g* is not an ineluctable entity; it represents one mathematical solution among many equivalent alternatives. The chimerical nature of *g* is the rotten core of Jensen's edifice, and the entire hereditarian school." (p. 320). Gould was asserting that Thurstone's model was just as good a fit to the positive manifold as the Spearman model.
(c) belief in *g* constituted an error of reification—"the notion that such a nebulous socially defined concept as intelligence might be identified as a "thing" with a

> locus in the brain and a definite degree of heritability—and that it might be measured as a single number, thus permitting a unilinear ranking of people according to the amount they possess." (p. 239).

Despite the certainty with which these points were advanced they can be addressed fairly easily.

Item (a) is false. Given that Gould is known for being a science historian one wonders why he failed to note that before Spearman most commentators on mental faculties assumed they were independent. This view was called "faculty psychology" and the idea goes back at least to Aristotle. This idea also motivates the modular approach to the mind put forth by Fodor in the book, *The modularity of mind: An essay on faculty psychology* (1983). An excellent discussion of this point can be found in Chabris (2007).

The first sentence in item (b) is false, as not all models fit equally well. Some models are much more *parsimonious* than others (elegant and economical rather than elaborate). Using confirmatory factor analysis, it can be shown empirically that *g* theory fits various mental ability correlation matrices far better than any other conceptual model (Major et al. 2012). In addition it has been be shown that *g* is not chimerical as the *g* from various batteries of tests is virtually identical (Salthouse 2013). It is worth noting that Gould's discussion of factor analysis was far from contemporary. In the words of one statistician, "Gould was half a century out of date" (Bartholomew 2004, p. 70).

Item (c) the error of reification is an interesting mixture of philosophical reasoning (Gould cites J. S. Mill—"to believe that whatever received a name must be an entity or being, having an independent existence or its own" (p. 151), the idea here is misplaced concreteness) and political posturing; that is, using the Marxist dogma "reification is invalid" (see Google "Marxist reification" for numerous references) to invalidate research on human intelligence and behavior genetics. Whether intelligence is a "thing" or only a useful construct or something else is an empirical question. As a historian of ideas Gould certainly was familiar with the arguments of Lysenko and the soviet Marxists who argued that genes and viruses (*theoretical constructs* with only a name at the time) were the metaphysical constructs of bourgeois science or reifications (Soyfer 2001). Few scientists today would deny the existence of genes and viruses, even though we still do not understand all there is to know about them. A construct specifies the result we would expect to observe if the construct were real. Constructs are an integral tool in science.

*g* is a theoretical construct and the idea is to test it, not reject it on an ideological basis. As Korb (1994) points out, "If we assume that the factor model is a true partial model, then such further investigation cannot be based upon a fallacy of reification unless there is no physical substructure to intelligence at all—a claim that only an extreme Cartesian dualist could countenance" (p. 121).

Interestingly, Gould asserted that biology could help us decide between models. "In the absence of corroborative evidence from biology for one scheme or the other, how can one decide?" (p. 314). As I will show the evidence from genetics and brain research overwhelmingly supports both a *g* and a hereditarian point of view (Jensen's rotten edifice, according to Gould).

It is curious how critical non-experts in psychology and even some experts are about factor analysis and its descendants (structural equation modeling, path analysis) without acknowledging the fact that human beings are in part correlation machines and that these methods are simply attempts, fallible just as humans are, to systematize ideas and theories about clustering and causation in their efforts to fathom the structure of the physical, social and psychological worlds. Discussing this issue Gower (1972) pointed out that, ''… the human mind distinguishes between different groups because there are correlated characters within the postulated groups.'' Some assert that it will never be possible to test causal ideas in psychology from observational data. Pearl (2009) disagrees and it should be kept in mind that astronomy qualifies as a science even thought it is largely observational. It has scientific status in part because of its links with physics. The same may eventually be said about parts of psychology through its links with genetics and biology in general (Lee 2012).

## Theoretical arguments about the structure of mental abilities: splitters versus lumpers

### *J. P. Guilford: the structure-of-intellect model*

At the extreme end of the splitters the distinguished psychometrician Guilford (1985) argued that there were a very large number of facets of ability (eventually well over 120) but there was no *g*. Although he modified his theory somewhat over time, including the year he passed away (Guilford 1988) he never believed in *g* in spite of devastating criticisms of his methods. The most crucial of these was the argument that his methods were entirely subjective (Horn and Knapp 1973). Eventually even his close colleagues acknowledged the validity of this criticism and demonstrated that his own data yielded a hierarchical model with *g* at the top (Chen and Michael 1993). Guilford's theory still has adherents and it illustrates the fact that, "Theories in psychology are like old soldiers: They are not refuted or replaced—they don't die—they only fade away" (Lykken 1991, p. 7). Perhaps a better characterization is that

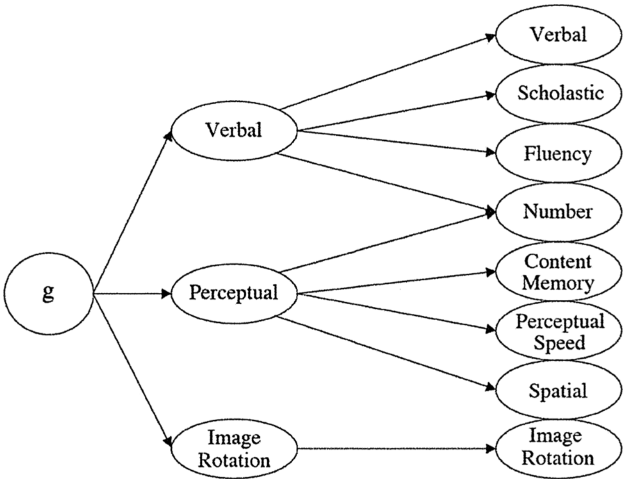

**Fig. 1** The verbal, perceptual, rotation (VPR) model

psychology is full of "Undead Theories" (Ferguson and Heene 2012).

*Cattell and Horn: fluid and crystallized intelligence*

Cattell and Horn argued in favor of a limited number of higher-order factors, but no *g* factor in much the same way as Thurstone and Thurstone (1941). More specifically Horn argued that the *g* factor extracted in various studies differed from one battery of tests to another and consequently the various g's lack invariance and therefore the status of a scientific construct (Horn 1989). This argument has now been decisively refuted. The *g* factor derived from well developed batteries of mental ability tests correlates almost perfectly and the results have been replicated numerous times (Johnson et al. 2008; Salthouse 2013).

*John Carrol: the three-stratum theory of intelligence*

Many theorists assumed that the structure of mental abilities, whatever the details, was a three stratum model with Stratum I being defined by tests, Stratum II being defined by lower-order factors and Stratum III being defined by *g*. This model was most fully elaborated by Carroll (1996; 2003a, b). McGrew (2009) has presented a model, the CHC theory that integrates Cattell-Horn and Carroll and provides a very useful taxonomy of abilities. It has been replaced by a Four-Stratum model.

*Philip Vernon: the verbal-perceptual-rotation (VPR) model*

Contrary to the expectations of many factor theorists, when enough tests and a large sample are used, a four-stratum model emerges. That model (Johnson and Bouchard 2005) which has been constructively replicated a number of times (Major et al. 2012) is shown in Fig. 1.

A number of points about the model should be made here.

First, this model is not original. It is a modification of an early model proposed long ago by Vernon (1965).

Second, and contrary to Gould's claims of arbitrariness, this model fits the many data sets to which it has been applied significantly better than well specified competing theories, specifically the Carroll Three Stratum Model, and the Cattell–Horn Fluid–Crystallized theory. This is, in part, because the studies designed to test and possibly refute the VPR model, had considerable statistical power (Matzke et al. 2010).

Third, the model is about variance in human abilities not a cognitive theory about how intellectual processes in the brain function (Jensen 2000). The same is true for the behavior genetic models to be discussed below. Variance component analysis applies to populations not individuals. Erroneous thinking about this matter continues to abound. Consider the comment by a previous president of the Association for Psychological Science, in which he repeats an old saw. "…partitioning the determinants of behavioral characteristics into separate genetic versus environmental causes is no more sensible than asking which areas of a rectangle are mostly due to length and which to width" (Mischel 2005, p. 3). While Mischel was citing someone else, he clearly accepted the criticism. The rectangle example is an old and long refuted rhetorical argument put forth by people whose fundamental argument is interactionist—that everything is complex and contingent—and then they assert that you need both environment and heredity. Well you need 2 equal lengths and 2 equal widths to define a rectangle but you can easily estimate the contribution of length and width to the area of a population of rectangles. In addition unless you can estimate a genetic contribution and an environmental contribution you cannot estimate the magnitude of an interaction. Mischel and his ilk have confused process within individuals with differences between individuals. What he should say is that organisms transact with their environments (e.g., eat food to grow, read and/or listen in order to acquire a vocabulary) and we would like to know the details of this process within individuals in order to estimate the degree to which it influences the variance in a trait within a population. I know of no one who disagrees with this latter point. It does not, however, invalidate the question, "how much does variation in their genes and their environment (food, exposure to words) contribute to individual differences within a population"? If genes contribute to population variance it is almost certain that the processes within individuals vary from person to person as a function of how the relevant genes influence the transaction by which the trait develops and manifests itself. We know very little about how genes actually influence most traits, be they physical or psychological. We do know from developmental twin and family studies, some of which are discussed below, that different genes come into play at different times during the development of morphological traits and intellectual skills (Wilson 1983).

Fourth, the model does not prove that *g* exists as a unitary entity. It may be that the positive manifold is best explained by hypothetical bonds (Bartholomew et al. 2013), mutualism (van der Maas et al. 2006) or neural network models (Chabris 2007). Choosing between these theories is difficult and will require much more precise knowledge of how the brain works (Hampshire et al. 2011). Of course once we know precisely how the brain works, including how it processes information obtained from the world, the positive manifold, the *g* factor and the structure of mental abilities will simply be a natural outcome of the underlying processes.

Fifth, if the model is correct the stratum II and III factors should correspond to some fundamental features (modules?) of the human brain and its evolutionary history. An example would be Spatial Ability (Lubinski 2010).

One lesson factor models teach us is that studies that employ a single test or task to represent a construct, a procedure widely used in experimental work dealing with cognitive processes, especially in animal studies, can be highly misleading as virtually all tests of mental ability have a large *g* loading. The higher the *g* loading the greater the complexity of the task, but no task is entirely *g* loaded and quite different tasks have equally high *g* loadings. For example the Raven Progressive Matrices is often cited as the test with the highest *g* loading. In fact the Thurstone Pedigrees test usually has a *g* loading equivalent to the Raven (Elebedour et al. 1997; Johnson et al. 2007) as do many verbal tasks. It is widely believed that *g* loadings are unstable and vary as a function of what tests are in a test battery. This is not true, *g* loadings are to a large extent a characteristic of the test itself (Floyd et al. 2009). Consequently, when using only one test or task it is difficult to know if the effect found is due to *g* or a more specific ability. A particular task or experimental manipulation is always a specific and error prone indicator of the latent construct of interest to an investigator (Loehlin 2004). Latent traits assessed with multiple indicators always provide more reliable and generalizable results. There is simply no substitute for the adequate measurement of constructs (Borsboom 2006).

## Brain size and *g* in humans: the controversy (Gould again!)

The fact that the increase in brain size of homonids over evolutionary time was driven by evolutionary processes and reflects an increase in cognitive skills is widely accepted. Consequently one might expect that brain size would correlate with *g* in contemporary populations and this should not be difficult to determine. As Van Valen (1974) put it:

> 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.

In spite of Van Valen's assertion that estimating the correlation between brain size and IQ should not be "overly difficult" the idea has been very controversial. Gould's (1981, 1996) attack on this idea was perhaps the sharpest and most influential. It also turns out in retrospect that it is among the most erroneous. In addition to being wrong about the relationship between brain size and IQ, Gould was wrong about a number of related issues. Consequently they deserve some discussion. One otherwise excellent and critical review of Gould's first edition by Spuhler (1982) asserted that "accounts of Morton, Broca, and Goddard contain fresh discoveries". Interestingly, two of these three discoveries have been shown to be false or seriously misleading so Gould's claims are a good place to start. Gould claimed that the data on the brain size of various groups gathered and compiled by the famous 19th-century physician and physical anthropologist Samuel George Morton reflected preconceived bias that was so strong "that it directed his tabulations along pre-established lines". It is now clear that Gould's claim is false and that it is more likely that Gould is the one who biased his measurement. An early study by an undergraduate student first called Gould's work into question (Michael 1988). An even more thorough analysis by a team of senior investigators lead to a conclusion that was opposite of that claimed by Gould, namely that; "Morton's methods were sound, and our analysis shows that they prevented Morton's biases from significantly impacting his results. The Morton case, rather than illustrating the ubiquity of bias, instead shows the ability of science to escape the bounds and blinders or cultural contests." (Lewis et al. 2011, p. 6). Goddard was accused of "skullduggery" (Gould 1981, p. 171) by manipulating photographs to "produce an appearance of evil or stupidity" (p. 172). A good case has been made that this accusation is as much bias on Gould's part as it is on Goddard's (Fancher 1987; Zenderland 1988). In addition Glenn and Ellis (1988) showed empirically that contemporary individuals are more likely to judge the individuals in the doctored photographs as "very bright" rather than as "retarded" and "kind" as opposed to "evil". Perhaps the photographs function as a projective test onto which different people impose their beliefs. Gould's erroneous interpretation is not uncommon. The use of drawn images versus photographs has been more of a problem in the history of science than generally realized and Daston and Galison (2007) provide a thoughtful discussion of the problem. Since we will be discussing the brain shortly it is worth noting that a bitter battle took place in Stockholm in 1906 between two Nobel prize winning neuroscientists—the Spaniard Santiago Ramón y Cajal and the Italian Camillo Golgi. Golgi defended a holistic view of the brain, a diffuse nervous network. Cajal defended a discrete model, the doctrine of the neuron. It was one battle in "an all out image war" that lasted a lifetime (Daston and Galison 2007, p. 119). I am not aware of any reanalysis of Gould's treatment of Broca, but Gould gives Boas credit for refuting "craniometric arguments". To quote Gould,

> The American anthropologist Franz Boas, for example, made short work of the fabled cranial index by showing that it varied widely both among adults of a single group and within the life of an individual (Boas, 1899). Moreover, he found significant differences in the cranial index between immigrant parents and their American-born children. The immutable obtuseness of the brachycephalic southern European might veer toward the dolichocephalic Nordic norm in a single generation of altered environment (Boas, 1911).

Put simply Gould argued that the Boas data proved "Cranial plasticity" across one generation. Freeman (2000) called this "21st Century Boasian Culturism" and indeed it has been cited for a hundred years as proof of environmental influence on head size and shape. The problem is that the Boas' data show no such thing. Sparks and Jantz (2002) reanalyzed the Boas data set and concluded that;

> Results indicate the relatively high genetic component of the head and face diameters despite the environmental differences during development. Results point to very small and insignificant differences between European- and American-born offspring, and no effect of exposure to the American environment on the cranial index in children. These results contradict Boas' original findings and demonstrate that they may no longer be used to support arguments of plasticity in cranial morphology. (p. 14636)

The narrow heritabilities for head length, head breadth and face breadth were estimated to be .55, .61 and .49. The authors admit that Boas was one of the most statistically and quantitatively oriented anthropologists of his time, and they make it clear that they are not claiming that Boas made "deceptive or ill-contrived conclusions", only that "the results were presented in a manner making the data look as convincing as possible" and that "when his data are subjected to a modern analysis, they do not support his statement about environmental influence on cranial form" (p. 14638). Holloway (2002) provides an informative perspective on this episode. Gould appears to have found nothing wrong with the Boas report. Gould is also guilty of selective reporting. He spent an entire chapter attacking Burt's study of monozygotic twins reared apart and failed to even mention the other well documented studies of twins reared apart.

Given the problems with Gould's treatment of Morton and Goddard, his failure to detect anything wrong with the Boas data, his selective reporting and his failure to meaningfully update the second edition of his book (Rushton 1997), one has to wonder about the validity of the rest of his reporting.

## Brain size and *g* in humans

The relationship between brain size and general mental ability is now a well-established fact and Van Valen's prediction of a correlation of about .30 turns out to be close to the mark. The correlation between external head measurements and *g* is .20 (weighted mean of 59 studies of children, adolescents and adults) (Rushton and Ankney 2009). Fortunately we can now do better than external measurement. McDaniel (2005) conducted a meta-analysis of 37 studies that used in vivo measures of brain volume. The mean correlation was .29 (.33 corrected for range restriction). Rushton and Ankney (2009) using a more select sample than McDaniel report a weighted mean correlation of .38. These values are often belittled as to small to be meaningful. This is a serious error. Møller and Jennions (2002) carried out a meta-analysis to estimate "How much variance can be explained by ecologists and evolutionary biologists?". They concluded the following, "Looking at all the different possible analyses, the 95 % confidence intervals for mean $|r|$ always fell between 0.14 and 0.22" across a range of fields in biology. (p. 497).

## The location of *g* within the human brain

Once it has been demonstrated that *g* is correlated with total brain size it is natural to ask, What is the correlation between *g* and cognitive activity in individual parts of the brain? Richard Haier and Rex Jung have worked this problem out in some detail in their Parieto-Frontal Integration Theory (P-FIT) of intelligence (Jung and Haier

2007). This theory is in its early stages as is the body of data on which it is based. A key feature of the theory is that the correlates of $g$ are widely distributed across the brain. Numerous studies support this model in its more general form, but the most important point is that the theory is supported by studies making use of quite different methods (lesion mapping and neuroanatomical correlates) (Barbey et al. 2012; Glascher et al. 2010; Goh et al. 2011; Karama et al. 2011). This is what one would expect of a distributed/integrative system (Shaw 2007; Sherrington 1906). Unfortunately these studies do not share a coherent theoretical framework and are therefore the results are difficult to integrate (Colom and Thompson 2011; Johnson and Bouchard 2007b).

## Animal studies of cognition: massive modularity versus $g$

As Darwin (1871, pp. 101–111) pointed out long ago one of the most compelling lines of evidence for quantitative genetic influence on behavior was the successful domestication of animals. Darwin, citing Galton, did not hesitate to generalize these findings to human beings.

> With man we see similar facts in almost every family; and we know through the admirable labors of Mr. Galton that genius, which implies a wonderfully complex combination of higher faculties, tends to be inherited; …

Surprisingly, there has been much more work on quantitative genetic influence on animal personality (van Oers and Mueller 2010) than on animal intelligence. Examples of personality research include fish (Bell 2009; Chervet et al. 2011), birds (Herbron et al. 2010; Kurvers et al. 2009), primates (Freeman et al. 2013; Rogers et al. 2008), and dogs (Jones et al. 2008). Not surprisingly animal personality is a domain also explored by Galton (1871) who reported on "gregariousness" in cattle. A wide range of studies can be found by searching "personality" in the journal Animal Behaviour and the web site—http://homepage.psy.utexas.edu/homepage/faculty/gosling/animal_personality.htm.

There is a great deal of work on cognition in animals (see the journal *Animal Cognition*) but only a limited amount of it deals with the $g$ factor. The reason for this has been the presumption of most investigators that the mental skills of animals are highly specific and unrelated (massive modularity as opposed to domain general mechanisms). That is, each ability is seen as a specialized adaptation optimized to deal with specific features of the animals environment and largely independent of every other mechanism. Massive modularity is the mantra of evolutionary psychology as propounded by Tooby and Cosmides (2005) and their followers (Platek et al. 2007). There is, however, considerable evidence that suggest that animals do have a domain general mental ability (Macphail and Bolhuis 2001) as well. Cosmides et al. (2010) have made a strong case for a number of highly modular abilities in humans. How many there are is an open question. A recent example might be human face recognition (Wilmer et al. 2010) which the authors argue is not $g$ loaded and highly heritable. I would reserve judgment regarding this particular conclusion as I never regard a single study as definitive. Contrasting views on this issue can be found in Lee (2009) and Shettleworth (2012).

## Has the Positive Manifold Been Demonstrated in Animals?

Chabris (2007) summarized the literature, through 2005 on mice (8 studies), dogs (2 studies), cats (2 studies), Rhesus monkeys (2 studies). The results are quite variable but generally support a $g$ factor. He concluded as follows:

> … in all but one of the studies, the average inter-task correlation is positive, and in the majority of studies (12 out of 21), the first principal component accounts for more than twice as much variance as the second principal component—the Law of General Intelligence appears to hold across species.

Lee (2007) has discussed the primate data in some detail and concluded that "the data suggest a generality of $g$ (or something like it) even wider than has been supposed" (p. 253). I extend the work of Lee and Chabris to a somewhat wider range of animal species. A drawback of most animal studies is the same one that plagued early studies of human intelligence. Data based on small samples and instruments with poor reliability leads to construct proliferation and unnecessary levels of complexity (Schmidt 2010). This problem has also plagued breeding and treatment studies in animal behavior genetics (Crabbe et al. 1999; Wahlsten et al. 2003). As the psychometric properties of the measures improve the findings should become more definitive. Nevertheless, there is already little doubt that $g$ (or something like it) characterizes a large number of animal species. I illustrate this argument with a brief discussion of a number of recent studies.

### *Mice*

Matzel and colleagues (2011; Wass et al. 2012) have regularly found a $g$ factor which accounts for around 40 % of the variance in the performance of mice on a variety of tasks. They summarize their research program as follows; "In total, this work indicates that learning abilities, attentional control, and the capacity for reasoning, features that constitute both colloquial and formal definitions of human intelligence, are commonly regulated in individual genetically heterogeneous mice." (Wass et al. 2012, p. 36). The use of genetically heterogeneous mice in these studies is important. While inbred strains are very useful for some purposes they are not informative with regard to generalizations about outbred organisms as they are genetic anomalies (Bouchard 1993). See Chabris (2007), for a summary of the earlier studies of mice.

### *Birds*

The authors of bird studies have no difficulty talking about "smart birds". There are apparently more smart birds than mammals (Isler and van Schaik 2009). Crows, for example, appear to be able to reason about hidden causal agents (Taylor et al. 2012) and parrots can count (Pepperberg & Carey, 2012). There is a small bird literature dealing with the positive correlation between pairs of abilities (Bouchard et al. 2007; Lefebvre et al. 2004). When the abilities of birds are examined in detail it is possible to classify behaviors as technically innovative versus simply reflecting the species ordinary repertoire. The findings are quite interesting.

> Our results demonstrate that larger-brained species perform a wider variety of innovative behaviour, but we can only speculate on the factors driving this relationship. Selection for increased behavioural flexibility may have driven accompanying changes in brain size. Alternatively, selection for large brain size, driven by another unexamined factor, may be accompanied by an increase in behavioural flexibility. That is, innovativeness may be a 'spandrel', a by-product of selection for other cognitive abilities (Gould and Lewontin 1979). Measures of cognition are often correlated with one another (Lefebvre et al. 2004), suggesting that selection may act on some measure of general intelligence rather than on innovativeness per se. (Overington et al. 2009) (p. 1008).

Note the explicit use of the term general intelligence and the term innovativeness in the same sentence and the belief that they are somehow quite distinct. In fact intelligence and the personality trait of Openness to Experience (O) are related in humans and some personality theorists subsume intelligence under this personality trait (DeYoung 2011). A somewhat broader conceptualization of this close linkage is called "cognitive flexibility" (Barbey et al. 2013).

### *Dogs*

Although dogs have been under study for a very long time there are few data on the correlation between measures of abilities in dogs. A study of word learning in a domestic dog (Rico) reported that dogs exhibited "fast mapping" of words (a process common in children, namely the acquisition of the rough meaning of a word after one exposure). The authors concluded that "Fast mapping thus appears to be mediated by *general learning and memory mechanisms* (our italics) also found in other animals and not by a language acquisition device that is special to humans." (Kaminski et al. 2004). Rico knew the labels of over 200 different items, a feat which led to a publication in Science. Chaser, the erudite border collie, learned the name of 1,022 objects and the investigators training her made it clear that this did not indicate a cognitive limit, they simply could no longer invest the time necessary to train her (Pilley and Reid 2011). A variety of experiments "provide clear evidence that Chaser acquired referential understanding of nouns, an ability normally attributed to children" (p. 12). Chaser has shown that the abilities of dogs have been severely underestimated. Nippak and Milgram (2005) also demonstrated, using beagles, strong correlations between response latencies to several cognitive tasks that assessed cognitive difficulty. Fast mapping has been shown in mice and related to mouse *g* (Wass et al. 2012). There are some 500 stray dogs living in the Moscow metro stations. Approximately 20 of them have learned how to ride the trains (Sternthal 2010). Dogs and mice appear to have gotten much smarter as investigators became more willing to put in the necessary observation time and work required to elicit their abilities.

### *Primates*

In an analysis of "ecologically relevant" behavior across non-human primates (behavioral innovation, tool use and social learning) the authors found that the three measures were correlated across species (Reader and Laland 2002). All three measures correlated with brain size. This finding supports the idea of *g*. In addition, contrary to the social brain hypothesis there was no correlation between social learning and social group size (105 species, r = .00). This is a striking refutation of a strong form of the social brain hypothesis. The authors concluded that, "The ability to learn from others, invent new behaviors, and use tools may have played pivotal roles in primate brain evolution." (p. 4436).

Banerjee et al. (2009) studied the performance of New World monkeys on a variety of tasks and concluded that "Individual differences in cognitive abilities within at least one other primate species can be characterized by a general intelligence factor, supporting the hypothesis that important aspects of human cognitive function most likely evolved from ancient neural substrates."(p. 1).

In a rather unique, Baysian rather than correlational, meta-analysis of cognition in nonhuman primates (Deaner et al. 2006) the authors conclude that some taxa do have better domain-general cognition than others. More interestingly, these authors did not find evidence for any domain-specific abilities. As they point out these findings do not refute the existence of modules, but they do refute the strong modularity hypothesis. Contra Tooby and Cosmides they argue that, "there are no compelling theoretical reasons to assume that domain-general cognition is restricted to primates or even mammals" (p. 178–179). Indeed there is a known genetic mechanism, *relationship Quantitative Trait Loci* (rQTL), that cause traits under simultaneous directional selection to be more highly correlated than traits not under simultaneous selection (Pavlicev et al. 2011).

We note that a rather heroic study by Herrmann and Call (2012) and Herrmann et al. (2010) failed to find a *g* factor both in samples of chimpanzees and very young children. The alpha coefficients, however, were quite low for most of the tests administered to the chimpanzees and a number of the tests administered to the children.

Again as investigators get smarter and invent new methods of investigation animals get smarter also (Gazes et al. 2013; Martin-Ordas et al. 2013).

## Comparing Across Taxa

There should not be any presumption that the various species developed "complex cognition" in the same manner. It is much more likely that convergent evolution is the underlying process. In 2004 two different research groups reported comparisons of complex cognition across taxa, one paper in *Science* and the other in *Brain Behavior and Evolution*. The *Science* paper by Emery and Clayton (2004) was titled "The Mentality of Crows: Convergent Evolution of Intelligence in Corvids and Apes". The authors concluded, "Because corvids and apes share these cognitive tools, we argue that complex cognitive abilities evolved multiple times in distantly related species with vastly different brain structures in order to solve similar socioecological problems." (p. 1903). Interestingly, at the time of this paper it was believed that birds did not have a neocortex and the authors speculated that intelligence "can evolve in the absence of a prefrontal cortex". We now know that the cell types that underlie the neocortex in mammals are present but organized into a different architecture in birds and reptiles (Dugas-Ford et al. 2012). The paper in *Brain Behavior and Evolution* by Lefebvre et al. (2004) was titled "Brains, Innovations and Evolution in Birds and Primates". The authors concluded, "In both birds and primates, innovation rate is positively correlated with the relative size of association areas in the brain, the hyperstriatum ventrale and neostriatum in birds and the isocortex and striatum in primates. Innovation rate is also positively correlated with the taxonomic distribution of tool use, as well as interspecific differences in learning. Some features of cognition have thus evolved in a remarkably similar way in primates and at least six phyletically-independent avian lineages." (p. 233). A more recent summary of work by Lefebvre and his colleagues leads to a conclusion entirely consistent with the thrust of this paper;

> These correlations suggest that many aspects of cognition might be better understood in terms of general processes (also termed *g*) rather than modules. This is not to say that some cognitive processes are not specialized and domain-specific, but the idea that all cognitive and neural systems are necessarily modular is increasingly being criticized as oversimplified. (Lefebvre 2011, p. 2)

This general theme has been elaborated in additional papers (Lefebvre 2013; Overington et al. 2008).

Based on their work with dolphins, Marino (2002, 2005) have come to a similar conclusion, namely that, "Cortical evolution… proceeded along very different lines than in primates and other large mammals. Despite this divergence, many cetaceans evince some of the most sophisticated cognitive abilities among all mammals and exhibit striking cognitive convergences with primates, including humans." Bearzi and Stanford (2010) in their book—*Beautiful Minds: The parallel lives of great apes and dolphins*—devote an entire chapter to this issue.

In the interest of space I will not take the time to discuss a variety of other species except to cite a few relevant references regarding pigs (Kornum and Knudsen 2011), raccoons (Pettit 2010), meercats (Thornton and Samson 2012), opposums (Kimble 1997), marsupials (Bonney and Wynne 2004), reptiles (Mueller-Paul et al. 2012; Wilkinson and Huber 2012) jellyfish (Albert 2011) and bees (Raine and Chittka 2008).

## Conclusion: *g* may well exist in many taxa

The reports cited above demonstrate that there is now a considerable body of evidence across a broad range of species that favors the idea of a "general biological intelligence" that characterizes any biological organism with more than a rudimentary central nervous system. While our definition of intelligence differs from that of Fodor, this construal of intelligence and the empirical evidence is in stark contrast to the modularity claim put forward by Fodor (1983). Namely that,

> …in all other species cognitive capacities are molded 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)

In addition this construal of the structure of the nervous system of organisms with some yet undefined level of complexity does not deny the existence of modules as such. It simply asserts that the massive modularity claim is too restrictive and fails to account sufficiently for a very large body of data.

## Intelligence: evolutionary considerations

### The mosaic evolution of the brain: size is not enough

Evolutionists ever since Darwin have been concerned with human intelligence.

> Of the importance of the intellectual faculties there can be no doubt, for man mainly owes to them his preeminent position in the world (Darwin 1871. p. 159).
> I believe that important insights can still be obtained from theoretical studies of some of the same questions that Darwin discussed in 1859. Similar attention should be devoted to… …the origin of any really outstanding characters such as human intelligence…." (Williams 1992, pp. 27–272).

As the studies discussed above demonstrate a great deal of interest in intelligence has focused on the size of the brain. As Holloway (2008) has pointed out "Most biological anthropologists ignore organization and cathect on brain size. ……" (p. 7). The same is true of psychologists. Size dominates the literature not simply because it is important in its own right, but because it is easy to measure both in live organisms and in endocasts. It must be kept in mind that comparative studies across the mammalian line involve organisms that have unique evolutionary histories since the time they shared common ancestors. Given that they all have unique behavioral repertoires, it is almost certain that their brains have reorganized in important ways relative to common ancestors. This idea is called mosaic evolution and there is considerable evidence for it (Barton and Harvey 2000; Oxnard 2004; Smaers and Soligo 2013) even though there is tight linkage between the various parts of the brain. This idea has been championed for many years by Holloway and has recently come back into fashion. According to Rakic (Rakic 2009, Box 2) "During evolution, the neocortical surface expands by the addition of radial columns……, but the composition of the columns also undergoes changes. The notion of the homogeneity of the columns has been abandoned in favor of their heterogeneity, both in different functional areas of an individual, as well as across species." See also papers in (Jones and Rakic 2010). An illuminating discussion of the kinds of changes that can occur in the neo-cortex is provided by Krubitzer and Kaas (2005).

Because the primary focus of this paper is on distal causes and space is limited I cannot spend much time on processes and mechanisms as that would require a paper longer than this one. Nevertheless, a few comments are necessary to round out the discussion. Even investigators who have focused on the correlation between brain size, cortical convolutions and cortical thickness make it clear that they believe these measures are only relevant because they reflect the structural integrity of these regions and they hypothesize that other micro-anatomical characteristics as well a neuronal circuitry will prove to be important (Luders et al. 2007, p. 2022). This prediction has proven to be true as Jolles et al. (2011) have recently shown that functional connectivity differences between brain regions cannot be explained by gray matter density alone.

Neural circuitry is currently being conceptualized in terms of "graph theory" models widely used in studies of telecommunications (the world wide web), power grids, bioinformatics, neurobiology (neural network of Caenorhabditis elegans) and molecular biology (Kim and Przytycka 2013; Varki et al. 2008). These networks have "small world properties" and it has been suggested that the brain possesses similar networks. Such networks are highly clustered with a short path length between them (Yan et al. 2011). This type of network allows for both modularization and efficient interconnection (Bassett and Bullmore 2006) or as Bullmore and Sporns (2009) put it "although functional properties are expressed locally, they are the result of the action of the entire network as an integrated system. Structural connectivity places constraints on which functional interactions occur in the network."(p. 192).

Some findings suggest that, "human intellectual performance is likely to be related to how efficiently our brain integrates information between multiple brain regions. Most pronounced effects between normalized path length and IQ were found in frontal and parietal regions. Our findings indicate a strong positive association between the global efficiency of functional brain networks and intellectual performance". (van den Heuvel et al. 2009, p. 7619).

Li et al. (2009, p. 2) report similar findings.

> "We consistently found that the high intelligence group's brain network was significantly more efficient than was the general intelligence group's.

> Moreover, IQ scores were significantly correlated with network properties, such as shorter path lengths and higher overall efficiency, indicating that the information transfer in the brain was more efficient. These converging evidences support the hypothesis that the efficiency of the organization of the brain structure may be an important biological basis for intelligence."

Changes in gray matter during development also show stunning differences between levels of intelligence. As Gogtay and Thompson (2010) put it more intelligent children demonstrate "a particularly plastic cortex with an initial accelerated and prolonged phase of cortical increase followed by a particularly vigorous phase of cortical thinning suggesting a highly plastic response in the brain." (p. 7).

Again size alone is not enough.

Another illustration of why too great a focus on size can be misleading can be found in studies of the brains of the elephant and parasitic wasps. Of the terrestrial mammals elephants have the largest brains. Like humans and great apes they are long lived and their offspring are altricial. Nevertheless, their neural cytoarchitecture is dramatically different from that of primates (Hart et al. 2008). Although elephants display a wide variety of abilities (use of tools, modification of tools, long term memory, high spatial/mapping skills, social strategies, anticipatory planning, problem solving, etc. (Byrne et al. 2009; Foerder et al. 2011)). I have been unable to find evidence of the correlation between abilities in this spectacular animal. The parasitic wasp Trichogramma evanescens has a miniaturized brain that is marginally larger than a single human pyramidal motor neuron. While the body volume of genotypically identical wasps can vary up to a factor of 7, even the small female phenotypes, "display a rich behavioral and cognitive repertoire similar to much larger insects, including flight, walking, courtship, deciding over the size and sex of their progeny, vision, olfaction, learning and long- and short-term memory formation" (van der Woude et al. 2013, p. 88). Scaling the size of parts of the brain against behavioral adaptations makes numerous unspecified assumptions and can often be misleading (Barton 2012; Willemet 2013).

## The brain is not a simple adaptation. It is embedded in a set of complex co-adapted traits

While it is asserted by many that the large human brain is one of our specie's unique features (Ayala 2010; Foley and Gamble 2009; Hill et al. 2010; Varki et al. 2008) it is important to recognize that brain size is not a dichotomous character that separates us from our ancestors. As Haile-Selassie et al. (2004) point out, "Bipedality might be an arbiter of hominid status, but "bipedality" involves a large and complex set of anatomical traits and is not a dichotomous character." Indeed a number of archaic hominins were bipedal (Wood 2010). The same is true for the brain, a variety of other hominid characteristics that served as constraints would have to have changed simultaneously with brain size; examples include female pelvic size and shape as well as related features of parturition, capacity for heat dissipation, diet and related metabolic processes related to energetic demands, length of intestines, dentition as related to diet etc. This might lead us to assume that the evolution of the human brain size should take a very long time. Interestingly, however, the evidence demonstrates that evolution can be dramatically accelerated on islands with small mammals getting larger and large mammals getting smaller. Some species can evolve faster than expected when there is rapid change in their environment. On islands this includes reduced predation, reduced interspecific competition, a change in diet, different pathogens, etc. (Millien 2006). Cochran and Harpending (2009) make a strong case for the influence of civilization as an accelerant of human evolution. The number of traits that tend to distinguish us from other apes is quite long (Trinkaus 2007). Carroll (2003a, b, Box 1) lists 15 and does not even mention bipedality. Laterality is a particularly distinguishing characteristic (Smaers et al. 2013). Laterality is related to differential control and motor control and is seldom related to higher cognitive functions even though it is related to language and tool making among other things. A large body of evidence now contradicts that view (Radman 2013). A Barton puts it, "… the evolution of large brains was associated with the elaboration of sensory–motor mechanisms for the adaptive control of bodies in their environments" (Barton 2012, p. 2104). Put simply, plants do not have brains.

## Energetics: the expensive tissue hypothesis

Apart from its possible relation to intelligence the evolution of the brain is of interest because of its energetics. The brain uses 10 times the amount of energy predicted by its weigh alone (2 % of body weight vs. 20 % of the energy consumed) (Clark and Sokoloff 1999; Holliday 1986). This estimate is derived from studies of the basal metabolism (resting rate) and does not reflect the amount of energy dedicated to active cognitive work. The latter may be very small and indeed more efficient brains may use less energy than less efficient brains (Jung and Haier 2007). The energetic demands of the brain have led to the "expensive brain hypothesis". Seldom mentioned in this literature is the fact that the liver and gastro-intestinal tract are as expensive as the brain. Perhaps it should be called the

"Expensive Tissue Hypothesis". There is a great deal of evidence that organ systems that no longer serve an adaptive purpose and are no longer selected for on a day-to-day basis degenerate. The classic examples are eyes in cave fish (Niven 2008) and the naked mole rat (David-Gray et al. 1998). Another example would be loss of pigmentation in pearlfish. This commensal fish lives within its host during the day and exits at night to forage. This behavioral strategy (an adaptation) is thought to have developed in order to avoid predation as the pearlfish is rarely found in the stomach of predaceous fish. In addition there are evolutionary trade-offs. As adaptive fitness improves in one environment there is often loss of fitness in other nonselective environments (Bennett and Lenski 2007). Indeed there is good evidence that under some selective pressures brains shrink in size (Niven 2005).

According to Isler and van Schaik, the expensive tissue hypothesis,

> predicts that relatively large brains can evolve only when either energy input increases (Isler and van Schaik 2006b) or there is an allocation shift from another expensive body function, such as the digestive tract in primates (Aiello and Wheeler 1995; Fish and Lockwood 2003) or the pectoral muscle in birds (Isler and van Schaik 2006a). To our knowledge, this framework is the only one that accounts for the well-known correlation between life history patterns and brain size (Barrickman et al. 2008; Deaner et al. 2003), while at the same time incorporating the energetic consequences of lifestyles that are influenced by ecological conditions of habitat and diet. (Isler and van Schaik 2009, p. 127).

This hypothesis has great verisimilitude as it incorporates life style and life history variables such as alloparenting in altricial birds and humans (Hrdy 1999; Kruska 2005), the extended family (Allman 2000, p. 198), the invention of cooking as a means of increasing the quality of diet (Allman 2000, p 194; Carmody and Wrangham 2009) and life span (Barrickman et al. 2008). The important point being made here is that a concrete feature of the brain (cost) is shown to systematically explain a series of correlations or what might best be called functional relationships. Selection for one characteristic has implications for a number of others. Any theory about the evolution of the brain or intelligence should have similar implications. Very few do. Nevertheless, brain size is only a crude index of cognitive functionality, other features of the brain (duplication of features such as visual cortical maps and interconnectivity) must therefore be quite important especially in the very small brains of insects which allow them to perform spectacular feats (Chittka and Niven 2009; Wiederman and O'Carroll 2013). The details of the energetics of neurons and the brain are beginning to be better understood (Niven and Laughlin 2008). The expensive tissue hypothesis implies that there must be strong selective forces that maintain big brains and that in the absence of such forces brains would rapidly shrink in size. It does not explain the increase in brain size per se.

## The rate of brain evolution: how fast?

It is often said that the brain size of *homo sapiens* increased at a staggering rate or that there was runaway selection. The actual facts, however, are quite different. As Williams (1992, p. 132) points out with only conservative assumptions about selection and the heritability of brain size, "An early homonid brain could have increased to modern size, and back again, about 21 times while the actual evolution took place". This is a point that had been independently made by Van Valen and cited above. I address the question of the heritability of brain size in contemporary human [and other primates (Rogers et al. 2007)] below. This argument that the brain could have evolved as rapidly as described is, of course, too simple. As pointed out above, a variety of other homonid features would probably have to have evolved alongside brain size. While cranial capacity of Pleistocene *homo* has increased in size since 200 ka (Lee and Wolpoff 2003), the absolute brain size of homo sapiens (and body size) has decreased over the past 35,000 years (Holloway 2008, Table 3) and the brain of *H. neanderthalensis* was much larger than those of *Homo sapiens* and that difference has not been explained (Carroll 2003a, b, Table 1; Roth and Dicke 2005, Table 1). The evidence seems to suggest "a stasis in relative brain size within homo between 1,800 and at least 600 kyr BP" (note added: 600 thousand years before present) (Ruff et al. 1997). This may well explain why contemporary data suggest that the brain may be under strong stabilizing (average-is-better) selection rather than directional (more-is-better) selection (Miller and Penke 2006).

## Some random thoughts on the evolution of big brains: adaptations, design, tinkering, kludges and bricolage

A further argument against a strong form of the massive modularity hypothesis (adaptations are finely tuned mechanisms optimized to solve a specific problem) comes from the large body of evidence that the brain is at least partially a kluge (Marcus 2008) constructed through a process similar to bricolage (Wilkins 2007). Bricolage is a term widely used in the visual arts and refers to creation of a piece of art from a diverse collection of things that happen to be available. What is available, of course reflects the interests and preoccupations of the particular artist. The artist we call Mother Nature using natural selection has built an unimaginably large number of creatures through a similar process called by Darwin "modification by descent". Wilkins has summarized this point elegantly;

> In reality, although organisms often seem designed efficiently for one trait, much is clearly suboptimal and many morphological/anatomical traits are baroque in their construction, defying the simplest notions of what constitutes good design. Furthermore, even the optimality of the well-designed features is often at the slight expense of other traits, the phenomenon of ''tradeoffs'' (20). In contrast, the alternative metaphor of evolution as a tinkerer, engaged in piecemeal construction or bricolage, seems at first to be more apposite than that of design. Evolution clearly works by adapting preexisting structures to new purposes, many in ways that no sensible human engineer would have used (p. 8591).

Thus natural selection should be seen as a tinkerer (Jacob 1977) who makes mistakes (Avise 2010) as much as a designer. One of the consequences of the process of modification by descent is that genes and gene complexes evolved for one purpose tend to be used over and over for other purposes and appear to be highly conserved.

Consider the case of the development of the size of the mammalian brain, it can be efficiently described by two factors, the first, brain size, encompassing 9 of 11 brain structures which have increased in size and a second olfactory bulb factor (Finlay 2007). The parts of the brain in the first factor appear to be tightly linked for a reason that is common across mammalian species. Selection for any one facet of the first factor leads to coordinated enlargement of the whole brain in a predictable manner (concerted evolution). Contrary to what would be predicted by the modularity hypothesis, "No mammal has found it advantageous to enlarge any brain structure preferentially over the cortex." (p. 297). Thus selection on any of the parts not just the neocortex (also called isocortex) leads to the large neocortex found in humans. There is no claim that the linkage cannot be broken (the fact that the olfactory bulb has decreased in size strikes us as proof positive), only that it has remained rather tight for quite a long time.[1]

This finding is consistent with the well-known developmental plasticity of the mammalian cortex. The best evidence is that different sensory modalities can be coopted depending on trauma and experience (Krubitzer and Kaas 2005). Developmental plasticity creates a mechanism that "facilitates rapid adaptation to novel environmental circumstances without substantially affecting the total energetic cost of sensory processing within the brain." (Niven and Laughlin 2008, p. 1802). The general-purpose functioning (plasticity) of the brain is also strikingly shown by the remarkable performance of children who suffered surgery or serious brain injury in early life (Bates et al. 2001). An alternate conception of this feature of the brain is neural reuse (Anderson 2010). Nevertheless, it does not entirely prevent specialized evolution from occurring. Trichromatic color vision has evolved independently in monkeys but not in other mammals (Jacobs and Rowe 2004). Interestingly, this evolution takes place at the sensory surface and not deep in the brain. This can be demonstrated by introducing a form of color vision from one species (human) into another species (mouse) that does not have it. The "mice apparently acquired an added dimension of sensory experience, implying that the mammalian brain has the innate ability to extract information from novel and qualitatively different types of visual input." (Jacobs and Nathans 2009). This certainly gives the impression that parts of the brain function as a general-purpose (domain general) device.

Behavior genetic studies of the tight linkage between parts of the brain in humans are consistent with those of Finlay discussed above. Because they can estimate genetic influence they can make additional claims.

> Behavioral genetic data supports the hypothesis that the human brain is a work in progress, as the extraordinarily high metabolic cost of brain tissue should place a selective pressure towards smaller brains and ultimate fixation of genetic polymorphisms affecting brain volumes. In contrast, imaging data has established that genetic variance not only persists but is by far the predominant determinant of brain size. (Schmitt et al. 2010, p. 121)

No one would have dreamed of making this claim even a few years ago.

Brain size in mammals has increased over evolutionary time (Yao et al. 2012). As a consequence a very large number of evolutionary scenarios predict a larger brain because the behavior selected for increases the fitness of ancestors. A number of examples are cited and described by Finlay (2007) and Charvet and Finlay (2012). I have counted 21 non-independent theories and there are likely many more. Most of the theories are difficult to test (Stanford 1995), they all however, assume that big brains contribute to survival and that prediction can be tested.

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[1] An interesting case of increase in the size of one part of the brain over other parts is the increase in cerebellum size with bower complexity in bowerbirds (Day et al. 2005). Sexual selection has let to an increase in the skills necessary to build intricate and precisely decorated bowers, but it is only reflected in an increase in cerebellum size. Such birds do have larger whole brains relative to other birds that live in similar habitats but do not build bowers. This appears to be an androgen triggered process.

### Do big brains contribute to survival?

Many of the theories can also be unified by the "brain size-environment change theory" (BS-EC theory). The argument is that organisms with greater cognitive complexity, facilitated by larger brains, are better able to cope with novel environments than those with smaller brains. This hypothesis has been tested four times using a quasi-experimental design in natural settings and the results have been positive in three of the four instances. The idea is that big-brained species should show higher survival than small brain species when introduced into novel environments. Sol et al. (2005) demonstrated this for avian species (>600 introduction events) and further demonstrated that the effect was mediated by cognitive (innovative propensity) rather than non-cognitive mechanisms. Sol et al. (2008) replicated this finding with mammals (>400 introductory events). The range of mammalian brain sizes studied was quite representative and the findings held when a variety of possible confounds were controlled. The authors make a strong case for the argument that, "The selective pressure to deal with novel or altered circumstances may have been a powerful evolutionary force for increasing the size of the brain." Amiel et al. (2011) have replicated these findings for ectothermic terrestrial vertebrates (amphibians and reptiles). Drake (2007) using a large data base failed to find the effect with multiple species of fish. Shumway (2008), however, has shown that brain size is related to habitat complexity in African cichlid fish. As far as I am aware there is no data on the relation between brain size and cognitive ability in fish (Bshary et al. 2002).

In her discussion of the implications of the bird findings, Marino (2005) explicitly proposed that the findings support the concept of "*g*" or general intelligence rather than "highly specialized domains of memory or calculation such as seed caching." She specifically cites studies that demonstrate the positive correlation between measures of cognitive ability (i.e., the positive manifold). As Marino pointed out only two taxa had been studied (birds and primates at the time she wrote). She suggested that other taxa such as cetaceans and invertebrates be studied in the same way in order to assess the possibility that "there are truly "universal" patterns of causation across brain, behavior and ecology on Earth" (p. 5307). The extension of these findings to mammals in general as well as amphibians and reptiles lends strong support to her hypothesis. Marino et al. (2007) and Connor (2007) provide additional discussion of convergent brain evolution in multiple taxa. There is also now some evidence for domain generality in invertabrates—cephalopods (Mather 2008).

The intuitively plausible idea that big brains contribute to survival (are adaptive) due to the fact that they allow organisms to cope more effectively with complex environments has a reasonable amount of support. The specific mutations that facilitate the process are likely to be many and varied, perhaps quasi-infinitesimal and remain to be explicated.

## Intelligence: genetic considerations

### The first law of quantitative genetics: every trait in every species is heritable

The heritability coefficient indexes the magnitude of genetic influence (as a proportion of variance) on a quantitative (generally polygenic) trait. It tells us how much of the variance (differences among individuals) in a population is due to genetic factors. It is a population statistic and while it describes individual differences, it does not apply directly to individuals. It is useful to distinguish between "broad heritability" and "narrow heritability". Narrow heritability consists of the additive effects of genes that cause most of the observed similarity between relatives except for monozygotic twins who are similar for both additive and non-additive genetic reasons (Visscher et al. 2008).

One conclusion often drawn from the massive modularity hypothesis is that any trait or character with high heritability cannot be an adaptation because if it were it would have reached fixation due to its contribution to fitness. This is alleged to flow from Ronald Fisher's Fundamental Theorem of Natural Selection. As Feldman, et al. (2000) put it in a critique of Bouchard's (1994) discussion of the heritability of personality (they call it a mistaken evolutionary interpretation),

> The theorem states that the rate of change in the mean fitness is equal to the additive genetic variance in fitness. Thus, if a trait truly had an effect on fitness (i.e., if the degree of adaptation did depend on the trait value), then the additive genetic variance would be dissipated by natural selection. Eventually we would be left only with non-additive genetic variance, genotype by environment interaction, and cultural or environmental variability. You cannot have it both ways: high additive genetic variance means not very important to natural selection, whereas low additive genetic variance means not very interesting to Bouchard. …… *In short, the prediction to be drawn from the premise that IQ or behavioral traits were selectively important in our ancestors is that there should be little additive genetic variability remaining for these traits among modern humans.* (*p. 76*)

As Edwards (1994, 2004, p. 111) notes this is a misappropriation of the theorem, one that is widely shared, particularly by evolutionary psychologists. As Fisher pointed out long ago natural selection alone is not evolution. The model cited by Feldman et al. is called a “Hard Sweep” and it underlies the view that all humans are virtually alike everywhere and evolution has ended. A huge body of evidence which flows from genome wide data suggest that there is considerable local adaptation and rather than human differences being only skin deep they probably permeate both the mind and the body (Cochran and Harpending 2009). The empirical evidence shows that neither directional artificial selection nor natural selection appear to exhaust genetic variance. Crow (2008, 2010) provides references and a number of theoretical reasons why this appears to be the case.[2] Standing genetic variation (heritability) is endemic and does not indicate evolutionary un-importance. More generally evolution has not ended.

Fortunately there is much to learn and considerable reason to believe Bouchard can “have it both ways”. Recent theorizing (Pritchard et al. 2010) and data (Hancock et al. 2010) suggests an important role for “Soft Sweeps” and “Polygenic Adaptation”. These models allow for a great deal of standing genetic variance in adaptive traits.

Consider the following abstract from a recent study of bumble-bee colonies.

> Despite the widespread assumption that the learning abilities of animals are adapted to the particular environments in which they operate, the quantitative effects of learning performance on fitness remain virtually unknown. *Here, we evaluate the learning performance of bumble-bees (Bombus terrestris) from multiple colonies in an ecologically relevant associative learning task under laboratory conditions, before testing the foraging performance of the same colonies under the field conditions.* (our emphasis) We demonstrate that variation in learning speed among bumble-bee colonies is directly correlated with the foraging performance, a robust fitness measure, under natural conditions. Colonies vary in learning speed by a factor of nearly five, with the slowest learning colonies collecting 40 % less nectar than the fastest learning colonies. Such a steep fitness function is suggestive of strong selection for higher learning speed. (Raine and Chittka 2008)

This much variation strongly suggests the trait is polygenic. Consequently, even in an ancient order of insects there is significant heritable variation in an important behavioral trait (colonies are the conceptual equivalent of individuals in other species) one that is demonstrably related to fitness.

I have provided examples of what has been called the First Law of Quantitative Genetics (Bouchard 2007); virtually every trait in every species is heritable. This is a generalization of Turkheimer’s (2000) First Law of Behavior Genetics (all human behavioral traits are heritable). As Lynch and Walsh (1998) put it,

> If one’s sole interest in performing a quantitative-genetic analysis is to demonstrate that the character of interest is heritable, there is probably little point in expending the effort. The outcome is virtually certain. Almost every character in almost every species that has been studied intensively exhibits nonzero heritability.” (p. 174)

In addition, the variance in most complex traits appears to be largely additive in nature (Hill et al. 2008). This point of view is shared by many others. In a massive study of flowering time in corn Buckler and 35 colleagues (Buckler et al. 2009) conclude that;

> Our results suggest that for the outcrossing species maize, the genetic architecture of flowering time is dominated by small additive QTLs with few genetic or environmental interactions (within the tested range of environments). Human height may have a similar genetic architecture… (p. 718).

There is every reason to believe that the important traits that distinguish us from other primates are also highly polygenic (Carroll 2003a, b, p. 853).

## The interesting scientific question is, why so much genetic variability?

If this argument is correct then few if any quantitative traits have achieved fixation in the sense that all individuals are genetically alike. The pervasiveness of genetic variability for traits that are very likely, on other grounds, to be adaptive is the interesting scientific question (Gangestad

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[2] According to Crow, “All that is required is that there be a substantial supply of rare alleles, many of them perhaps in a mutation–selection balance that was reached before the current selection program started” (p. 1242). James Lee (Personal Communication, 2013) has provided me with the following formulation based on Crow’s argument. “Even if the mean of a trait has been consistently increasing in one direction over time, the additive genetic variance does not necessarily decline because there are loci where the “plus” allele was initially rare but then increased in frequency. The contribution of such loci to the additive genetic variance increases rather than decreases, until the plus allele passes the frequency of 0.50. And unless all possible ways to increase the value of the trait have been exhausted, there will always be new mutations entering the population to replenish the variance lost as a result of plus alleles going from 0.50 eventually to fixation. The equilibrium additive genetic variance depends only on the effective population size, and given a size of 10,000 (good enough for humans) a heritability of 0.60 or so is not at all anomalous.” Brem and Kruglyak (2005) provide empirical evidence for the existence of the necessary alleles for a large and unbiased sample of quantitative traits in yeast that are highly heritable (>69 %). Rockman (2012) discusses the general issue within a larger historical context.

2010; Rockman 2012, p. 9–10). Examples include brains (this paper), Warbler wing length in wild birds (Tarka et al. 2010), the timing of reproduction in the wild great tit (Nussey et al. 2005) and perhaps most interestingly the high heritability of beak size in Darwin's finches (Grant and Grant 2006).

Note that the same question permeates plant genetics. Kliebenstein (2010) in a recent theoretical paper dealing with natural genetic variation asserts that, "Despite the ubiquity of this variation, little is known about the molecular underpinnings of natural genetic variation or the forces behind its maintenance or generation." (p. 480). Krubitzer and Kaas (2005) refer to the same question regarding the structure of the brain, "Once we appreciate the degree to which certain gene expression patterns vary, for example, we could then determine how this variation is related to variation in aspects of cortical organization, connections and functionality."

Until very recently it was widely believed that human evolution had stopped. Indeed this assumption underlies Feldman et al.'s criticism. What was forgotten was that both adaptive processes such as selection, and non-adaptive processes such as mutation, migration and assortative mating are always at work changing gene frequencies both in an absolute and a relative sense (Alonso-Nanclares et al. 2008; Brandon 2006; Draghi et al. 2010; Gerhart and Kirschner 2007). McShea and Brandon (2010) have made a strong case for the argument that complexity has increased in evolutionary systems and this seems to be true (Russell 1983). All of evolutionary change, however, need not be caused by the evolution of adaptations (Bonner 2013; Lynch 2007).

Evolution is now seen to be a much more rapid process than previously believed (Cochran and Harpending 2009; Hawks et al. 2007; Wang et al. 2006) and relevant empirical findings are appearing almost everyday. A recent example is the unique adaptations to high altitude by Tibetans and Andeans, adaptations with fitness consequences (Simonson et al. 2010; Yi et al. 2010). This topic was initially explored in an interesting paper by Beall (2007). She demonstrated that there were very large differences between Tibetans and Andeans, who lived at very high altitudes, in a number of functional (oxygen transport) traits. The effect sizes were very large. She also showed that if the trait had been studied by quantitative geneticists it would have been shown to be heritable. Some of the genes underlying these adaptations are now known and they reflect rather rapid evolution.

The arguments that the high heritability of a trait in a population deems it non-adaptive, that all adaptive traits will quickly move to fixation, and that human populations do not differ genetically are simply false (Edwards 2003).

## The heritability of brain size: animal data

Before turning to the human data it is of interest to report on two recent genetic studies of brain size in primates.

The first study (Rogers et al. 2007) measured brain size using MRI data obtained from one-hundred and nine (51 males and 58 females) adult Baboons in a 40 year old colony who lived in large outdoor enclosures. By taking account of the known multigenerational pedigree of the colony it was possible to estimate the heritability of brain size (controlling for age, sex, and age × sex). The heritability of Total brain volume was .82.

Remarkably similar results were obtained by Fears et al. (2009) using a colony of 357 Vervet monkey and similar procedures. The heritability of Total Brain Volume (controlling for sex, age and weight) was .99.

The authors ascribe the somewhat higher heritability than previous studies to the increased precision of their MRI procedures and the highly controlled environment of the colony. Other older studies of the heritability of primate brain size include Cheverud et al. (1990) and Mahaney et al. (1993).

## The heritability of brain size: human data

An early study of a very small group of monozygotic twins ($N = 10$) suggested that size of the surface area of the cortex and the folding may be under genetic influence (Tramo et al. 1995). A further study of this sample (Tramo et al. 1998) reported non-significant correlation between various brain measures and *g*. All studies since then have reported sizeable positive correlations between brain size measures and *g*.

Using a full twin design, but still with small samples (a reading disabled group and a normal control group) Pennington et al. (2000) measured the volume of thirteen brain regions and a factor analysis of the total sample yielded two factors: a cortical factor (basically all the Gray matter) and a sub-cortical factor (largely defined by white matter). The heritabilities for the two factors and cerebral total as well as their correlations with *g* are shown in the top section of Table 1. The heritabilities for the volume measures are quite high and the results are surprisingly similar to the Baboon and Vervet data presented above. The correlations with *g* are in the range expected from the meta-analysis presented earlier.

A twin study of this sort allows one to compute the genetic correlation between two variables, in this case head size and *g*, the genetic correlation $r_g$ is .48. This means that about half the genetic influence is common between cerebral volume and *g*. This phenomenon is best called statistical pleiotropism as it does not necessarily guarantee that the same genes cause the correlation (Carey 1988). It is also possible to calculate how much of the phenotypic overlap between brain size and *g* is due to shared genes. In this instance it is 80 %.

**Table 1** Heritabilities of various brain region volumes and their correlation with *g* and genetic correlations for studies with all measures

| Brain measure | Heritability | Correlation with *g* | Genetic correlations |
|---|---|---|---|
| Pennington et al. (2000) (combined samples) | | | |
| Cerebral total | .89 | .37 | Not reported |
| Cortical factor | .67 | .15 | .48 |
| Subcortical factor | .78 | .38 | Not reported |
| Posthuma et al. (2002a, b) | | | |
| Whole-brain gray matter | .82 | .25 | .29 |
| Whole-brain white matter | .87 | .24 | .24 |
| Betjemann et al. (2010) | | | |
| Total brain volume | .80 | .28[a] | .50 |
| Neocortex | .30 | .20[a] | .70 |
| White matter | .60 | .26[a] | .45 |
| Prefrontal cortex | .38 | .21[a] | .62 |

[a] Mean of verbal and perfomace IQ correlations. They did not report full Scale IQ

These results suggest that the correlation between brain size and *g* is substantively mediated by genes.

Two additional studies have reported heritabilities for brain size, correlations with *g* and genetic correlations (Betjemann et al. 2010; Posthuma et al. 2002a, b). They are shown in the middle and lower section of Table 1. The heritabilities for the total measures are around .80 and the correlations with *g* are a bit lower than those reported in the meta-analysis cited earlier. In both studies the phenotypic correlations with *g* can be entirely accounted for by genes.

In 2001 Thompson et al. (2001) using a very small sample of twins (10 MZ and 10 DZ) reported that genetic factors "significantly influenced cortical structure in Broca's and Wernicke's language areas, as well as frontal brain regions". They also showed that frontal gray matter volume correlated .45 (based on a *N* of 20, Twin 1) and .37 (the remaining *N* of 20, Twin 20) with a measure of *g*. In a constructive replication of the Thompson et al. study the Amsterdam Group (Posthuma et al. 2002a, b) using a large extended family design found a heritability of .82 for Whole-brain gray matter, .87 for Whole-brain white matter and .86 for *g*. Whole-brain gray matter and white matter correlated .25 and .24 with *g*. Both correlations are mediated entirely by common genetic factors rather than environmental factors. These latter results are similar to those of Frangou et al. (2004) who reported a correlation of .34 between gray matter volume and *g*. Similar results have been reported by Hulshoff Pol et al. (2006). These findings are in the same range as those reported in Table 1. A review of the literature on the heritability of various parts of the brain (including the total brain) can be found in Peper et al. (2007). I have summarized their data in the stem and leaf diagram shown below.

| Frequency | Stem and leaf |
|---|---|
| 3.00 | Extremes (.0, .0, .07) |
| 1.00 | 3. 1 |
| 2.00 | 4. 09 |
| 3.00 | 5. 568 |
| 4.00 | 6. 3569 |
| 4.00 | 7. 0799 |
| 11.00 | 8. 12225788899 |
| 8.00 | 9. 00122447 |

The mean heritability is .71 with 95 % confidence interval of .62–.80. Given the skewness of the distribution, the median is a more representative descriptor and the median heritability is .82. Most studies contributed a number of estimates so the values are not independent. We can, however, conclude that most brain structures are significantly heritable and the effect size is in the range of heritability found for *g*.

Panizzon et al. (2009) reported a heritability of .78 for total brain volume based on 110 MZ and 92 DZ male adult twins (Vietnam Era Twin Study) with an average age of 55.8, thus replicating the results reported above The purpose of this study, however, was to test the hypothesis that volume measures of brain regions reflect two different and distinct genetic influences. The hypothesis flows from the idea that surface area and thickness are driven by two different processes, the radial unit hypothesis proposed by Rakic, with volume being the product of the two. They confirmed this hypothesis as the heritability of the surface area for total gray matter was .89 and the heritability of cortical thickness was .81, but the genetic correlation between the two was very small .08. The idea that different genes or genetic processes drive the two components is consistent with the evolutionary evidence that the first enlargement of the human cortex involved expansion of the surface area with only a modest increase in thickness (Rakic 2009, Fig. 1). The increase in thickness came later. Obviously it would be useful to know the extent to which the two components correlate with *g*. If the influences are independent and additive, the results would not support the hypothesis that *g* is a unitary phenomenon, but rather a multiple causation hypothesis such as that of Godfrey Thompson's bond theory (Bartholomew et al. 2013). This is, however, a single study and replication is mandatory.

In summary the average heritability of brain volume based on ten twin studies is .84 (Baare et al. 2001; Bartley

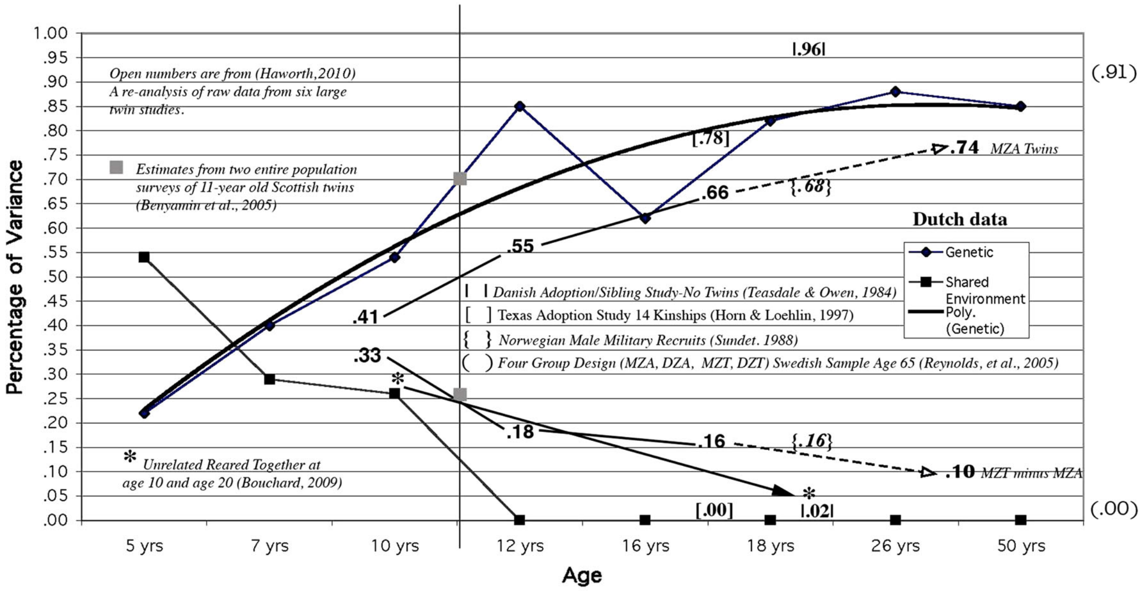

**Fig. 2** Estimates of genetic and shared environmental influence on *g* by age. The age scale is not linear. (see original paper for references and discussion)

et al. 1997; Betjemann et al. 2010; Carmelli et al. 1998; Geshwind et al. 2002; Hulshoff Pol et al. 2006; Panizzon et al. 2009; Pennington et al. 2000; Pfefferbaum et al. 2000; Posthuma et al. 2002a, b). The heritability appears to remain high (.77) even in the later years (68–77 years of age) (Lessov-Schlaggar et al. 2012) although the sample size in this last study is small. Smit et al. (2010) report similar results for the heritability of head size in two large twin and family studies.

The heritabilities of the volume of specific brain regions and their correlations with *g* are quite variable. This is in part due to small samples. I expect it will require more studies, better psychometric measurement, and a meta-analysis before we can be confident of the meaning of the findings. The variability could easily be an artifact. It would be highly desirable if investigators used a *g* factor score in place of IQ as an estimate of *g* (Bartholomew 2004) and lower order factor scores free of *g* for specific abilities. For examples of the improved theoretical clarity produced by such procedures, particularly with regard to sex differences, see Reeve et al. (2006) and Johnson and Bouchard (2007a).

## The heritability of *g*: human data

The evidence for genetic influence on *g* has been reviewed in detail elsewhere (Bouchard 2009a, b) and much of the data reported in that paper is summarized in Fig. 2 from Bouchard (2013)

What does this Figure tell us? It tells us two things, both of which were intuitively implausible to many psychologists and thus adamantly denied for many years. The first is that *g* is very significantly heritable beginning at least at age 9 and heritability increases with age until late adulthood when it reaches the mid-seventies and higher for some populations. Interestingly the picture changes very late in life, but as one would expect attrition changes the characteristics of the sample. Nevertheless, heritability is still quite high (.62) for 80 year old twins when both individuals are free of major motor, sensory or cognitive impairment (McClearn et al. 1997). The observed changes cannot be explained by changes in brain size as brain volume does not increase over the age period 8–22 years of age (De Bellis et al. 2001, Fig. 1; Giedd et al. 1999, Fig. 1), although the relative size of different parts does change (Castellanos et al. 2002; Schmithorst and Yuan 2010) and after age 20 parts of the brain decline in volume (Raz et al. 2004). Study of the developing brain is now an important part of the research agenda for developmental neuroscientists (Luciana 2010). The changes must be due to changes in the internal structure of the brain. The second is that shared environmental influence, while higher than genetic influence at age 5 decreases linearly and rapidly with age, reaching about 10 % by age 17 and is probably somewhat less in middle adulthood. These results are robust as they do not depend on a single design. Adoption studies with various combinations of kinships, not including twins, yield the same results as twin studies. It is worth noting that we are not the only ones who have observed such effect. Scott (1990), who carried out classic work on the behavior genetics of behavior in dogs, reports that,

> We thought that the best time to study the effects of genetics would be soon after birth, when behavior

> still had little opportunity to be altered by experience. On the contrary, we found that the different dog breeds were most alike as newborns; that is genetic variation in behavior develops postnatally, in part as a result of the timing of gene action and in part from the interaction of gene action and experience, social and otherwise. (p. vii)

These two processes, timing of gene action and interaction of genes and experience (I prefer the term transaction to interaction) are now called innovation and amplification. A meta-analysis of longitudinal twin and adoption data (Briley and Tucker-Drob 2013) supports the idea that genetic innovations explain the results in Fig. 1 up to age 8 and amplification after that point. Amplification processes may reflect the fact that organisms create their own effective environments via selective transactions. As Martin et al. (1986) put it "humans as exploring organisms whose innate abilities and predispositions help them select what is relevant and adaptive from the range of opportunities and stimuli presented in the environment. The effects of mobility and learning, therefore, augment rather than eradicate the effects of the genotype on behavior" (p. 4368). This idea has been elaborated in some detail by Scarr (1996) who has argued that people make their own environments, and Bouchard (Bouchard 1997; Bouchard et al. 1996; Johnson 2010) who has elaborated the Experience Producing Drive Theory of Hayes (1962). Amplification may also be facilitated by entended sensitive periods for intellectual development (Brant et al. 2013) and perhaps other mechanisms.

Amplification is often hailed as highlighting the importance of the environment relative to genes (Dickens and Flynn 2001), but I tend to side with Roberts (1967) on this issue:

> The genotype may influence the phenotype either by means of biochemical or other processes, labeled for convenience as "developmental," or by means of influencing the animal's choice of environment. But this second pathway, just as much as the first is a genetic one;… (p. 218).

Roberts treats this as a definition issue, environmental effects are those effects unrelated to the genotype. This stance can also be defended from a causal point of view. Consider the following thought experiment. If the genes that influence the trait (choice of environment, an example would be the beavers choice of waterways for their home as opposed to dry ground as illustrated by marmots) are replaced by null genes then the effect disappears. The real question, however, is malleability (Sesardic 2005). If we could easily influence the animal's choice of environment, other than by severely restricting it (Vonnegut 1961), this pathway could justifiably be regarded as a source of environmental influence. This has been difficult to achieve both at the individual level (Lee 2010) and the societal level (Firkowska et al. 1978; Firkowska-Mankiewicz 2011). More importantly, however, if we can specify the causal pathways, describing precisely how things work (the true goal of science) the question becomes moot.

Nevertheless, environments are not unimportant. It is important and necessary to specify the populations to which the results in Fig. 2 can be generalized and not misinterpret what they mean. The samples were drawn almost exclusively from western industrial democracies. These settings have characteristic environments. Only a few of the participants were raised in real poverty or by illiterate parents. This is the domain to which we can generalize. The results do not mean that environments are irrelevant. The proximate causes of variance in *g* are the "cognitively stimulating experiences" that the individual experiences.

More generally a number of behavioral phenotypes show similar age related changes in heritability (Bergen et al. 2007). There may be a common mechanism underlying the effect or multiple mechanisms.

## Mechanisms and causes

The term mechanism is somewhat ambiguous, particularly with regard to causation. This is especially true when the data relevant to the mechanism have not been gathered in an experimental context. I use the term mechanism to describe any specific pattern of observed relationships, not necessarily a path model or acyclic graph. Such a pattern may suggest a particular part of a chain of causation, but is typically no more than a hypothesis about causation. A nice example is the somewhat different pattern of brain activation data in females versus males. Females have smaller brains than males yet there is at most a small difference in *g* in adulthood (Johnson and Bouchard 2007a; Keith et al. 2008).[3] This finding has long been a paradox. Recently, however, a diffusion tensor imaging study of "small world" cortical networks "found that females had significantly greater local network efficiencies than males. Moreover, smaller brains showed higher local efficiency in females but not in males, which implies an interaction between sex and brain size." (Yan et al. 2011, p. 8). If replicated this work specifies mechanisms and may have solved the paradox. There is also an overwhelming body of data that suggests that the maturation and functioning of

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[3] Keith et al. (2008) have demonstrated that it is important to use a latent trait model to explore questions regarding sex differences as methodological differences (composite scores vs. *g* scores, different methods of dealing with missing data, etc.) strongly influence the findings.

the brains of males and females follow a different time line and that female brains are structurally different from male brains. Examples include;

(1) Cortical synaptic density (men higher) (Alonso-Nanclares et al. 2008)
(2) Cortical convolution (different correlations with *g*) (Luders et al. 2007)
(3) Different levels of resting EEG activity as related to *g* (Jaušovec and Jaušovec 2005)
(4) The correlations between g and gray matter and white matter differ for men and women. This suggests that there is a different brain architecture for men and women (Haier 2009; Schmithorst and Yuan 2010)
(5) There is a sex by age interaction for the reduction in gray matter and increases in white matter (De Bellis et al. 2001)
(6) There are differences in interconnectivity of the brains of males and females (Duarte-Carvajalino et al. 2012; Schmithorst 2009)

There is also data suggesting that male and female primate brains could have been under different selection pressure (Lindenfors et al. 2007).

The bottom line here is that studies of brain functioning using samples that have combined males and females may well have produced misleading results. It will be critical in the future to carry out separate analyses of males and females. More interestingly it appears that if one were to try to predict *g* from physical properties of the brain, quite different properties would likely have to go into the equations for males and females. If this proves to be true it raises the question, would one expect different genes to be responsible for the differences in brain development of the two sexes? Given such data it is easy to assume that men and women use their brains differently. They may, but the data are descriptive and not proof of causation.

Almost all descriptive data sets are consistent with a number of different causal mechanisms. It is easy to think that because two things are both highly heritable and genetically correlated (brain size and IQ) both are directly influenced by the same genes in a mechanistic manner. Things are probably more complicated than that. As Peper et al. point out:

> It might be, for example, that a higher level of cognitive functioning leads a person to select an environment that also increases brain size. The genetic influence on brain size then simply reflects the genetic influences on cognition. Thus, the specific mechanism, pathways, and genes that are involved in human brain morphology and its association with cognitive functions remain elusive. (Peper et al. 2007, p. 469–470)

This is another description of Experience Producing Drive theory discussed above. Wilson (1985) put a very similar idea into an evolutionary context although he did not give it a name or work out the necessary details. It is now called “behavioral drive”—“The second pressure to evolve comes from the brain of mammals and birds. This internal pressure, a consequence of the power of the brain to innovate and imitate, leads to culturally driven evolution” (p. 172). Much of the animal/brain size research cited earlier in this manuscript flows from this hypothesis. Dawkins (1982) called a more refined version of this idea “The Extended Phenotype”, but it might be better called “the extended genotype” (Krueger et al. 2003). These ideas all attempt to capture the empirical phenomenon of genotype x environment correlation.

## Molecular genetics and intelligence

The high heritability of *g* has made it a popular target in the search for genes that influence behavior. In spite of numerous studies with sufficient power to detect rather small effects, the results to date have been dismal in comparison with expectation (Deary et al. 2009). Flint and Munafo (2013) commenting on a recent very large scale study (Rietveld et al. 2013) that they describe as a possible “successful backdoor study of IQ” (the actual phenotype was educational attainment) point out that the effects are tiny and an order of magnitude smaller than the findings for height and weight. Nevertheless, adding together the influence of the variants found increases the accuracy of prediction, suggesting that the trait is highly polygenic. It is worth noting that height is largely due to combing the length of a limited number of bones. The brain, on the other hand, is an exceedingly complex organ in which thousands of genes are expressed. It may be the case that the near infinitesimal model of quantitative genetics applies to the genes that influence *g*, work in other domains provides a perspective on this issue.

For example, the corn study mentioned earlier found 333 genetic loci influencing flowering time. This is probably a minimum estimate and clearly supports the near infinitesimal model of quantitative genetics for this trait in this species (Kliebenstein 2010). Human disease genes also appear to fit this model (Marigorta and Navarro 2013). Even though we know of about 50 genes for height and their effect size is larger than those found for educational attainment, they explain a small fraction of its heritability. McEvoy and Visscher (2009) point out that there well may be thousands of genes influencing height.

## The rate of evolution of cognitive process in various species

If there are only about 22,333 human genes (the grape has 30,434) (Pertea and Salzberg 2010) then most if not every gene must be pleotropic and doing more than one task. If most genes are pleotropic then selecting for a trait influenced by a subset of genes implies that one is selecting for many other traits as well. Given that so many genes appear to underlie complex traits one would imagine that the effect of such selection would be very weak. This, however, turns out not to be true for some traits. Consider the classic study initiated by Dmitry K. Belyaev who selected foxes for tameness over a 40-year period, less than a blink of the eye in evolutionary time. Selecting for tameness dragged along a series of other traits including a reduction in brain size and the manifestation of novel traits characteristic of other domesticated species (Trut 1999). It is well known that the skull size of domesticated species is reduced relative to their wild ancestors. This reduction is greater in species with greater encephalization than those with less encephalization (Kruska 2005). Indeed the skulls of male foxes became somewhat "feminized" (a decrease in the sexual dimorphism of the skull). I am willing to speculate that the same thing has happened to the male human skull during the process of civilization (assumption: I equate civilization with domestication/feminization), which has probably entailed indirect selection against within-group aggression. Recall that human brain size has decreased over the last 35,000 years. Allman (2000, Chap. 7) has put forth a similar argument. This change was probably due to genetic changes during the timing of developmental events causing the organism to maintain a more juvenile form (neoteny). Neoteny appears to be one of the processes that influence the evolution of the human brain. Note, however, that this process was not general across all human traits. As Caroll (2003a, b) points out;

> Importantly, all of the skeletal changes associated with bipedalism are structural innovations independent of neoteny. These observations suggest that the human brain is not a product of simple shifts in growth relationships, but of multiple, independent and superimposed modifications. (p. 851).

This is another description of "bricolage".

There is also experimental evidence based on the Russian tame fox population for a correlated by product effect on cognition.

> sociocognitive evolution has occurred in the experimental foxes, and possibly domestic dogs as a correlated by-product of selection on system mediating fear and aggression, and it is likely the observed social cognitive evolution did not require direct selection for improved social cognitive ability. (Hare et al. 2005, p. 226)

It should be clear that there is much to learn about the genetic processes underlying the evolution of cognitive process in all species.

## A Dieu

I can't resist mentioning Steven J. Gould a last time[4]. The title of Gould's book (1981, 1996), *The Mismeasure of Man*, tells us the purpose of the book—to denigrate the measurement of intelligence. We find section headings in Chapter 3—Measuring Heads, like "The allure of numbers", "Numbers do not guarantee truth". It should be clear to the reader that the achievements discussed in this paper could simply not have been attained without succumbing to "the allure of numbers". Numbers may not guarantee truth, but progress in science is impossible without numbers and measurement, as words and rhetoric are not enough. Everything discussed in this paper was aimed at facilitating a causal understanding of human intelligence along the lines sketched by Lee (2012, Fig. 1). I have, however, only touched on some of the nodes and edges.

**Conflict of interest** The author declares that he has no conflicts of interest.

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[4] For readers who may not be familiar with Gould's book I should explain my reason for choosing it as a foil. Gould was without doubt among the most influential scientific intellectuals of the 20th century, and he shaped the thinking of huge numbers of people not trained in science (Shermer 2002) as well as a large number of those trained in science. An example of an important scientist/administrator/textbook author influenced by Gould would be Richard Atkinson. He was Director of the National Science Foundation and President of the University of California System and author of a widely used introductory psychology textbook (Atkinson et al. 2000). When asked about IQ testing he "frequently referred then to Stephen Jay Gould's book *The Mismeasure of Man*, published in 1981; it is a remarkable piece of scholarship that documented the widespread misuse of IQ tests (Atkinson 2005, p. 16). During Bouchard's career he was repeatedly confronted by people who cited Gould in opposition to his work with twins reared apart. Indeed Chapter six of *The Mismeasure of Man* begins as follows:

"If I had any desire to lead a life of indolent ease, I would wish to be an identical twin, separated at birth from my brother and raised in a different social class. We could hire ourselves out to a host of social scientists and practically name our fee. For we would be exceedingly rare representatives of the only really adequate natural experiment for separating genetic from environmental effects in humans–genetically identical individuals raised in disparate environments."

Bouchard's study of monozygotic twins reared apart had been running for 2 years when this was published and Gould was well aware of the study. He certainly never asked Bouchard what the twins were paid, it was a pittance (Segal 2012). Bouchard finds the claim of venal motivation on the part of twins insulting to say the least.

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