Cognitive and Neurobiological Mechanisms of the Law of General Intelligence

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Introduction

Why do scores on most cognitive ability tests correlate positively? The fact that people who score highly on one test tend to score highly on others—that some people are more intelligent than others—is now so intuitively obvious that most psychologists, at least since it was first discovered by Spearman (1904), take it for granted. They are not interested in talking about, much less thinking about, let alone investigating, individual differences in cognitive ability. And there is nothing wrong with this; research topics and approaches fade in and out of popularity. Even the harshest critics of IQ profess no surprise at the positive correlations among tests; Stephen J. Gould (1981, p. 315) wrote, "The fact of pervasive intercorrelation between mental tests must be among the most unsurprising major discoveries in the history of science." But if we could step out of our normal modes of thinking, if we could free our minds of the "debauchery of learning" that William James famously noted (1890, as quoted by Cosmides & Tooby, 1994), we might wonder why there should be any correlation among cognitive tests, let alone the strong, consistent, positive correlations found in hundreds of studies over the past century (Carroll, 1993).

Evolutionary psychology, with its emphasis on specialised adaptations and instincts forged in a long-ago stone age, has little to say about current variation in intelligence. Few theories in cognitive psychology specify how their component processes or representations might vary from person to person. Neuroscience likewise gives short shrift to individual differences, though it would appear to contain within its ranks fewer outright opponents of the very concept. Notwithstanding the plea of Cronbach (1957) for unification of the "two disciplines" of psychology, instances of collaboration between students of human commonalities and students of human differences, or instances of individual researchers who effectively operate within both of these camps, are still the exception, not the rule. Those who employ the Analysis of Variance rarely actually *analyse variance* (Plomin & Kosslyn, 2001).

The ubiquitous positive correlations among cognitive tests are a challenge for theories of how the mind works that focus on independent, domain-specific, encapsulated processes, or "modules"

(Fodor, 1983) as the elementary units of study. This is especially so if one believes that these modules must have evolved to solve critical problems rapidly and efficiently (Cosmides & Tooby, 1994): Why should there be *any* correlated variation in the efficacy of all of these carefully designed processes? Paradoxically, the notion of intelligence as an individual difference, a fact that most humans take for granted, is outside the predictive power of one of the leading theoretical frameworks in modern cognitive psychology.

Two general approaches have been taken toward reconciling modularity with general intelligence. One is to argue that the general factor revealed by the correlations among cognitive tests—the *g* factor—is a psychometrically unitary construct, but that it is caused by multiple biological factors (Jensen, 1998a). In a letter to *Commentary* (included in Chabris et al., 1998, pp. 20–21), Arthur Jensen elaborated on this hypothesis:

> … the design features of the brain—its neural structures and functions—that are necessary for the many distinct processes that enter into information-processing, or intelligence (such as attention, perception, discrimination, generalization, learning, memory, language, thinking, problem-solving, and the like) are essentially the same for all biologically normal Homo sapiens, i.e., those free of chromosomal and major gene anomalies or brain damage.
>
> Correlated individual differences in the functioning of these various information processes are a result of other quantitative biochemical and physiological conditions in the brain, most of them highly heritable, that are separate from the brain's essential design features, or "hard-wiring," but are, as it were, superimposed on all of them in common, and affect the overall speed and efficiency of their functioning.

The domain-general "speed and efficiency" of neural functioning can be assessed in several ways: by measuring speed of response in simple cognitive tasks, by measuring speed of perceptual intake via a simple psychophysical task, by measuring nerve conduction velocity, and the like. Global neural resources can be quantified by measures such as total brain volume, total grey matter, and total white matter. Indeed, numerous studies support the correlation between these sorts of measures and performance on intelligence tests, especially the general factor.

The alternative approach is that certain neural systems, perhaps ones that are only semi-modular, are especially related to *g* because they are responsible for controlling the operation of other processes, or for managing limited central resources that other processes require in order to function optimally. Variability in the efficacy of these special systems could account for *g* (e.g., Kyllonen & Christal, 1990). As others have noted, this view encompasses two distinct ideas: that of a limited pool of central memory capacity, perhaps also constraining the action of domain-specific processes, versus that of a limited ability of a central process to control the operation of domain-specific processes (e.g., Thomas & Karmiloff-Smith, 2003). Region-specific neural resources corresponding to these processes could be indexed by the volumes of specific structures, or the degree to which those structures are activated in response to specific cognitive challenges.

Each of these approaches (general neural efficiency versus central resources or processes) has the potential to reconcile the modular view of the mind—an orchestra of multiple independent processes designed for specific purposes and playing specific parts in the overall performance of

behaviour—with the fact of general intelligence. In this chapter I will selectively review the evidence in favour of each of these hypotheses, focusing on recent studies of brain anatomy and function. This evidence indicates that these hypotheses are not in contradiction, and that both are likely to be true. However, I will show that we have not collected the data needed to determine the relative importance of all the neurobiological factors potentially underlying *g*, nor have we applied the best tools for modeling the human cognitive architecture to the problem of understanding the causes of *g*. I will outline a research program for the next stage of research on the mechanisms of human intelligence, and conclude with a reminder of what intelligence is *not*.

The Law of General Intelligence

As Brand (1996) eloquently points out, a folk-psychology understanding of cognition need not predict a general intelligence:

> … a normal expectation is that time spent in one activity is time that is lost for another: an evening spent doing crossword puzzles or metaphysics is an evening lost to practising jigsaws or swatting up metallurgy. Thus, in so far as 'practice makes perfect' and time is finite, the pervasive intercorrelation between mental abilities should actually tend to be negative; and a prediction of negative correlation should particularly made by anyone who, like Gould, is inclined to treat measured IQ-type abilities as collections of attainments.

Contrary to this, in the preface to his masterful volume *The g Factor*, Jensen (1998a, p. xii) remarked almost offhandedly:

> I have come to view *g* as one of the most central phenomena in all of behavioral science, with broad explanatory power at least as important for understanding human affairs as E. L. Thorndike's Law of Effect (or Skinner's reinforcement principle). Moreover, it became apparent that the *g* construct extends well beyond its psychometric origin and definition. The *g* factor is actually a biologically based variable, which, like any other biological functions in the human species, is necessarily a product of the evolutionary process. The human condition in all its aspects cannot be adequately described or understood in a scientific sense without taking into account the powerful explanatory role of the *g* factor.

In essence, Jensen proposed that the concept of *g* was sufficiently established and important to merit the status of a behavioural or biological law. Needless to say, this suggestion has not been taken up enthusiastically, or even half-heartedly, by psychologists. But even though only eight years have passed, the evidence in favour of a "law of general intelligence" has increased markedly. This law would state that *measurements of cognitive ability tend to correlate positively across individuals*, with a corollary that the first principal component or general factor extracted from any such correlation matrix—assuming a diverse battery of mental tests and a diverse sample of subjects—will account for a substantial fraction of the variance.

The proposal that general intelligence is a behavioural law contrasts sharply with the suggestion by Ardila (1999, p. 117) that "the psychometric concept of general intelligence should be deleted from cognitive and neurological sciences." It is good to be reminded that, despite its seeming

ubiquity, *g* is not an automatic, trivial consequence of other established theories and findings in cognitive science: In our world, cognitive abilities could be correlated or uncorrelated, and whether they in fact are correlated is still a point of controversy (Chabris, 1998; Korb, 1994). In this regard the Law of General Intelligence lacks the widespread acceptance of Weber's Law, the Matching Law, or any of the other major behavioural laws (reviewed by Teigen, 2002). In this section I will review evidence in favour of the Law of General Intelligence and argue that it is likely to apply not just to human beings, but to all species with sufficient cognitive complexity to allow for individual differences in problem-solving behaviour.

General intelligence in humans

The Law of General Intelligence is illustrated in a straightforward way by **Table 19.1a**, a correlation matrix from a Scottish population sample performing the WAIS-R, a prominent intelligence test. In this case all 55 correlations among the subtests are positive, although they range from .14 to .72. This is the "positive manifold" typically observed in IQ tests. **Table 19.1b** demonstrates that the law is in effect even when evidence for it is not being sought. I collected these data (in collaboration with several colleagues and research assistants) as part of a study of individual differences in decision-making in a sample of students and adults in the Boston area. Correlations are shown among seven cognitive tasks, none of which is traditionally included in IQ tests, ranging from –.02 to .48, with 19 out of 21 positive. Note that although the samples are different (population sample in Scotland versus convenience sample in the U.S.), the tests are different (psychometrically-validated IQ subtests versus mainly cognitive tests), and the context is different (mainly untimed, verbal responses versus mainly timed, computerised administration), the overall patterns are strikingly similar. When the correlation matrices are subjected to principal components analysis,[1] the first component accounts for 48% of the total variance in Table 19.1a and 36% in Table 19.1b. The differences can partly be explained by the superior reliability of the WAIS-R as a test battery, and range restriction in the smaller, more idiosyncratic Boston sample.

Some correlational studies of cognitive tasks in humans have failed to find a general factor, but upon closer examination, they turn out to be the exceptions that prove the rule. For example, Kosslyn et al. (1984) administered a set of mental imagery tasks to 50 subjects, mostly not students, and reported correlations among the 13 derived measures ranging from $r = -.44$ to .79, with a mean of .28. According to a re-analysis of their published matrix, the first three principal components account for 22%, 18%, and 13% of the total variance. However, most of the measures derived from the various tasks were not absolute performance levels, such as total accuracy, but rather theoretically-relevant measures such as slopes of mental rotation functions, or introspective judgments of the blurriness or vividness of mental images. [Indeed, Kosslyn et al. report analyses confirming a good fit between (1) the observed correlations and (2) predictions derived from a detailed computational model of visual mental imagery processing.] Slopes or change scores inherently tend to be independent of individual differences in total speed or accuracy, and introspective judgments are not necessarily measurements of performance that would be regarded as demonstrating "intelligence" in the same way as speed or accuracy of responding. If one considers only the tasks for which objective total performance measures are given,[2] all 10 correlations are positive, and the first principal component accounts for 45% of the variance, results in line with the Law of General Intelligence. Adding the performance measures from the four non-imagery tasks also used by Kosslyn et al. results in 33 out of 36 positive

correlations, and 35% of the variance accounted for by the first principal component, comparable to the pattern in Table 19.1b—again, from a dataset using entirely different tasks and subjects, collected for a purpose other than discovering a *g* factor.

Extensive cross-cultural studies (reviewed by contributors to Irvine & Berry, 1988) have established that the *g* factor is observed whenever a battery of diverse, complex cognitive tasks is administered to a human sample. For example, Reuning (1988) summarised eight years of studies administering custom-designed mental tests to 512 Kalahari Bushmen and concluded that "the patterns of intercorrelations suggest that a fairly strong general intellectual factor is operative in all sets of data" (p. 479) with positive correlations among cognitive and perceptual tests ranging from .20 to .78—almost the same range as shown in Table 19.1a. Standardisation samples for IQ tests confirm that the factor structure is also consistent across sexes and ethnic groups within the United States and other countries (e.g., Taylor & Ziegler, 1987), and that cognitive ability level can be measured with high reliability (Mackintosh, 1998, pp. 55-62). And intelligence has been repeatedly shown to be the best psychometric predictor of job success (Ree & Earles, 1992) and many other important life outcomes, both positive and negative (Gottfredson, 1997; Herrnstein & Murray, 1994), as diverse as the propensity to invest in financial markets (Benjamin, Brown, & Shapiro, 2006; see also Frederick, 2006 on intelligence and normative decision-making) and the risk of developing mental illness in response to traumatic stress (Macklin et al., 1998). Even death is a higher risk for individuals of lower intelligence (e.g., Deary et al., 2004). [See also Brody, Chapter 18, and Gottfredson, Chapter 20, this volume.]

So far we have seen how the Law of General Intelligence describes a regularity of human behaviour. Note that this regularity applies not to patterns of behaviour within an individual, in contrast to Weber's Law or the Power Law of Practice, but to patterns across individuals. In this way it resembles the "three laws of behavior genetics" proposed by Turkheimer (2000), which describe regularities in how trait variance appears to be caused by genetic, shared environmental, and nonshared environmental variance. It is a quantitative law, in that it describes a systematic relation among quantities (test scores), but like Turkheimer's laws, and qualitative statements such as the Gestalt laws of perceptual organisation, it does not make specific numerical predictions of empirical results.

General intelligence in other species

Thousands of studies have been conducted to demonstrate the existence of *g* in human samples, and to measure the reliability and validity of intelligence measures. Arguments that *g* is a mere statistical artifact or is necessarily bound to possibly racist Western notions of measurement or ability (e.g., Gould, 1981) have been refuted (Bartholomew, 2004; Chabris, 1998; Davis, 1983; Korb, 1994), but there has been relatively little work on *g* in nonhuman species (Locurto, 1997; Plomin, 2001). Note that the question of animal *g* is not the same as whether different species are on average more or less "intelligent" (MacPhail, 1987), or whether different breeds within a species seem to differ in "intelligence" (e.g., Coren, 1994). The case for a Law of General Intelligence would be strengthened considerably by finding a consistent *g*-factor in animals, such that the individuals within a species who perform well on one "cognitive" task are likely to perform well on other tasks.

Table 19.2 shows data from a study of 84 outbred laboratory mice (Galsworthy et al., 2005) in which each animal performed six tests of learning and problem-solving that are typically used in cognitive studies with mice. Paralleling Table 19.1, all 15 correlations are positive (r = .05 to .52) and the first principal component accounts for 35% of the variance. Indeed, the three datasets shown so far differ in so many respects on the surface that their fundamental similarity should be striking. Despite the idiosyncrasy of species, nationalities, sampling methods, and tasks, the correlation matrices share the properties of having almost all positive correlations (55 out of 55, 19 out of 21, and 15 out of 15) and of the first principal component accounting for between one third and one half of the total variance.

Table 19.3 summarises published studies of *g* in animals, conducted to the end of 2005. Several noteworthy points emerge from an examination of these results. First, 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. Second, there are more studies on mice than on all other species combined, and all but one of these have been conducted in the past ten years. The earliest study was conducted by Bagg (1920), but he did not present his data in a correlation matrix format. Galsworthy et al. (2005) report a re-analysis of Bagg's data in this format, as well as two studies of their own, and observe that the first principal component (1st PC) accounted for 61%, 41%, and 23% of the variance in the three studies. The most recent common ancestor of mice and humans lived 80 million years ago, and many cognitive capabilities—or modules—found in the two species must have evolved separately, during that time, to face different environments and challenges. Nonetheless, as with humans, mice display correlated variation in mental ability levels across domains: the grand average inter-task r across the studies of mice is .28 (weighted by sample size, r = .24).

Third, as shown in **Table 19.4**, in one case the same test battery was applied to samples of rhesus monkeys—a fairly close primate relative—and human children. In each case the average task correlations were positive; however, this pattern was much stronger in the human sample (perhaps due in part to these being low-birthweight children at risk for low intelligence). The human sample also completed a standard, age-appropriate IQ test, which correlated strongly with each of the tasks in the battery that loaded on its *g*-factor. Taken together, these results link the *g* factors found in animals and humans. Finally, it should be noted that most of the studies reported here may be biased against finding a general factor, because laboratory animals are raised in environments that are not only somewhat impoverished but also identical, or at least very similar across individuals, removing a major source of individual differences, and increasing the homogeneity of behaviour.

There was a small vogue for studying *g* in rats and chickens during the 1930s and 1940s, but, as Locurto (1997) points out in a review of comparative studies of intelligence, few lessons can be drawn from this work because it often used inbred, mutant (e.g., albino), or poorly-characterised laboratory animals, or focused exclusively on different maze-running tasks (see also Plomin, 2001). Samples with artificial genetic similarity, which include even the more recent, well-designed studies of rats (e.g., Anderson, 1993, 1995), are less likely to reveal a *g* factor, as are studies without a diverse set of cognitive challenges (these could instead identify a factor specific to the type of task used). Interestingly, two large recent studies that failed to find strong evidence of *g* in the Sprague-Dawley rat strain did find a positive manifold when animals were subjected to a variety of brain lesions early in development, a treatment that presumably increased the

diversity of their surviving brain function by counteracting the effects of genetic similarity (Crinella & Yu, 1995; Thompson, Crinella, & Yu, 1990). Crinella and Yu (1995) present data from Thompson et al. (1990) comparing the unlesioned animals ($N = 75$) to the full sample ($N = 424$) on four performance measures; the average correlation among tasks in the unlesioned group is $r = .01$, compared to .24 for the full sample. In a replication with seven measures intended to sample a broader range of *g*-loadings, Crinella et al. found an average correlation of $r = .02$ in 24 unlesioned animals, increasing to .19 when 96 lesioned animals were added to the sample.[3]

Hints of evidence for general intelligence have also emerged in recent studies of non-mammals, specifically insects. Honeybees were divided into two groups according to their performance on a test of latent inhibition (high or low inhibition); the offspring of these groups showed a similar difference on latent inhibition, and high-inhibition bees performed worse on a reversal learning task (Chandra, Hosler, & Smith, 2000; but see Ferguson, Cobey, & Smith, 2001 for inconsistent findings). While this study observed a positive association between just two tasks, it is intriguing that reversal learning is a test of executive function, which is related to fluid intelligence in humans (see next section). The development of more diverse batteries of tests, as has been done for mice, could facilitate studies of general intelligence in suitable insect species, such as honeybees and fruit flies, as well as other species in which individual differences have been found at the single-neurone level, such as molluscs (Matzel & Gandhi, 2000).

The recent focus on mice has enabled the development of consensus methodologies (e.g., Crawley & Paylor, 1997) and a database of relatively comparable results, as well as facilitating the study of genetic modifications (e.g., Tang et al., 1999), but it cannot address some issues as well as can work on other species. Nonhuman primates such as monkeys should be studied further because of their close evolutionary relationship and neuroanatomical similarities to humans.[4] Dogs present an interesting case for several reasons, including their high social ability and co-evolution with humans (Hare & Tomasello, 2005), as well as their potentially greater suitability as a model for understanding human cognitive diseases and for developing therapies (e.g., Milgram et al., 2005; Tapp et al., 2004, 2006). Studies of dogs, and other non-primate species that show comparable cognitive and neurological complexity to primates, such as dolphins (Marino, 2004), and even highly intelligent non-mammals such as corvids (e.g., crows and ravens; Clayton & Emery, 2005), afford the opportunity to ask whether *g* represents a universal property of diverse brains that evolved on long-separate lineages. Many specific cognitive abilities have evolved convergently, such as self-recognition in cetaceans and primates (Marino, 2002), and tool use and episodic memory in corvids and primates (Emery & Clayton, 2004). There appear to be considerable differences among ravens in their ability to solve a novel, complex problem (gathering up a string with their bills and feet to acquire a piece of meat tied to the end; Heinrich & Bugnyar, 2005). It is therefore plausible that covariation among cognitive abilities, perhaps due to their need for shared central information processing resources, can arise separately within species as well.

Cognitive and Neurobiological Mechanisms

A second important corollary of the Law of General Intelligence is that individual differences in *g* result from differences in the amount or efficiency of information-processing resources brought to bear in solving problems. These resources could be specified at the cognitive or biological levels.[5] Jensen (1998a) devoted 99 pages to the correlates of *g*, focusing on brain volume, brain

electrical activity, processing speed, and working memory. In the ensuing years, the biological foundation of *g* has been strengthened considerably, and it has been broadened by the use of new brain-imaging technologies, primarily based on magnetic resonance imaging (MRI), and new cognitive approaches. Also important is the identification by Duncan and colleagues (Duncan, Burgess, & Emslie, 1995; Duncan et al., 1996), and others, of executive function, as mediated by the frontal lobes, as being critical for general fluid intelligence (*gF*).[6]

Table 19.5 summarises recent empirical studies of the major cognitive and neurobiological correlates of general mental ability. In some cases, such as brain volume, the results of a meta-analysis are given, while in others, such as response time, the results of a single, large, well-designed study are presented. In the case of some newer MRI technologies, only a single small study may have been reported to date. In this section I will review some of the most important studies of the major dimensions of cognitive and neurobiological variation that have been shown, or proposed, to correlate with general intelligence.

Brain volume

The idea that greater information-processing resources should facilitate greater cognitive ability is a simple one—so simple that it appears simplistic. Yet the fact that brain volume is correlated with intelligence comes as a surprise to many contemporary cognitive scientists, who have apparently absorbed critiques of allegedly "racist" studies conducted a century ago (e.g., Gould, 1981). Their attitude is well-expressed by Budiansky's (1998) assertion: "Correlation between intelligence and brain size has been soundly rebuffed in humans." According to a press release (dated 29 March 2006), Elias A. Zerhouni, the head of the U.S. National Institutes of Health, believes this to be the conclusion of empirical research: "Studies of brains have taught us that people with higher IQs do not have larger brains." The general ethos of modularity that prevails in cognitive psychology and evolutionary psychology, and which is in opposition to notions of equipotentiality, also feeds skepticism of the importance of global parameters of brain function and structure. Nonetheless, beginning with Andreasen et al. (1993), a lengthening series of studies using quantitative analysis of structural magnetic resonance images and modern psychometric tests has documented a robust association accounting for about 10% of the variance in IQ, according to a meta-analysis of 37 studies involving 1530 subjects (McDaniel, 2005). Controlling for height (as a measure of body size) typically does not alter the results (e.g., Witelson, Beresh, & Kigar, 2005). An earlier meta-analysis by Gignac, Vernon, and Wickett (2003) showed that the IQ-volume association was the same for grey matter (which consists mainly of the cell bodies of neurones) and white matter (which consists of axons and myelin, which carry information between neurones). As we shall see, however, properties of the white matter other than its total volume may be critical for intelligence.

Modern image analysis technologies allow the volumes of particular structures and regions to be estimated from structural MRI data. Using such a method, Thompson et al. (2001) reported a correlation of .41 between frontal lobe volume and IQ (controlling for whole-brain volume), which was the largest and only significant relationship of cortical lobe volumes to IQ. Studies using more automated techniques, such as voxel-based morphometry (VBM; Ashburner & Friston, 2000), have revealed varying patterns of results. In a study of 146 children aged 5 to 19, Wilke et al. (2003) found that grey matter volume was most strongly correlated with IQ in the anterior cingulate cortex (ACC; $r = .29$). Interestingly, this correlation was highest in the oldest

third of the subjects (r = .53). Frangou, Chitins, and Williams (2004) used a similar technique with 40 older children (ages 12 to 21) and replicated the correlation between IQ and ACC grey matter volume. They also found IQ correlations with orbitofrontal (bilateral), precuneus, thalamic, and cerebellar grey matter volume.

In contrast to these developmental studies, Haier et al. (2004) used VBM analysis from different sites with two adult samples (total N = 47) and found much more widespread regions of IQ-volume correlation, in both grey and white matter. As shown in **Figure 19.1**, the strongest correlations between grey matter concentration and IQ occurred in the medial prefrontal cortex, and the superior, middle, and inferior frontal gyri bilaterally. White matter concentration correlations with IQ were strongest in the frontal and temporal lobes. Using both VBM and a manual technique, Gong et al. (2005) found a correlation only in the medial PFC (specifically the anterior cingulate cortex) between grey matter volume and *g*. Thus, while these studies disagree in the particulars of their findings, the overall pattern is consistent with Thompson et al.'s conclusion that frontal cortex grey matter is closely related to IQ. The disagreement may result from the differing samples: During development, the frontal cortex continues to mature, so the IQ-volume effect may grow more apparent with increasing age. It is also possible that the reliability of automated warping techniques like VBM is sufficient to capture robust trends of correlation over large regions, such as the lateral or medial prefrontal cortex (PFC), but not smaller areas such as specific gyri.

Information processing speed

Just as a larger brain can be a more intelligent brain, a faster brain can also confer greater cognitive ability. This has been found even for the most simple measurements of processing speed. Deary, Der, and Ford (2001) administered a task with two conditions to a representative population sample of 900 Scottish adults aged 54 to 58. In one condition, subjects had to press one of four buttons according to which of four corresponding lights illuminated on each trial; in the other, only one light and one button were involved, so there was no "choice" component involving a decision of which button to press. Response time (RT) on the 4-choice condition correlated r = –.49 with IQ (higher-IQ subjects responded faster), but this correlation remained at r = –.31 on the simple reaction time condition. Higher-IQ subjects also showed less variable response times (r = –.26 between IQ and the standard deviation of RT). Notably, IQ explained at least thirteen times more variance in RT parameters than it did in accuracy on the 4-choice task, ruling out the possibility of a speed-accuracy trade-off.

RT is not necessarily a pure measure of information processing speed. Despite the apparent simplicity of even the simple RT task, it requires the sequencing of several operations (from detection of the light to initiation of the motor response, plus the speed of moving one's fingers). The "inspection time" (IT) task aims to measure a circumscribed component of perceptual processing by separating out the motor response component. On each trial, following a cue, two line segments are presented side by side on a screen for a very brief period of time, followed by a masking stimulus; the subject must decide which segment is longer. The dependent measure, IT, is not speed of response, rather it is the minimum stimulus display time at which the subject can reach a predefined accuracy criterion, such as 75% of trials correct. Early studies reported IT-IQ correlations as high as r = –.85 (higher-IQ subjects are able to reach criterion at shorter stimulus display times; Deary, 2000), but a more recent meta-analysis of 92 studies, involving 4197

subjects, estimated the population correlation at –.51 (Grudnik & Kranzler, 2001), essentially the same as the correlation between choice RT and IQ found by Deary et al. (2001).

White matter efficacy

Larger brains and faster brains are both associated with higher IQ, as demonstrated by the volume, RT, and IT findings. Even so, it is not clear whether larger brains should equate with being faster ones. But faster processing could certainly result from the more efficient function of white matter—the axons that communicate information between neurones, and the myelin that insulates the axons to prevent signal degradation over distance. Miller (1994) argued that the biological substrate for IQ differences should be found in white matter, and as we have seen, white matter volume, both globally and in specific regions, does predict IQ. Two of the white-matter factors presented in Table 19.5 have small correlations with *g*. Nerve conduction velocity, which can be measured in different ways, shows a consistent but very small association with *g*, as illustrated by the large recent study of Reed, Vernon, & Johnson, (2004). The presence of white matter lesions, which are areas of hyperintense MRI signal, and are often associated with ageing, correlates weakly with *g*, though perhaps more highly with executive function, according to a meta-analytic review (Gunning-Dixon & Raz, 2000). However, two newer MRI techniques enable direct measurement of the efficacy and integrity of white matter tissue.

Diffusion tensor imaging (DTI) measures how much water diffuses in different directions within each voxel (three-dimensional "chunk") of the tissue being sampled. Water diffuses more along the direction of axon projection than perpendicular to it, since the perpendicular direction may be restricted by the axon membrane and the surrounding myelin sheaths. Fractional anisotropy (FA) is the degree to which water diffuses in a single direction. Thus, if a voxel contains mainly axons lined up in a single direction, it should have high FA. Klingberg et al. (2000) treated FA as an individual-differences parameter that indexes the integrity of the microstructure of white matter, and found that FA in a region of the left temporal-parietal cortex correlated as high as $r = .84$ with reading test score in a sample of 17 adults. Tuch et al. (2005) directly related FA to response time on a 4-choice task in 12 young adults aged 19-26, and observed negative correlations (faster responders had higher FA values) in left parietal and superior temporal areas (cf. Madden et al., 2004). Finally, Schmithorst et al. (2005) measured FA and IQ (using the Wechsler Intelligence Scale for Children-III) in 47 children aged 5 to 18. In addition to a bilateral region in the frontal lobes, several areas of positive correlation between FA and IQ were found in areas associated with visual-spatial processing, such as the right occipital-parietal region, with a collective average correlation of $r = .44$. (See Shenkin et al., 2003, 2005 for further studies of FA and intelligence in samples of older adults.)

Magnetic resonance spectroscopy (MRS) measures the relative concentrations of different molecules in tissue, but typically cannot be performed with the same resolution or whole-brain coverage as structural MRI, DTI, or functional MRI (fMRI). A typical study samples from one or a few large regions of interest (ROIs) in the brain. Only certain molecules have spectroscopic signatures that enable quantification; the most commonly used is N-acetyl-aspartate (NAA), which is a marker of neuronal health. In the most recent MRS study of intelligence, Jung et al. (2005) measured NAA in an ROI in a right occipital-parietal white matter region, and observed a correlation of $r = .51$ with IQ in a sample of 27 adults (cf. Jung et al., 1999a). When the same region was examined in a separate study of 45 college students (Jung et al., 1999b), performance

on a set of timed cognitive tasks was more highly correlated with NAA (r = .65) than was performance on a set of untimed tasks (r = .28), a specificity to processing speed consistent with the ROI's placement within white matter.

Working memory and cognitive control

IQ differences may arise from variation in information processing efficiency across brain areas (as measured by RT or IT), which may in turn reflect differences in available neural resources (as measured by global or region-specific brain volume, or white matter efficacy). Two complementary possibilities are that IQ differences arise from variation in the capacity of limited resource pools—collectively described as working memory (WM)—that are used by multiple other processes, or from variation in the efficacy of supervisory processes (executive function or cognitive control) that regulate the operation of other processes (Duncan & Owen, 2000).[7] In either case, the requirement that the limited resource or specific process be used to perform many different cognitive tasks would explain the positive correlations among cognitive tests.

Working memory is assessed, albeit crudely, by the digit span test that is standard in IQ batteries like the WAIS. The relationship between IQ and working memory capacity is so well-supported by empirical evidence that some theorists have argued the two concepts are coextensive (e.g., Kyllonen & Christal, 1990), but current views are less radical (Conway, Kane, & Engel, 2003). The connection between IQ and executive function is a more recent development. Classical neuropsychological dogma claimed that measured IQ did not significantly decrease after lesions to the prefrontal cortex (e.g., Warrington, James, & Maciejewski, 1986). Paradoxically, a separate specific neuropsychological evaluation, such as the Wisconsin Card Sort Test (WCST), was required to detect frontal damage. In the WCST, the subject must learn to sort cards into piles by inferring a simple rule the examiner has in mind, such as sorting by the number of shapes on the card (1, 2, 3, and 4) rather than the collar of the shapes (red, blue, green, or yellow). After the subject has followed the rule correctly for a series of trials, the examiner changes the rule. Perseverative errors—continuing to follow the old, invalid rule—are made by patients with frontal damage, and are interpreted as reflecting decreased executive function. Duncan et al. (1995) resolved this paradox by showing that frontal damage impairs performance on tests of *fluid intelligence* disproportionately, compared to the overall IQ score, which in traditional test batteries such as the WAIS was weighted towards measures of *crystallised intelligence* such as vocabulary. Frontal lobe patients scored significantly lower on the Culture-Fair test than on the WAIS, whereas matched control subjects, and non-frontal patients, performed similarly on the two tests. The Culture-Fair test includes "matrix reasoning"—the quintessential measure of fluid intelligence, and the measure that typically loads most highly on the *g* factor in a battery of cognitive tests. A matrix task requires subjects to examine an array, whose nonverbal elements are linked by (unstated) rules, and determine which of several options is the correct one to fill an empty space in the array. Items get progressively harder as the test proceeds. [The newest edition of the WAIS, the WAIS-III, has added a matrix reasoning test.] Duncan et al. (1996) showed that frontal patients and low-IQ subjects exhibited a phenomenon of "goal neglect"—an impairment of cognitive control, in which instructions to switch attention between two different stimulus streams are ignored, even though they are understood.

A recent study by Gray, Chabris, and Braver (2003) illustrates the relationship between IQ, WM, and cognitive control. 58 adults completed Raven's Advanced Progressive Matrices (RAPM, the

leading matrix reasoning test) and the 3-back working memory task. For this task, in each of a series of trial blocks, the subject views a series of words and presses one button if the current word is the same as the one that came three earlier, and another button if it is different. This is a deceptively difficult task; in addition to keeping three words in memory while waiting for the next one, which is relatively easy by itself, the subject must discard the oldest word and add the new one while keeping the order correct. Accuracy on this task across all trials correlated $r = .34$ with RAPM score. The task was made even more difficult by the inclusion of "lure" trials, in which the stimulus is the same as the one seen two, four, or five trials earlier. On these trials, the familiarity of the word tempts the subject to respond incorrectly that it is the 3-back word, and performance is worse. On "nonlure" trials, when the stimulus matches that from one, six, or seven trials back, or is entirely new, performance is better. Cognitive control must be selectively increased on lure trials to suppress the incorrect response; indeed, RAPM score explained more variance on lure trials than on nonlure trials (partial $r = .27$ for the RAPM-lure correlation when controlling for nonlure accuracy).

Functional brain architecture

Several lines of evidence reviewed thus far point to the prefrontal cortex and cognitive control as critical anatomical and cognitive substrates of *g*. Gray et al. (2003) tested the hypothesis that individual differences in fluid intelligence are mediated by differences in the functioning of the neural system responsible for working memory. This system involves the lateral frontal cortex, anterior cingulate cortex, and cerebellum. 48 of the subjects who performed the 3-back task discussed above had their neural activity measured with fMRI on a trial-by-trial basis, and activity during lure trials was correlated with RAPM scores. The WM task activated a widespread network of brain regions, and RAPM predicted lure trial activity in the expected lateral frontal, ACC, and cerebellar regions, as well as several other regions, especially in the parietal lobes. **Figure 19.2** illustrates this effect for an ROI in the left lateral frontal cortex, in which the percent signal change from baseline correlated $r = .55$ with RAPM score. High-*gF* subjects increased activation of this area during lure trials, while low-*gF* subjects actually *decreased* activation.[8] These correlations between *gF* and lure trial activity remained in analyses controlling for activity on other trial types, as well as for accuracy on lure trials.

Two separate relationships have been established thus far: (1) RAPM predicts WM performance, especially on lure trials; and (2) RAPM predicts neural activity specific to lure trials, especially in the lateral PFC. These findings are consistent with the idea that increased activation of this network explains why high-IQ subjects perform better on lure trials. To demonstrate directly that this neural activity is responsible for the relationship between fluid intelligence and working memory, Gray et al. (2003) used mediation analysis. Mediation occurs when the relationship between two variables, A and B, is transmitted through a third variable C, that is correlated with both A and B (MacKinnon et al., 2002). Activity differences in three regions—the left lateral PFC region highlighted in Figure 19.2, as well as a left parietal and right parietal region—collectively accounted for nearly all of the relationship between *gF* and lure trial accuracy. Interestingly, the coordinates of these critical regions, whose activity reflects individual differences in fluid intelligence, are similar to those identified in an fMRI study of task-switching (Sohn et al., 2000), consistent with the findings of Duncan et al. (1996) on goal neglect.

Further evidence that the lateral frontal cortex and parietal cortex mediate general intelligence comes from studies using what Jensen (1998a) has described as the *method of correlated vectors*. According to Jensen, if a biological variable is related to *g*, its relationship with test performance should strengthen as the test's *g*-loading increases; that is, a vector of test *g*-loadings (vector A) should correlate significantly with a vector of correlations between the test scores and the biological variable (vector B). Lee et al. (2005) had 36 high school-age subjects complete the WAIS-R and RAPM, and then perform a matrix reasoning task during fMRI. Vector A contained the *g*-loadings of the WAIS-R subtests and the RAPM (as reported in a published psychometric study). They selected a set of five brain ROIs in which activity was greater during a difficult than during an easy version of the matrix task; these areas were the ACC, left and right PFC, and left and right posterior parietal cortex. For each of these ROIs, they created a vector of correlations between performance of the WAIS-R and RAPM tests and activity in that ROI (each of these is a Vector B1, B2, … B5). Finally, when Vector A was correlated with each of the Vector Bs, the highest correlations were observed for posterior parietal cortex ROIs bilaterally. That is, in the parietal cortex, as the *g*-loading of a test increased, so did the relationship between the test score and neural activity: The most *g*-loaded tests were the best predictors of individual differences in neural activity in this ROI compared with elsewhere in the brain.

Duncan and Owen (2000) recorded neural activity with positron emission tomography (PET) while 13 young adults performed two pairs of tasks, one spatial pair and one verbal pair. Within each pair, one of the tasks had a higher *g*-loading than the other (spatial: .59 versus .37, verbal: .55 versus .41). The dorsolateral PFC was the only brain area in which activity was greater in the higher-*g* than in the lower-*g* version of *both* tasks. This conjunction criterion eliminated areas of activity specific to particular stimulus and response types. Neither of these two studies agreed completely with the Gray et al. (2003) findings, but each had a smaller sample size than Gray et al., and the lateral PFC and posterior parietal cortex were each strongly implicated in two out of the three studies.

Several other small studies relating neural activity to individual differences in intelligence have recently been reported. In a sample of 19 adults, Horn et al. (2003) measured IQ using the National Adult Reading Test (NART) and neural activity using fMRI during a response-inhibition task, which demands cognitive control. NART predicted activation in a left lateral frontal area, as well as a precentral gyrus region on the same side. Geake and Hansen (2005) had 12 subjects perform a "fluid analogy" task involving nonsense letter strings during fMRI, and found that a measure of verbal intelligence predicted task-specific activation in two left lateral frontal areas. Despite possibly being weighted towards crystallised rather than fluid *g*, the results of these two studies are broadly similar to those of Gray et al. (2003). Haier, White, and Akire (2003) took a different tack from other studies by measuring *g* with RAPM and correlating it with PET activity while the 22 subjects simply watched videos, without performing any task. In contrast with the results discussed so far, this study's strongest finding was a difference in activation between high- and low-*g* subjects in an occipital-temporal region, likely involved in object recognition.

The broad pattern that emerges from these studies of the functional architecture of *g* is in line with the studies of regional grey matter volume: The prefrontal cortex is the most critical node in a network that implements working memory and cognitive control, which are intimately related to each other and to fluid intelligence (Kane & Engle, 2002). However, there is heterogeneity of *g*-related function in the frontal lobe, with the lateral frontal cortex appearing more closely

related to individual differences than is the medial frontal or anterior cingulate cortex. The best evidence for this PFC-*g* relationship comes from the mediator analyses reported by Gray et al. (2003): as a rule, such analyses provide a stronger understanding of the neural mechanisms of *g* because they can reveal those mechanisms that account for the relationship between *g* and specific aspects of cognitive task performance, such as cognitive control. The evidence for posterior parietal cortex association with *g* comes from Gray et al. and from Lee et al. (2005), especially the correlated vectors analysis performed in the latter study. Interestingly, the parietal region does not show as strong a volumetric relationship to *g* as does the frontal cortex; perhaps variability in parietal function does not depend on its size, whereas frontal function increases with size. Future studies of the functional architecture of *g* should explore these frontal and parietal regions, as well as the thalamus, basal ganglia, and cerebellum, using multivariate methods such as mediation and correlated vectors analyses.[9]

Learning ability and "neural plasticity"

The possibility that general intelligence results from variation in the ability to learn new skills and facts has been raised repeatedly, from Spearman (1927) to Garlick (2002, 2003). Garlick offers "neural plasticity," measured by a learning rate value in a model neural network, as a single "golden parameter" (Thomas & Karmiloff-Smith, 2003) to explain *g*. In support of this hypothesis, he demonstrates that simple neural networks, using error-feedback learning rules, reach asymptotic performance with less training when their learning rates are higher. Garlick's learning rate parameter would seem to correspond most closely to the speed of acquisition of simple associations, or to the speed of conditioning. The idea that *g* reflects learning ability is entirely reasonable (Mackintosh, 1998) and accords well with common sense, but learning ability is conspicuously absent from Table 19.5. One reason is that whereas the ability to learn complex material invokes a variety of cognitive abilities, and does correlate with *g* (Jensen, 1998a), it is not easy reliably to measure elementary parameters of learning, such as acquisition rates or conditionability, that might underlie or explain individual differences in intelligence. This difficulty arises because measures of change, difference, or slope are inherently less reliable than measures of absolute performance level (Jensen, 1998b). For example, the reliability of a difference score depends on the reliabilities of two separate measures, and subtracting the two measures essentially sums the "noise" associated with each. Thus, IQ may appear to correlate poorly with a measure of learning simply due to poor reliability. Future research on learning and *g* might profit from developing reliable and valid ways to measure an individual subject's learning rate.

Garlick's specific proposal is problematic for at least two reasons. First, as the above discussion implies, there is little direct evidence that IQ or *g* predicts performance on elementary learning tasks. Studies of implicit learning, which is an unconscious, associative process, have demonstrated only modest IQ correlations (e.g., $r = .25$ in Reber, Walkenfeld, & Hernstadt, 1991; $r = .05$ in Feldman, Kerr, & Streissguth, 1995; and $r = .12$ in McGeorge, Crawford, & Kelly, 1997). Second, Garlick's neural models confirm nothing more than a tautology: that for some tasks, increasing the learning rate leads to faster learning. This fails to account for situations in which learning is too rapid and results in overfitting (learning associations that are too specific to the training examples provided, and thus generalise poorly to novel situations), or in a failure of the model to reach a stable solution. Learning ability is undoubtedly related to intelligence, but undoubtedly not in such a simplistic way.

Overview and Future Directions

Across the wide variety of different measures reviewed here, a remarkably consistent result holds: virtually all of the cognitive and neurobiological variables correlate with IQ in the range of $r = .30$ to .50. This implies that both of the proposed accounts of the mechanistic basis of the Law of General Intelligence are correct, as the measures related to overall neural efficiency (e.g., gross brain volume, response time) and the measures of common resources or control processes (e.g., frontal lobe volume, working memory) are equally predictive of *g*. As a rule, none of the measures in Table 19.5 is able to go far beyond the .50 threshold, and some that come close (e.g., fMRI and DTI measures) come from regions of interest in the brain that are selected post-hoc, and thus may represent overestimates of correlations that would be found with prospectively chosen ROIs.

One's interpretation of this general pattern may depend on one's prior beliefs about how strong correlations "should be" to be taken seriously. Some might argue that doing complex medical scans, at several hundred dollars per subject, or behaviourally testing a sample of several hundred individuals, and explaining "only 9 to 25%" of the variance in IQ is an unimpressive feat. But if *g* were a simple, linear product of a simple, obvious biological variable, that variable would probably have been identified already, and the Law of General Intelligence would be much less interesting than it actually is.

While some of the correlations reported here are based on meta-analyses of numerous studies, others need further replication and generalisation. Establishing firm empirical bases for the roles of white-matter efficiency and region-specific brain structure and function are important goals for further research, as are expanding the study of *g* to neural features such as cortical thickness and shape. In the remainder of this section I will propose three other critical questions regarding the mechanisms of *g*, and discuss possible means of answering them.

Mechanisms of g *in other species*

First, as the Law of General Intelligence appears to apply to other species as well as it does to humans, its corollary on information processing efficiency should likewise be species-general. There are some indications from the limited literature on animal *g* that this is the case. The relationship between *g* and working memory is observed in mice (Kolata et al., 2005), and frontal cortex volume predicts performance of working memory and executive function tasks in dogs (Tapp et al., 2004). As Thomas and Karmiloff-Smith (2003) note, novelty-preference in human infants predicts higher intelligence at later ages. Likewise, across at least two studies (Matzel et al., 2003; Kolata et al., 2005), the propensity of mice to explore in an open field is correlated significantly with performance on multiple cognitive tasks. Anderson (1993) found that in a sample of 20 Long-Evans rats, brain volume correlated significantly with the general factor, derived from a battery of four measures designed for high *g*-loading.[10] This battery included a novelty-preference measure, which loaded .43 on the *g* factor.

Future studies of *g* in animals, as proposed earlier, should incorporate biological measures whenever possible; given the availability of MRI and PET devices designed for mammals, it is possible to obtain virtually the same range of neurobiological assays that can be studied in humans, as well as additional measures that cannot be performed on humans. For example,

Anderson (1995) observed significant variability across individual Long-Evans rats in the degree of dendritic arborization, but did not find differences in this measure between small groups of high-*g* versus low-*g* animals. In principle, such micro-anatomical features and cellular mechanisms, such as firing rate and long-term potentiation, could be measured in individual animals and correlated with differences in cognitive ability, affording examination of the mechanisms of *g* at a level of detail that is difficult to reach in human studies.

Discovering new mechanisms of g

Second, as illustrated by the unique possibilities of animal studies, we must continue to seek new mechanisms that could underlie *g*. New technologies and discoveries in cognitive neuroscience may come with obvious applications to understanding individual differences—but researchers interested in individual differences must monitor these developments, because most cognitive neuroscientists and neuroimaging specialists are not interested in individual differences. But instead of merely waiting for new developments in other fields, students of human intelligence might use heuristic strategies for identifying factors likely to covary with *g*. For example, cognitive ability, especially fluid intelligence, tends to decline with age. There is a burgeoning literature on age-associated changes in the brain, and in specific cognitive processes. We should ask which of these specific brain changes parallel those in general cognitive ability. Neurone number decreases by approximately 10% from age 20 to 90 (Pakkenberg & Gundersen, 1997), as does the number of glial cells (Pakkenberg et al., 2003), but total myelinated fibre length decreases by 40 to 50% during ageing (Marner et al., 2003). These findings are consistent with the known association of brain volume and IQ, and point to white matter factors as potentially even more important, given their greater sensitivity to ageing.

As well as asking how the brain changes with age, one could ask how the human brain differs from that of other species. In human studies, brain volume is correlated with IQ, with or without correcting for individual differences in body size. In comparative studies of brain evolution, however, the large differences in body size among species must be taken into account. Brain and body size tend to scale together within a lineage, so that species in which the brain is larger than "expected" given the body size can be identified as outliers that have developed unusually large cognitive capacity. Humans rank highest in this measure of "encephalization quotient." However, some species have larger brains than humans in terms of absolute volume, yet do not appear to have greater cognitive abilities, to the extent that species can be compared in "intelligence." Whales, bottlenose dolphins, and African elephants have brains that are at least as large as the human brain, but the human brain probably has slightly more cortical neurones (Roth & Dicke, 2005). However, neurone count is not the only difference between the human and other large brains: As a rule, white matter volume scales up faster than grey matter as total brain size increases (Bush & Allman, 2003). Axons are thicker in primates than in cetaceans and elephants, resulting in greater conduction velocity, and distances are shorter (due to the packing of more neurones into a smaller volume), resulting in more efficient communication and synchronisation between computational modules (Roth & Dicke, 2005). Thus, evidence from brain evolution and brain ageing converge to highlight white matter as a potentially crucial source of individual differences in intelligence. Further comparative research combining behavioural measures of processing speed and histological measures of white matter structure may shed light on these relationships.

Not all parts of the brain have evolved in parallel. In particular, in primate evolution, the cortex has grown more rapidly than subcortical structures, and the frontal cortex has grown more rapidly than the rest of the cortex (Bush & Allman, 2004; see also Schoenemann et al., 2005). One can also ask which new features of the brain evolved most recently, and could still vary widely within the human population. Allman and colleagues (Allman, Hakeem, & Watson, 2002; Allman et al., 2005) have proposed that a brain region (Brodmann area 10) and a cell type (known as "spindle neurones" or "Von Economo neurones")—found only in great apes and humans—may be associated with cognitive capacities in which humans excel, such as self-control.[11] Area 10 is at the frontal pole, and Von Economo neurones are found in the ACC and fronto-insular cortex, all in or near regions of the frontal lobe associated with intelligence. Area 10 is at least twice as large in humans (as a fraction of brain size) as in apes, and Von Economo neurones are about 25 times more numerous in humans than in apes. Studies of ageing again converge nicely with the general evolutionary finding: The frontal cortex declines in size with age faster than any other cortical region (Allen et al., 2005, found that age explained 37% of the variance in frontal lobe grey matter volume, compared with 32%, 22%, and 8% for the temporal, parietal, and occipital lobes).

Further application of the ageing and evolution heuristics may point to factors other than white matter and the frontal cortex, and there are doubtless other useful heuristics that may be used to search for novel mechanisms of general intelligence. Genomic investigations may prove especially fruitful in this regard (Gilbert, Dobyns, & Lahn, 2005).[12]

Developing statistical and computational models of g

The most critical question about all the current (and future) studies that find "moderate" correlations of $r = .30$ to .50 may be whether they are really all rediscovering the same correlation, or whether they are identifying substantially independent contributors to variation in cognitive ability. That is, does having a larger brain *and* more efficient white matter yield higher intelligence than just having one or the other? If so, what are the independent contributions of these two variables, and do they interact, or are they merely additive? The same can be asked of response time, working memory capacity, cognitive control, and all the cognitive and neurobiological factors associated with *g*. And exactly *how* do these interact?

The answers to these questions can only come from developing detailed models of general intelligence (Gray & Thompson, 2004). These must be of two types: statistical and computational. A statistical model would specify the relationships *among* the many cognitive and biological factors associated with *g*. Such a model cannot be constructed from data in published studies, since these almost always evaluate only the relationship between a *single* measure and *g*. There are scattered recent examples of studies that relate IQ to multiple covariates (e.g., Deary et al., 2006; Gray et al., 2003; Schretlen et al., 2000), sometimes in genetically-informative designs (e.g., Hansell et al., 2005), but these studies rarely incorporate more than one measure of brain function. [A notable exception to this rule is the work of Walhovd et al., 2005, who showed that cortical volume and a measure of brain electrical activity were additive in explaining variance in performance IQ.]

What is needed is a single study in which the same sample of subjects receives a comprehensive battery of assessments including gold-standard IQ tests (e.g., the WAIS-III, Raven's APM),

cognitive measures (e.g., response time, working memory, inspection time, novelty preference, inhibition, and implicit learning), and a wide-ranging neurofunctional examination comprising at least high-resolution structural MRI, fMRI during performance of cognitive tasks with varying *g*-loadings, diffusion MRI, and MR spectroscopy, as well as EEG measures of the latency of various elementary processes. The best practices currently followed in each of these specific research areas should be adopted, beginning with the collection of a participant sample that is demographically representative of a large population, such as a medium-size city and its environs. Multivariate analyses such as regression, structural equation modeling, mediator and path analysis, and even factor analysis of the biological measures would be applied. With sufficient funding, subjects could be followed over time so that changes in biological and cognitive factors could be related to changes in intelligence, as well as to life outcomes. On the model of the National Longitudinal Survey of Youth (NLSY), that has been mined for numerous studies on intelligence (e.g., Herrnstein & Murray, 1994; Benjamin, Brown, & Shapiro, 2006), such a study would generate a unique resource for current and future investigators, yielding returns far beyond the required initial investment.

A statistical model of the factors that correlate with individual differences in cognitive ability will not provide a complete picture of the nature of *g*. The crucial missing element is a computational model—a simulation of interacting neural mechanisms that is sufficiently complex to allow all of the relevant factors to be specified and manipulated (see Newell, 1990, for discussion of the value of computational models in psychology). The statistical model, as well as hierarchical factor analyses of cognitive tasks, would serve as constraints on the class of acceptable models. A diverse set of cognitive tasks would be chosen such that they could be implemented within the model and could be administered in a battery to human subjects so as to measure the task *g*-loadings. Parameters of the model would then be manipulated to simulate individual differences in *g*-related factors, such as the size of different brain regions, or the speed of information processing, or the efficiency of communication between processes. To the extent the model is valid, varying the parameter should produce an expected change in performance of the model on the simulated tasks. Critically, performance changes on specific tasks should be related to how *g*-loaded the tasks are. For example, if the model included a parameter for the size of the frontal cortex, which correlates with IQ (Thompson et al., 2001), then increasing this parameter—within some reasonable range—should improve performance on the simulated tasks, with the greater improvements on highly *g*-loaded tasks, like working memory, than on simpler tasks like perceptual completion.

Several existing frameworks could be used to model individual differences in cognitive ability, including ACT-R (Anderson et al., 2004; Daily, Lovett, & Reder, 2001), but neural network models may be the best choice. These are abstract simulations of networks of simple processing units reminiscent of neurones: many such interconnected units all operate in parallel, computing simple transformations of input to output and communicating signals of information to one another. A further advantage of these models is the correspondence between their tunable parameters and the factors known to correlate with *g*. O'Reilly and Munakata (2000) describe a neural network framework in which a wide variety of tasks, of varying levels of complexity, have been implemented. **Figure 19.3** shows a model developed using this framework by O'Reilly et al. (2002) to simulate the intradimensional/ extradimensional (ID/ED) set-shifting task, which is sensitive to frontal lobe damage (and can be learned by animals). The task model includes, in addition to representations of the input and output, four separate modules of processing units, each corresponding to a different anatomical region: orbital frontal cortex,

lateral frontal cortex, the ventral tegmental area, and a generic "posterior cortex." Unidirectional and bidirectional connections within and between some of these modules are also implemented. The details of the model implementation are not essential here; what is more important is the fact that, in principle, the size and processing efficiency of each module, as well as the quality of connections among the modules, can all be varied. Modules can also, of course, be added or removed to simulate different strategies, or combinations of processes, that might be used to complete a task.

A simple qualitative analysis suggests that neural network models can account for some of the major findings regarding *g*. For example, consider three of the tasks included in the battery whose data are shown in Table 19.1b: 3-back working memory, categorical spatial encoding, and coordinate spatial encoding. The latter two tasks, which involve deciding whether a dot is above or below a line (categorical encoding), or whether it is within a certain precise distance from the line (coordinate encoding), had the lowest *g*-loadings of the battery (.20 and .25). The 3-back working memory task (which was essentially the same task used by Gray et al., 2003) had the second highest *g*-loading (.46); the first principal component accounted for over three times as much variance in 3-back performance as it did in either spatial encoding task. Kosslyn et al. (1992) and Baker, Chabris, and Kosslyn (1999) implemented network simulations of the spatial encoding tasks, and were able to account for several aspects of human performance with a simple feedforward network consisting of input, output, and two "hidden" layers. O'Reilly and Munakata (2000, Ch. 9) implemented a simplified model of working memory involving four neural modules in addition to input and output, a level of complexity comparable to that of the ID/ED model in Figure 19.3 (but simpler than would be required for a full-scale 3-back task). As one would expect, simulating the more highly *g*-loaded task requires a more complex model; moreover, if all three tasks were implemented within a sufficiently sophisticated model—with "posterior cortex" corresponding to the hidden layers in the original models of the spatial tasks—there would be more potential sites of damage that would impair performance of the 3-back than the spatial encoding tasks. This is precisely what was found in the lesion studies of rat *g* that were mentioned earlier (Crinella & Yu, 1995; Thompson et al., 1990): the more highly *g*-loaded a task, the more anatomical locations to which damage impaired the task. And in humans, Colom, Jung, and Haier (2006) report that the *g*-loading of a WAIS-R subtest predicts the number of areas in the brain where grey matter concentration correlates with test performance.

More complex models than that shown in Figure 19.3, including well over 200 processing units, can be readily simulated with currently-available computational resources (e.g., O'Reilly & Frank, in press). Similar models have been used to simulate the effects of Parkinson's disease on learning (Frank, Seeberger, & O'Reilly, 2004), self-organisation of task-specific rules in the frontal cortex (Rougier et al., 2005), the interactions of the hippocampus and cortex in recognition memory (Norman & O'Reilly, 2003), and the relationship between behavioural and fMRI data (e.g., Herd, Banich, & O'Reilly, 2006). The discovery of parameters within these models that explain individual differences may suggest novel experiments in human subjects, including neuroimaging studies to test specific hypotheses about the activation of systems during *g*-related tasks, and the relationship between neural activity, *g*, and task performance (that is, the models may generate predictions that can be tested by studies designed similarly to Gray et al., 2003). Finally, the learning process in such a system can itself be modified, to properly test the hypothesis that differences in learning can account for differences in intelligence (Garlick, 2002).

Conclusion

General intelligence is a property of the web of positive correlations among performance scores on cognitive tasks. The general factor that invariably emerges—in humans and possibly other species—is itself embedded in a larger web of correlations with basic properties of information processing (speed, working memory, control, learning) and of the brain (total and regional volume, white matter integrity, neurochemical concentrations). Surprisingly, these latter correlations are all within a relatively narrow range, with no single variable explaining more than 25% of the variance in intelligence. Nonetheless, they establish a biological basis for *g* that is firmer than that of any other human psychological trait. The challenges for future research on the Law of General Intelligence are to establish its species-universality, to discover its cognitive and neurobiological mechanisms, to quantify the relative importance of those different mechanisms, and to model the mechanisms underlying *g* with biologically plausible computer simulations.

As Jensen (1998a) pointed out, there is no real conflict between the notion of the mind as a collection of separate processes or modules, and the notion of correlated individual differences in the efficiency of cognition. Evolution has provided us all with bodies constructed according to the same genetic design: we all have two arms, two legs, one liver, one heart, and so on, but some of us are faster, stronger, and healthier than others. The Law of General Intelligence does not stand in contradiction to the hypothesis of a mind that has evolved via adaptation to solve specific problems, any more than a "law of general athletic prowess"—that people who perform well in one sport will tend to perform well in others—clashes with the modular construction of human musculature. Biological studies indicate that individual genes and molecules have functions in multiple organ systems of the body, so it is natural to believe that within the brain, mechanisms will have considerable generality and overlap—it would be difficult for a biological system to develop for one specific purpose, except by piggybacking on other existing functions and using genes and pathways already established (for example, the Notch signaling pathway is involved in both cell differentiation during development, and memory formation during adulthood; Costa, Drew, & Silva, 2005). Given this principle of the re-use of existing mechanisms for new functions, it is inevitable that variation in the existing mechanism will transfer to variation in the new one, yielding correlated individual differences in mental ability. This outcome is in clear opposition to extreme notions of domain-specificity that assert each module's complete independence from other cognitive and neural mechanisms.

Although this chapter has made the case for a Law of General Intelligence, it will end with a caution against putting intelligence, IQ, or *g* on a pedestal above the many other dimensions along which individual human beings differ, such as creativity, personality, confidence, patience, ethicality, and the like. Intelligence may be the single best predictor of many life outcomes, but those of us who study intelligence should be especially vigilant against the tendency to associate it with moral worth or to exalt it as the only important human trait. Rather than rename other mental abilities like social skill as "intelligences" and pit them against general intelligence (Gardner, 1993; Goleman, 1995), we should study each for its own value in understanding the diversity of human behaviour.

Finally, research on individual differences in cognition is often decried because of the belief that such work inevitably implicates genetic mechanisms, and thus it will further the agenda of those who seek to discriminate on the basis of ethnicity (Chabris et al., 1998). But a true understanding of differences among *individuals* is actually inimical to a racist agenda: People must be

evaluated, rewarded, punished, and treated according to their own personal actions and abilities, not to those of whatever groups they have involuntarily joined. More information about how people differ in intelligence, and why, can only help to replace false beliefs with knowledge. The right response to the overuse of stereotypes is not to pretend that all people are the same, but to discover precisely how each person is truly unique.

Endnotes

[1] There are many methods of factor analysis that can be used to discover the architecture of a correlation matrix of mental tests. Here I use only unrotated principal components analysis (PCA) because it is the simplest, and involves no decision-making on the part of the analyst. The general factor extracted as the first principal component is essentially the same no matter what analytic method is used (Ree and Earles, 1991).

[2] These measures are: Line Drawing Memory, Line Drawing Time, Reorganisation Probe, Nonreorganisation Probe, and Form Board (see Kosslyn et al., 1984, for details).

[3] This effect is reminiscent of Spearman's (1927) finding that the average inter-task correlation is larger in low-scoring than in high-scoring groups of human subjects.

[4] In addition to the batteries of tasks tested on rhesus monkeys mentioned earlier, a version of the CANTAB neuropsychological test battery has been developed with eight tests suitable for rhesus (Weed et al., 1999) and perhaps marmosets. Later studies of similar tasks have shown considerable individual differences among monkeys (Taffe et al., 2004), but no factor analyses of inter-task correlations with this battery have been published.

[5] Note that other biological differences between people, such as genotypes, nutrition, general health, hormones, and other physiological biomarkers are not considered here, because their effects on intelligence differences must in some way be mediated by differences in brain structure or function.

[6] In discussing variables that are correlated with intelligence in this chapter, I use "*g*," "IQ," "cognitive ability," and similar terms interchangeably. However, this does not mean that they are synonymous. Bartholomew (2004) points out that measures of *g* based on factor analysis are normally superior to IQ scores, which are not necessarily constructed to optimally measure the general factor. Also, in some cases correlations with second-level factors such as general *fluid* intelligence, or general *crystallised* intelligence, or performance IQ (reflecting the nonverbal abilities measured by an IQ test) will be specified rather than correlations with measures of the *g*-factor itself.

[7] For the purposes of this chapter I will consider "executive function" and "cognitive control" to be synonymous, but in the broader literature they are not always taken to mean the same thing. Executive function may be viewed as a large-scale category of neuropsychological functions, which itself can be fractionated into subcomponents (Miyake et al., 2000), each of which may correlate more or less with general intelligence. Indeed, Friedman et al. (in press) report that measures of the ability to update working memory correlate significantly with IQ, while measures of set-shifting and inhibitory abilities do not.

[8] This study, and the other fMRI studies reviewed in this section, report that neural activity is positively correlated with *g*. This appears to contradict the findings of several studies that measured neural activity in terms of cerebral glucose metabolism with PET, and consistently found negative correlations with *g* (for a review, see Haier, 1993). Gray et al. (2003) and others actually show that *differences* in activity between difficult and easier task conditions correlate

positively with *g*, whereas the PET studies tend to show that the *absolute* glucose metabolic rate correlates negatively with *g*. Larson et al. (1995) used PET to compare glucose metabolism between difficult and easy versions of a digit span test customised to the ability level of each of 28 subjects. High-RAPM scorers showed higher brain-wide activity in the difficult condition than in the easy condition, but low-RAPM scorers showed *lower* activity when the task was more difficult—analogous to the pattern observed by Gray et al. (Figure 19.2).

[9] Studies of individual differences in neural activity to date have focused on variability in the *magnitude* of activation within regions, but it is also possible to explore the *distribution* of activation across the brain. For example, variation in locations, in correlations between locations, and in other properties (e.g., Glabus et al., 2003).

[10] Shirley (1928) reported that "the relationship between maze learning and brain weight, in so far as one exists at all, is, then, the heavier his brain, the more the rat blunders" (p. 194). One imagines a rat with an oversized, overweight head causing it to stumble around a maze, bumping off walls as though drunk. As with negative studies of rat *g* around the same time, the cognitive measures were insufficiently diverse, and the genetic history of the animals insufficiently specified, to allow any conclusions to be drawn from this work.

[11] We may not think of ourselves as creatures with great self-control, but compared to some other primates, humans are extremely patient, as are adults compared to children. Cotton-top tamarin monkeys, with extremely small frontal lobes, apparently cannot learn to wait more than about eight seconds for a food reward, even if doing so would triple the reward's size (Stevens, Hallinan, & Hauser, 2005).

[12] According to one research group, genes that are found to have evolved unusually rapidly in the primate lineage, or to show evidence of ongoing selection in the human population, are plausible candidates to explain individual differences in human phenotypes. Dorus et al. (2004) argue that genes involved in nervous system development are undergoing extra-rapid evolution (compared to genes for neural transmission, and to genes for cellular "housekeeping" processes), and Mekel-Bobrov et al. (2005) and Evans et al. (2005) claim that two of these genes, whose mutations cause microcephaly, are still undergoing selection.

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Table 19.1. Correlation matrix of scores, with loadings on the first principal component (1st PC), from two batteries of cognitive tests administered to human adults. *(a)* Data from a population sample of 365 Scottish subjects completing all 11 subtests of the Wechsler Adult Intelligence Scale-Revised (principal component analysis calculated, and correlations redisplayed, from data presented in Deary, 2000, p. 7). The 1st PC accounts for 48% of the variance. *(b)* Data from 111 Boston-area subjects (54 males, 57 females; age range 18 to 60; approximately one-half students) completing seven timed cognitive tasks as part of a larger study. All tasks except Raven's APM and verbal fluency were conducted by computer. The 1st PC accounts for 36% of the variance. *Notes:* For all tasks, higher scores correspond to better performance. Correlations are uncorrected for attenuation in range. Those in boldface are significant at $p < .05$ or better.

(a)	V	S	I	C	PA	BD	A	PC	DSp	OA	1st PC
Vocabulary											.83
Similarities	**.67**										.80
Information	**.72**	**.59**									.80
Comprehension	**.70**	**.58**	**.59**								.75
Picture arrangement	**.51**	**.53**	**.50**	**.42**							.70
Block design	**.45**	**.46**	**.45**	**.39**	**.43**						.70
Arithmetic	**.48**	**.43**	**.55**	**.45**	**.41**	**.44**					.68
Picture completion	**.49**	**.52**	**.52**	**.46**	**.48**	**.45**	**.30**				.68
Digit span	**.46**	**.40**	**.36**	**.36**	**.31**	**.32**	**.47**	**.23**			.56
Object assembly	**.32**	**.40**	**.32**	**.29**	**.36**	**.58**	**.33**	**.41**	**.14**		.56
Digit symbol	**.32**	**.33**	**.26**	**.30**	**.28**	**.36**	**.28**	**.26**	**.27**	**.25**	.48

(b)	Raven's	WM	Verbal	RT	Rotation	Coord	1st PC
Raven's Matrices (12-item APM)							.50
Working Memory (3-back d')	**.39**						.46
Verbal Fluency	**.36**	**.48**					.42
Response Time	**.41**	**.28**	**.41**				.39
Mental Rotation	**.41**	**.29**	.15	**.21**			.34
Coordinate Spatial Encoding	**.32**	**.30**	.07	–.02	.04		.25
Categorical Spatial Encoding	**.21**	.12	–.02	.13	.16	**.21**	.20

Table 19.2. Correlation matrix of scores, with loadings on the first principal component (1st PC) from 84 outbred heterogeneous stock mice (42 males, 42 females) completing a battery of six cognitive tests (redisplayed from Study 1 of Galsworthy et al., 2005). For all tests, higher scores correspond to better performance. The 1st PC accounts for 35% of the variance. Correlations are uncorrected for attenuation in range. Those in boldface are significant at $p < .05$ or better.

	BP	HWM(l)	PP	HWM(e)	MWML	1st PC
Burrowing puzzle (latency)						.66
Hebb-Williams maze (latency)	.21					.65
Plug puzzle (latency)	**.52**	**.30**				.62
Hebb-Williams maze (errors)	.12	**.32**	.13			.60
Morris water maze learning (latency)	**.25**	**.39**	.05	.18		.56
T-maze (errors)	.10	**.22**	.06	.17	.14	.40

Table 19.3. Studies of general cognitive ability in nonhuman species. Studies were only included if there were at least two published studies for a particular species, if they presented quantitative performance data (on at least three tasks) in correlation matrix form suitable for factor analysis, and if they were known not to have used inbred or mutant strains. Measures of performance on problem-solving tasks were included; measures of global activity, preference, "personality," and the like were excluded (see notes). Analysis is based on product-moment correlations (*r*) unless otherwise noted; mean *r* was calculated using z_r transformation. Columns indicate the number of subjects in the study, the number of measures included in the analysis, the number of positive correlations and total number of correlations, the mean *r* among measures, and the percentage of variance accounted for by the first principal component (numbers in parentheses indicate studies in which this was *less* than twice the variance accounted for by the second principal component). The final three entries summarise the human data from Table 19.1 and Table 19.4b, for comparison.

Reference	Subjects	Measures	+ out of total correlations	Mean *r*	1st PC % variance
Mice					
Bagg (1920) *a*	71	8	28/28	.58	.61
Locurto & Scanlon (1998) *b*					
Sample A (F_2 cross)	34				
Speed		6	15/15	.51	.58
Accuracy		4	6/6	.26	(.44)
Sample B (CD-1 outbred)	41				
Speed		6	15/15	.47	.55
Accuracy		4	6/6	.31	.48
Galsworthy et al. (2002)	40	8	26/28	.20	(.31)
Locurto et al. (2003) *c*	60	6	11/15	.13	(.27)
Matzel et al. (2003)	56	5	10/10	.22	.38
Galsworthy et al. (2005)					
Study 1	84	6	15/15	.22	(.35)
Study 2	167	11	41/55	.09	(.18)
Kolata et al. (2005) *d*	21	7	21/21	.35	.45
Locurto et al. (2005) *c*					
Experiment 1	47	5	4/10	–.03	(.28)
Experiment 2	51	5	9/10	.15	(.34)
Dogs					
Anastasi et al. (1955) *e*	73	10	30/45	.10	(.26)
Nippak & Milgram (2005) *f*	13	3	3/3	.89	.92
Cats					
Warren (1961) *g*	21	6	14/15	.50	.57
Livesey (1970) *g*	8	4	5/6	.40	.58
Rhesus monkeys					
Paule (1990)	44–69	5	8/10	.16	(.36)
Herndon et al. (1997)					
Analysis 1	30	6	n/a	n/a	.48
Analysis 2 *h*	53	3	n/a	n/a	.62
Humans					
WAIS-R data (Table 19.1a)	365	11	55/55	.43	.48
Cognitive test data (Table 19.1b)	111	7	19/21	.24	.36
Operant battery data (Table 19.4b)	85	5	10/10	.24	.42

Notes: (a) From data presented by Galsworthy et al. (2005). (b) Activity measures excluded. (c) Activity, Stress, and Anxiety measures excluded. (d) Open-field measure excluded; working-memory measures included. (e) Subjects were from six different breeds; leash control, motor skills, and obedience measures excluded. (f) All subjects were beagles; 30-second delay version of the delayed non-match to sample task was used; all measures were speed. (g) Based on rank correlations. (h) Subjects were a superset of those in Analysis 1, adding individuals who only completed three of the six total tasks.

Table 19.4. Correlation matrices of scores, with loadings on the first principal component (1st PC), on a battery of five operant tasks designed for toxicology studies with monkeys. *(a)* Data from 69 male rhesus monkeys (aged 2–3 years) completing the battery over the course of one year (redisplayed from Paule, 1990). For all tests, higher scores correspond to better performance. The 1st PC accounts for 35% of the variance. Correlations are uncorrected for attenuation in range. Those in boldface are significant at $p < .05$ or better (for some task pairs, only 44 or 64 subjects did both tasks). *(b)* Data from 85 preterm, low-birthweight human children tested on an analogue of the monkey battery at age 6.5 years (additional data provided by authors from Paule et al., 1999). An additional column shows the correlation of each test with full-scale IQ obtained at age 5 years with the Wechsler Preschool Primary Scale of Intelligence (WPSSI). For all tests, higher scores correspond to better performance. The 1st PC accounts for 42% of the variance. Correlations are uncorrected for attenuation in range. Those in boldface are significant at $p < .05$ or better.

(a)	PR	DMTS	TRD	CPR	1st PC
Progressive ratio					.75
Delayed match to sample	**.31**				.71
Temporal response differentiation	**.40**	.21			.64
Conditioned position responding	.18	**.36**	.14		.57
Incremental repeated acquisition	**–.25**	–.04	.02	.21	.56

(b)	IQ	PR	DMTS	TRD	CPR	1st PC
Progressive ratio	.08					.13
Delayed match to sample	**.41**	.01				.76
Temporal response differentiation	**.40**	.10	**.23**			.53
Conditioned position responding	**.48**	.02	**.54**	**.32**		.84
Incremental repeated acquisition	**.46**	.09	**.37**	.17	**.48**	.72

Table 19.5. Selected estimated simple correlations between full-scale IQ scores or other measures of general intelligence and possible causal factors.

Measure	Correlation (*r*) with IQ	Reference	Notes
Whole brain volume	.33	McDaniel (2005)	meta-analysis of 37 MRI studies, N=1530
Grey matter volume	.27	Gignac et al. (2003)	meta-analysis of 7 MRI studies, N=428
White matter volume	.31		
Frontal grey matter volume	.41	Thompson et al. (2001)	N=40 (20 twin pairs)
Response time (RT):		Deary et al. (2001)	N=900, population sample aged 54 to 58, modified Hick task
simple reaction time	–.31		
4-choice RT	–.49		
variability of RT	–.26		
number of 4-choice errors	.07		
Inspection time (IT)	–.51	Grudnik & Kranzler (2001)	meta-analysis of 92 studies, N=4197, attenuation correction (uncorrected *r* = –.30)
Nerve conduction velocity	.10	Reed et al. (2004)	N=387, P100 VEP latency, average over 3 stimulus conditions
White matter lesions	.09	Gunning-Dixon & Raz (2000)	meta-analysis of 11 studies (4 crystallised, 7 fluid intelligence)
White matter organization	.44	Schmithorst et al. (2005)	N=47, DTI of FA, average of 7 brain areas showing positive correlations
White matter integrity	.51	Jung et al. (2005)	N=27, proton MRS of NAA in occipital-parietal region
Working memory (WM):		Gray et al. (2003)	N=58, averaged across 3 trial types
accuracy in 3-back task	.34		
RT in 3-back task	.01		
Frontal activity during WM:		Gray et al. (2003)	N=48, fMRI signal, weighted average of 10 significant clusters
specific to control	.51		
sustained across tasks	–.11		

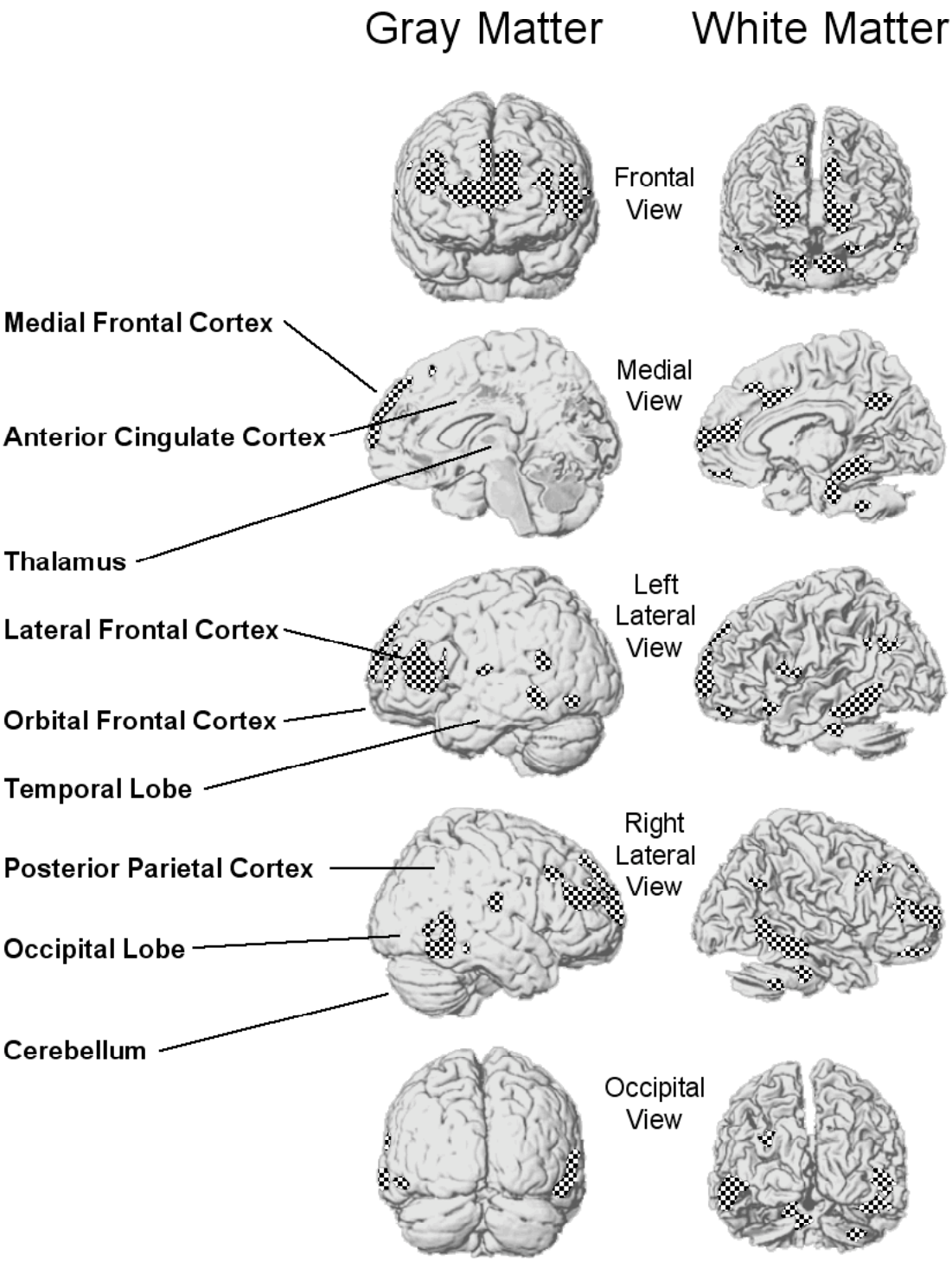

Figure 19.1. Maps of brain areas, shown by chequered regions, where tissue volume correlates with full-scale IQ, in each of two separate samples totaling 47 adults (Haier et al., 2004). Labels indicate regions associated with general intelligence in this and other studies discussed in the text.

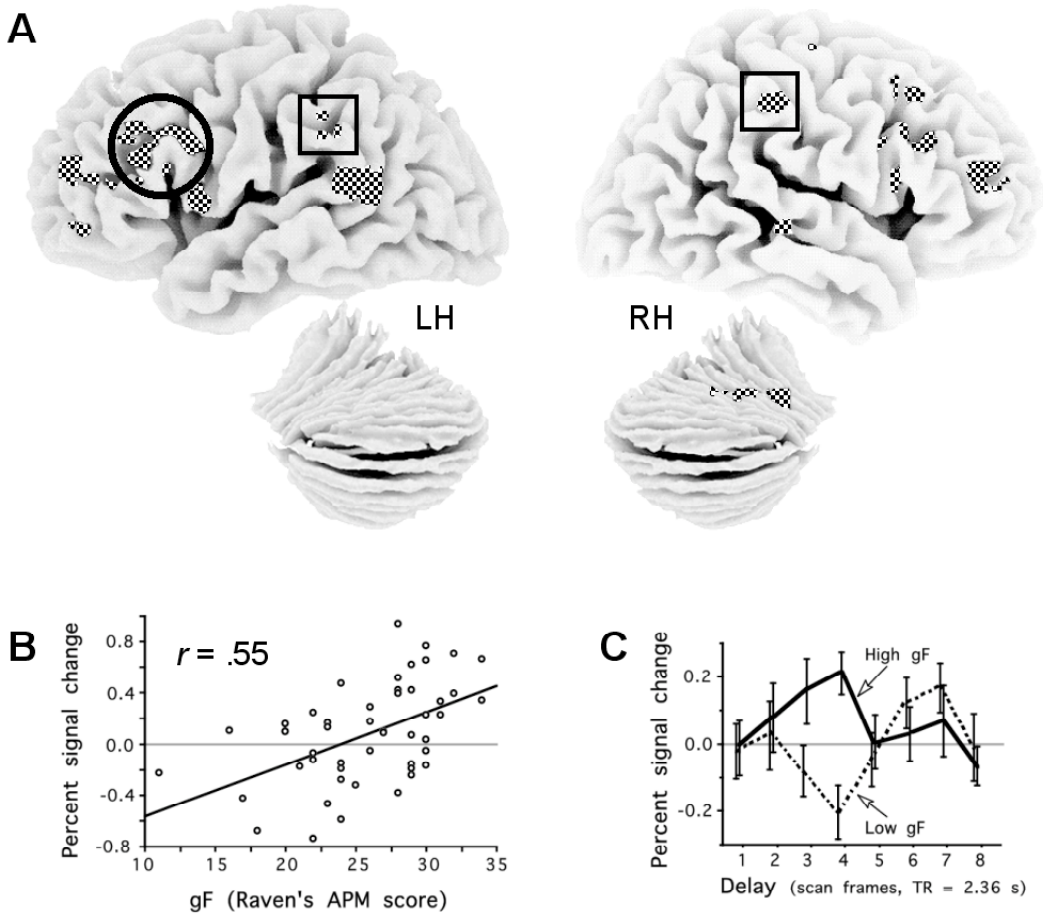

Figure 19.2. Results of an individual differences study of the neural mechanisms of general fluid intelligence (Gray et al., 2003). *(A)* Chequered areas indicate brain regions in which *gF*, measured by Raven's APM score, predicted neural activity on the high-interference lure trials of a 3-back working memory task. Lateral views of the cerebral cortex (top) and cerebellum (below) are shown for the left hemisphere (LH) and right hemisphere (RH). In addition to the regions shown here, *gF*-activity correlations were also observed in the left anterior cingulate cortex (not pictured). The three highlighted regions in the left frontal, left parietal, and right parietal cortex collectively mediated nearly all of the behavioural correlation between *gF* and 3-back lure trial accuracy. *(B)* Positive relationship between *gF* and neural activity (% signal change from baseline) in the circled region of the left lateral frontal cortex (lure trials). Note that sustained activity during the 3-back task (compared to periods of rest) was not significantly correlated with *gF* in this region. *(C)* Contrasting activation time courses of high-*gF* and low-*gF* groups (defined by a median split on RAPM score) during performance of lure trials.

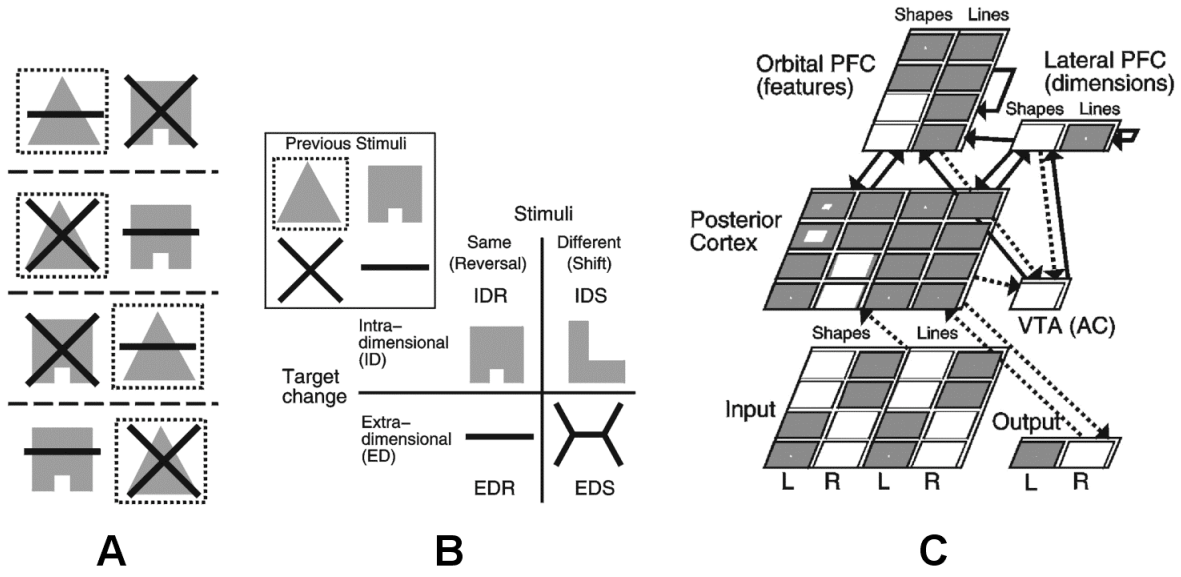

Figure 19.3. A biologically plausible model of the intradimensional/extradimensional set-shifting (ID/ED) task (reprinted from O'Reilly et al., 2002). This task is similar to the Wisconsin Card Sort Task in its sensitivity to frontal cortex damage, but it can be applied to animals as well as humans. *(A)* Four consecutive trials in which the correct response is "left" for the first two and "right" for the last two, because the grey shape dimension is selected and the triangle is the target shape. *(B)* At random intervals the decision rule is changed, and the subject will commit errors before adjusting. The change may be one of four types: (1) an intradimensional reversal to selection of the previously ignored stimulus within the same dimension (the other grey shape); (2) an extradimensional reversal to selection of a previously irrelevant stimulus within the other dimension (the black line figures); (3) an intradimensional shift to a new stimulus within the same dimension (a new grey shape); or (4) an extradimensional shift to a new stimulus within the other dimension (a new black line figure). *(C)* A neural network model of performance on the ID/ED task, incorporating specific computational roles and interconnections for the orbital and lateral prefrontal cortex (PFC), as well as the ventral tegmental area (VTA) and a generic posterior cortical area.