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The Parieto-Frontal Integration Theory (P-FIT) of intelligence: Converging neuroimaging evidence

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Abstract: "Is there a biology of intelligence which is characteristic of the normal human nervous system?" Here we review 37 modern neuroimaging studies in an attempt to address this question posed by Halstead (1947) as he and other icons of the last century endeavored to understand how brain and behavior are linked through the expression of intelligence and reason. Reviewing studies from functional (i.e., functional magnetic resonance imaging, positron emission tomography) and structural (i.e., magnetic resonance spectroscopy, diffusion tensor imaging, voxel-based morphometry) neuroimaging paradigms, we report a striking consensus suggesting that variations in a distributed network predict individual differences found on intelligence and reasoning tasks. We describe this network as the *Parieto-Frontal Integration Theory* (P-FIT). The P-FIT model includes, by Brodmann areas (BAs): the dorsolateral prefrontal cortex (BAs 6, 9, 10, 45, 46, 47), the inferior (BAs 39, 40) and superior (BA 7) parietal lobule, the anterior cingulate (BA 32), and regions within the temporal (BAs 21, 37) and occipital (BAs 18, 19) lobes. White matter regions (i.e., arcuate fasciculus) are also implicated. The P-FIT is examined in light of findings from human lesion studies, including missile wounds, frontal lobotomy/leukotomy, temporal lobectomy, and lesions resulting in damage to the language network (e.g., aphasia), as well as findings from imaging research identifying brain regions under significant genetic control. Overall, we conclude that modern neuroimaging techniques are beginning to articulate a biology of intelligence. We propose that the P-FIT provides a parsimonious account for many of the empirical observations, to date, which relate individual differences in intelligence test scores to variations in brain structure and function. Moreover, the model provides a framework for testing new hypotheses in future experimental designs.

Keywords: diffusion tensor imaging (DTI); functional magnetic resonance imaging (fMRI); *g*; genomics; intelligence; IQ; magnetic resonance spectroscopy (MRS); positron emission tomography (PET); reasoning; structural magnetic resonance imaging (sMRI); voxel-based morphometry (VBM)

> Is there a biology of intelligence which is characteristic of the normal human nervous system wherever it is found? Does it contribute to man's survival as an organism? Is it different in degree, in kind, or in both from that possessed by members of other surviving species? Is it unitary or comprised of multiple factors? More practically, can convenient indices be found which, like blood pressure, accurately reflect the normal and pathological range of variance for the individual? Is there a pathology of biological intelligence which is of significance to psychiatry and to our understanding of normal behavior?
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> — Ward Halstead (1947), *Brain and Intelligence*

1. Introduction

"Where in the brain is intelligence?" This question has vexed researchers for at least the last two centuries, as phrenological inquiries (Gall 1825) gradually gave way to eloquent studies of particular brain–behavior relationships characterized by the observations of Broca (1861) and Wernicke (1874), and the unfortunate case of Phineas Gage (Harlow 1848; 1868), to name a few iconic examples. Subsequently, two richly articulated schools of thought emerged regarding localization of higher cognitive function, including intelligence, within the brain: one implying that the brain works in harmony as a single entity (Flourens 1824; Jackson 1932; Lashley 1929), the other articulating discrete cortical regions underlying higher cognitive functions (Broca 1861; Gall 1825; Kleist 1934). Pavlov (1949) synthesized these previously discordant viewpoints, summarizing brain function as comprising distributed interactions between cortical regions united to perform a common cognitive task, a conceptualization that persists to the present day (Detterman 2000).

This iterative interplay of reductionism and a systems approach provides the conceptual framework that is the

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basis for most modern neuroimaging studies of intelligence and reasoning. Moreover, this approach expands on earlier studies of whole brain size, which have established the robust, if statistically modest, observation that larger brain size is related to higher intelligence (Jensen 1998). Most of our review is focused on fine-tuning this general observation by identifying the discrete brain regions that are particularly related to individual differences on measures of intelligence and reasoning within the human brain. First, however, we wish to provide a larger context by summarizing the evidence that bigger brains provide some species-general cognitive advantage.

2. Larger brains are "smarter" across species and across evolutionary time

Archeological and anthropological evidence has supported the notion that, within the genus *Homo*, evolutionary constraints have generally selected for larger brain size relative to body size over time (although see *Homo floresiensis*). Indeed, Charles Darwin writes in *The Descent of Man* that,

> As the various mental faculties gradually developed themselves the brain would almost certainly become larger. No one, I presume, doubts that the large proportion which the size of man's brain bears to his body, compared to the same proportion in the gorilla or orang, is closely connected with his higher mental powers. (Darwin 1871, p. 37)

Researchers have long attempted to study brain physiology and determine specific correlates of intelligence using technology available during their times. Earliest endeavors (Galton 1869) focused on brain size, crudely approximated by measures of head size. All modern studies but one (Tramo & Gazzaniga 1999) have found positive correlations between magnetic resonance imaging (MRI) measures of brain volume and intelligence. Indeed, a recent meta-analysis of some 37 neuroimaging studies (McDaniel 2005) demonstrates a small, yet consistent relationship between whole brain volume and psychometric measures of intelligence ($r = .33$). Moreover, the relationship between brain size and IQ appears to be rather equally distributed across tissue types, with unweighted mean correlation values of .31 for white matter volume and .27 for gray matter volume (Gignac et al. 2003).

This relationship between total brain volume and intelligence is compelling in light of the evolutionary record. Two candidate genes have been identified that appear to be important in the regulation of brain size, *microcephalin* and *ASPM* (Evans et al. 2005; Mekel-Bobrov et al. 2005). *Microcephalin* mutation, causing primary microcephaly (severe reduction in brain size, mental retardation, although preserved lobar structure), is found prominently within the germinal matrix of the developing forebrain (Jackson et al. 2002), the expression of which results in brain size comparable to early hominids (Wood & Collard 1999). A particular haplotype of the *microcephalin* locus (i.e., G37995C) was noticed to have a much higher frequency, the age of emergence estimated as being ~37,000 years ago (Evans et al. 2005). A homozygous null mutation of *ASPM* (i.e., A44871G and C45126A) hypothesized to regulate neural stem cell proliferation/differentiation also is associated with microcephaly; it was estimated by the same group of researchers to have emerged merely 5,800 years ago (Mekel-Bobrov et al. 2005). Thus, there exists tentative support linking discrete candidate genes, brain size, and the temporal development of cognitive skills associated with relatively modern (i.e., ~5,800–37,000 years ago) human endeavors over the course of evolutionary history.

Although humans classically have been considered to be the most intelligent species within the *scala naturae*, they do not possess the largest brain (e.g., sperm whale) or cortical volume (e.g., elephants, whales). What is unique to human brain structure is the relatively large number of cortical neurons (~11,000 million), and relatively high conduction velocity between those neurons (Roth & Dicke 2006). Hence, the general notion that "bigger is better" will certainly benefit from a more fine-grained regional analysis of brain–behavior relationships, as reviewed herein. Moreover, whole brain observations also overlook significant connectivity (Schmithorst et al. 2005) and biochemical (Rae et al. 1996) contributions within cerebral white matter that may critically constrain the development of intelligence across species and across evolutionary time. Furthermore, the prevailing lore is strongly prejudiced toward the relatively massive (when compared with other species) human frontal lobes as causally related to intelligence. Whereas early researchers found relatively larger frontal cortices in humans compared with other primates (Brodmann 1912), more contemporary research finds little evidence of proportional differences among primates when great apes are included in the sample (Semendeferi et al. 2002), except for Brodmann area (BA) 10, which is relatively larger in humans (Semendeferi et al. 2001). This same

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group has found that gyral white matter (white matter immediately underlying cortical gray matter) was larger than expected in humans in the frontal and temporal lobes (Schenker et al. 2005), potentially allowing for increased intracortical connectivity within these brain regions.

Another research group, while focusing on the relatively larger frontal white matter in humans compared to other species, notes the importance of connecting frontal with posterior brain regions to facilitate the evolution of language skill disproportionately evident within the human species (Schoenemann et al. 2005). Finally, cortical thickness and white matter microstructure vary substantially across species, with cetaceans (e.g., dolphins and whales) having thinner cortices (Haug 1987) and lower levels of myelin thickness (Zhang & Sejnowski 2000) than primates, in spite of the relatively high level of encephalization (1.8–5.3), total brain size (1,350–9,000 g), and overall number of cortical neurons (5,800–11,000 million) in cetaceans. Thus, the cognitive capacities shared among cetaceans, nonhuman primates, and humans – including self-recognition, symbol-based communication, abstraction, and complex social structures (Marino 2002) – are associated with markedly different brain features than mere size alone.

3. Definitions and perspectives from previous reviews

The study of intelligence has labored under various challenges of definition, from "that which intelligence tests measure" (Thorndike 1921), to finite aspects of cognition consisting of numerous facets or independent abilities (Gardner 1993a; Sternberg 2000). Others advocate that intelligence is synonymous with working memory (Colom et al. 2004; Kyllonen & Christal 1990), whereas a recent review makes the case for a distinction between working memory/executive functioning and general intelligence (Blair 2006). A consensus panel of the American Psychological Association (APA) defined intelligence in this way: "Individuals differ from one another in their ability to understand complex ideas, to adapt effectively to the environment, to learn from experience, to engage in various forms of reasoning, to overcome obstacles by taking thought" (Neisser et al. 1996). This view of general intelligence has widespread appeal. In addition, the empirical evidence overwhelmingly supports the concept of a *general* factor (*g*) of intelligence, first defined by Spearman (1904), underlying performance on most (if not all) measures of higher cognitive functioning (Jensen 1998). "General intelligence" more aptly refers to intelligence in general, and it is not the same as *g*. The neural basis of general intelligence has been the focus of most early neuroimaging/intelligence research; however, as we understand more fully the importance of individual differences across a wide range of cognitive tasks, the neural basis of *g* has become a more recent focus. Although some neuroimaging studies have specifically tried to assess *g* (Colom et al. 2006a; 2006b; Duncan et al. 2000), most studies use single or composite indices of intelligence in general derived from tests such as the Raven's Progressive Matrices Test or Full Scale Intelligence Quotient (FSIQ) scores obtained from the Wechsler Intelligence Scales.

There is a theoretically informative distinction, relevant to the current review, between intelligence in general (e.g., FSIQ) and a general intelligence factor (*g*). As noted by Jensen, the *g*-factor should be conceived as a "distillate of the common source of individual differences in all mental tests, completely stripped of their distinctive features of information content, skill, strategy, and the like" (Jensen 1998), p. 74). As noted by Colom et al. (2006), whereas the scientific construct of *g* relies upon the correlations among test scores, intelligence in general is merely a summation of standardized mental test scores. However, the simple sum of various test scores cannot be considered the optimal measure of *g*, but rather considered a measure of intelligence in general. Intelligence in general means *g* plus several more specific cognitive abilities and skills. Typical IQ scores comprise a complex mixture of those abilities and skills (Colom et al. 2002). Although IQ scores have high *g*-factor loadings, IQ scores only approximate *g*.

Most previous reviews concerned with the neural basis of intelligence have not focused on such distinctions. Rather, they have addressed the biological correlates of intelligence and reasoning from several different perspectives: For example, (1) positron emission tomography (PET) studies of cerebral glucose metabolic rate (Haier 1993b); (2) the speed and efficiency of brain functioning inferred from reaction time (Jensen 1998) or assessed by electrical propagation of nerve impulses through the brain (Deary & Caryl 1997); (3) the commonality of frontal lobe recruitment across a wide range of cognitive demands (Duncan & Seitz 2000), including intelligence (Duncan 2005; Duncan et al. 1995; Kane & Engle 2002); (4) genetic bases underlying the neurobiology of intelligence (Gray & Thompson 2004; Toga & Thompson 2005); (5) common fronto-parietal integration underlying a vast array of cognitive demands (Naghavi & Nyberg 2005); and most recently, (6) an attempt to reconcile concepts of cognitive processing efficiency and general intelligence (Chabris 2006).

Summarizing these reviews is well beyond the scope of this paper: Suffice it to say that each of these other reviews has posited discrete brain regions as being associated with intelligence as inferred from the use of noninvasive neuroimaging paradigms, adding incrementally to our understanding of where in the brain intelligence might reside. Our task here is to articulate, for the first time, commonalities across the wide array of neuroimaging studies to date which use a range of measures of intelligence and reasoning, and myriad techniques amenable to structural localization, including structural magnetic resonance imaging (sMRI) and its recent application of voxel-based morphometry (VBM), activation studies of cerebral blood flow and glucose metabolism using positron emission tomography (PET) and functional magnetic resonance imaging (fMRI), chemical inquiries using magnetic resonance spectroscopy (MRS), and measures of water movement using diffusion tensor imaging (DTI).

Due to space limitations, we specifically exclude measures of electroencephalography (EEG) and magnetoencephalography (MEG), both of which provide excellent temporal resolution but, due to the inverse problem (Balish & Muratore 1990), provide relatively

low spatial resolution as compared to other neuroimaging modalities.

4. A discrete parieto-frontal network underlies human intelligence

Following the 100th anniversary of development of the first psychometric test of intelligence by Alfred Binet (see Binet 1905), we appear poised to answer the question of where individual differences in intelligence might arise in the human brain. This progress is due to the steady increase, starting in the latter part of the twentieth century, in neuroimaging research designed to correlate measures of higher cognitive functioning with both structural and functional attributes of discrete brain regions. Indeed, in December 2003, a symposium brought together for the first time many researchers engaged in neuroimaging of intelligence (Haier et al. 2003a). That meeting was the genesis of this paper; when the two of us, Jung and Haier, found ourselves independently presenting parallel reviews and hypotheses tentatively locating individual differences in intelligence within a network including both frontal and posterior brain regions. Our comprehensive review here of 37 neuroimaging studies – which include measures of both fluid and crystallized intelligence, measures of reasoning, measures of *g*, and measures of games of reason (i.e., chess and GO) – identifies several discrete brain regions, distributed across the entire brain, and articulates a surprising commonality of these areas across studies and methods.

We propose a model – the *Parieto-Frontal Integration Theory*, or P-FIT – that elucidates the critical interaction between association cortices within parietal and frontal brain regions which, when effectively linked by white matter structures (i.e., arcuate fasciculus, superior longitudinal fasciculus), underpins individual differences in reasoning competence in humans, and perhaps in other mammalian species as well (see Fig. 1). We arrive at this model based on the 37 neuroimaging studies of intelligence and reasoning reviewed here and guided conceptually by the recent and extensive review by Cabeza & Nyberg (2000) of cognitive neuroimaging research summarizing the functional correlates of brain activity, by lobe, at the level of Brodmann areas.

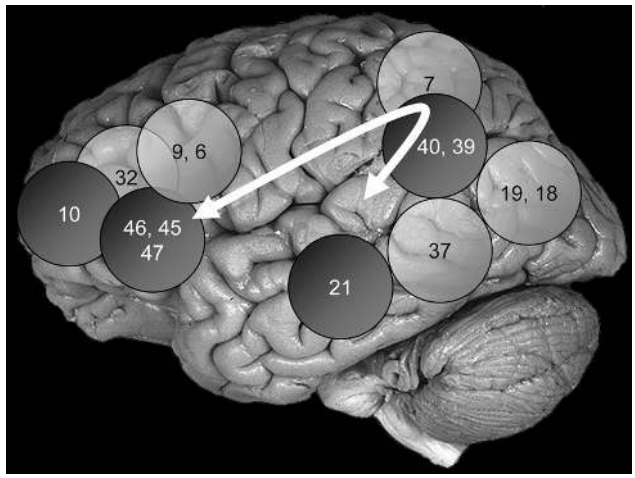

Figure 1. Brain regions by Brodmann area (BA) associated with better performance on measures of intelligence and reasoning that define the P-FIT model. Numbers = BAs; dark circles = predominant left hemisphere associations; light circles = predominant bilateral associations; white arrow = arcuate fasciculus. This figure is derived from data presented in Figure 5.

The importance of the P-FIT model to intelligence and reasoning can be summarized as follows: (1) We begin with the assumption that humans gather and process cognitively salient information predominantly through auditory and/or visual means (usually in combination) – therefore, particular brain regions within the temporal and occipital lobes are critical to early processing of sensory information: the extrastriate cortex (BAs 18, 19) and fusiform gyrus (BA 37) involving recognition and subsequent imagery and/or elaboration of visual input, and Wernicke's area (BA 22) involving analysis and/or elaboration of syntax of auditory information. (2) We assume this basic sensory/perceptual processing is then fed forward to the parietal cortex, predominantly the supramarginal (BA 40), superior parietal (BA 7), and angular (BA 39) gyri, wherein structural symbolism, abstraction, and elaboration emerge. (3) We further assume the parietal cortex interacts with frontal regions (i.e., BAs 6, 9, 10, 45–47), which serve to hypothesis test various solutions to a given problem. (4) Once the best solution is arrived upon, the anterior cingulate (BA 32) is engaged to constrain response selection, as well as inhibit other competing responses. (5) Finally, we propose that this process is dependent upon the fidelity of underlying white matter necessary to facilitate rapid and error-free transmission of data from posterior to frontal brain regions.

Following our review of the neuroimaging evidence upon which the P-FIT model is based, we will review supporting evidence from brain lesion and genetic imaging studies.

5. Review of neuroimaging literature

5.1. Voxel-based morphometry: Beyond "bigger is better"

Beyond the observation that total brain size weakly correlates with intelligence (Van Valen 1974), major progress on particular structure-function relationships relied heavily upon lesion analysis (Halstead 1947; Luria 1973), and upon groundbreaking work regarding lateral asymmetry (Geschwind & Levitsky 1968) and cortical disconnection syndromes (Geschwind 1965). This approach changed dramatically with the introduction of MRI to clinical neurology and psychiatry, offering the possibility of imaging brain structures in both disease and health in living human subjects. In the first study designed to assess the relationship between brain size and intelligence *in vivo* (Willerman et al. 1991), total brain volume in 40 college students (mean age $\pm$ SD = 18.9 $\pm$ 0.6) was measured with MRI and correlated to performance on four subtests of the Wechsler Adult Intelligence Scale-Revised (WAIS-R). These researchers found a pooled (across sex) correlation of .51 between IQ scores and brain size, although they did note that selection of extreme IQ groups for their sample likely amplified the degree of correlation (estimated r = .35 for a more representative sample). Following Willerman et al., the first so-called *in vivo* autopsy was conducted to

determine brain-intelligence correlates in 67 healthy individuals (mean age ± SD = 38 ± 16) without a history of medical, neurological, or psychiatric disease. Subjects completed the WAIS-R (mean IQ ± SD = 116 ± 14) and a standard MRI scan, the results of which indicated modest positive correlations (i.e., .32 to .46) between FSIQ and the volume of specific brain structures including the temporal lobes, hippocampus, cerebellum, and total gray matter (Andreasen et al. 1993). A subsequent study (Flashman et al. 1997), in which lobar volumes (i.e.., frontal, temporal, parietal, occipital, cerebellum) were correlated with IQ measures in 90 normal subjects (mean age ± SD = 27 ± 10), found that volumes of frontal (r = .24), temporal (r = .28), and parietal (r = .24) cortices were predominantly correlated with measures of nonverbal reasoning (i.e., performance IQ). These authors hypothesized that the remaining variance between IQ and brain structure would likely reside in the "quality" rather than "quantity" of brain tissue as found in such variables as circuit complexity, dendritic arbor, myelin thickness, and other neurotransmitter/neurochemical factors.

In spite of the important differences in regional cellular organization reported by Brodmann (1912), the brain is not easily segmented into readily identifiable cortical regions. The measurement of discrete cortical and subcortical neuronal-axonal populations required an advance in image analysis, recently realized with voxel-based morphometry (VBM), a method by which standard images may be automatically segmented into tissue compartments (i.e., gray, white, cerebrospinal fluid) using measures of voxel intensity at the millimeter level of resolution (Ashburner & Friston 1997). Images from individual subjects are imported into a freely available analysis program (i.e., Statistical Parametric Mapping, or SPM), spatially normalized in stereotactic space (i.e., Montreal Neurological Institute), segmented and smoothed, and subjected to voxel-wise statistical comparisons with either a comparison group or an external variable (Ashburner & Friston 2000). This development has resulted in a veritable explosion of clinical VBM studies designed to assess volumetric consequences of various neurological and psychiatric diseases, with more than 200 peer-reviewed research reports containing "voxel-based morphometry" within their abstracts between the years 2000 and 2006. Of note, this methodology is not without controversy (Allen et al. 2005; Ashburner & Friston 2001; Bookstein 2001; Davatzikos 2004), although several recent studies have compared VBM to traditional region-of-interest (ROI) tracing techniques in the same subjects and determined generally good correspondence between methods (Giuliani et al. 2005; Good et al. 2002; Testa et al. 2004).

To date, seven studies have appeared in the literature designed to assess the volumetric correlates of intelligence in the normal human brain (see Table 1). The first study (Wilke et al. 2003) was of 146 children (mean age ± SD = 11.7 ± 3.5) of above average intellectual attainment as measured with the Wechsler Intelligence Scales (mean IQ ± SD = 113.8 ± 13.8). Significant correlations (r = .30) were found between measures of FSIQ and gray matter within the cingulate (BA 32). Our study of 47 adults (age range = 18–84) of high average intelligence (mean IQ ± SD = 116 ± 14.4) found correlations between gray matter volume within frontal (BAs 9, 10, 46), temporal (BAs 21, 22, 37, 42), parietal (BAs 3, 43), and occipital (BA 19) regions, with significant white matter–IQ correlations observed near BA 39 (Haier et al. 2004). Moreover, these areas differed in young and old adults and also between men and women (Haier et al. 2005). A third study (Frangou et al. 2004) of 40 young subjects (mean age ± SD = 14.9 ± 2.6) of average intelligence found correlations with gray matter volume within the cingulate (BAs 24, 31, 32), frontal (BAs 9, 10, 11, 47), and parietal (BAs 5, 7) cortices. Lee et al. (2005) studied 30 older subjects (mean age ± SD = 61.1 ± 5.18) and found regional correlations between performance IQ and brain volume limited to the posterior lobe of the right cerebellum. A fifth study (Gong et al. 2005) of 55 adults (mean age ± SD = 40 ± 12) of above average intelligence (mean FSIQ ± SD = 117 ± 11) found gray matter volume correlates with IQ limited to the anterior cingulate (BAs 24, 32) and medial frontal (BAs 8, 9, 10) regions. We have since reanalyzed our VBM data using the method of correlated vectors (i.e., correlating the rank of *g*-loadings for each test in a group of tests to the rank of the same test correlation to any external variable such as age or brain size; Jensen 1998). We found that *g* accounted for many of the FSIQ correlations with gray matter in the anterior cingulate (BA 24), frontal (BAs 8, 10, 11, 46, 47), parietal (BAs 7, 40), temporal (BAs 13, 20, 21, 37, 41), and occipital (BAs 17, 18, 19) cortices (Colom et al. 2006b). Moreover, in a separate analysis, we found a nearly perfect linear relationship between *g*-loading of each subtest of the WAIS and the amount of gray matter correlated to each subtest score (Colom et al. 2006a).

Finally, a newly published study of cortical thickness demonstrates that we are entering the next phase of neuroimaging research on intelligence: longitudinal studies of brain and cognitive development with a large sample size (Shaw et al. 2006). In this study, 307 normally developing children (mean age at first scan ±SD = 13 ± 4.5) were scanned on multiple occasions to determine correlates between measures of cortical thickness and performance on standardized measures of IQ. The strongest and most consistent correlations between cortical thickness and IQ were obtained during late childhood (age range = 8.6–11.7 years), with regions throughout the brain showing positive correlations. Using the supplementary Table 1 of their report, we have converted the regional areas identified to Brodmann areas, resulting in distributed brain regions association with intellectual performance in late childhood across frontal (BAs 4, 6, 8, 10, 11, 44–46), parietal (BAs 1–3, 5, 39, 40), temporal (BAs 21, 37), and occipital (BAs 17, 18, 19) cortices. These authors note a striking difference in trajectory of high-IQ subjects compared to their more average counterparts, with "an initial accelerated and prolonged phase of cortical increase, which yields to equally vigorous cortical thinning by early adolescence" (Shaw et al. 2006). Cortical thickness was correlated with IQ, but there was a clear developmental sequence showing a dynamic relationship between regional brain structure and intelligence as the brain matures through childhood and adolescence. This finding corresponds to our own data showing different, but overlapping brain regions associated with intelligence across young and older adults (Haier et al. 2004). Similarly, the cortical thinning finding is consistent with some of

Table 1. *Structural neuroimaging studies demonstrating relationships between discrete Brodmann areas (BAs) and measures of intelligence and reasoning*

	N	Age of cohort	AC/PC	Frontal	Parietal	Temporal	Occipital	Reasoning measure
Morphometry								
Wilke et al. (2003)	146	11.7 ± 3.5	B32					WAIS/WISC
Frangou et al. (2004)	40	12–21	B24, 31, 32	B9, 11, 47 L10	B5, 7			WISC/WAIS
Haier et al. (2004)	47	43.5 ± 20.3		L8, 10, 45, 46 R9	L39, 40 R3, 43	L21, 22, 37, 42 R21	L19	WAIS
Lee et al. (2005)	30	61.1 ± 5.18					RCb	WAIS
Gong et al. (2005)	55	40 ± 12	B24, 32	B8, 9, 10				CCFT
Colom et al. (2006a)	47	43.5 ± 20.3	L24	B10 L11, 46, 47 R8	B40 L7	L20, 21, 37, 41 R13	B18, 19 R17	*g*
Shaw et al. (2006)	307	13 ± 4.5		B11, 44–46 L10 R4, 6, 8	B5, 39, 40 R1-3	L21, 37	B18 L17, 19	WPPSI/ WISC /WAIS
^{1}*H-MRS*								
Jung et al. (1999)*	26	22 ± 4.6			L39/40			WAIS
Pfleiderer et al. (2004)*++	62	20–75	L24/32	L10/46				WAIS Vocabulary
Jung et al. (2005)*	27	24.8 ± 5/9			L39/40			WAIS
DTI								
Schmithorst et al. (2005)*	47	11.0 ± 3.3	R31	B9 R3	L13, 39/40	L30		WISC

Note: AC/PC = anterior cingulate/posterior cingulate; B = bilateral; L = left lateralized; R = right lateralized; WAIS = Wechsler Adult Intelligence Scale; WISC = Wechsler Intelligence Scale for Children; RCb = right cerebellum; CCFT = Cattell Culture Fair Test; *g* = general intelligence factor; WPPSI = Wechsler Preschool and Primary Scale of Intelligence; *white matter regions with closest approximate BAs identified; ++women only.

our earlier observations regarding brain efficiency as evidenced by inverse correlations between brain activity and psychometric intelligence scores (Haier 1993b; Haier et al. 1988; see also Neubauer & Fink 2003; Neubauer et al. 2002; 2004).

5.2. White matter studies and intelligence

The relative contribution of white matter to higher cognitive functioning has remained relatively understudied compared to gray matter research linking particular cortical regions to performance. However, several lines of inquiry would suggest that the integrity of myelinated axons plays a critical role in intellectual attainment (Miller 1994). For example, myelin thickness is correlated to axonal size (Bishop & Smith 1964; Friede & Samorajski 1967; Mathews 1968), and larger axonal diameter is associated with increased nerve conduction speed (Aboitiz 1992). The simultaneous increases in myelination and axonal diameter have been hypothesized to play a critical role in cognitive development. For example, one group has found significant age-related increases in white matter density within the bilateral internal capsule and the posterior aspects of the left arcuate fasciculus (which links anterior and posterior language cortices) in a young (age range = 4–17 years) normal cohort (Paus et al. 1999). At the other end of the developmental continuum, age-related cognitive decline has been linked to general slowing of brain processes (Hale et al. 1987), with concordant linear decreases in myelination initiated around the fourth decade (Bartzokis et al. 2003). Indeed, reviews of the research literature have found that nearly the entire decline in intellectual functioning observed among the elderly may be accounted for by reductions in processing speed (Lindenberger et al. 1993; Salthouse & Coon 1993).

One technique particularly amenable to the interrogation of white matter neurochemical integrity is magnetic resonance spectroscopy (MRS). This technique predates MRI, although its use in brain research only began in earnest in the latter part of the twentieth century in parallel with the broad application of conventional brain MRI (Bottomley et al. 1985). Two major MRS modalities exist – proton and phosphorous spectroscopy (^{1}H and ^{31}P, respectively), which comprise the vast majority of clinical and normal human studies in the research literature. N-acetylaspartate (NAA), the main metabolite visible within the ^{1}H-MRS spectrum, is found only within neurons and mature oligodendrocytes (Urenjak et al. 1993) and has been established as a marker of neuronal density and/or viability in numerous disease states (Barker 2001). In the first study linking brain chemistry to intellectual performance in normal subjects using ^{31}P-MRS, Rae et al. (1996) studied 42 boys (age range = 7.4–13.2 years), comparing measures of pH and performance on the Wechsler Intelligence Scale for Children–3rd Edition (WISC-III). They found a significant positive correlation between pH in a large volume spanning the

fronto-parietal cortex and IQ ($r = .52$, $p = .0008$), the association of which was subsequently determined to be specific to children (Rae et al. 2003b). It should be noted that the MRS technique used to date allows only for placement of a single voxel within predominantly white matter regions, and that other brain regions have not been adequately assessed for NAA–IQ relationships. This is a major limitation of this imaging technique, although several groups are implementing spectroscopic imaging techniques that will allow for multi-voxel acquisition across a slab of tissue (Gasparovic et al. 2006), and eventually we may expect full coverage across the entire brain parenchyma.

Using ^{1}H-MRS, our group first studied 26 healthy college students (mean age $\pm$ SD = 22.0 $\pm$ 4.6), comparing brain metabolites with performance on the Wechsler Adult Intelligence Scale–3rd Edition (WAIS-3). We obtained measures of NAA from a voxel placed within the left occipito-parietal white matter, a region underlying the angular and supramarginal gyri (BAs 39, 40). In this neurologically and psychiatrically normal cohort, we found a significant, positive relationship between NAA and IQ ($r = .52$), equally predictive of verbal ($r = .48$) and nonverbal ($r = .45$) measures of intellectual performance (Jung et al. 1999). We have since replicated and extended these findings in a new normal cohort of 27 college students (mean age $\pm$ SD = 24.8 $\pm$ 5.9), showing specificity of the NAA–IQ relationship to left occipito-parietal white matter (when compared to bilateral samples of frontal white matter), as well as stronger NAA–IQ relationships in women compared to men (Jung et al. 2005). A second group (Pfleiderer et al. 2004) studied the relationship between NAA within bilateral dorsolateral prefrontal and left anterior cingulate cortices and the Vocabulary subtest of the WAIS-R (high *g*-loading) in 62 healthy adults (age range = 20–75). They found significant correlations between NAA in voxels underlying left BAs 10 and 46 ($r = .53$) and 24 and 32 ($r = .56$) and the Vocabulary subtest scores for women, but not for men. Other groups have since confirmed broader NAA–cognition relationships across a wide array of cognitive tasks in both younger (Yeo et al. 2000) and older (Ferguson et al. 2002; Valenzuela et al. 2000) experimental cohorts, as well as across myriad neurological and psychiatric patient samples (Ross & Sachdev 2004).

A second major modality by which the white matter integrity is measured is diffusion tensor imaging (DTI), an imaging technique that measures the coherence of water movement through the white matter of the brain and that can facilitate *in vivo* white matter fiber tracking. A single, recent study (Schmithorst et al. 2005) attempts to link measures of white matter status to measures of intelligence in a normal pediatric cohort. This study included 47 children between the ages of 5 and 18 who underwent MRI with DTI and whose intelligence was assessed with the WISC-III. Measures of fractional anisotropy (FA), defined as a measure of white matter fiber "coherence" (i.e., directional organization), were calculated within white matter across all brain regions (frontal, temporal, parietal, and occipital). Results indicated a positive correlation between measures of FA, bilaterally, within frontal and occipito-parietal white matter, a region that the authors concluded to be representative of the arcuate fasciculus. They also noted a stronger correlation between measures of FA and verbal intellectual ability ($r = .57$) as compared to nonverbal ability ($r = .33$). Thus, the integrity of white matter connecting Broca's area (BA 44) to Wernicke's area (BA 22) appears to be sensitive to individual differences in intellectual attainment in this young cohort (Schmithorst et al. 2005). We have since used the Talairach coordinates, obtained from Schmithorst et al. (2005), to determine the nearest gray matter regions overlying the white matter DTI-intelligence regions, which include left hemisphere BAs 13 and 30, right hemisphere BAs 3 and 31, and bilateral BAs 9, 39, and 40 (see Table 1), underlying frontal, parietal, and temporal cortices. Although DTI is an exciting new technique to assess white matter orientation and integrity over the entire brain, the reliability of this technique has yet to be established within discrete white matter tracts (e.g., arcuate fasciculus). That being said, DTI studies potentially may result in substantial contributions linking higher cortical functioning, including intelligence, to white matter fidelity.

5.3. Summary of structural correlates of intelligence

As shown in Table 1 and Figure 2, several commonalities are apparent when assessing structural (i.e., VBM, MRS, DTI) characteristics of the brain that have been associated with intelligence. For example, of the 11 studies reviewed, more than 40% implicate left BA 10 (frontal), 39, and 40 (parietal); specifically, the tissue density and white matter integrity within these regions correlate substantially to performance on the Wechsler Intelligence Scales both in young cohorts (Schmithorst et al. 2005) and within adult samples ranging in age from 18 to 84 (Haier et al. 2004). Similarly, tissue density and chemical composition for left hemisphere BAs 24 and 32 (cingulate) and 46 (frontal) and right hemisphere BA 9 (frontal) were correlated to FSIQ in more than 30% of the studies. Overall, the structural studies did not tend to implicate common temporal or occipital lobe regions as being correlated to intellectual performance. This may be due to the static nature of structural imaging – participants are not performing tasks while being scanned; rather, their intellectual capacity is assessed and they are scanned on separate occasions. Therefore, it is possible that temporal and occipital lobe relationships to intelligence may be functional and "task dependent" upon the sensory modality (auditory or visual, respectively) employed, as discussed in the next section. However, these structural studies do support frontal (BAs 9, 10, 46), parietal (BAs 39, 40), and anterior cingulate (BAs 24, 32) aspects of the P-FIT model as important to individual differences in performance on standardized intelligence tests such as the WAIS. The combined use of DTI, VBM, and MRS across the entire brain in future studies would allow for simultaneous assessment of water diffusion, tissue density, and chemical composition on a voxel-by-voxel basis, and their simultaneous application would substantially improve our understanding of the structural correlates of intelligence.

5.4. Functional imaging studies using PET

William James (1890, p. 99) first remarked that "blood very likely may rush to each region of the cortex according as it

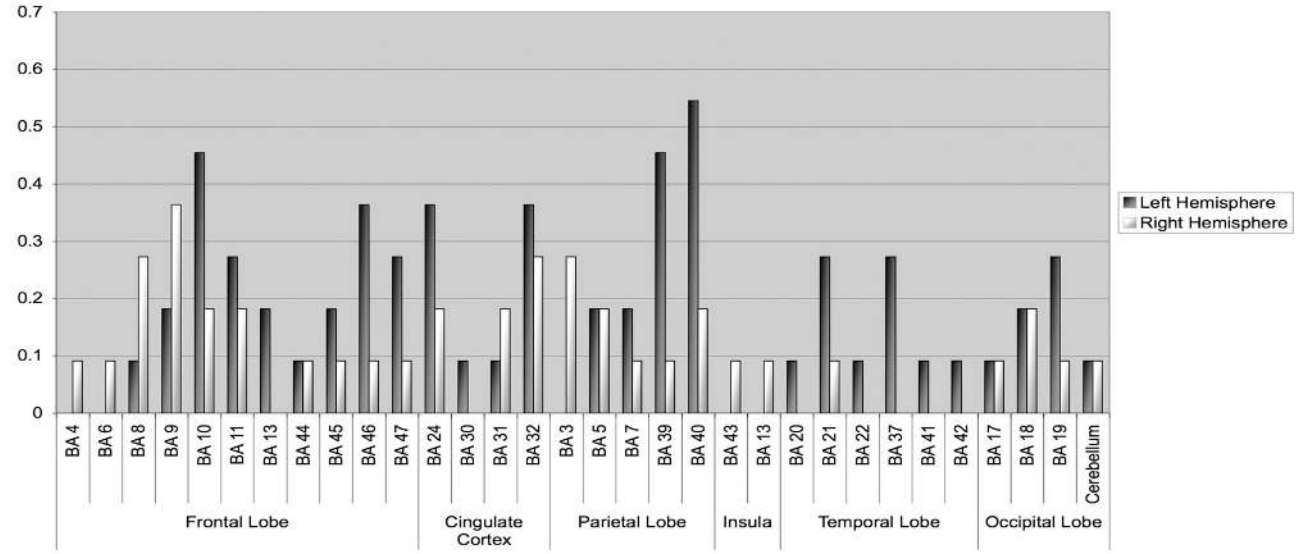

Figure 2. Graphical representation of the proportion (Y-axis) of structural neuroimaging studies describing relationships between intelligence and/or reasoning and discrete Brodmann areas by lobe (X-axis).

is most active," a supposition that remained empirically elusive until the introduction of relatively sensitive and accurate measures of regional cerebral blood flow (rCBF) (Lassen et al. 1963a; 1963b). Early research (Ingvar & Risberg 1967; Risberg et al. 1968) demonstrated that performance of cognitive tasks was accompanied by increases in regional circulation, hypothesized to correspond to changes in gray matter neuronal activity. One of the earliest imaging techniques had subjects breathe oxygen labeled with the short half-life radioactive isotope ^{133}Xenon, the decay of which could be recorded from detectors surrounding the head. Positron emission tomography (PET) evolved from these early rCBF studies, allowing for greater sensitivity and spatial localization of neuronal uptake through labeling of glucose utilization or blood flow (Sokoloff 1981).

The first PET study, designed to formally assess brain–intelligence links in normal subjects in the entire brain, was undertaken in eight young men (mean age $\pm$ SD = 22.4 $\pm$ 2.3) by utilizing ^{18}fluoro-2-deoxyglucose (FDG) uptake during performance on a high *g*-loaded test of nonverbal abstract reasoning, the Raven's Advanced Progressive Matrices (RAPM), over a period of 32 minutes, while subjects worked at their own pace (Haier et al. 1988). The most notable finding from this study was widespread *inverse* correlations between regional glucose metabolic rate (GMR) and performance on the RAPM. Thus, high scores on the RAPM were related to *lower* GMR, a finding thought possibly to reflect increased "neuronal efficiency" in subjects with better performance (Haier 1993b; Haier et al. 1988). This study used a first-generation PET scanner that imaged only nine axial brain slices, one slice at a time, with relatively poor spatial resolution. (Modern PET scanners image the entire brain simultaneously, with considerably higher spatial resolution.) In this first RAPM study, regional GMR was assessed in only three of the nine axial slices using a stereotactic method, quite primitive by today's standards. In approximate BA terms, the most significant inverse correlations were bilateral in BAs 9/46, 39/40, 22/42, 21/22, and 37/19. A subsequent re-analysis of these data (Haier 1993b) used a more anatomically refined three-dimensional method of anatomical localization which used all nine axial slices instead of only three individual ones (still primitive by today's standards). Of 32 possible correlations (four areas within each of four lobes, left and right hemisphere), 12 were significant (all negative) – six of these were in temporal and parietal lobes (approximate BAs 21, 22, 37, 38, 39), four in the occipital lobe (BAs 18, 19), and two in the frontal cortex (BAs 9, 10) (Haier 1993b). At the time, the inverse correlations were surprising, even as the exact anatomical localization of the most significant areas was unsatisfactory. A similar PET study of 16 normal volunteers performing a high *g*-loaded verbal fluency test, however, also showed significant inverse correlations in frontal, temporal, and parietal lobes (Parks et al. 1988). These authors also interpreted the inverse correlations as an indication of brain efficiency. Hypothesizing that mental retardation may be associated with increased brain inefficiency and greater brain activity, Haier et al. (1995) reported higher glucose metabolism throughout the brain in a small group of subjects with IQs between 50 and 75. The regional results of these studies are difficult to convert to BAs; they are discussed in more detail elsewhere (Haier 2003).

Although inverse correlations between brain function and cognitive performance also have been reported in EEG studies (Neubauer & Fink 2003), most functional imaging studies of cognition compare a task and a control condition and do not examine individual differences in the performance of the task as a variable. In fact, most tasks used in cognitive imaging studies are chosen to minimize performance differences among subjects. Such cognitive tasks are not tests of intelligence per se, but several other studies have linked performance of various "reasoning" tasks to brain activation utilizing PET. One such study (Ghatan et al. 1995) using the perceptual maze task (PMT), a measure of frontal lobe function and visuo-spatial reasoning, was performed by

eight middle-aged volunteers (mean age = 49.1; age range = 41–59 years) during [^{15}O] butanol PET. When compared with a motor control "sham" condition, performance of the PMT resulted in increased uptake within bilateral anterior cingulate (BA 32), medial (BAs 6, 8) and right frontal (BAs 4, 49), superior and inferior parietal (BAs 7, 40), inferior temporal (BA 37), and superior occipital (BAs 18, 19) cortices.

Haier and Benbow (1995) used FDG PET to study mathematical reasoning in college men (N = 22) and women (N = 22). Half of each group were selected for high or average mathematical ability on the basis of college entrance SAT-Math scores (SAT-M scores more than 700 for the high groups; between 410 and 540 for the average groups). During the PET procedure, each subject completed a new SAT-M test during the 32-minute FDG uptake period. In men, there were significant correlations between the math score and glucose metabolism in the temporal lobes bilaterally (middle, inferior, and posterior; analogous to BAs 20, 21, 22). There were no correlations in the women, showing a clear sex difference. In a separate PET study of eight normal males, Haier et al. (1992a) assessed functional brain changes after the learning of a complex visuo-spatial task (i.e., Tetris), and reported decreased cerebral metabolism after practice. Of interest here, the decreases in several brain areas were larger in the subjects with higher scores on the Raven's Advanced Progressive Matrices (Haier et al. 1992b). The regions of decreased metabolism over time were based on a stereotactic method and are not amenable to BA conversion.

Verbal and nonverbal reasoning have also been studied using PET. For example, one group of researchers conducted two studies assessing deductive/inductive reasoning and analysis of verbal syllogisms (Goel et al. 1997; 1998) in samples of 10 (mean age $\pm$ SD = 28.4 $\pm$ 4.03) and 12 young adult subjects (mean age $\pm$ SD = 28.2 $\pm$ 2.6 years), respectively, measured with [^{15}O]H_2O PET. In the first study, compared to baseline, inductive reasoning was associated with activations in the left frontal (BAs 8, 9, 10, 24, 32, 47), temporal (BA 20), and occipital (BA 19) lobes. In the second study, the researchers found activations inclusive of the left frontal (BAs 45, 46, 47), left temporal (BAs 21, 22), and left cingulate (BAs 24, 32) gyri. In a ^{15}O PET study of two frontal lobe nonverbal reasoning tasks – the Wisconsin Card Sorting Test and the Raven's Progressive Matrices Test – Esposito et al. (1999) studied 41 healthy volunteers. In their young adult cohort (age range = 18–42 years), they found converging bilateral activations across tasks within the dorsolateral prefrontal (BAs 9, 46), inferior parietal (BAs 39, 40), anterior cingulate (BA 32), inferior/lateral temporal (BAs 21, 37), and occipital cortices (BAs 18, 19), suggestive of a common neural network underlying diverse problem-solving tasks and matching key components of the P-FIT.

The understanding of analogical reasoning, a high *g* ability, has been of keen interest within the cognitive neurosciences for several decades, with at least one group speculating that the left angular gyrus may be "hard-wired" for analogical reasoning (Gur et al. 1994). Indeed, several early ^{133}Xenon blood flow studies indicated that verbal analogical reasoning activated predominantly left hemisphere regions, particularly the left inferior parietal cortex and Wernicke's area (Gur & Reivich 1980; Gur et al. 1982; 1987; 1988; Risberg et al. 1975). However, spatial localization was quite primitive when compared to modern PET and fMRI techniques. In the only PET visual analogical reasoning study to date (Wharton et al. 2000), researchers studied 12 young adult subjects (mean age = 26 years) while they observed a source picture comprised of nameable geometric objects (e.g., triangle) and decided whether it was an analog of a target display of geometric objects. When comparing analogical reasoning to literal conditions (i.e., target matches source exactly), Wharton et al. found activations within the left middle frontal (BAs 6, 8) and inferior frontal (BAs 10, 44, 45, 46, 47) gyri, the anterior insula, and inferior parietal cortex (BA 40). These authors concluded that "analogical mapping is produced by an integrated network formed from the left parietal and frontal cortices. Further, it may be that the left parietal and frontal cortices mediate automatic and controlled aspects of mapping respectively" (Wharton et al. 2000).

In a widely cited study, Duncan et al. (2000) reported [^{15}O] butanol PET activations associated with reasoning performance in 13 young adult subjects (mean age = 26 years). Their protocol used high *g*-correlated and low *g*-correlated items sampling both verbal and visuo-spatial domains. They focused the interpretation of their results on the predominantly frontal commonality of activation seen in both the verbal and spatial reasoning conditions (BAs 46, 47). However, their "high" *g* task resulted in activations spread across frontal (BAs 6, 8, 10, 45, 46, 47), parietal (BAs 7, 40), and occipital (BAs 18, 19) cortices. Nonetheless, Duncan et al. concluded that *g* was almost exclusively related to the frontal lobe, a view at odds with most prior and subsequent neuroimaging studies. Recently, Duncan has modified his view (Duncan 2005; also see a critique of this study by Colom et al. 2006a).

Finally, Haier et al. (2003b) assessed whether individuals with higher scores on the high *g*-loaded test, the Raven's Advanced Progressive Matrices Test (RAPM), process information differently even when no problem solving is explicitly involved in task performance. For this experiment, 22 young adults (mean age $\pm$ SD = 22.1 $\pm$ 2.6) were studied with FDG PET as they viewed two videotapes, including narratives, with content consisting of either emotional or no emotional valence. Prior to the PET session, subjects completed the RAPM, with a 40-minute time limit, to assess intellectual functioning. Interestingly, significant positive correlations (common across both conditions) were found between RAPM scores and glucose uptake in several posterior brain regions, including bilateral parietal (BA 7), temporal (BAs 22, 37), and occipital (BAs 18, 19) cortices. Negative correlations were found in left BA 39 and right BA 7, BA 18, and the left parahippocampus (only positive correlations are included in the Table 2, although the interaction of reduced "activation" and function is of increasing interest to the cognitive neurosciences). Moreover, the strongest functional connectivity differentiating high- and low-RAPM subjects was found between BAs 19 and 37 and the left anterior cingulate/medial frontal gyrus. These authors offer several possible hypotheses for the importance of these posterior areas for intelligence, including that "individual differences in the ability to resolve competition among incoming visual stimuli may be a component of *g*" (Haier et al. 2003b).

Table 2. *Positron Emission Tomography (PET) neuroimaging studies demonstrating relationships between discrete Brodmann areas (BAs) and measures of intelligence and reasoning*

	N	Age of cohort	AC/PC	Frontal	Parietal	Temporal	Occipital	Reasoning measure
PET								
Haier (1988/1993b)	8	22.4 ± 2.3		B9, 10	B39	B21, 22, 37, 38	B18, 19	RAPM
Ghatan et al. (1995)	8	49.1	B32	B6, 8 R4, 49	B7, 40	B37	B18, 19	PMT-sham
Haier & Benbow (1995)	22	20 ± 1.7				B20, 21, 22§		Math Reasoning
Goel et al. (1997)	10	28.4 ± 4.03	L24, 32	L8, 9, 10, 47		L20	L19	Inductive/Deductive Reasoning
Goel et al. (1998)	12	28.2 ± 2.6	L24, 32	L45, 46, 47		L21, 22		Verbal Syllogisms
Esposito et al. (1999)	41	18–42	B32	B9, 46	B39, 40	B21, 37	B18, 19	WCST/RAPM
Wharton et al. (2000)	12	26		L6, 8, 10, 44, 45, 46, 47	L40			Analogy Reasoning
Duncan et al. (2000-V)	13	26		L10, 46, 47				Letter Sets
Duncan et al. (2000-V/S)	13	26		B8, 46, L47 R6, 45	B7, R40		B18, 19	CCFT
Haier et al. (2003b)	22	22.1 ± 2.6			B7	B22, 37	B18, 19	RAPM

Note: AC/PC = anterior cingulate/posterior cingulate; B = bilateral; L = left lateralized; R = right lateralized; RAPM = Raven's Advanced Progressive Matrices; PMT = perceptual maze test; V = verbal; V/S = visuo-spatial; WCST = Wisconsin Card Sorting Test; CCFT = Cattell Culture Fair Test; § = men only.

5.5. Summary of PET correlates of intelligence

One striking element in the summary of PET studies of intelligence is the general gradient of bilateral activations within posterior brain regions and the predominantly left hemisphere activations within the frontal lobes, apparent in Table 2 and Figure 3. Half of the studies reported bilateral activations within BAs 18 and 19 within extrastriate cortex, as well as predominantly left hemisphere activation

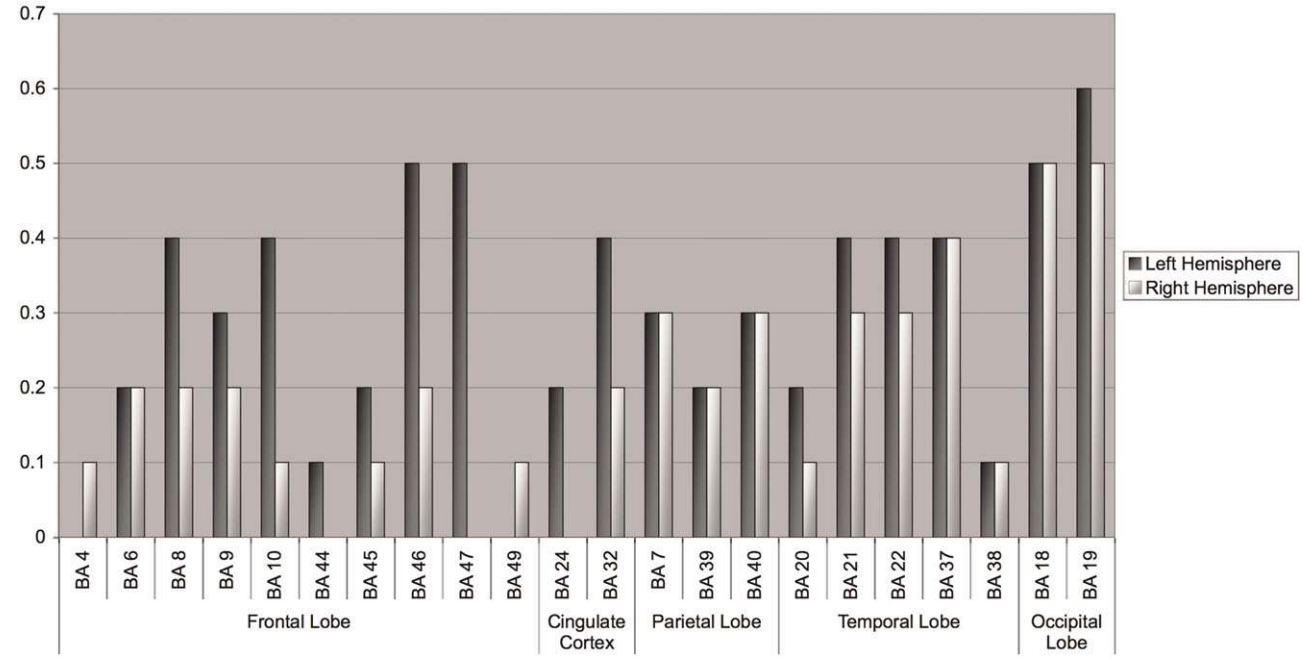

Figure 3. Graphical representation of the proportion (Y-axis) of PET neuroimaging studies describing relationships between intelligence and/or reasoning and discrete Brodmann areas by lobe (X-axis).

within either BAs 46 or 47. Forty percent (40%) of studies revealed left greater than right activation within frontal BAs 8 and 10, the anterior cingulate gyrus BA 32, and temporal BAs 21, 22, and 37, comprising the ventral "what" stream of visual information processing (Ungerleider & Mishkin 1982). Interestingly, these activations were not limited to strictly visual tasks (see Goel et al. 1997; Wharton et al. 2000). Finally, 30% of studies reported activations within predominantly the left lateralized frontal cortex (BA 9) and the bilateral posterior parietal cortex (BAs 7, 40). Overall, these PET studies largely conform to the P-FIT model. The relative invasiveness of PET studies (i.e., exposing subjects to radioactive isotopes), as well as the long period of uptake within the brain (i.e., ranging from 2 minutes to 32 minutes), would tend to limit future research to targeted hypotheses within relatively small subject groups designed to elucidate the entirety of brain networks associated with a given reasoning and/or intelligence task. However, this area of research is critically important to future studies, as it exploits direct precursors limiting the performance of neuronal work (e.g., oxygen/glucose) as opposed to measures hypothesized to be indirectly linked to neuronal work (e.g., blood oxygen level dependent [BOLD] response). In combination with new labeling agents and other imaging modalities possessing millisecond time resolution (e.g., magnetoencephalography), PET studies are likely to continue to contribute to understanding the neural basis of intelligence and reasoning.

5.6. Functional imaging studies using fMRI

Functional studies of human cognition required technology unavailable at the beginning of the twentieth century. However, in perhaps the first report on the association between blood flow and cognition in humans, John Fulton, a neurosurgery resident, described a patient who presented with decreasing vision due to an arteriovenous malformation (AVM) in the occipital cortex (Fulton 1928). Surgical removal of the AVM was attempted but unsuccessful, leaving a bony defect in the occipital bone through which a prominent bruit (i.e., rushing of blood) could be heard at auscultation. In a subsequent detailed analysis, Fulton found that the amplitude of the bruit was well correlated with the patient's mental activity. For example, opening of the eyes would elicit a moderate increase in blood flow sounds, whereas reading corresponded to dramatic increases. This initial finding foreshadowed the potential of tools which could make such assessments of blood flow – as later demonstrated by the accumulated work of several Nobel laureates (e.g., Felix Bloch and Edward Purcell [Nobel Prize – 1952], and Paul Lauterbur and Peter Mansfield [Nobel Prize – 2003]), and numerous other, less recognized contributors to the nascent field, in developing imaging technology that would allow visualization of brain parenchyma *in vivo*. Out of their collective work emerged magnetic resonance imaging (MRI), and later functional MRI (fMRI), a neuroimaging technique that exploits the increase in blood flow to the local vasculature that accompanies neural activity in gray matter regions of the brain.

In the first fMRI study of the neural substrates of reasoning, Prabhakaran et al. (1997) had seven young adult subjects (age range = 23–30 years) perform three types of problems (i.e., match, figural reasoning, analytical reasoning) selected from the RAPM while undergoing fMRI. Match problems required the subject to merely match a figure to an identical exemplar. Figural problems required predominantly visuo-spatial analysis to determine the right answer. Analytical problems required abstraction and reasoning beyond mere perceptual analysis. Fluid reasoning (i.e., analytic–figural) resulted in activations within frontal (BAs 6, 9, 44, 45, 46), parietal (BAs 7, 39, 40), temporal (BAs 21, 37), and occipital (BAs 18, 19) cortices, with only the parietal activation limited to the left hemisphere. These authors conclude that the neural network underlying RAPM performance overlaps substantially with verbal working memory networks, even during analytical reasoning regarding nonverbal patterns; therefore, a strong link exists between neural systems underlying working memory and reasoning. Another group (Kroger et al. 2002) used fMRI to study neural correlates of visual reasoning during performance of matrix problems of increasing levels of difficulty by eight young adults (age range = 19–32 years). They found that a measure of "relational complexity," associated with solving matrix problems, resulted in activations within the bilateral frontal (BAs 6, 9, 47), left frontal (BAs 44, 46), bilateral parietal (BA 7), and bilateral anterior cingulate (BA 32) cortices.

Proficiency in the game of chess has long been equated with superior intelligence and keen reasoning skill, and attempts have been successful in creating a computer that can defeat even the most accomplished human opponent (i.e., IBM's Deep Blue). The neural substrates of such games of reason are now under study with neuroimaging. One group of researchers studied fMRI activations associated with the games of chess (Atherton et al. 2003) and GO (Chen et al. 2003). In the first experiment, six male novice chess players (age range = 24–33 years) were scanned as they determined the best move for white to make in a middle game position. When this condition was contrasted with a condition in which chess pieces were dispersed randomly across the board, significant activations were observed within bilateral regions of the parietal (BAs 7, 39, 40), occipital (BA 19), and left frontal (BAs 6, 8, 9) cortices, as well as the left cerebellum. In the second study, six amateur GO players were scanned under realistic and random game positions. When game conditions were compared with random board conditions, significant activations were observed within the left frontal (BAs 44, 45), bilateral frontal (BAs 6, 9), posterior cingulate (BAs 30, 31), parietal (BAs 7, 40), temporal (BA 37), and occipital (BA 19) cortices. Chen et al. noted the relative "paucity of activation in the frontal lobes" across studies, as well as lack of hemispheric specialization, although both games are considered to be strategic and spatially oriented. They made special note "that the so-called '*g*' areas in the frontal lobe reported and emphasized by Duncan et al. (2000) are not consistently activated in either GO or chess cognition" (Chen et al. 2003).

Several studies have been undertaken to study logical reasoning with fMRI. For example, Goel and Dolan (2001) used measures of either concrete or abstract "relational reasoning" problems (e.g., "the apples are in the barrel; the barrel is in the barn; the apples are in the barn," or $A > B$; $B > C$; $A > C$) to measure brain

activation in 14 subjects (mean age ± SD = 28.6 ± 4.6). These authors found that logical reasoning elicited activations within the bilateral frontal (BAs 6, 9), parietal (BAs 7, 40), left (BAs 17, 18) and bilateral occipital (BA 19) cortices, as well as in the bilateral subcortical (e.g., caudate/nucleus accumbens) and cerebellar regions. In a study of 10 male subjects (age range = 20–25 years), Luo et al. (2003), used Chinese verbal analogies to assess brain activations associated with reasoning, finding significant activations within the left frontal (BA 9), left parietal (BAs 7, 40), bilateral fusiform (BA 37), and left (BA 18) and bilateral (BA 19) extrastriate cortices. Using an assessment of conditional verbal reasoning, Noveck et al. (2004) studied 16 subjects (mean age ± SD = 26.7 ± 5.9) using measures of verbal "if-then" statements derived from symbolic logic (e.g., *modus ponens/modus tollens*). Subtraction of straightforward if-then inferences (e.g., *modus ponens*) from conditional inferences (e.g., *modus tollens*) yielded activations within the left frontal (BAs 9, 47), parietal (BA 40), and cingulate (BA 32) cortices. These authors noted that parietal activations were associated with "arbitrary" content such as found with symbolic relations (e.g., if A then B; A// therefore B), whereas frontal activation was observed as the reasoning problems became more similar to conversational exchanges. In a separate study by the same group (Goel & Dolan 2004) of 16 subjects (mean age ± SD = 27.5 ± 6.4), the main effect of reasoning was associated with activations in the bilateral frontal (BAs 6, 45), parietal (BAs 7, 40), temporal (BA 37), and occipital (BA 18) cortices.

Another group of researchers have used fMRI in a series of studies to ascertain brain regions associated with deductive reasoning, usually by way of presenting premise statements from which a subject is to draw a "relational" conclusion (e.g., [1] Bob is taller than Bill; [2] Bill is taller than Brian; [3] is Bob taller than Brian?). Knauff et al. (2002) studied 12 right-handed, male subjects (mean age ± SD = 23.9 ± 3.3) as they performed verbal or spatial-relational word problems. Activations were observed in the bilateral frontal (BAs 6, 9), anterior cingulate (BA 32), temporal (BAs 21, 22), parietal (BAs 7, 40), and occipital (BA 19) brain regions. This same group (Ruff et al. 2003) studied 12 volunteers (mean age ± SD = 24.0 ± 3.21) using problems of relational inference (e.g., left of, right of, overlaps from the left) that supported either a single conclusion (i.e., "determinate") or several conclusions (i.e., "indeterminate"), presented in an auditory format. They observed activations within the bilateral frontal (BAs 6, 10) and bilateral posterior cingulate (BA 31) cortices, the right parahippocampus, and the bilateral occipital (BAs 18, 19) cortex. Moreover, performance on the Block Design subtest of the WAIS (high *g*-loading) covaried negatively with precuneus (BA 7) activations during the reasoning task. A third study by this group (Knauff et al. 2003) used verbal relational reasoning problems (e.g., Bob is taller than Bill, etc.) to study brain activations in 12 German native speakers (age range = 21–35 years). These researchers found that performance of all inference problems compared to rest intervals was associated with activations in the left frontal (BAs 46, 47), right frontal (BA 6), bilateral parietal (BA 7), and both bilateral (BA 21) and left (BA 38) temporal cortices. Most recently, this group (Fangmeier et al. 2006) has hypothesized a three-stage model of deductive reasoning involving (1) premise processing, (2) premise integration, and (3) a validation phase. In 12 subjects (mean age ± SD = 22.4 ± 1.98), across all reasoning phases (as opposed to maintenance phases analogous to working memory), Fangmeier et al. found that brain activations were significantly predicted by performance of the high *g* Block Design subtest of the WAIS within the left cingulate cortex (BAs 23, 24, 31), frontal cortex (right BAs 4, 6, 8, 9, 10; left BA 46), bilateral precuneus (BA 7), basal ganglia, and thalamus. They noted a shift of activation from initial temporal-occipital activation, to frontal activation, and finally to parietal activation, the last of which they surmised is central to the reasoning process, as it is active only during reasoning, and not during working memory processes.

Gray et al. (2003) studied the relationship between working memory and intelligence with fMRI in a sample consisting of 48 young adults (age range = 18–37 years) who performed the RAPM while outside the scanner, and performed a three-back working memory task, comprised of either recurring words or faces, while undergoing the imaging protocol. "Target" trials consisted of stimuli repeated at three intervals following initial presentation; "lure" trials consisted of trials in which previously viewed stimuli were seen again, although not in the third position from initial presentation. Analysis of the data determined voxels of activation in which the magnitude of brain activity while performing "lure" trials of the three-back test was significantly correlated with performance on the RAPM. Results unconstrained to brain region indicated broad activation on the "lure" trials consisting of frontal (left BAs 45, 46; right BA 4), parietal (right BA 31, left BA 39, bilateral BA 40), and bilateral temporal (BA 22) cortices – areas consistent with earlier studies (Haier et al. 1988; Prabhakaran et al. 1997), although Gray et al. (2003) do not report evidence of an inverse relationship in these areas between activation and performance. Indeed, when controlling for lure-trial brain activity, activation within three regions including the left lateral prefrontal cortex and bilateral parietal cortex predicted 99.9% of the relationship between fluid intelligence and accuracy on the working memory trials with high interference, the strongest of which was the right medial parietal region (BA 31, r = .60). These authors concluded that fluid intelligence differences in brain activity emerged "almost exclusively" on working memory trials in which high interference was a factor; and that the lateral prefrontal cortex, "a key brain region suspected to support reasoning and novel problem solving ability," substantially mediates the control over such interference in attaining cognitive goals. This finding appears to contrast with that of the previous study (Fangmeier et al. 2006), which found reasoning to be associated with late parietal activation and working memory to be associated with frontal activation.

Geake and Hansen (2005) used measures of "fluid analogies" comprised of letter sequences in which the one right answer, of four possible choices, is inferred from an example problem and solution (e.g., abc → abd, ijk → ?). Twelve subjects (age range = 18–54 years) of above average intelligence (mean FSIQ = 119) were studied. At least two interesting findings emerged from this study. First, the regions in which fluid analogy

problem solving elicited activations were within predominantly bilateral frontal (BAs 8, 10, 12, 45, 47; also left BA 44, right BA 46), parietal (BAs 7, 40), and occipital (BAs 17, 18) regions, as well as the bilateral anterior cingulate cortex (BA 32). Second, these researchers found a linear relationship between a measure of verbal IQ (New Adult Reading Test) and the percentage change in the blood oxygen level dependent (BOLD) signal in several discrete frontal brain regions (BAs 9, 45, 46). Geake and Hansen concluded that their findings are consistent with research highlighting activation of the inferior parietal lobe and precuneus being related to solving visually presented, quasi-spatial problems (Goel & Dolan 2001; Knauff et al. 2002), and frontal activations being associated with working memory demands (Cabeza & Nyberg 2000).

Another fMRI study (O'Boyle et al. 2005) compared six mathematically gifted males with six average controls (mean age = 14.3). Math-gifted participants performed at the 99th percentile on both the Australian version of the SAT math section and on the Raven's Progressive Matrices test; average participants performed at the 50th and 70th percentiles, respectively, across measures. Subjects performed a mental rotation task while undergoing fMRI, and groups did not differ across accuracy or processing-time measures. Whereas both groups activated a similar fronto-parietal network during performance of the mental rotation task (i.e., BAs 6, 7, 9, 40), activations were significantly greater for gifted subjects in three brain regions: the right anterior cingulate (BA 32), left inferior parietal lobe (BA 39), and left premotor cortex (BA 6). Moreover, no significant group differences were found during a simple matching task relative to baseline. O'Boyle et al. noted that gifted individuals recruit a "quantitatively and qualitatively different brain network than [do] those of average math ability," with more bilateral activation, extensive activation of the parietal lobes, and "selective activation of the anterior cingulate and frontal cortex." They hypothesized that bilateral activation of the parietal, frontal, and cingulate cortices may be critical components of an "all-purpose" information processing network, "relied upon by individuals who are intellectually gifted, irrespective of the nature of their exceptional abilities."

Using a similar design, Lee et al. (2006) studied 18 gifted and 18 average Korean adolescents (mean age $\pm$ SD = 16.5 $\pm$ 0.8) as they performed *g*-loaded visual tasks of low and high difficulty. All subjects were administered the RAPM outside of the scanner, as well as the Korean version of the WAIS-R. Gifted subjects had exceptional performance on both the RAPM and the WAIS-R (>99th percentile), whereas average subjects were at the 60th and 63rd percentiles, respectively. The first finding of note was that a positive correlation was found between individual difference in *g* and cortical activation during a reasoning task, in apparent contrast to previous studies reflecting "neuronal efficiency," reported in non-gifted subjects (Haier et al. 1988), but consistent with other studies which also selected subjects on high and average ability (Haier & Benbow 1995; Larson et al. 1995). There were greater regional activations in the gifted group in the bilateral anterior cingulate (BA 32), prefrontal (BAs 6, 8, 9, 45, 46), parietal (BAs 7, 39, 40) and occipital (BA 19) cortices. When individual difference-based activations were correlated with individual *g* level, the activations were limited to a bilateral region within the superior parietal lobe (BA 7), the right inferior parietal lobe (BA 40), and the precuneus (BA 19). Lee et al. (2006) interpreted their findings as reflecting the neural underpinnings of superior intellectual ability, with robust activation of a fronto-parietal network, particularly the posterior parietal cortex. Whereas earlier work of one of these authors (Gray et al. 2003) focused predominantly on frontal regions underlying intelligence, their current work is consistent with a distributed view and implicates parietal regions consistent with the P-FIT proposed here.

Finally, in what can only be described as an fMRI "tour de force" (Schmithorst & Holland 2006), 323 children between the ages of 5 and 18 (mean age $\pm$ SD = 11.8 $\pm$ 3.7) performed a silent verb-generation task while undergoing a "child-friendly" (Holland et al. 2001; Petersen et al. 1988) functional MRI session. All subjects completed either the WISC or WAIS (mean IQ $\pm$ SD = 111.6 $\pm$ 13.9) and underwent fMRI scanning during which they silently generated appropriate verbs (e.g., "throw") associated with aurally presented nouns (e.g., "ball"). Across both sexes, significant activations were associated with intellectual performance during verb generation within the left frontal region (BAs 6, 44, 45), left anterior cingulate (BAs 24, 32), left (BA 21) and right (BA 22) temporal lobes, and left precuneus (BA 19). Schmithorst and Holland conducted connectivity analyses in which the main effect of FSIQ revealed connections between the precuneus and medial frontal gyrus (relative weighted functional connectivity = 1.0), with weaker connections between the medial frontal gyrus and cingulate (relative weighted functional connectivity = .25) and between the precuneus and medial temporal gyrus (relative weighted functional connectivity = .25). Sex differences were also found, although these are beyond the scope of this review. These authors hypothesized a developmental course of functional connectivity between posterior and anterior regions, mediated by sex, during the performance of a "low-*g*" task. They noted that the lack of activation within the lateral prefrontal and inferior parietal lobes is consistent with the Gray et al. (2003) study which showed activation within these regions related to performance of a high *g*-correlated working memory task. In contrast, according to Schmithorst and Holland, individual differences in "low-*g*" information-processing abilities like those studied by Haier et al. (2003b) appear to mediate the functional connectivity between visual association regions with the anterior cingulate and medial frontal gyri.

5.7. Summary of fMRI correlates of intelligence

As shown in Table 3 and Figure 4, the fMRI studies articulate the most broadly distributed network of regions associated with reasoning measures including tasks similar to the RAPM, visual and verbal analogical reasoning, logical reasoning, and playing reasoning games of chess and GO. Similarly, research in which subjects' performance on high *g* (i.e., working memory) or low *g* (i.e., verb generation) tasks was constrained by individual differences on intelligence measures in such a way as to articulate similar aspects of the P-FIT, particularly bilateral regions within the frontal and parietal cortices.

Table 3. *Functional magnetic resonance imaging (fMRI) studies demonstrating relationships between discrete Brodmann areas (BAs) and measures of intelligence and reasoning*

	N	Age of cohort	AC/PC	Frontal	Parietal	Temporal	Occipital	Reasoning measure
fMRI								
Prabhakaran et al. (1997)	7	23–30		B6, 9, 44, 45, 46	L7, 39, 40	L > R21, 37	L > R18, 19	RAPM
Goel & Dolan (2001)	14	28.6 ± 4.6		B6, 9	B7, 40		L17, 18 B19, Cb	RR
Knauff et al. (2002)§	12	23.9 ± 3.3	B32	B6, 9	B7, 40	B21, 22	B19	RR
Kroger e al. (2002)	8	19–32	B32	B6, 9, 47 L44, 46	B7			Matrix Reasoning
Gray et al. (2003)	48	18–37		L45, 46 R4	B40 L39 R31	B22		WM/RAPM
Atherton et al. (2003)§	6	24–33		L6, 8, 9	B7, 39, 40		B19 LCb	Chess
Chen et al. (2003)	6		B30, 31	B6, 9 L44, 45	B7, 40	B37	B19	Game-Random Condition
Luo et al. (2003)	10	20–25		L 9	L7, 40	B37	B19 L18	Analogies
Ruff et al. (2003)	12	24.0 ± 3.21	B31	B6, 10		R parahipp	B18, 19	Verbal Reasoning vs. Rest
Knauff et al. (2003)	12	23.7		L46, 47 R6	B7	B21 L38		Visual Inference vs. Rest
Goel & Dolan (2004)	16	27.5 ± 6.4		B6, 45	B7, 40	B37	B18	Inductive/ Deductive
Noveck et al. (2004)	16	26.7 ± 5.9	L32	L9, 47	L40			Conditional Reasoning
Geake & Hansen (2005)	12	18–54	B32	B8, 10, 12, 45, 47 L44 R46	B7, 40		B17, 18	Fluid Analogies
O'Boyle et al. (2005)	12	14.3	R32	L6	L39			Math Gifted vs. Normals
Lee et al. (2006)	36	16.5 ± 0.8	B32	B6, 8, 9, 45, 46	B7, 39, 40		B19	Visual Reasoning
Fangmeier et al. (2006)	12	22.4 ± 1.98	L23, 24, 31	R4, 6, 8, 9, 10 L46	B7		BG Th CC	Deductive Reasoning
Schmithorst & Holland (2006)	323	11.8 ± 3.7	L24, 32	L6, 44, 45		L21 R22	L19	WISC Verb Generation

Note: AC/PC = anterior cingulate/posterior cingulate; B = bilateral; L = left lateralized; R = right lateralized; RAPM = Raven's Advanced Progressive Matrices; RR = relational reasoning; WM = working memory; WISC = Wechsler Intelligence Scale for Children; parahipp = parahippocampus; Cb = cerebellum; Th = thalamus; BG = basal ganglia; CC = corpus callosum; § = men only.

As shown in Figure 4, more than 70% of these studies included activations within BA 7, and more than 60% activations within frontal BA 6 and parietal BA 40, providing strong evidence for posterior parietal lobe involvement across a vast array of reasoning tasks. Substantial bilateral activations (i.e., >40% of studies reviewed) were also observed within the frontal (BA 9) and occipital (BA 19) cortices, again left tending to be greater than right. Other regions in which activations were observed on a consistent basis (i.e., >30% of studies reviewed) included left > right parastriate cortex (BA18), left dorsolateral prefrontal cortex (BAs 45, 46), and the left anterior cingulate cortex (BA 32).

With these summary activation patterns in mind, we must not lose sight of the truism that all neuroimaging research is correlational by nature. However, fMRI has been under increasing scrutiny due to its high reliance upon inferences drawn from blood flow as opposed to neuronal processes per se (Arthurs & Boniface 2002; Logothetis & Wandell 2004). This potential problem is compounded by the rather infrequent reference to lesion studies in fMRI research to support such inferences (Fellows et al. 2005). Therefore, following the next section, we pay particular attention to lesion data towards the purpose of supporting the inferences used to define the P-FIT model.

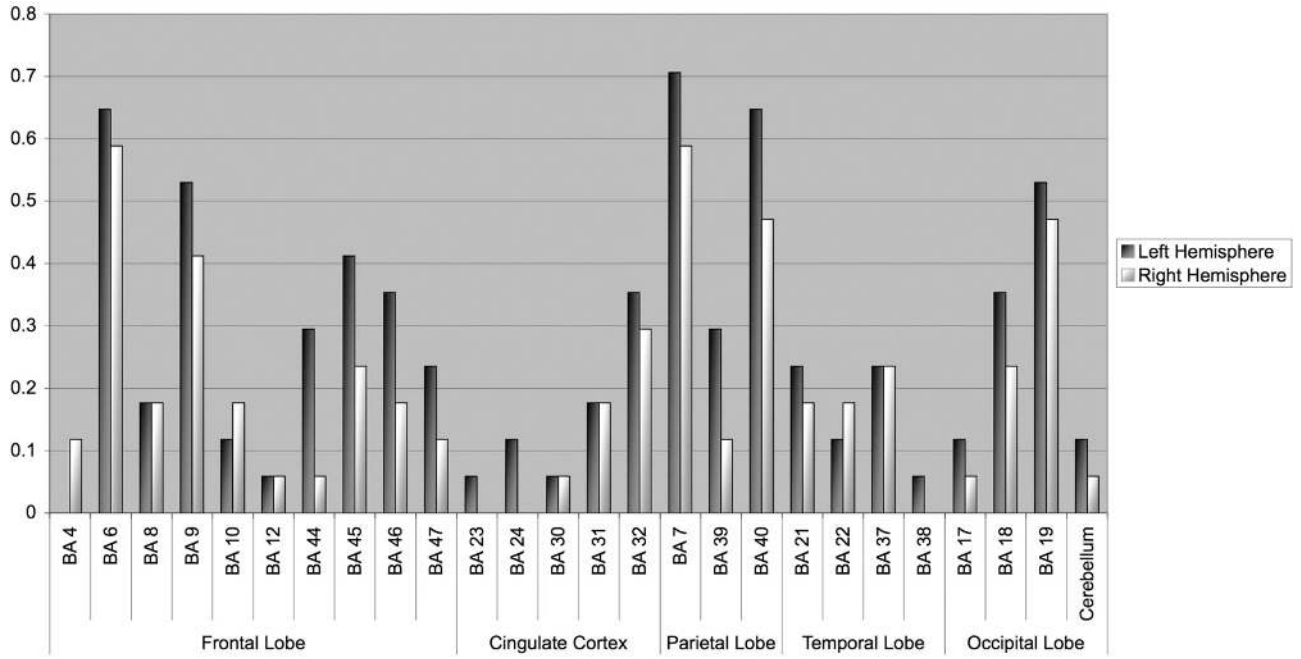

Figure 4. Graphical representation of the proportion (Y-axis) of fMRI neuroimaging studies describing relationships between intelligence and/or reasoning and discrete Brodmann areas by lobe (X-axis).

6. Where in the brain is intelligence? A tabulation of 37 neuroimaging studies[1]

To facilitate identifying common areas across studies, Figure 5 shows the overall tabulation of these brain areas from Tables 1 to 3, separately by hemisphere. Where studies explicitly identified such BAs, as commonly found in fMRI and VBM experiments, they are listed by region including anterior cingulate, frontal, parietal, temporal, and occipital cortices, as well as the cerebellum. In studies where such regional detail is not explicit, as found in some PET, DTI, and MRS studies of white matter, the nearest BA has been estimated.

Several interesting features are evident within the tables, summarized within Figure 5. For example, of the 37 studies identified, all but 10 found parietal activations/volume correlates with intelligence centered around BAs 7 and 40 but also inclusive of BA 39. Similarly, all but 11 of the studies were associated with frontal lobe activations/volume correlates relatively equally distributed between BAs 6 and 9, with somewhat fewer studies suggesting the addition of BAs 45 to 47. Occipital regions including BAs 18 and 19 were represented consistently across studies more than 30% and 40% of the time, respectively. Temporal BAs 21 and 37 also were well represented, although not quite as consistently. These occipital and temporal areas implicate early sensory processing, especially the ventral "what" and dorsal "where" circuit, which may be more subject to individual differences than previously appreciated (Haier et al. 2003b). Finally, the anterior cingulate (BA 32) was consistently related to intelligence measures across more than 30% of studies reviewed; it remains a strong biological correlate of intelligence, as both volume and activation of this structure were found across several studies. Overall, the network of brain regions that we designate as the P-FIT, summarized in Figure 1, appears to underlie individual differences in intellectual functioning in humans across the preponderance of studies. There is substantial overlap with brain regions associated with language functioning, including Wernicke's area (BA 22), the angular and supramarginal gyri (BAs 39, 40), white matter regions including the arcuate fasciculus, and Broca's area (BAs 44, 45).

The notion that parieto-frontal interaction underpins higher cognitive functioning is not a new one. To be sure, the interplay between parietal and frontal association cortices, evident across both human and nonhuman primates, has been described as both central to behavioral guidance (Kandel et al. 2000) and critical to maintenance of neuronal firing beyond the bounds of overt environmental stimulation (Goldman-Rakic 1987). Indeed, the very notion of consciousness was hypothesized to be related to interactions between parietal and frontal association cortices linking sensory with motor systems, respectively (Jackson 1932). Recent reviews regarding neuronal underpinnings of higher cognitive functioning, including the constructs of attention, episodic memory, working memory, consciousness, and intelligence, have touched upon various elements of this parieto-frontal integration, with most emphasizing predominantly frontal control over parietal integration (Deary & Caryl 1997; Duncan & Owen 2000; Gray & Thompson 2004; Naghavi & Nyberg 2005), although the directionality of control and how feedback loops moderate these interactions remain empirical questions.

Finally, on an ideographic note, we observe that a postmortem study found that Albert Einstein's brain was 15% larger than controls in the parietal lobe (Witelson et al. 1999), although this observation is not without controversy (Galaburda 1999; Hines 1998) and inferences from one exceptional intellect should be treated with caution (Burrell 2005).

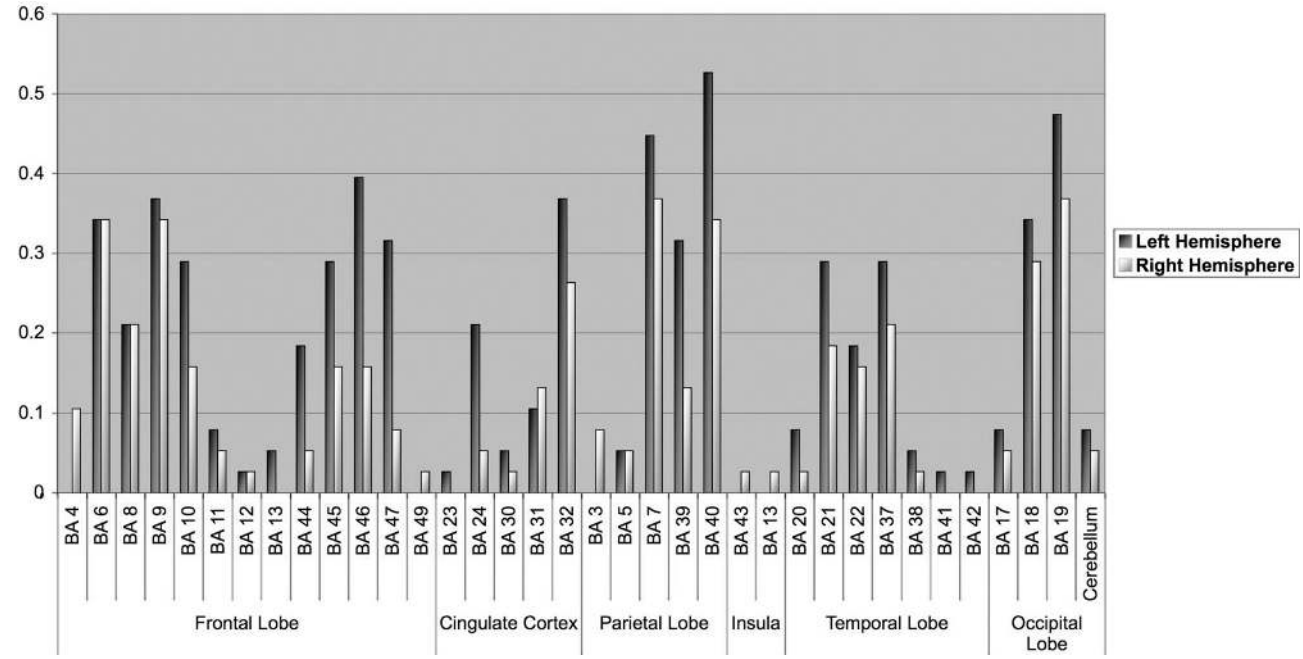

Figure 5. Graphical representation of the proportion (Y-axis) of all reviewed structural, PET, and fMRI studies describing relationships between intelligence and/or reasoning and discrete Brodmann areas by lobe (X-axis). These studies represent 1,557 subjects.*

*Brodmann areas (BAs) in which greater than 25% of studies found significant relationships between intelligence/reasoning and neuroimaging measures were included in Figure 1 as comprising the P-FIT. Furthermore, within a given BA that met this threshold, if hemispheric asymmetry ratio exceeded 10:7, then predominantly left hemisphere asymmetry was assumed. In BAs where the hemispheric asymmetry ratio was less than 10:7, bilateral symmetry was assumed.

7. Perspectives on the P-FIT network

7.1. Brain lesion studies

Lesion studies provide an excellent set of data to help evaluate the model that discrete regions distributed throughout the brain underlie intelligence, as opposed to the brain in its entirety or localization being in only the frontal lobes. The specific model we shall examine predicts that lesions within dorsolateral prefrontal (BAs 9, 45–47) and/or parietal (BAs 7, 40) regions will result in a decline in intelligence, whereas lesions outside of these regions will result in relative intellectual stability. The first test of the model may be inferred from the effects of high-velocity focal missile wounds incurred during the two world wars of the last century (Newcombe 1969). The advantage of this type of study is the relatively discrete nature of the injury, as opposed to large territory destruction resulting from other traumatic or cerebrovascular etiologies. Indeed, studies by Poppelreuter (1917), Kleist (1934), Goldstein (1942), Head (1926), and Luria (1963) added substantially to the field of behavioral neurology in explicating various structure–function relationships associated with discrete brain lesions. Germane to the current discussion, Weinstein and Teuber (1957) reported on a sample of 62 men who took the Army General Classification Test both before and after incurring missile wounds. After controlling for the presence of aphasia, only individuals with left parietal or parieto-temporal lesions had lower verbal intelligence than controls (for a review, see Newcombe 1969). In the largest sample of its kind, 97 servicemen from World War II with missile wounds (53 left hemisphere, 44 right hemisphere) were subjected to an extensive battery of psychometric measures (including the Raven's Progressive Matrices Test) and compared with age- and education-matched controls. Individuals with aphasia were excluded from the analysis. Of the lesion sites evaluated, those within right posterior brain regions were associated with the greatest difference in IQ between patients and controls, although the general conclusion was that missile injury was not associated with intellectual decline (Newcombe 1969).

Frontal leukotomy was a technique developed by Antonio Egaz Moniz to "calm" neuropsychiatric patients (a finding that won him the Nobel Prize in 1949), later popularized by Walter Freeman and James Watts in the United States. This technique involves severing the fronto-thalamic white matter connections, thus isolating the frontal lobes from other brain regions. Ward C. Halstead (1947), from whose work the opening epigram of this article is drawn, reviewed several studies in which psychometric measures were used to study patients undergoing prefrontal leukotomy (Freeman & Watts 1942; Hunt 1940; Hutton 1942; Kisker 1943; Porteus 1944; Porteus & Kepner 1944; Strom-Olsen et al. 1943). Indeed, for the Stanford-Binet test, postoperative IQs reported in the literature at that time ranged from 54 to 152, with a mean value of 108; the average drop in IQ postoperatively measured one point across studies. Several subsequent studies have confirmed that minimal if any decline in IQ results from frontal lobotomy (Cochrane & Kljajic 1979; Cumming et al. 1995; Stuss et al. 1983). Across several decades of study on the subject,

the generally accepted doctrine has remained that IQ scores are relatively impervious to damage of the frontal lobes, although more specific neuropsychological skills (e.g., judgment, planning, accommodation of novelty) may be affected adversely. Indeed, when intellectual deficits are reported following frontal lobe lesions, they almost invariably involve dorsolateral (BAs 44–47) cortical lesions.

Several studies have sought to determine the effects of temporal lobectomies on intellectual performance, providing another test of our model. A standard anterolateral temporal lobectomy involves removing 4 to 5 cm of lateral cortex (superior, middle, and inferior temporal gyri) and the parahippocampal formation (parahippocampal gyrus and hippocampus), thus leaving relatively intact the BA 37, as well as posterior aspects of BAs 21 and 22. Pediatric epilepsy is often treated with excision of the "lesioned" tissue, and the location of the lesion has been associated with intellectual deterioration: Children with posterior foci are at some threefold greater risk for intellectual disability than those with frontal or temporal loci (Helmstaedter & Lendt 2001). In a review of the available literature on intellectual changes following temporal excision, Lah (2004) reports that of 16 studies available, 3 showed a significant change in IQ post-surgery, and that those three studies suggested *increased* IQ compared to pre-surgical levels (Lewis et al. 1996; Miranda & Smith 2001; Westerveld et al. 2000). This finding is generally borne out in adult studies, which also find stability or even a slight *increase* in IQ following temporal lobe resection (Alpherts et al. 2004; Suchy & Chelune 2001; Wachi et al. 2001). Therefore, removal of the anterior portions of the temporal lobe does not appear to adversely affect intellectual performance.

Finally, we evaluate the P-FIT model with lesions to the dorsolateral and inferior parietal/superior temporal cortices, as often is found in populations suffering from acquired aphasia as a result of stroke. Research regarding the effects of aphasia on intelligence has been murky, with several researchers demonstrating decreased performance of aphasics on the Raven's (Costa et al. 1969), while others find no such differences (Archibald et al. 1967; Arrigoni & De Renzi 1964; Boller & Vignolo 1966; De Renzi & Faglioni 1965; Piercy & Smyth 1962), although aphasia type (i.e., expressive *versus* receptive) likely plays a role. Indeed, in an early study of 111 aphasic patients separated by type (i.e., global, Wernicke's, transcortical, Broca's, conduction), researchers Kertesz and McCabe (1975) found that individuals with global, transcortical, and Wernicke's aphasias performed significantly worse than those with Broca's or conduction aphasias or the controls on the Raven's Coloured Progressive Matrices (RCPM) test, a finding which they interpreted as reflecting the combined need for comprehension and visuo-spatial relations to perform the task well. Subsequent studies (Gainotti et al. 1986) have confirmed that Wernicke's and global aphasias preferentially affect intellectual performance independent of the effects of unilateral spatial neglect, although apraxia may play a role (Basso et al. 1981). Lastly, in an elegant study of the effects of lesion site upon performance of the RCPM in 159 unilateral brain damaged patients in which the presence of aphasia and visual field defects were controlled for, it was found that patients with aphasia performed worse on the task regardless of whether the visual fields were intact or not (Basso et al. 1973). These authors conclude that

> there is one region of the brain, overlapping the language area, which plays a major role in several different intellectual tasks, independent of their specific features. This might mean that several intellectual abilities are focally organized in this area, or, more likely, that the area sub-serves a super-ordinate ability entering into every intelligent performance and identifiable with the factor designated as "*g*" by psychologists. (Basso et al. 1973)

We should note at the conclusion of this "lesion" section that the increasing availability of rapid transcranial magnetic stimulation (rTMS) provides a further avenue to explore mechanistic relationships between discrete brain regions and intelligence. More experimental control is possible with rTMS than with lesion studies, the vast majority of which traverse several BAs and involve reorganization of function in patients over time. Although the state of rTMS research largely has been limited to discrete single stimulation points, we are quickly moving towards the ability to perform multichannel rTMS, by which discrete nodes within a network can be "lesioned" temporarily in a sequence guided by information provided by EEG/MEG during performance of a behavioral task. Experiments of intelligence and reasoning carried out with rTMS, then, may provide information regarding the necessary and/or sufficient contribution of discrete nodes, and the time-course of their involvement, within the network identified by the P-FIT as they relate to the manifestation of intelligent behavior.

7.2. Imaging genomics

A major domain of interest regarding biological mechanisms underlying intelligence and reasoning must include genetic inquiries, although this area of research is not without controversy (Gray & Thompson 2004). Indeed, a gradual evolution has occurred regarding "genetic determinism," wherein the paradigm has moved away from "one gene equals one protein" to multiple possible transcripts, alternate splicing, multiple proteins, and hence multiplicity of possible functions (Silverman 2004). Environmental factors likely interact with gene expression in a critical and complex interplay, which, at the level of an individual, weakens the notion of genetic determinism. Silverman (2004) took a strong position on the changing view of genetic determinism based on the extreme disparity between the relatively small number of human genes and the vast number of gene products:

> The evolutionary and developmental implications of multiple expression variants are profound and suggest a tectonic shift from sole reliance on single mutations or nucleotide polymorphisms as a source of potential variation. Through combinatorial interactions, these expression variants increase, by a million fold or more, the raw material for evolutionary development. (p. 32)

This exponential variability of genetic variation is a model that offers the requisite number of possibilities for natural selection to occur (on the order of billions as opposed to 30,000), and suggests that microevolutionary events can occur within the scale of human existence, leading to the expression of intelligence associated with massive brain expansion.

That being said, several studies comparing monozygotic twins have indicated a strong heritability of gray matter, white matter, and total brain volume, ranging from .6 to .9 (Winterer & Goldman 2003). Moreover, both total brain volume and intelligence have been found to be under substantial genetic influence (Pennington et al. 2000; Posthuma et al. 2002; Thompson et al. 2001; Tramo et al. 1995), although two studies do not support such an association (Reiss et al. 1996; Schoenemann et al. 2000). More specifically, the heritability of white matter volume/intelligence relationships is complicated by the relative lack of localization ability when compared with gray matter volumes. However, in a recent study of 24 monozygotic twin pairs, 31 dizygotic pairs, and 25 sibling pairs (Posthuma et al. 2002), researchers found that the observed volume/intelligence correlations were roughly equal across both gray and white matter volumes ($r = .25$ and .24, respectively). Recalling our earlier discussion of two genes associated with total brain size which have recently emerged (Evans et al. 2005; Mekel-Bobrov et al. 2005), we would also anticipate that the *ASPM* and *microcephalin* genes are strong candidates for mediating the relationship between gray and white matter volumes within discrete brain regions identified within the general P-FIT.

Specific to regional gray matter volumes, one important study outlining genetic contribution to brain volume was carried out in 40 individuals: 10 monozygotic and 10 dizygotic twin pairs (Thompson et al. 2001). These researchers found that frontal gray matter volume was most related to FSIQ ($F = 9.37$, $p < .0176$ corrected for multiple comparisons). Interestingly, they found that gray matter volume was under "significant genetic control" in regions including frontal and language-related cortices. More specifically, gray matter volumes of monozygotic twins were correlated 95% to 100% in frontal lobe (BAs 9 and 46), linguistic areas including Broca's (BA 45) and the supramarginal region of Wernicke's areas (BA 22), and parieto-occipital association cortices. Fraternal twins had 90% to 100% convergence in gray matter volumes in the supramarginal (BA 40), angular (BA 39), and Wernicke's (BA 22) areas of the brain. These regions largely overlap the major regions identified by the P-FIT model, which suggests the possibility of major genetic contributions to intellectual functioning associated with dorsolateral, linguistic, and parieto-occipital association gray matter volume. It should be noted that correlations between measures of FSIQ and gray matter volume were significant only for the frontal lobes when whole brain size was controlled statistically; however, the relatively low statistical power may have limited the ability to detect such relationships in other brain regions (e.g., temporal gray matter volume in this study reflected a statistical trend of $p = .06$).

The mechanisms by which genetic factors interact with environmental constraints to affect gray matter volume within the P-FIT (and thus intelligence) are currently unknown. We are not aware of any studies combining neuroimaging, genetics, and assessment of individual differences in intelligence simultaneously. Future studies using broad measures of cognitive functioning, from which a measure of *g* might be extracted, in large samples of monozygotic and dizygotic twins, undergoing various neuroimaging paradigms, will be important. Such studies would be powerful in providing data to address which aspects of greater cortical volume are salient for the reported relationships with intelligence.

8. Concluding remarks

Despite the sometimes contentious controversy about whether intelligence can or should be measured, the array of neuroimaging studies reviewed here demonstrates that scores on many psychometrically based measures of intellectual ability have robust correlates in brain structure and function. Moreover, the consistencies demonstrated among studies further undermine claims that intelligence testing has no empirical basis. Schizophrenia research in the 1970s moved beyond controversies of whether it was a brain disease or a social construct following studies of genetic and biological correlates. Intelligence research also now can move beyond skepticism of psychometrics to detailed explorations of individual differences in the brain. In fact, the cognitive problems associated with schizophrenia and the loss of cognitive abilities that characterizes dementia are the other side of the coin to understanding the neural basis of normal intelligence.

Most of the neuroimaging research on intelligence is in a nascent stage. As shown here, various image-acquisition methods are available, each with relative strengths and weaknesses. Similarly, various image-processing and statistical techniques also are available, each requiring different assumptions. The technical issues raised by each approach are quite numerous and complex and, therefore, were not detailed in this review. They include, for example, how best to correct for multiple comparisons, and how and when to correct for whole brain size. There are also different approaches to assessing intelligence, the *g* factor, and reasoning. Study designs also differ; some compare tasks that are differently related to intelligence measures, whereas others compare subjects who differ on intelligence measures.

Despite these issues, there is much neuroanatomical consistency among results, which we have described as defining a specific frontal/posterior network we term "the P-FIT model." We emphasize that this is very much still a hypothesis and much additional research will be needed to further explicate the neural basis of intelligence. The provisional empirical support we have reviewed may become more compelling as new neuroimaging studies of intelligence are completed using much larger sample sizes, and which incorporate experimental research designs to help determine the relationships between the salient brain areas and the cognitive processes they enable or control. Many of the areas implicated by the P-FIT, for example, have been related to fundamental cognitive processes including working memory and attention (Cabeza & Nyberg 2000; Chabris 2006; Naghavi & Nyberg 2005), although a comprehensive discussion of this literature is beyond the scope of this review.

It must also be noted that there are likely other brain regions critical to intelligence and the implementation of intelligent behavior, including regions identified in studies of discrete cognitive processes, such as the basal ganglia, thalamus, hippocampus, and cerebellum. Based on the research designs of the neuroimaging studies reviewed, we believe that the P-FIT regions are those in

which individual differences account for intellectual performance, especially areas of association cortex which serve to integrate information among brain areas. That is to say, other brain regions are so critical to brain functioning in general that individual differences in chemical composition, diffusion anisotropy, volume, and blood flow are minimized to ensure reliability across fundamental functions. What the P-FIT likely represents are brain areas in which individual differences are expressed less encumbered by day-to-day housekeeping or maintenance operations. Such a differentiation is somewhat similar to one based on a systematic study of the effects of lesions on problem-solving performance in rats (Thompson et al. 1990). Thompson et al. showed that six brain areas loaded on a *g* factor extracted from performance on many problem-solving tasks), whereas eight areas were important for performance on all problems. The former areas (parietal cortex, occipitotemporal cortex, posterior cingulate, dorsal hippocampus, posterolateral hypothalamus, superior colliculus) were termed necessary for "psychometric" intelligence; the latter eight areas (substantia nigra, ventral lateral thalamus, globus pallidus, dorsal caudatoputamen, median raphe area, superior colliculus, pontine reticular formation, ventral tegmental area) were termed "biological" intelligence (see also Haier 1993a).

Although we have chosen not to include data from EEG and MEG studies in this review due to space limitations, it is important to recognize that only by integrating the spatial localization provided by the studies reviewed herein with the temporal resolution possible with EEG/MEG, may we truly talk about "networks" in the brain underlying intelligence, reasoning, and higher cognitive functioning. For example, we have hypothesized that some activations within certain experimental paradigms might be "task dependent." By integrating spatio-temporal information (e.g., simultaneous EEG-fMRI or cross-platform fMRI-MEG experiments) one might expect to see a clarification of the relationships between performance and brain function/structure both within and outside of the network identified in the P-FIT. Indeed, several newer studies are beginning to integrate fMRI with MEG information to exploit their relative spatial and temporal strengths (Huang et al. 2005). We would expect that the integration of spatial and temporal techniques will be an area of keen interest to intelligence research, as it may shed light upon the interactions of reaction time with *g* (Thoma et al. 2006), further our understanding of "neural efficiency" in the brain (Grabner et al. 2006), and may even outline productive genetic inquiries regarding mechanisms by which intelligence is manifested in the brain.

Although this review emphasizes the consistencies among studies, there are important inconsistencies and potential conflicts to resolve. For example, as noted by Haier et al. (2004), higher intelligence appears to be related both to increased gray matter and to decreased GMR under certain conditions, the latter finding often interpreted as evidence of brain efficiency (Haier et al. 1988; Neubauer et al. 2002). Brain efficiency (i.e., lower GMR in subjects with higher intelligence) may result because the availability of more gray (or white) matter resources in finite areas reduces the overall brain work required to address a specific problem. A related issue of great importance is whether gray matter increases as a result of practice and learning, as suggested in recent research (Draganski et al. 2006). Such plasticity would challenge some of the relatively simple ideas about how the genetic contributions to intelligence may work, especially as a limiting factor, and lead to rethinking genetic determinism, as suggested by Silverman (2004).

Another central issue of potential inconsistency relates to possible sex differences regarding the strength and/or applicability of the P-FIT. Indeed, our group of researchers has found that sex differences exist with regard to PET activations during mathematical reasoning (Haier & Benbow 1995), with respect to relative tissue volume correlates of intelligence (Haier et al. 2005), and with regard to the strength of chemical correlates of intelligence within frontal lobe white matter (Jung et al. 2005). Several other groups have noted sex differences related to intelligence and higher cognitive functioning (e.g., Gur et al. 1999; Pfleiderer et al. 2004). Sex differences were not noted in the recent Shaw et al. (2006) study of brain development and cortical thickness, although strong sex differences were found in our structural study of adults (Haier et al. 2005) and in Schmithorst and Holland's (2006) fMRI study of young people. Although most research shows no sex difference in FSIQ, there is some suggestion that there may be a small difference favoring males (Nyborg 2005), so whether the P-FIT applies equally to both males and females is an open question, and we expect that the P-FIT will be modified as more data become available. At this point, it does appear that, across several studies and groups, the relationship of intelligence to white matter volumes, chemical composition, and perhaps water diffusivity may be higher in women than in men.

9. The future

In addition to age and sex analyses in larger samples, future studies should also use multiple measures of cognitive skill and intellectual ability so the *g* factor can be extracted separately from measures of general intelligence and from specific cognitive abilities. Finally, individual differences in intelligence measures among subjects must be studied as they relate to differences in brain characteristics not easily assessed with current technology, such as the size or efficiency of specific networks or characteristics of individual neurons (e.g., mitochondria activity). Once the relevant parameters are established, drug challenges to excite or inhibit specific pathways in combination with neuroimaging techniques may provide the experimental data necessary to identify specific neurochemical mechanisms that underlie intelligence (Mozley et al. 2001). These studies may be particularly informative in groups defined by neurological conditions such as mental retardation, as well as for those in the normal range of intelligence. This new phase of research will move beyond the current correlational limitations of neuroimaging studies, which address questions of individual differences and of "where" in the brain is intelligence. Rather, this next generation of research will engage individual differences in a direct manner, perhaps articulating for the first time "how" intelligence evolved, how brain development influences intelligence, and how neurological and psychiatric diseases cause cognitive decline. As neuroimaging and molecular techniques advance, each generating

hypotheses to inform the other, the scientific study of intelligence is poised to exceed the hopes of pioneers such as Spearman, Binet, and Halstead.

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NOTE

1. We consider Duncan et al. (2000) to comprise one study of two distinct experimental conditions. Although we refer to them separately in the table, we consider this to be one study as related to the discussion in section 5.4.

Open Peer Commentary

Inherent limits on the identification of a neural basis for general intelligence

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Abstract: The target article provides a thoughtful review and synthesis of studies examining the neural basis of cognitive abilities associated with intelligence test performance. In its attempt to present a new or generative theory of the neural basis for intelligence, however, the review faces specific limits to its theoretical model that relate to processes of development and the role of automaticity in cognition.

When Jung & Haier (J&H) provide a brief summarization of the P-FIT model in the target article (sect. 4, para. 3), they are describing one aspect of what can be considered intelligence. Their focus is on reasoning abilities and on what are referred to as effortful cognitive processes: early attentionally directed processing of information in the parietal cortex and coordination of information, information maintenance, and inhibition of prepotent or distracting information and responding through interconnected frontal and parietal cortical circuitry. The broad aspect of cognitive ability that is the focus of their review is generally referred to as working memory, executive function, or fluid cognition and can be considered quintessential higher-order cognition. However, although fluid abilities, broadly speaking, have been assumed to underlie general intelligence, a variety of information indicates this is not the case. As I outlined in a prior target article in this journal (Blair 2006), despite numerous studies indicating near unity between working memory and general intelligence (e.g., Colom et al. 2004), an equally numerous body of studies both with special populations (Duncan et al. 1995; Waltz et al. 1999) and with historical cohort data (Flynn, in press) indicate dissociation between fluid cognitive abilities and general intelligence. Accordingly, the P-FIT model could more accurately be described as a theory of the neural basis for working memory/executive cognitive abilities, and as such generally has broad consensus.

As the data presented in the target article indicate, reasoning ability, measured in a variety of ways, is associated with a distributed cortical network primarily involving fronto-parietal circuitry. It is interesting to note, however, that early research on the neural basis for working memory focused primarily on the frontal cortex, and that the role of the parietal cortex in individual differences in working memory and reasoning ability has only recently become clearer. Specifically, several studies indicate that a higher level of ability/expertise, both within and between age groups, is associated with increased parietal – as much as or more so than frontal – cortical activation (Klingberg et al. 2002; Lee et al. 2006). An anterior to posterior shift with increasing expertise is a characteristic of learning and improved performance on a wide variety of cognitive tasks. As tasks become less difficult, individuals utilize posterior cortical regions more so than frontal ones. This focus on individual differences and task difficulty has been an important advance in research on the neural basis for fluid cognition. It is one that highlights the role that method and experimental design play in attempts to identify the neural bases for a given cognitive ability. In relation to the neural basis for individual differences in working memory or relational reasoning, it is necessary to ask: Should the focus of imaging research be on brain areas active in response to the most difficult problems that only high-IQ individuals can solve? Or should it be on differences in brain activity in high- and low-IQ individuals in response to problems that are solvable by most people? The two approaches are likely to lead to different conclusions about brain areas associated with intelligence. For working memory, prefrontal cortical activation primarily discriminates high- from low-IQ individuals when problem difficulty is increased by highly distracting elements (Gray et al. 2003). Among reasoning problems, however, when difficulty pertains primarily to complexity of relations among problem elements, activation in the parietal cortex primarily discriminates high- from low-IQ individuals (Lee et al. 2006).

From the foregoing, one might conclude, contrary to J&H, that the neural basis for individual differences in intelligence relates not to particular brain areas but in the application of relevant brain areas to a given task or problem. As with one of the target author's prior findings for glucose metabolic rate using PET (Haier et al. 1988; Haier et al. 1995), higher-IQ individuals require fewer, not greater, resources to solve problems that are generally solvable by most people. This likely has important implications for the investigation of the neural bases of other aspects of cognition associated with intelligent behavior, such as memory, language, inspection time, speed of processing, and so on. It may also suggest that there are no specific cortical areas that underlie intelligence, but that individual differences in intelligence reflect aspects of brain function that enable more efficient use of cortical structures and resources that are associated with specific cognitive abilities.

Future work that takes a resource utilization/efficiency approach to the study of the neural basis for reasoning could profitably consider processes of development and automaticity. Developmental imaging studies of reasoning abilities, such as simple relational reasoning or basic mathematical calculation (i.e., single-digit addition or subtraction), indicate a frontal to parietal shift with age. In these tasks, age is negatively correlated with frontal and striatal activation and positively correlated with parietal activation (Eslinger et al., submitted; Rivera et al. 2005). Significantly, these differences are observed even in the absence of a relation between accuracy in problem solving and age. These findings suggest a process in which the less-expert problem solver relies on active, more resource-intensive processes of information maintenance and coordination of procedural knowledge required for problem solution associated with the frontal cortex and striatum. In contrast, the more-expert problem solver requires presumably fewer cognitive resources and exhibits increased parietal activation associated with a more automatic

and efficient arrival at problem solution. But does this mean that the more-expert, older problem solver is more intelligent than the less-expert, younger problem solver? The differences in brain activity are associated with age and experience, not intelligence – at least not as the construct is commonly understood. Traditional theories of general intelligence have struggled to incorporate development and experience in meaningful ways and have never really succeeded in doing so, despite an excellent start in this direction (Hunt 1961). Attempts to consider the neural basis for general intelligence must also clearly articulate a clear understanding of the role of experience and development.

In conclusion, consideration of development and automaticity in brain function points to an overarching issue for the P-FIT theory – specifically, the idea that general intelligence is a mathematical abstraction, not a thing in itself. As such, the search for its neural basis may ultimately prove futile. In contrast, the search for the neural basis for components of intelligence, for specific cognitive abilities, has been and will likely continue to be very productive.

Selecting between intelligent options

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Abstract: In this commentary we make two rejoinders to Jung & Haier (J&H). First, we highlight the response selection component in tasks as a confounding variable that may explain the parieto-frontal involvement in studies of human intelligence. Second, we suggest that efficient response selection may be an integral part of the definition of intelligence.

Jung & Haier (J&H) have reviewed 37 neuroimaging studies and concluded that the parietal cortex is part of a network associated with better performance in intelligence and reasoning tasks. Moreover, they have suggested that the interaction between the parietal cortex and the prefrontal regions supports the existence of a parieto-frontal integration theory (P-FIT) of intelligence. The meta-analysis approach that J&H have adopted is most welcome. However, we would like to point out that the activation of this same neuronal network is common to many mental operations that may not be related to intelligence. As there is therefore no unique relationship between the parieto-frontal network proposed and intelligence, we need to ask what other functions provide a competing fit.

J&H adopt the American Psychological Association (APA) definition of intelligence, according to which, "Individuals differ from one another in their ability to understand complex ideas, to adapt effectively to the environment, to learn from experience, to engage in various forms of reasoning, to overcome obstacles by taking thought" (target article, sect. 3, para. 1). A striking omission, or at least ambiguity, in this (most agreed upon) definition is the lack of a clear role for *response selection*. Response selection is interface between perception and action that allows one to choose the most adequate response among alternatives. Crucially, response selection in tasks recruits the parietal cortex, as well as the prefrontal lobe (Bunge 2004; Bunge et al. 2002b; Cohen Kadosh et al. 2007; Göbel et al. 2004; Jiang & Kanwisher 2003; Rosenthal et al. 2006). Moreover, it seems that a parieto-frontal network is activated under conflict situations and when response selection is required (e.g., Brass & von Cramon 2004; Cohen Kadosh et al. 2007; Rushworth et al. 2001; Zysset et al. 2001). In terms of the definition of intelligence adopted in the target article, one could rewrite that in order to "adapt effectively to the environment, to learn from experience, to engage in various forms of reasoning, to overcome obstacles by taking thought" one must *respond effectively to the environment, learn which responses to (not) use again, and overcome obstacles by taking action.* Indeed, the greater number of behavioural alternatives an intelligence can generate, the more important is the role of selection between possibilities.

In general, the neuroimaging studies reviewed by J&H did not control for a response selection component in their measurement. Hence, the correlation between IQ and the parieto-frontal network, as assessed by structural changes (e.g., voxel based morphometry [VBM], diffusion tensor imaging [DTI]) or functional neuroimaging (PET, fMRI), may suffer from confounding of IQ and response selection. If IQ and response selection tap different mental processes, future studies aimed at revealing the brain mechanisms underlying IQ should take into account this possibility in order to unconfound response selection and IQ – if indeed one thinks it desirable to take action out of intelligence.

We would argue that it is possible and desirable that response selection should be regarded as an integral part of intelligence. Indeed, most of the tests, assumed to measure intelligence, request that the participants choose among alternatives and take into consideration the number of correct answers and speed of processing in calculating one's IQ score. Moreover, at least in Western culture, the ability to quickly choose a correct response is a virtue that can help in various areas such as driving, shopping (very important), and other tasks which enhance life. Having response selection as an important component of intelligence would necessitate casting a different eye over the finding that a parieto-frontal network appears to be related to intelligence. It is important to establish, for example, whether these structures are involved in IQ only because of the response selection component of IQ tasks or also because of other aspects of IQ. Moreover, it would be interesting to find out how much of the variance in IQ is contributed by the various components. This could help us understand the relationship between the parieto-frontal role in IQ and the role of the parieto-frontal network in human mental experience in general.

The argument made by J&H is therefore, in our view, limited in two ways. We can either conclude that the network outlined is no more than an amalgam of areas involved in many task components that may be related to intelligence in some way. Or we may conclude that the network lacks specificity because an important component of intelligent *behaviour* is not taken into account.

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Intelligence? What intelligence?

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Abstract: Neuroimaging evidence, both within and between research strategies, is largely heterogeneous. This results from the way the

construct of interest (i.e., intelligence) is measured. Every single available measure comprises several cognitive abilities, although the so-called *g* factor is always present. Here I suggest that studies must always control for this empirical fact to arrive at solid conclusions.

Theories are necessary for stimulating scientific inquiry. We have mountains of data, but weak theories. Therefore, the theoretical attempt by Jung & Haier (J&H) must be applauded. The search for converging evidence from a wide variety of empirical studies about the biological substrate for the psychological construct of intelligence is welcome.

However, I found some problems seeing the convergence J&H support. Only a very small number of discrete brain areas approach 50% of convergence across published studies employing the same neuroimaging strategy. First, structural studies nominate 32 brain areas, but only Brodmann areas (BAs) 10 and 39 to 40 50% of convergence. Second, PET studies nominate 22 brain areas, but only BAs 18 to 19 and 46 to 47 enjoy 50% of convergence. Third, fMRI studies summarily nominate 26 brain areas, but only BAs 6, 7, 9, 19, and 40 reach 50% of convergence. Furthermore, structural and functional results are not consistent. Of those brain areas approaching 50% of convergence, no one overlaps across neuroimaging research strategies. These empirical facts are not a good basis to support an integration theory of intelligence. Admittedly, this is not the authors' fault, but rather, a result derived from the heterogeneity of the available evidence.

My view is that (a) the proposed theory may or may not be correct, and (b) its likelihood cannot be supported (or rejected) by the collected data. I do think the theory is promising, but expressly designed empirical studies to appropriately test it are strongly required.

The P-FIT model postulates that, at a first stage, temporal and occipital brain areas process sensory information: BAs 18, 19, and 37 for visual material and BA 22 for acoustic processing. The second stage implicates integration and abstraction of this information by parietal BAs 7 and 39 to 40. Further, these parietal areas interact with the frontal lobes, which serve for problem evaluation. Frontal BAs 6, 9, 10, and 45 to 47 are highlighted by the P-FIT model. The anterior cingulate (BA 32) is then invoked for response selection and inhibition of alternative responses. Finally, white matter plays a critical role for a reliable circulation of information across these brain processing units.

Nevertheless, J&H do believe that not all these brain areas are really germane for human intelligence. Actually, they predict that only the discrete brain regions of the dorsolateral prefrontal cortex (BAs 9, 45 to 47) and the parietal cortex (BAs 7 and 40) will affect intelligent performance. However, examining the collected structural and functional evidence, it is difficult to conclude that their view is supported.

First, the strongest structural data points to frontal (BA 10) and parietal (BAs 39, 40) areas, relatively consistent with the authors' prediction. However, the PET data are consistent only with the authors' prediction regarding frontal BAs 46 and 47, not regarding the occipital BAs 18 and 19. The fMRI data are consistent with the authors' prediction with respect to frontal BA 9 and parietal BAs 7 and 40. But BAs 6 and 19 are not within the authors' framework. Therefore, only a minority of the identified brain areas overlaps with the central brain areas proposed by the P-FIT model. Structural and functional data identify a great number of discrete brain areas (see Figs. 2, 3, and 4 of the target article) and only a small number overlap with the P-FIT model.

Why is the evidence so heterogeneous? Several are the tentative alternatives, such as age, sex, and representativeness of the analyzed samples; but I think the key resides in the measurement of the construct of human intelligence.

Intelligence can be defined as a "general mental capacity . . . involving the ability to reason, plan, solve problems, think abstractly, comprehend complex ideas, learn quickly, and learn from experience" (Gottfredson 1997, p. 13). However, this definition neglects the theoretically important distinction between "intelligence in general" and "general intelligence" (Colom et al. 2002; 2006a; 2006b; Jensen 1998). Typical psychometric intelligence scores, such as Full Scale IQ, measure "intelligence in general" comprising an array of cognitive abilities and skills in addition to general intelligence, or the *g* factor. We already know that (a) the *g* factor is the main component of the intelligence construct (Lubinski 2004) and (b) not all intelligence tests measure the *g* factor of intelligence to the same degree (Jensen 1998).

Intelligence tests can be classified according to the degree to which they involve the *g* factor. The *g*-loading for test X relates to its average correlation with all the remaining tests in a comprehensive test battery: the higher its average correlation, the larger its *g*-loading. From a theoretical standpoint, a high *g*-loading for test X can only result from the fact that it shares a large amount of mental processes with the other tests in the battery (Arend et al. 2003). Therefore, a test with a perfect *g*-loading should comprise most of the mental processes germane to the general factor of intelligence (*g*). Available measures of human intelligence confound *g* with other cognitive abilities and skills (Colom et al. 2002).

Neuroimaging studies on human intelligence must refine the way this construct is measured. Different measures will result in different structural and functional correlates. We do need to know the causes underlying these discrepancies, and J&H are sensitive to this central issue. Actually, we have shown that as the *g*-loading of a given intelligence measure increases, more widespread discrete brain areas become involved (Colom et al. 2006a). Importantly, this increased recruitment is not related to the superficial characteristics of the measurements, like their verbal or nonverbal nature.

In conclusion, not every intelligence measure taps the intelligence constructs in the same way. Heterogeneity is an inevitable result derived from the lack of consensus regarding the question of the most appropriate avenue to get measures of the complex construct of human intelligence. If the *g* factor is its core component, but available measures tap this component to quite different degrees, then obtained data will be hardly comparable.

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A roadmap for integrating the brain with mind maps

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Abstract: This commentary compares the P-FIT model with psychometric and developmental models of intelligence and shows that there are isomorphisms and divergences between them. All three models involve some common dimensions, but the P-FIT model lacks many of the dimensions of the other models. Then we point to research that can lead to the integration of brain models with cognitive-developmental models.

This commentary discusses the target article from the point of view of a cognitive-developmental theory of intelligence. We first examine whether the P-FIT model is consistent with psychometric and developmental models of intelligence. Then we show the limitations of the P-FIT model and raise questions that must be answered to ameliorate these limitations.

Mapping the P-FIT model onto a PSY-DEVO model. The target article claims that general intelligence is distributed over a wide network of brain areas (see Fig. 1 of the target article) that serve different functions and are associated with different stages in information processing. Individual differences in the volume, quality, efficiency, and connectivity of the neuronal ensembles involved, and the underlying white matter, are associated with individual differences in general IQ. This architecture is generally consistent with the architecture of intelligence as suggested by psychometric (Carroll 1993; Jensen 1998; Gustafsson & Undheim 1996) and development research (Demetriou 2006; Demetriou et al. 2002; Demetriou & Kazi 2006), hereafter called the PSY-DEVO model.

Our Figure 1 summarizes this model. The model involves four kinds of factors: (1) A set of first-order factors (PS) standing for content-free processes common to all cognitive tests, such as processing speed, inhibition, and working memory. These processes define psychometric *g* (Jensen 1998) and fluid intelligence (Blair 2006). (2) A set of first-order domain-specific factors (DS) standing for specialized mental abilities, such as spatial, categorical, verbal, numerical, causal, and social reasoning. (3) A set of second-order factors (REAS) standing for reasoning processes. (4) A set of higher-order hypercognitive factors (HC) standing for processes used to monitor, regulate, and coordinate the processes underlying all the other factors.

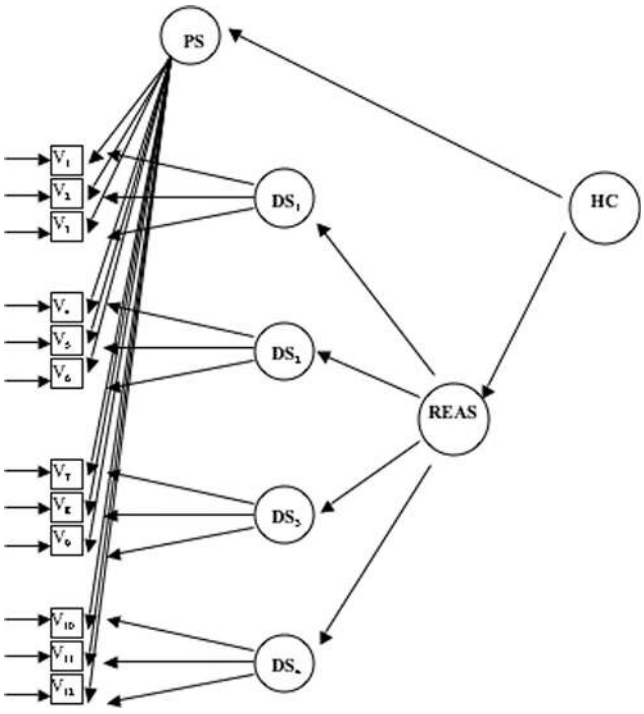

Figure 1 (Demetriou). Abstract representation of the psychometric-developmental architecture of the mind. PS represents a set of first-order factors standing for processing efficiency and capacity. DS represents domain-specific factors standing for different domains of thought. REAS represents second-order factors standing for inductive and deductive reasoning. HC represents factors standing for hypercognitive self-monitoring and self-regulation processes. V stands for observed variables.

In developmental time this architecture remains fairly stable, but the state of the processes and their interrelations change. Specifically, speed of processing increases, efficiency of inhibition and executive control improves, working memory expands, inferential processes become increasingly complex and abstract, and awareness and self-regulation of mental processes become increasingly refined and effective (Demetriou et al. 2002; Demetriou & Kazi 2006). Changes in speed and inhibition efficiency pave the way for working memory expansions and development in inferential processes. However, dynamic patterns of change vary with life phase. In childhood, development of reasoning depends extensively on the development of processing efficiency (55% of variance) and working memory (13% of variance), and a part of it (24% of variance) depends on changes that are specific to it (Demetriou et al. submitted; Mouyi 2007). However, changes in reasoning in adolescence and adulthood are associated with changes in self-awareness (circa 40%) rather than in efficiency (Demetriou & Kazi 2006).

Mapping the P-FIT onto the PSY-DEVO model suggests some interesting isomorphisms. Specifically, the sensory areas involved in the P-FIT model are more related to the domain-specific factors of the PSY-DEVO model. The parietal areas of the P-FIT model are related to the inferential and meaning-making processes applied on domain-specific content of the PSY-DEVO factors. The frontal areas of the P-FIT model are related to working memory, attention, and executive control of the PSY-DEVO model. Finally, the anterior cingulate of the P-FIT model is related to hypercognitive intentional planning and conscious selection of responses in the PSY-DEVO model. Changes in the state and interrelations of processes in the PSY-DEVO model are associated with changes in brain volume, myelination, connectivity, and neuronal pruning of the P-FIT model. These isomorphisms support Jung & Haier's (J&H's) conclusion that empirical evidence justifies detailed explorations of individual differences in the brain. Despite this optimism, however, a feeling of "so what?" remains after reading the target article, because very little is said about issues that are important for cognitive and developmental science. In the next subsection we formulate some of these issues.

Questions for a NEURO-PSY-DEVO model. It is noted, first, that there is more to the brain bases of general intelligence than is specified in the P-FIT model. According to Osherson et al. (1998), even very general inferential processes, such as inductive and deductive reasoning, are served by different neural networks (frontal gyrus and the right insular cortex for inductive reasoning and associative visual areas; the right superior parietal lobule and thalamus and the right anterior cingulate for deductive reasoning). Even the same type of reasoning, such as deductive reasoning, activates different networks depending upon the information to be integrated (Goel et al. 2000). Specifically, content-based propositions activate temporal (BAs 21/22) and frontal regions (BAs 44, 8, 9). Formal propositions activate occipital (BAs 18, 19), left parietal (BA 40), bilateral dorsal frontal (BA 6), left frontal (BAs 44, 8, 10), and right frontal (BA 46) regions. Moreover, both types of reasoning share a common network in the bilateral basal ganglia, right cerebellum, bilateral fusiform gyri, and left prefrontal cortex.

Therefore, depending upon the type of information to be processed, reasoning is both a linguistic syntactic system and a mental model system, which both draw upon an underlying logical interpreter.

How does each of the various networks involved at the successive stages of processing do its own job (e.g., in terms of rate coding)? How do the networks interact with one another (e.g., in terms of temporal coding)? How are they integrated into a final solution (e.g., in terms of synchronization)? What is the equivalent of the developmental patterns noted above in the organization and functioning of the brain networks involved? The research reviewed in the target article does not answer these questions. Moreover, it does not speak about what is truly general and what is truly specific in both the brain and the mind. Specifically, how much of psychometric *g* is associated with general brain qualities (i.e., sheer total brain volume, overall physical state of neurons and neurotransmitters, connectivity, etc.) and how much is accounted for by the fact that the brain regions specified in the P-FIT model are always engaged in cognitive processing? What are the specific networks serving the specialized reasoning domains specified in the PSY-DEVO model? For some domains (i.e., verbal, spatial, and numerical reasoning), the P-FIT model is reasonably informative. With regard to others (i.e., social, causal, and categorical reasoning), it is silent.

Also, common processes, such as executive control, planning, or response selection, specified in the PSY-DEVO model, depend on recurring patterns of coactivation of the associated regions specified in the P-FIT model. How is this neuronal dialogue orchestrated and executed? How are variations of it subjectively differentiated so that intentional decisions can be made in advance which can then be tested so that some of them are selected and others rejected? What other regions, in addition to those specified in the P-FIT model, are involved when processing surfaces to consciousness? Does awareness emerge from particular networks, such as those specified in the P-FIT model, or does it result from particular coactivation patterns that may involve alternative networks? In conclusion, the grand neuro-cognitive-developmental theory of intelligence to come would have to integrate brain maps with functional and subjective maps of mental functions into a common landscape.

P-FIT: A major contribution to theories of intelligence

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Abstract: The P-FIT model is a major step forward in understanding biological causes of intelligence. It is consistent with evidence on the influence of working memory and speediness upon intelligence, and with models that emphasize the role of interaction between modules to produce intelligence. The contribution to understanding genetic contributions is problematical, due to the difficulty of isolating the genes involved.

The Jung & Haier (J&H) P-FIT model shows how far we have progressed toward understanding the biological basis of intelligence. Twenty-five years ago researchers in the field were engaged in an unedifying discussion of the relation between skull sizes and intelligence test scores. By taking advantage of the huge advances in measurement of the brain that have occurred in the past quarter century, J&H can take the far more sophisticated view that individual differences in intelligence depend, in part, upon individual differences in specific areas of the brain and in the connections between them.

J&H's view is consistent with convincing psychological evidence that general intelligence depends upon two information-processing functions: working memory capacity and general speediness. The P-FIT model provides a way of understanding why this might be true. Working memory is closely connected to the simultaneous abilities to store relevant information for temporary manipulation and at the same time suppress irrelevant information. The information being maintained or suppressed may either come directly from the environment or be the result of activation of memories stored throughout the cortex. There is some gross evidence that general speediness, as reflected in complex problem-solving behaviors, may be linked to neural conductance. J&H's discussion of the varied roles of gray and white matter, and of the importance of measuring connections between areas of the brain, points the way toward the use of new technologies that can much improve upon arguments that rely on crude measures such as simple reaction times, or on external measurements of nervous system responses, such as the galvanic skin response (GSR). The P-FIT model, with its emphasis on interaction between parts, is also consistent with recent theoretical modeling (van der Maas et al. 2006) that has shown that the statistical phenomenon of general intelligence (*g*) could be produced by interaction between component modules, rather than by a general property underlying a variety of cognitive skills.

In theory, the P-FIT model and others like it might move discussions of the genetic basis of intelligence beyond discussions of the percentage of variance in intelligence that is due to genetics (a measure that is restricted to the population measured) to an understanding of the mechanisms by which genes influence intelligence. However, this is likely to be a slow, hard process, because isolating the genes involved is not going to be easy. For example, J&H cite reports that the *ASPM* and *microcephalin* genes, which are involved in pathologically small brain sizes, might be involved in establishing variations in intelligence within the normal range. Alas, recent evidence, which probably was not available when J&H wrote their article, indicates that such involvement is complex, that the alleles involved are not clear, and that the overall involvement, if it exists at all, is very small (Mekel-Bobrov et al. 2007; Rushton et al. 2006; Woods et al. 2006). Tracing out the biological pathways involved in the genetics of intelligence is going to be a long and arduous task, simply because the genetic component is likely to be due to very small contributions by very large numbers of genes.

The problem is made even more complicated by the fact that different brain mechanisms may be crucial for intelligence at different times, and that the relative importance of brain areas may differ between men and women. See, for instance, Gernsbacher's (2007) light-hearted discussion of whether it is good or bad to have a thick cortex.

All this tells us is that the P-FIT model is a very useful step toward a model of the biological causes of intelligence, but there are many steps to come. I believe J&H would agree.

Finally, it is important to remember that the P-FIT model, and similar models to come, are models of the biological causes of intelligence. Although there is a sense in which everything, even knowledge of the arcane rules of American football, must have a biological basis, socio-cultural effects, most definitely including education, are important too. A complete understanding of variations in human cognition will not be reached until we

have models of both environmental and biological influences and their interactions.

Obviously the P-FIT model is addressed solely to biological concerns. However, its development has analogical meaning for studies of the environment. The P-FIT and similar models are possible only because of the major advances that have been made in biological measurements of brain processes. Models of social influences will require similar detailed measurements, both of intelligence and of related social phenomena. Given the amount of recording that is routinely done for social transactions today, the gathering of such data is conceivable. However, actually gathering the data, and for that matter, the measurement of intelligence itself, is hampered by bureaucratic concerns for privacy that go far beyond what is needed to satisfy a legitimate concern for confidentiality. Until this problem is solved, we are unlikely to have the data needed to match the sophistication of biological models with equally sophisticated environmental models.

The sleeping brain, the states of consciousness, and the human intelligence

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Abstract: A large number of experimental results clearly indicate that sleep has an important role for human intelligence. Sleep-wake stages and their specific patterns of brain activation and neuromodulation subserve human memory, states of consciousness, and modes of information processing that strongly relate to intelligence. Therefore, human intelligence should be explained in a broader framework than is implicated by neuroimaging data alone.

Jung & Haier (J&H) propose a theory based on an excellent review of modern neuroimaging data. In their model, the parieto-frontal (P-F) cortical areas are mainly implicated in human intelligence, although other brain regions also can be engaged. In particular, the amygdala is shown to be involved in emotional intelligence (Bar-On et al. 2003; Brierley et al. 2004; Shaw et al. 2004). Combining strong neuroimaging evidence with developmental and neurogenetic implications, J&H address the fundamental question of how brain and behavior are associated through the expression of intelligence and reason in an advantageous way.

However, one very important issue is generally ignored in their theory, namely the role of sleep for human intelligence. In fact, we spend a substantial part of our life in sleep. A large body of data clearly demonstrates that sleep does have an essential role for different types of learning and memory, and, likewise, for our intelligence (Hobson 2005; Maquet 2001; Stickgold 2005; Stickgold & Walker 2005). Moreover, sleep is an active brain state consisting of different stages (Steriade & Hobson 1976), and it is recently becoming evident that these different sleep stages affect various types of human cognition dissimilarly. For example, whereas rapid eye movement (REM) sleep has been implicated mostly in procedural learning and memory, non-REM (NREM) sleep has been shown to modulate the consolidation of declarative (or explicit) learning and memory (Born et al. 2006; Plihal & Born 1999; Walker & Stickgold 2004). More specifically, the declarative memories benefit from stage two of NREM sleep, as well as from the sleep spindles in this stage and their grouping by slow cortical oscillations (Clemens et al. 2005; Gais et al. 2002; Marshall et al. 2006; Schabus et al. 2004). Some empirical results concerning the association between sleep and intelligence are to be further emphasized. For example, it has been elegantly demonstrated that sleep inspires insight, an important aspect of human intelligence (Wagner et al. 2004), and revives emotional representations (Wagner et al. 2002; 2006). More importantly, recent studies show a strong and positive correlation between individual intelligence and the amount, quality, and quantity of sleep (Alchanatis et al. 2005; Bodizs et al. 2002; 2005; Schabus et al. 2006). Also, preceding learning has been found to produce quantitative electroencephalographic changes during subsequent sleep periods (Huber et al. 2004; Molle et al. 2004). Therefore, there is unambiguous evidence that sleep strongly impacts on human intelligence.

Concerning further the nature of human intelligence, it is well documented that brain physiology and neuromodulation considerably differ across sleep-wake stages. Importantly, the majority of neurotransmitters involved in these regulatory processes originate from nuclei located in the brain stem, projecting their activity to the cortex; in this manner, they modulate cortical activation (Gottesmann 1999; Hobson et al. 1975; Pace-Schott & Hobson 2002). Given the relevant contribution from subcortical regions to cortical plasticity, it may be a limitation to regard the P-F cortical areas as the only neuroanatomical source of human intelligence, as J&H propose.

Further, the processes involved in sleep-wake regulation also have been implicated in the states of consciousness (Hennevin et al. 2007; Hobson et al. 2000; Tononi 2005). Accordingly, the brain activation, the information flow, and the neurochemical mode of modulation, all in combination, may determine specific states of mentation (Hennevin et al. 2007; Hobson et al. 2000). Therefore, the processes of sleep-wake regulation and their corresponding states of consciousness may have much in common with human intelligence.

Taking all these considerations together, it may be concluded that the neuroimaging data incorporated in the model of J&H could hardly explain the nature of all aspects of human intelligence. This limitation leads to the following question: How do sleep, states of consciousness, and their regulatory mechanisms relate to human intelligence? This question is certainly of relevance and mandates further investigations.

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What about the neural basis of crystallized intelligence?

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Abstract: General intelligence is largely based on two distinguishable mental abilities: crystallized intelligence (*gC*) and fluid reasoning ability (*gF*). The target article authors' P-FIT model emphasizes a network of regions throughout the brain as the neural basis for fluid reasoning and/or working memory. However, it provides little significant insight into the neural basis of *gC*, or how or why *gC* is more stable than *gF* across the life span.

In their target article, Jung & Haier (J&H) propound "the P-FIT model" implicating a variety of cortical nodes as the network responsible for supporting general intelligence and reasoning. This model, however, appears insufficient to explain the neural basis for general intelligence, although it could successfully underpin fluid reasoning function or working memory.

As J&H mention, "general intelligence" refers to intellectual ability in general, which is conceptually somewhat different from the general factor *g* or fluid reasoning ability. In the

psychometric tradition, it is widely accepted that there are two related but distinct components of general intelligence, referred to as "fluid (*gF*) and crystallized (*gC*) general intelligence" (Cattell 1963; 1987). *gF* generally refers to reasoning and novel problem-solving ability, to be able to see relationships, as in analogies and letter and number series, which is independent from prior experience and learned knowledge. In contrast, *gC* is cognitive functioning based on previously acquired knowledge available in long-term store, including semantic knowledge and episodic memory. Indeed, most psychometric batteries for general intelligence (i.e., IQ tests; for example, the Wechsler-derived batteries, the Thorndike test, the Kaufman test) contain diverse verbal subtests to assess the cognitive skills belonging to *gC*, whereas pictorial, matrix-based reasoning tests such as the Raven's tests assess largely *gF.* Notably, factor analysis suggests that the Wechsler-derived batteries are biased toward crystallized content and even that the "verbal," or *gC*, factor is the most valid intelligence factor (Ashton et al. 2001; Robinson 1999; 2005).

More importantly, evidence on the two-factor theory has been provided by numerous longitudinal behavioral studies demonstrating that diverse cognitive skills and functions belonging to *gC* and verbal ability (such as performance on the WAIS verbal subtests), persist and even improve for decades after adolescence. In contrast, cognitive fluid reasoning and working memory peak in the third decade and then decline (Botwinick 1977; Dixon et al. 1985; Kaufman et al. 1991). This is thought to be a reason why scientists especially in quantitative disciplines, who need fluid intelligence, mainly produce their best work in their 20s and 30s, whereas those in the field of history and philosophy produce their best work in their 40s, 50s, and beyond as they have accumulated more knowledge.

More causal evidence for the *gC*/*gF* distinction has come from studies of patients with brain damage. Patients with prefrontal damage showed profound deficit in resolving many reasoning tasks, whereas those with anterior temporal lobe damage revealed bad performance on the tests of declarative knowledge (Waltz et al. 1999). Other lesion studies emphasized that the frontal lobe plays a crucial role in abstract reasoning but not in general intelligence as assessed by WAIS (Duncan et al. 1995; 1996). All these findings strongly suggest that the neural bases of fluid reasoning and crystallized knowledge are dissociable. Thus, to elucidate the nature of the biology of intelligence, at least two distinguishable mechanisms should be addressed.

Over the last decade, neuroimaging studies using various techniques, including anatomical MRI, fMRI, PET, and MRS, have rapidly unveiled the neurobiological bases of diverse cognitive functions such as fluid reasoning, working memory, and problem-solving ability (Gray & Thompson 2004). On the basis of commonality of the results from these studies, J&H have developed the integrated network model emphasizing functional connectivity to explicate the neural basis of general intelligence. However, this approach appears to have some intrinsic limitations to differentiate the neural basis of *gC* from *gF* or the unitary factor *g*.

First, almost all imaging data, regardless of both task modality and imaging method, is correlational rather than causal evidence. Commonality of these data is also correlational and therefore unable to articulate specific neural correlates of the diverse cognitive skills comprising general intelligence, although this concern could be tempered using a multiple regression approach. Second, individual differences in *gF* and *gC* exhibit robust intercorrelation in the normal cohort ($r = .7$ to .8; see Jensen 1998; Kaufman & Horn 1996). Their relation could be explained by the notion that *gF* plays a substantial role in encoding and retrieving information in long-term store and thereby in facilitating the accumulation and expression of *gC*, although there are distinct neural bases for these two functional domains of intelligence. Third, the typical crystallized knowledge content of WAIS subtests "Information" and "Vocabulary" reveals high *g*-loadings ($r = .6$ to .7) despite low reliance upon fluid reasoning ability and working memory capacity (Colom et al. 2006a; Lee et al. 2006). Therefore, to dissect the neural mechanism specific for crystallized knowledge, more sophisticated experimental paradigms and methods are required. Such an effort would allow us to formulate a combined model of *gF* and *gC* that accounts for dissociation of *gC* and *gF*, and further, provide better prediction for individual differences in general intelligence.

Where and how is crystallized knowledge organized in the human brain? Neurobiological studies on "learning and memory" in animal models have begun to shed light on closely related questions using diverse technical approaches based on genetics, electrophysiology, pharmacology, and anatomy (Frankland & Bontempi 2005; Miyashita 2004). Long-term memory, often referred to as "remote" memory in neurobiology, is fundamental for maintaining crystallized knowledge. Several lines of evidence have demonstrated that the hippocampus functions as a temporary store for new information, whereas more permanent storage depends on a distributed cortical network including the anterior cingulate, the lateral prefrontal, and the temporal cortices. In monkeys, memory traces representing repeated associations (likely the basis of semantic-like memory) are consolidated in the domain-specific regions in the temporal cortex (Sakai & Miyashita 1991; Yoshida et al. 2003). During memory consolidation, structural reorganization of cortical circuits occurs, which includes the addition/elimination of synapses and modulation of axonal dendritic growth through a cellular program of gene expression that eventually may lead to changes of cortical gray matter density and thickness (Chklovskii et al. 2004; Tokuyama et al. 2000).

Consistent with this account based on animal models, human functional neuroimaging studies suggest that the prefrontal and temporal lobes, particularly in the left hemisphere, may be involved differentially in semantic memory representation (Martin & Chao 2001; McClelland & Rogers 2003). The left inferior prefrontal cortex generally plays a crucial role in retrieving and manipulating lexical and semantic information stored elsewhere, whereas the temporal lobe integrates semantic information with increasing convergence along its posterior-to-anterior axis. Furthermore, evidence from studies on patients with semantic dementia emphasizes a pivotal role of the anterior temporal lobe in semantic working memory as well as memory storage (Gainotti 2006; Hodges et al. 1992; Mummery et al. 1999). Thus, individual differences in *gC* may depend on declarative knowledge stored in the temporal lobe and association areas, leading to structural differences across individuals. If this is correct, however, it is puzzling that the structural correlates of intelligence did not tend to implicate temporal regions, and that J&H interpreted the results to mean: "temporal and occipital lobe relationships to intelligence may be functional and 'task dependent' on the sensory modality employed" (sect. 5.3, para. 1).

A possible explanation is technical limitation of the voxel-based morphometry (VBM) method. As commented in the target article, there has been some dispute over the application of VBM, especially to characterizing group differences (Bookstein 2001; Davatzikos 2004; Mehta et al. 2003). Within individuals, this method would convincingly demonstrate longitudinal changes of cortical structure through scanning on multiple occasions before and after training (Draganski et al. 2004; 2006; Golestani et al. 2002). However, when used for group analysis, the results are vulnerable to systematic misregistration errors of the spatial normalization that are caused by simple cortical geometric differences across individuals. It, therefore, is unclear whether structural correlates based on VBM are relevant to changes of cortical gray matter density or to simple shape differences. In addition, the spatial normalization process based on the Talairach coordinate system provides just a rough registration without considering gyral and sulcal pattern variation. Even the standard Montreal Neurological Institute (MNI) template is not

exactly the same size or shape as the model brain: In particular, the temporal lobe's discrepancy between the MNI template and the Talairach brain extends to about 10 mm (Brett et al. 2002; Westbury et al. 1999). This possibly contributed to the weaker implication of the temporal lobe regions in the structure correlates of intelligence as compared to other cortical regions.

Another potential problem could be the spatial resolution of anatomical images. Most structural studies of intelligence have employed T1-weighted images resolved into maximally 256 × 256 matrixes from 1.5-T MR scanners, and therefore a single voxel size is at least 1 mm^3. On the other hand, cortical gray matter thickness varies between 1 mm and 5 mm depending on the cortical regions (average thickness = 2.5 mm) (Fischl & Dale 2000). Notably, individual differences in cortical thickness are on the order of a few percentage points. Current resolution of anatomical imagery has been an obstacle in the way of detecting subtle structure changes in the cortex, especially the changes smaller than the voxel size.

In conclusion, methodological advances in both anatomical imaging and structural analysis would extend our understanding on the neurobiology of intelligence – including distinguishing among *g*, *gF*, and *gC*. For example, a high-Tesla scanner such as 7-T MRI, although still in a developing stage as regards human applications, could provide more detailed information about the structural correlates of *gC* and even about changes within the laminar structure of cortical gray matter; these already have been demonstrated using molecular and cellular imaging in experimental animals after semantic-like memory tasks or special working memory tasks (Maviel et al. 2004; Tokuyama et al. 2000). These future findings would open exciting avenues not only for establishing neurobiological model of general intelligence, but also for developing neurometric intelligence that explicates individual differences comparable to psychometric intelligence.

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Integrative action in the fronto-parietal network: A cure for a scattered mind

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Abstract: A large body of evidence supports the idea that a common fronto-parietal network is activated across a range of diverse cognitive functions. Jung & Haier's (J&H's) review demonstrates a very similar pattern of activity, which correlates with individual differences in intelligence. We propose that these converging lines of evidence are best interpreted as a general role of the fronto-parietal network in integration and control.

Comparison of brain imaging studies reveals that many cognitive functions tend to recruit overlapping neural regions (for reviews, see Cabeza & Nyberg 2000; Duncan & Owen 2000; Naghavi & Nyberg 2005). It is possible that the apparent commonalities reported in such between-studies assessments, at least in part, reflect activation of adjacent but distinct regions. However, several within-study PET and fMRI reports have also demonstrated overlap in activation patterns for different cognitive functions, such as attention, working memory, and episodic memory retrieval (e.g., Braver et al. 2001; Cabeza et al. 2002; 2003; LaBar et al. 1999; Nyberg et al. 2002; Ranganath et al. 2003). Common activations are particularly prominent in interconnected cortical regions in the frontal and parietal lobes, including the dorsolateral prefrontal cortex and posterior parietal cortex (see our Fig. 1). Reviewing 37 neuroimaging studies, J&H conclude that a very similar large-scale network mediates performance in tasks involving intelligent thought and reasoning. This conclusion suggests that an even broader range of conditions activate the fronto-parietal circuit, although within-study comparisons are needed to exactly and reliably define these similarities. The fronto-parietal recruitment is particularly salient for tasks having a high *g*-loading, thereby further strengthening the association between fronto-parietal activity and general-purpose higher-order cognitive functions.

What does the convergence of diverse cognitive functions in a large-scale fronto-parietal network imply? From a general point of view, common fronto-parietal activations reveal an important feature of how cognitive processes are distributed in the brain. Computational systems are traditionally thought of as devices in which distinct components are devoted to specific functions, with minimal if any overlapping localization of functions. The brain, however, appears to be designed in such a way that particular regions are concurrently involved in numerous cognitive functions (Duncan 2001; McIntosh

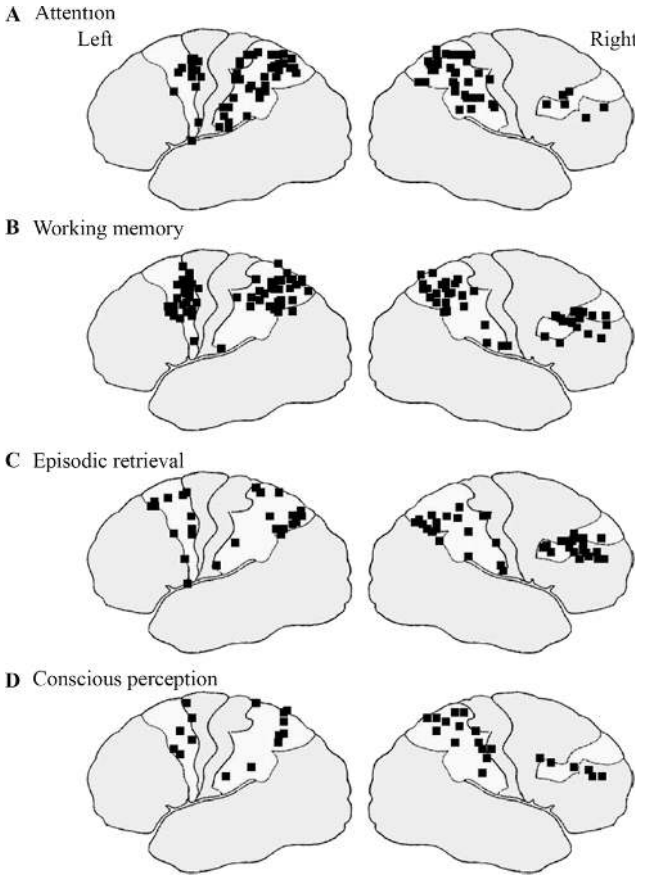

Figure 1 (Naghavi). Peaks of activation in fronto-parietal areas associated with: (A) attention, (B) working memory, (C) episodic retrieval, and (D) conscious perception, extracted from 47 fMRI and PET studies; blank areas indicate the regions with highest level of common regional brain activity across functions, namely bilateral BA 7 and BA 40, left BA 6, and right BA 9 (after Naghavi & Nyberg 2005; reprinted with permission from Elsevier).

2000). In fact, compelling evidence from neuroimaging and neuropsychological studies suggests that the frontal lobe, particularly the dorsolateral prefrontal cortex, and the parietal cortex, especially the intraparietal sulcus, collaborate tightly for directing a wide range of higher cognitive functions as well as sensory-motor processes (Bush et al. 2002; Collette & Van der Linden 2002; Culham & Kanwisher 2001). The notion of multifunctionality of the fronto-parietal network is also supported by single-cell studies in primates, which demonstrate the co-presence of neurons with different processing operations (Funahashi et al. 1989; 1990), and/or the presence of neurons with multiple processing operations (Fuster et al. 1982; Quintana & Fuster 1999; Rosenkilde et al. 1981) in regions in the prefrontal cortex and the parietal cortex. For example, in monkeys it has been shown that neurons in the lateral intraparietal area are activated across a wide variety of conditions, including visual, attentional, memory, and saccade-related tasks (Colby et al. 1996).

In spite of the apparent diversity of cognitive functions that correlate with fronto-parietal activity, these functions may fit into a unifying conceptual framework for integration and control of information. Such a capability is critical for optimal recruitment of internal resources to exhibit goal-directed behavior relevant to ever-changing environmental requirements (Miller & Cohen 2001). Examples of integration and control processes are: multimodal convergence of behaviorally relevant information in coherent representations; selective enhancement or inhibition of specific representations through feedback mechanisms; maintenance of information in a buffer system via sustained activity; and manipulation of information according to the cognitive demands. All of these processes should be carried out by a central system that has extensive access to both sensory and motor representations, and the fronto-parietal network is at an ideal site in the brain to subserve this end. Nodes of the fronto-parietal network are thoroughly and reciprocally connected with each other, as well as with other association cortices and subcortical areas, a property that allows widespread access to perceptual and motor representations at different levels. With this unique connectivity pattern, on the one hand, and specialization in a wide variety of higher-order processing operations, on the other hand, the fronto-parietal network can function as the source of integration and top-down control in the brain, orchestrating perception, thought, and action in accordance with internal goals.

Hence, J&H's conclusion that intellectual demands activate the fronto-parietal network is consistent with a general role of the fronto-parietal network in integration and control processes. However, it should be noted that a number of relatively basic functions, such as conscious perception (Rees et al. 2002), top-down attention (Pessoa et al. 2003), and eye movement control (Muri 2005), are also associated with activity in the fronto-parietal network. Therefore, whereas J&H argue for viewing the parieto-frontal network as a neural signature of intelligence, the association between fronto-parietal activity and intelligence may reflect only a specific, though important, aspect of a much more general role of the fronto-parietal network. As an integrative model, the fronto-parietal network can be seen as a core system equipped with diverse mechanisms that allow integration and control of distributed patterns of neural activity throughout the brain. Given the distribution of the fronto-parietal network in posterior and anterior parts of the brain, as well as its connectivities and functional specializations, this network might be conceived of as a backbone, located at the top of the hierarchical organization of the brain, by which the otherwise fragmented pieces of information as well as sensory-motor and cognitive processes are integrated and managed. Thereby, integrative action in the fronto-parietal cortex provides a cure for a scattered mind.

On images from correlations

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Abstract: The difficulty of making reliable interpretation from a dense cloud of unreliable correlations means that the grounds for making a testable "biological," or brain-based, theory of intelligence remain very shaky. We briefly discuss the conceptual and methodological problems that arise and suggest one possible alternative interpretation of the data.

This target article assumes that a mapping between individual differences in IQ and various brain characteristics constitutes a testable theory of intelligence. However, we would argue that even within the advent of the modern neuroimaging revolution, this is contestable on both conceptual and methodological grounds.

We remind readers that the modern notion of *g* is based on intercorrelation among test performances, but "*g* tells us little if anything about contents" (Jensen 1998, p. 92). The intercorrelation may be partially or entirely based on noncognitive factors, so there are still serious doubts whether the intelligence envisaged by Jung & Haier (J&H) exists (van der Maas et al. 2006). Critics say that indices of *g*, such as IQ test performance, measure degree of enculturation into specific linguistic and cognitive styles, together with motivational, anxiety-related, and other test-preparedness factors: in effect, it is a good measure of social class (not well measured by socioeconomic status [SES]; Cole 1999).

Just as interpretation from correlations among IQ scores is debatable, so is that from imaging data, as J&H recognize: "all neuroimaging research is correlational by nature" (sect. 5.7, para. 3). Yet their whole theoretical effort is based on correlations between those correlations. It is scarcely surprising that the results are mixed and inconsistent. As J&H say, in "more than 40%" of voxel-based morphometry studies, "tissue density and white matter integrity ... correlate substantially" with IQ (sect. 5.3, para. 1) – meaning that in nearly 60% of studies they don't. Similar interpretations apply to the fMRI, PET, and other data. What, for example, does "consistently related ... across more than 30% of studies" mean (sect. 6, para. 2)? Sometimes correlations are positive, sometimes negative (e.g., sect. 5.4, para. 2). Finding areas that are activated during cognitive tasks is intrinsically interesting. But that more than 20 different tasks were used, together with unreliability of methodology, makes interpretation difficult. (Giuliani et al. 2005, cited for reassurance in sect. 5.1, para. 2, actually say that "Although VBM is rapid and fully automated, it is not a replacement for manual ROI-based analyses. Both methods provide different types of information" [p. 135].) And all this must be appraised within the context of the "noise" created from a multitude of different complex cognitive tasks in different studies. Even fMRI studies on well-defined, replicable tasks, such as hand flexions/extensions, have stressed the interdependence between brain regions (Marrelec et al. 2006).

Even if the correlational patterns, and interpretations of them reported by J&H, were robust, we suspect that better explanations could be found within the "ecology" of IQ test preparedness and brain development. Both IQ and brain region volumes are experience dependent. For example, the high memory demands on London taxi drivers are reflected in bigger hippocampi (Maguire et al. 2000). In Western class-structured societies, the majority of developmental advantages and benefits are socially inherited, with huge psychological, as well as material, consequences affecting both IQ and brain development. For example:

1. Although the consequences of malnutrition for brain development are well known, risk factors are clustered in the lower class groups, primarily because their diet "provides cheap energy (sources) … lower in essential nutrients such as calcium, iron, magnesium, folate, and vitamin C than that of the higher socioeconomic groups" (James et al. 1997, p. 1545).

2. Adverse substance experience has higher incidence among lower SES groups. Alcohol abuse during pregnancy interferes with trophic factors that regulate neurogenesis and cell survival (Goodlett et al. 2005). Nicotine dependence affects N-acetylaspartate (NAA) levels in the frontal cortex (Gür et al. 2006). Similar findings have emerged from studies on drugs and exposure to environmental toxins, particularly lead (Grandjean & Landrigan 2006).

3. Stress arising from the poor sense of control over circumstances, including financial and workplace insecurity, affects children and leaves "an indelible impression on brain structure and function" (Teicher 2002, p. 68; cf. Austin et al. 2005). In childhood and later life, increased stress reactivity can impair aspects of test performance, including self-confidence, attention, and memory (Richardson 2002).

4. Experiences in working class situations create poor cognitive self-efficacy beliefs. These are passed from parents to children (Bandura et al. 1996), influencing levels of aspiration and self-confidence, as well as anxiety and distractiveness in test situations (for review, see Richardson 2002). They can deter children from specific kinds of cognitive experience, with consequences for brain development. For example, activity in anterior cingulate regions is related to confidence in cognitive tasks (Fleck et al. 2006).

Note that many experience-dependent effects have been discovered to be (non-genetically) transgenerational through what Harper (2005) calls "this all but ignored" pathway of influence from parents to children and successive generations. That is, parental experiences are reflected in gene regulatory (epigenetic) aspects of children's and even grandchildren's development.

Such considerations suggest that "bigger" brain areas are not a cause of higher IQ. Rather, both are consequences of social experience. Accordingly, J&H's theory merely redescribes the class structure and social history of society and its unfortunate consequences. It seems to us that a host of variables, terms, and ecological factors need to be clarified before their model can be entertained further.

We are also concerned about the empirical latitude permitted in this area, overall, where, for example, a simple vocabulary test, or even a reading test (e.g., sect. 5.6, para. 7), can be taken as a measure of general intelligence. Likewise, we would question J&H's appeal to twin studies which have been consistently criticised for poor empirical standards (Richardson & Norgate 2005).

Finally, we note that their whole model is based on a feedforward model of higher cerebral functions, which many would argue is outmoded. Looking for simple deterministic bases of intelligence variation does not reflect how the dynamics of the brain work (Freeman 2001). Having evolved to deal with changeable environments, cognitive systems must wring predictability from deep structures in the dynamic flow of information using massive reciprocal connections and cooperative processing between centres. This suggests quite different foundations for a theory of intelligent systems (Richardson 2006).

Intelligence and reasoning are not one and the same

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Abstract: Lest the conjunction "intelligence and reasoning" seduce readers into supposing that the two are of a piece, we point out that analyses made at the superset level concerning *intelligence* do not readily align with or outperform the scientific advances made via investigations of *reasoning*, which at best can be viewed as a subset of intelligent behaviour.

One of Piaget's better-known tasks is the class-inclusion problem, in which participants are shown, for example, five daisies and three tulips and asked, "Are there more flowers or more daisies?" Although the task's intended normative response is *flowers*, many (usually younger) participants say that there are more *daisies* – arguably because they understand *flowers* to mean *flowers-that-are-not-daisies* (for a recent review, see Politzer 2004).

The target article's reference to "intelligence and reasoning" harks back to Piaget's task, because the oft-used conjunction leaves the impression that the two represent a single area of study, when in fact the domain *Intelligence* is very large (the target article covers chess playing, Go, IQ tests, etc.) and perhaps *includes* reasoning. We argue that the presentation of *Intelligence* in this way is infelicitous, much like the option *flowers* in the class inclusion problem. More specifically, we ask the two following questions: First, are there advantages in studying a large area of cognitive performance over investigating one subpart (i.e., reasoning) alone? Second, do approaches that rely on individual differences (and primarily correlations among subtests) provide conclusions and insights that have greater validity or greater predictability than those drawn from investigations of a subset (i.e., reasoning)? It is our view that the answer to both questions is negative.

For better or worse, investigations into reasoning take a structural approach. The field breaks down reasoning into its component parts, both conceptually and empirically. Thus, reasoning researchers make the distinction between deductive and inductive reasoning (where the former concerns valid conclusions and the latter, conclusions that are more or less probable). Once in the deductive domain, which will remain our example, one then aims to determine the role played by factors such as logical validity, semantic content, development, as well as perceptual or belief biases that affect participants' responses. Generally speaking, reasoning researchers make the assumption that findings are universal. For example, it is generally accepted that Modus Tollens (*if p then q; not-q//Therefore, not-p*) is more difficult to carry out than Modus Ponens (*if p then q; p//Therefore q*). The literature on the neuroimaging of reasoning, which is covering the same ground as its cognitive forebears, also aims to depict the way the above factors play out, but with respect to the brain mechanisms or structures that are shown to be responsible for these universal effects. Neuroimaging has not only provided some specific findings that are inaccessible to classic cognitive paradigms, but has informed theory making as well.

For example, Prado and Noveck (2006; 2007) have demonstrated how participants are more prone to errors and are slowed down when features mentioned in a rule mismatch those in a test item (e.g., note how a test item depicting a *P-in-a-circle* verifies the rule *If there is not an H then there is not a square* while providing two mismatches). The neuroimaging experiment (Prado & Noveck 2007) revealed that an increase in mismatching leads to greater activity in the medial prefrontal cortex (PFC) and the right mid-dorsolateral PFC. This indicates that mismatching, rather than negation-interpretation, is likely critical to correct performance. Interestingly, this restricted network is basically the same as the one reported when prior beliefs interfere in evaluating logically valid conclusions (see Goel et al. 2000; Goel & Dolan 2003). This is also in line with growing evidence showing that the right lateral PFC is specifically involved in inhibiting a prepotent response (see Aron et al. 2004) and that its non-activation in children (8–12 years)

is linked to less effective attentional control when compared with adults (Bunge et al. 2002a).

By making distinctions between an attentional control system described above and the parietal-frontal system that is implicated in fundamental logical inferences such as Modus Ponens (Noveck et al. 2004), one gets an informed account of the way reasoning is distributed in the frontal and parietal lobes. This dual-system approach also describes some other novel findings. For example, it can explain (a) why solutions to insight tasks, which arguably benefit from having less attentional control, are more accessible to those who have lesions in the frontal cortex (Reverberi et al. 2005), and (b) why right lateral PFC activity is predictive of successful logical performance (Goel & Dolan 2003). Providing explanations for such non-intuitive findings is the hallmark of scientific advances. Most importantly, this indicates that correct performance on higher-level tasks has little to do with the better use of normative rules; it has more to do with avoiding biases while using such rules.

In contrast, studies that investigate cerebral correlates of *Intelligence* point to a large number of regions, but they hardly describe the role played by each. The upshot is that differences among individuals are linked to an entire system that fails to distinguish between its functionally distinguishable parts (e.g., rule access and perceptual integration). In fact, when intelligence research does aim to isolate factors, it largely confirms what is found through more structural approaches (e.g., Gray et al. 2003). The worry is that infelicitous analyses of brain function could lead to infelicitous theoretical claims (e.g., about evolution).

Although reasoning research has benefited from descriptions of individual differences (e.g., see Jackson & Griggs 1988; Stanovich & West 2000), such descriptions do not amount to a central strategy in investigations of reasoning (at least as far as WAIS-based tests are concerned). There are two viable reasons for this. First, quality of education and economic background are critical for better performance on standardized tests of intelligence (see Georgas et al. 2003; Shuttleworth-Edwards et al. 2004). This makes measures of intelligence unstable across populations. Second, as Georgas et al. (2003) report, of the 11 subtests that account for performance on the WISC-III, the two subtests that imply reasoning (and not necessarily deductive reasoning) – Mazes and Picture Completion – are among the least predictive of variance across the 12 large populations (and 15,999 people) studied. In other words, *reasoning* per se has a limited impact on standardized tests of intelligence.

Intelligence, hormones, sex, brain size, and biochemistry: It all needs to have equal causal standing before integration is possible

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Abstract: Recent brain imaging points to differences in brain structure that relate to intelligence, but how do we model their causal relationship within a coherent framework that circumvents classic dualist traps? A bottom-level nonlinear, dynamic, multifactor, multiplicative, multidimensional, molecular (ND4M) trait-covariance time-space model may accomplish this better than traditional approaches.

The evidence: Research on general intelligence (*g*), genes, sex, hormones, neurochemistry, and brain imaging finally converge. Spearman's (1904) and Jensen's (1998) psychometric *g* shows 40–80% adult heritability. Brain size is largely inherited (Pennington et al. 2000; Toga & Thompson 2005). Retarded brains use more glucose than normal ones (Haier et al. 1995). Jung & Haier (J&H) report positive correlations between the size of small gray brain matter areas and intelligence, and males (with greater brain structure volumes; e.g., Allen et al. 2003) have a slight mean *g* advantage and a flatter dispersion score than females do (Jackson & Rushton 2006; Lynn 1999; Nyborg 2003; 2005). Females use slightly different gray matter areas for *g*-loaded tasks than males do and also use more white matter (Gur et al. 1999; Haier et al. 2005). All these interdependent parameters may relate to permanent androgen priming of the fetal brain and dynamic adult steroid regulation of primary abilities (Kimura & Hampson 1994; Nyborg 1994).

The hard problem: How do we best relate the material basis for dynamic interactions among genes, hormones, nutrition, and learning to differences in brain size, structure, and neurochemistry and *g* (or mind)? This is a hard problem, as 2,400 years of dualist theory gave not a clue to how a nonphysical intellect (mind) interacts with its physical brain. The problem is outlined in Figure 1 (see also Nyborg 1997).

Top-level nonhierarchical models such as behaviorism or trait psychology only scratch the surface and fail to causally integrate behavior with its material basis. Top-down and bottom-up

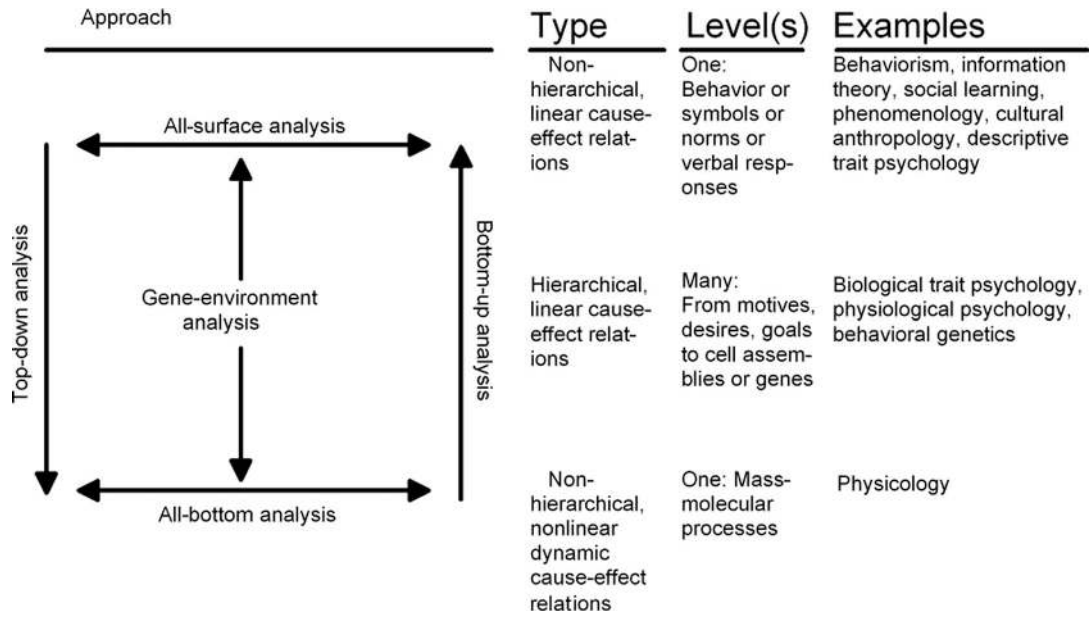

Figure 1 (Nyborg). Types of analytic approaches to abilities and personality (from: Nyborg 1997).

hierarchical models operate simultaneously with material and immaterial agents at a semi-causal level, fail to reflect causal integration, and commit a category error by assuming that mental and physical agents are causally equivalent. There is a way, however, to bypass these problems: an all-bottom model.

The solution: A nonlinear, dynamic, multifactor, multiplicative, multidimensional, molecular (ND4M) all-bottom model is presented in Figure 2.

The model uses Occam's razor principle to reduce intelligence (mind), the brain, and society to physical agents interacting within a trait-covariant nonhierarchical dynamic time-space-phase framework. All agents enjoy equal causal standing as they refer to locally or globally coupled molecular mass-interactions.

Thinking is represented by the pattern of locally constrained *intra-systemic* coupled transport of neurotransmitters, neurohormones, oxygen, glucose, and so on; behavior is *intra-systemic* coupled transport of parts or the full body of molecular conglomerates in space-time coordinates; social interaction is the *inter-systemic* coupled adjustments of mass molecular events in two or more organisms; the nonsocial environment is the *extra-systemic* molecular constellations of relevance for survival. More details are found in Nyborg (1994).

The ND4M model maps the causal basis for genotypes, hormotypes, neurotypes, and phenotypes (Nyborg 1997), and it predicts what will happen when the expression of parental genes is modified during ontogenetic development by plasma steroid hormones (themselves partly under genetic and environmental influence), and by molecular re-organization through learning. The ND4M model needs no theory and depends on only a few a priori assumptions:

1. *Stereotaxic affinity*: That is, each molecule has specific affinity for certain molecules enabling, say, steroid hormones to go everywhere in the body but to exert specific effects only in target organs inducing suitable receptor molecules; affinity dramatically reduces local entropy.

2. *Nonlinearity*: Most molecular mass-interactions are nonlinear (e.g., low hormone values exert small effects, higher values an "optimal" effect, and still higher values a neurotoxic effect); the curvi-linearity principle is generalized in the ND4M model.

3. *A limited energy budget*: Body development and behavior, including thinking, is costly; according to the Economy Principle (Nyborg 1994, Ch. 13): "strong development or activity in one area [has to be] traded off by less development or activity in other areas" due to obligatory nutritional and intra-systemic constraints. The General Trait Covariance (GTC) model (Nyborg 1994, Ch. 10) predicts, for example, that high early plasma sex hormone levels promote excessive sexual differentiation of body and behavioral development at the cost of reducing brain development relevant for the expression of *g*. Likewise, any deviation (up or down) from optimal DNA transcription of parental genes for *g* (related to other genes or to sub-optimal levels of hormones, neural plasticity, brain size, white matter involvement, glucose uptake, neural efficiency, or deficient nutrition or learning) will lower the expression of genomic *g*. Only if all or most metric states are at optimal levels may a genius appear (Nyborg 1997).

Most things in nature are continuously distributed. The model allows for smooth transitions among structure and function. "Solid" nerve cell walls are gradually built up by coupled molecules more or less permanently "frozen" in time-space coordinates after their stereo-specificity, and part of the wall is formed by channel-proteins that dynamically regulate the transport of neurotransmitters in accordance with complex signal systems.

Testing of the GTC and ND4M models depends on our ability to simultaneously keep track of multiple molecular events. This will tax our ingenuity for some time. Luckily, we do not have to monitor the behavior of each molecule. For example, labeled coupled multiple *s* molecular events behind sexual differentiation are fairly easy to map. Given sex-typical plasma hormone levels,

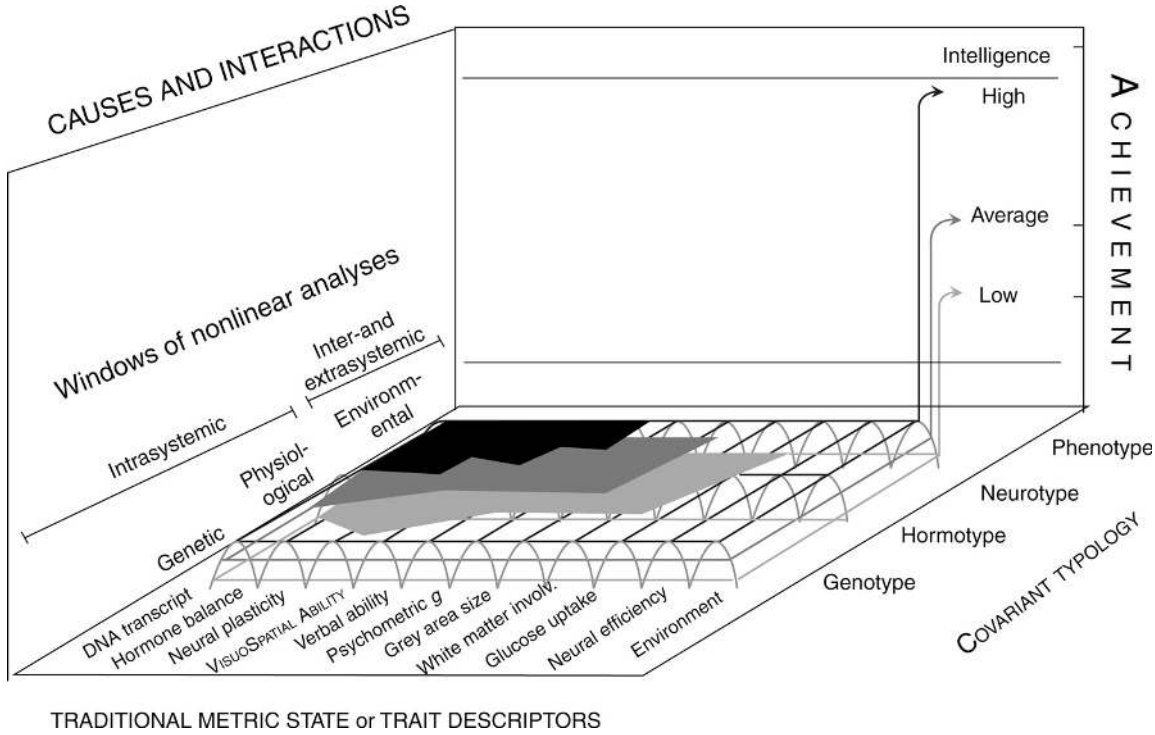

Figure 2 (Nyborg). A nonlinear, dynamic, multifactor, multiplicative, multidimensional, molecular (ND4M) model for the development of general intelligence, *g*. High intelligence is seen as a combined function of favorable gene products, moderate plasma sex hormones, low sexual differentiation, high adult neural plasticity and efficiency combined with optimal sizes in about 10 relatively small and widely distributed gray matter brain areas. The model mirrors multidimensional mass-molecular space-time-phase (x,y,z + time + phase) changes over long phylo- and shorter ontogenetic periods (modified from Nyborg 1997).

the sex-typical genotypes and phenotypes normally concur. However, if androgens are present during the 4 to 7 fetal weeks, we get a phenotypic boy whether "its" genotype is XX or XY; if receptor molecules for androgen fail to be induced, we get a phenotypic girl even if "her" karyotype is XY. Some individuals have low plasma hormones and display lower than average sexual differentiation (e.g., Nyborg 1983). The GTC model predicts high *g* in this group, as an excessive sexual differentiation does not detract from the costly build-up of *g*-related brain structures. A testable consequence of this is that androgynous males and females will have higher *g* and larger *g*-related gray matter brain areas than their more sex-typed brothers and sisters.

Obviously, the above mass molecular solution is just one way for solving pertinent dualist problems in the attempt to relate soft and hard sciences. The actual testing of the GTC and ND4M models requires powerful computers and bright minds with a keen eye for sorting out the tangled web of small partial correlations among quantifiable molecular parameters such as gene products, hormones, brain size, learning-related changes in the brain, neural efficiency, and *g*.

P-FIT and the neuroscience of intelligence: How well does P fit?

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Abstract: A well-recognized framework for modeling human intelligence centers around Spearman's *g*, a common central factor accounting for individual differences in cognitive performance across a variety of complex tasks (Spearman 1904). The neural basis of *g* may be better characterized by *posterior*-frontal integration, rather than parietal, which may be just one of many posterior regions that are controlled by the prefrontal cortex (PFC).

As summarized in Jung & Haier's (J&H's) review, there have been numerous studies aimed at the quantification of *g*. One observation that arises from their review is that it has been operationally defined in ways that are at least partly isomorphic with "supervisory attentional system" concepts as articulated by Shallice (1988). Therefore, *g* appears to be critical for such executive operations as supervision of diverse streams of information, goal management, cognitive control, and strategy shifting, independent of the format, or processing domain (e.g., verbal or spatial).

Attempts to elucidate the nature of *g* have taken two forms that may be characterized as either "top-down," or "bottom-up." In the top-down approach, complex tasks are used that require many cognitive operations to be implemented simultaneously. Conceptually, high-*g* executive processes are characterized as "domain-independent" and are distinguished from low-*g* "domain-dependent" processing of spatial, object, or verbal information. Empirically, high-*g* and low-*g* processes have often been distinguished by the use of subtraction techniques in neuroimaging data analysis. In one study, for example, Duncan et al. (2000) subtracted high-*g* (domain-independent + domain-specific) from low-*g* (domain-specific) versions of the tasks that spanned different processing domains (spatial, verbal, and perceptuo-motor). Two results from these studies are important for our present argument. First, both frontal and parietal activity was observed in the high-*g*/low-*g* subtractions. It is important to note, however, that parietal activity was observed only in the spatial tasks. Second, only prefrontal cortical (PFC) regions were consistently isolated when the subtraction analysis was applied. These results suggest a more intimate connection between frontal brain regions and *g*-related processes than between parietal regions. The apparent parietal fit noted by J&H may have been a consequence of the spatial nature of many high-*g* tasks.

In the bottom-up approach, simpler cognitive constructs have been utilized to isolate particular domain-independent *g*-related processes. In one of the earliest such approaches, subjects performed domain-specific processing tasks (either spatial rotation or semantic judgment tasks) in separate scans (D'Esposito et al. 1995). Domain-independent processing was evoked by the requirement to perform both tasks together. This "dual-task" requirement elicited activity in dorsal PFC regions, implicating a supervisory role (cf. Shallice 1988) for these regions, a function also closely related to *g*. Prabhakaran et al. (2000) utilized a similar strategy to show that integration of information in working memory can also be mapped to specific PFC regions, whereas posterior brain regions support domain-specific processing. Subjects performed tasks in which they maintained integrated or discrete verbal and spatial items in working memory, while load and duration of processing were controlled. It may be that PFC regions mediate the integrated representation that underlies the cognitive flexibility needed for domain-independent processing. Posterior brain regions may mediate discrete representations needed for domain-specific processing.

Intelligence research is rooted in attempts to identify factors that determine reliable performance differences between individuals. Such information, not readily available from the group-level analyses of data, yields a more nuanced picture of the neural basis of *g*. Our approach to exploring this question has been to account for individual performance variability in neuroimaging data. This approach has yielded important clues about the neural underpinning of intelligence.

Consistent with the P-FIT model, our initial study of the Raven's Progressive Matrices (RPM; Prabhakaran et al. 1997) uncovered a fronto-parietal network for analytic reasoning. Taking into account the relative difficulty of individual problems, as well as individual subjects' reaction time (RT) and accuracy, highlighted the importance of PFC regions (Christoff et al.

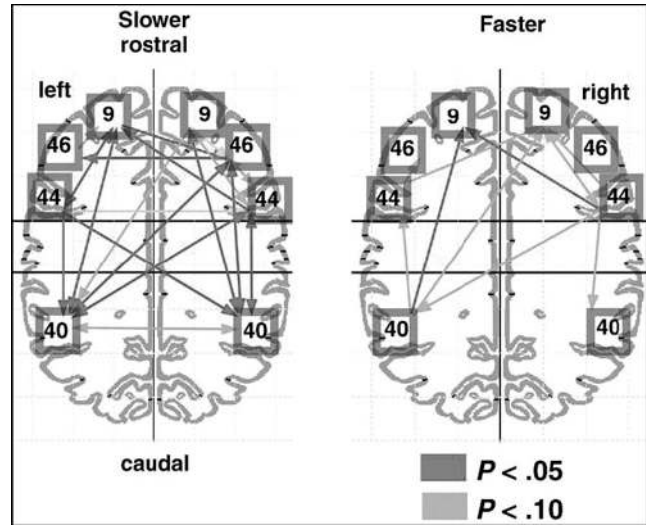

Figure 1 (Prabhakaran). Granger causality permits characterization of the strength and direction of influence between discrete brain regions. Influences were calculated separately for faster and slower subjects (grouped by median split). Influences were considered significant for $ps < .05$ and trends when $.05 < p < .10$.

2001). Importantly, a composite analysis of our reasoning studies (Prabhakaran et al. 2001) suggested consistent frontal-lobe involvement across tasks but more variable involvement of posterior brain regions, based on the specific processing domain of the task. These results are consistent with the P-FIT model insofar as prefrontal function is concerned, but they are less consistent with the model regarding parietal function.

Do frontal and parietal regions together perform the functions that we associate with *g* as P-FIT suggests? Or does it depend on the nature of the task and the characteristics of the individual? Data we have collected recently suggest that *g*-related functions may be mediated primarily by the PFC. Posterior regions including the parietal cortex play the major role when executive or supervisory requirements are minimal.

One study we conducted suggests that the prefrontal cortex exerts supervisory control over posterior parietal regions during visual search (Rypma et al. 2006). Subjects were scanned while they matched a "digit-symbol key" and a single digit-symbol probe that appeared below the key. Subjects performed this task with uniformly high accuracy. Reaction times were short but more varied between individuals than accuracy was. We used Granger analysis to test the hypothesis that, among slower individuals, PFC systems guide posterior systems (Fig. 1).

Consistent with the notion of PFC supervisory control, the results indicated there were more directed frontal-to-parietal influences in slower performers than in faster ones. Regression analyses indicated that, across individuals, PFC-parietal connectivity was associated with longer RT. This result supports the hypothesis that PFC exerts control over parietal activity in slower performers during visual search. For faster performers, posterior systems operate more automatically, independent of PFC control.

Another study (Prabhakaran et al. 2007) also shows increased frontal activity among poor performers (Fig. 2a). In this study, normal subjects and chronic stroke patients were scanned while they either subvocally generated words or rested passively. Normal subjects recruited a left-lateralized fronto-temporal network compared to rest. Chronic left Middle Cerebeal Artery (MCA) stenotic patients showed additional right fronto-temporal activity. In normal subjects, parietal regions actually showed more activity during rest than during word generation, suggesting a limited role in mediation of *g* functions and possibly reflecting a "default mode network" role for this region (Fig. 2b; cf. Raichle et al. 2001; Vincent et al. 2006).

We think that such results suggest modification of P-FIT. First, the observations made in the target article are consistent with the notion that *g* is mediated through the PFC. Second, we suggest that the parietal lobe is not a principal player in posterior mediation of *g* functions, but rather one stand-in among many that are called upon to mediate domain-specific task demands. Thus, the term "P-FIT" may be better phrased as a "*posterior*-frontal integration theory." We suggest that performance differences between high-*g* and low-*g* individuals may result from the extent to which domain-specific cognitive processes can be implemented relatively "automatically" (cf. Schneider & Shiffrin 1977) by posterior brain regions, independent of control exerted upon them by the PFC.

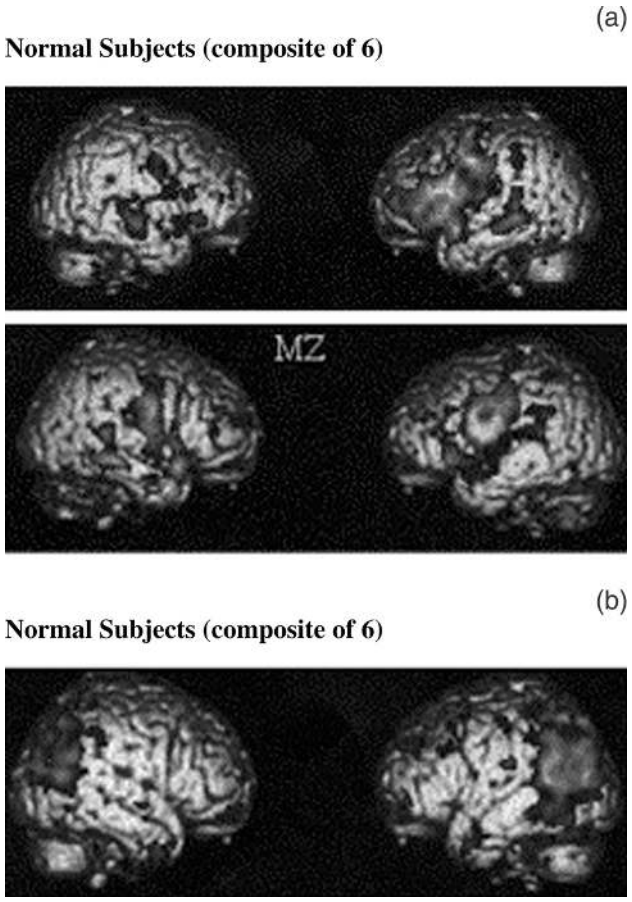

Figure 2 (Prabhakaran). (a) Blood oxygen level dependent (BOLD) effect for task versus rest at $p = 0.001$ (uncorrected). Top panel: Composite results of fMRI of normal subjects showing a left-lateralized fronto-temporal network of brain activity with predominantly frontal involvement.Bottom panel: fMRI result of one of the chronic left MCA stenotic patients MZ showing less lateralized fronto-temporal activity with increased right fronto-temporal/predominantly-frontal region involvement. (b) BOLD effect for rest versus task at $p = 0.001$ (uncorrected). Composite results of fMRI of normal subjects. Bilateral parietal regions were noted to show more activity in the rest than in the task state.

Piece of mind; a full systems approach is required

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Abstract: Intelligence studies are confounded by an inability to image the mind, as well as by heterogeneity in intelligence constructs, gender, and age. The ghost (of future, not past) sitting at the table is a molecular one. Biochemistry and molecular biology factors can contribute to or take away from intelligence to a great and not yet fully explored extent.

Jung & Haier (J&H) have done a nice job of collating the little data about the neural substrate of intelligence. It is useful and we do have to start somewhere; there are of course the usual reservations about drawing conclusions about the mind from images of the brain (Coltheart 2006; Seron & Fias 2006), but J&H have been suitably cautious, sieving the data down to groups of mutually inclusive spots.

The involvement of Brodmann area (BA) 39 is of interest. There is some very solid lesion data from aphasics to support involvement of this area in intelligence, but at least some of the circuitry therein may only have a peripheral role. This area is known to be significantly abnormal in dyslexic dysfunction (Rae et al. 1998; Rumsey et al. 1992), although there is a poor relationship (Gustafson & Samuelsson 1999) between the presence of dyslexia and IQ. (Albert Einstein is a topical case in point,

having both dyslexia and abnormal BA 39; see Kantha [1992]; did Einstein's abnormal brain development allow the increased development of other circuits, such as those dealing with mathematical reasoning?)

The very intelligent brain is an interesting thing and may not necessarily be wired the same way as the average one. This suggests that a continuum may not exist in neuroanatomical intelligence substrates (i.e., a very intelligent brain may not just be a supercharged version of an average one); male brains being a generalized case in point, where the IQ distribution has significant wings. The gender distribution among those with extreme mathematical ability (or extremely dull brains) is highly skewed towards males (Benbow & Stanley 1983). How does this happen? Why is the male brain more susceptible to disorders such as dyslexia (Rutter et al. 2004)? A clue may yet come from epigenetics.

It seems like stating the obvious, and J&H have highlighted it in their article, but the inherent fuzziness of the concept makes "intelligence" difficult to define (Sternberg 1990). J&H have identified intelligence as relating closely to *g*, itself a difficult to define concept. There is an argument to mount that heterogeneous functions in *g* (e.g., visuo-spatial vs. verbal) have different neural substrates (e.g., Benga 2006), and the data may be skewed by the tendency of researchers to use tasks loaded on visuo-spatial ability in their functional imaging studies simply because they are easier to implement in many cases than language tasks (e.g., the verb-generation task study [Schmithorst & Holland 2006] does not include BA 39). From an evolutionary perspective, spatial abilities were acquired by the brain earlier than verbal abilities, which appear wired into the brain (especially the female brain) wherever there is room! Overlaid on this is the effect of gender, where differences in brain regions involved in intelligence have been repeatedly shown. Furthermore, there is strong evidence of possible epigenetic effects (Davies et al. 2005; Davies & Wilkinson 2006). In the case of Turner syndrome, where persons have only one sex chromosome (45,X), evidence has emerged that the superior and middle temporal lobes are greatly enlarged (Rae et al. 2004). The bigger the lobe, the worse the performance on temporal lobe-related tasks (Rae et al. 2004) (another example of bigger not necessarily being better). The enlargement is related to the parent of origin of the lone X chromosome, and other lobes, such as the parietal lobe which is relatively smaller, are similarly affected (Cutter et al. 2006). These changes in brain volume are not insignificant and have the potential to influence attempts to measure changes in brain volume with intelligence. In males, where the parent of origin of the X chromosome is always maternal, this effect may be easier to deal with than in females, where X-inactivation is mosaicized and could have an infinite number of possible patterns. There are of course 23 other chromosomes, and not only gender effects but age effects, hormone effects, and the list goes on. It has recently been shown that just a single amino acid substitution in an enzyme can sharpen signal-to-noise characteristics in microcircuitry (Winterer et al. 2006).

Speaking of signaling efficiency (at the risk of overemphasizing my piece of the elephant), the emergent P-FIT model "elucidates the critical interaction between association cortices within parietal and frontal brain regions which, *when effectively linked* by white matter structures . . . underpins individual differences in reasoning competence in humans" (sect. 4, para. 2, my emphasis). Being *effectively linked* is obviously of importance, and structural and metabolic hot spots in functional imaging studies are not yet able to show how this linkage takes place. The size of the linking cabling shown up on the diffusion tensor image (Deary et al. 2006; Mabbott et al. 2006) and connectivity analysis approaches may in future illuminate how, when, and where this happens (Rypma et al. 2006). How one brain communicates more efficiently than another, virtually identical brain, is a question central to any query about intelligence. Brains with more bioenergetic capacity appear to work better (Jung et al. 1999; Rae et al. 2003b); indeed ability can be improved by as much as one standard deviation at a task heavily loaded on *g*, (Raven's Advanced Progressive Matrices), simply by adding spare bioenergetic capacity (creatine) (Rae et al. 2003a).

The P-FIT model is a good start given our limited data, but may also be a dangerous thing if taken too seriously. Is there really a one-size-fits-all? Do ultra-bright brains really fit inside the box, or do individual differences become more important at this end of the scale?

The bottom line is that, beyond all the other confounding factors, molecular and systems biochemistry also needs to play a bigger role in research into cognition and inform our theorizing about the basis of intelligent behavior. Systems approaches need to be expanded to include all major variables, and study-group sizes need to be a lot bigger to filter the doubt from the dogma. Otherwise we shall never know what the elephant really looks like.

Can the Parieto-Frontal Integration Theory be extended to account for individual differences in skilled and expert performance in everyday life?

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Abstract: Performance on abstract unfamiliar tasks used to measure intelligence has not been found to correlate with individual differences in highly skilled and expert performance. Given that cognitive and neural structures and regions mediating performance change as skill increases, the structures highlighted by parieto-frontal integration theory are unlikely to account for individual differences in skilled cognitive achievement in everyday life.

Jung & Haier (J&H) present an extensive review of brain activation during the performance of psychological tasks that have traditionally been assumed to reflect intelligence in general, such as IQ tests, logical reasoning, fluid-crystallized measures, and reasoning in games such as chess and Go. Although the authors document many important similarities in the location of relevant brain areas during the performance of many of these tasks, all the studies they reviewed are based on samples of untrained participants. This type of research cannot address the critical question of whether the same structures of parieto-frontal integration theory (P-FIT) would be activated, and thus mediate individual differences, in the execution of high levels of skilled performance.

Over the last two decades there has been remarkable progress in measuring expert performance scientifically (Ericsson et al. 2006), particularly in finding valid metrics of superior achievement. Reproducibly superior performance has been successfully captured by recreating ecologically valid and representative tasks in the laboratory (Ericsson 2006a; 2006b) that typically predict objective performance in skill domains far better than do subject metrics, such as social judgments of expertise. When we limit our review to only objective measures of performance in domains of skill, we find that traditional intelligence tests are not related to individual differences among skilled and expert performers. In general, our reviews show that although intelligence is frequently correlated with initial performance on an unfamiliar task, after extended periods of skill acquisition the

relation is no longer statistically reliable. For example, a recent longitudinal study of children's improvements in chess found that the predictive power of IQ diminishes dramatically as skill improves, and did not predict rate of improvement after accounting for practice activity (Bilalič 2006). Research on expert performance has also found that full-scale IQ tests and heavily *g*-loaded tests (e.g., Raven's matrices) are not reliably correlated with expert performance in many types of intellectual domains, such as chess (Doll & Mayr 1987), Go (Masunaga & Horn 2001), and several others (Ericsson & Lehmann 1996). Although a common objection to these findings is that the entire sample of skilled chess players have an average IQ that is higher than the mean of the general population (e.g., Doll & Mayr 1987), the lack of a relation persists even in samples that vary widely in skill and IQ (Grabner et al. 2006; Unterrainer et al. 2006), indicating that restriction of range cannot be the explanation. Additionally, IQ is not a requirement for high performance, given the numerous documented cases of individuals achieving extreme levels of achievement with IQs below 100. For example, some of the grandmaster chess players in Doll and Mayr's (1987) study had IQ scores below the normative mean; and even in the verbal board game SCRABBLE, some top players have below-average verbal ability (Tuffiash et al., submitted). That IQ and cognitive-ability tasks fail to reliably predict objective measures of domain achievement raises doubts as to whether the underlying mechanisms overlap.

Indeed, research on processes mediating reproducibly superior expert performance shows that the mediating mechanisms differ fundamentally from those used by novices (Ericsson 2006a) – that is, during years of practice and training, experts acquire elaborate mechanisms for encoding and maintaining flexible access to critical task information that bypass basic capacities, such as short-term memory capacity (Ericsson & Kintsch 1995). Moreover, there is an impressive body of evidence showing that with increasing level of skill there are changes in the patterns of neural activation (Hill & Schneider 2006); and some evidence even suggests that intense training can change functional and structural aspects of the brain (Ericsson 2006b). For example, early and extended training has been shown to change the cortical mapping of the brain area controlling fingers of string players (Elbert et al. 1995) and the flexibility of fingers (Ericsson & Lehmann 1996). Also interesting is the recent finding that intense music practice influences the development of myelin around nerves in critical brain regions (Bengtsson et al. 2005). Notably, several studies have also found that regions of brain activity may dramatically change as chess skill increases (Amidzic et al. 2001; Grabner et al. 2006; Volke et al. 2002), which further challenges the results based on novice samples reviewed by J&H. Other studies have shown evidence that experts use different neural regions than the ones novices use in many other intellectual domains as well, including memory (Maguire et al. 2003) and mental calculation (Pesenti et al. 2001), and even in taxi driving (Hartley 2003). In general, achieving expert proficiency in a domain requires thousands of hours of effortful *deliberate practice* involving problem solving and intense concentration (Ericsson 2006b; Ericsson et al. 1993), and critical changes in neural substrates will accumulate over this period of time, in a manner that cannot be elicited during a brief training period with the tasks.

If authentic skilled performance activates different brain regions than does unskilled performance on lab tasks, the regions outlined by P-FIT may not influence or constrain skilled performance in naturalistic settings. If extended *deliberate practice* can transform and adapt physical, cognitive, and neural structures, then the search for the ultimate neurological circuit or brain structure underlying intelligence may be misguided. We would recommend that J&H extend their research to brain activation during experts' performance on ecologically valid and representative tasks and compare these patterns to those activated by conventional tests of intelligence. We also believe that longitudinal studies of the decade-long acquisition of skilled and expert performance would be necessary to allow us to assess the changes in brain activation and their relation to extensive training periods. Ultimately, a general theory of mental ability and intelligence must account for individual differences in cognitive performance throughout skill development, from unskilled beginners to the highest levels of domain achievement.

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Functional connectivity in the brain and human intelligence

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Abstract: A parieto-frontal integration theory (P-FIT) model of human intelligence has been proposed based on a review of neuroimaging literature and lesion studies. The P-FIT model provides an important basis for future research. Future studies involving connectivity analyses and an integrative approach of imaging modalities using the P-FIT model should provide vastly increased understanding of the biological bases of intelligence.

Based on an exhaustive review of neuroimaging studies, including volumetric MRI (especially voxel-based morphometry [VBM]), diffusion tensor MRI (DTI), magnetic resonance spectroscopy (MRS), functional MRI (fMRI), and functional PET (fPET), as well as lesion studies, Jung & Haier (J&H) propose a parieto-frontal integration theory (P-FIT) model which underpins individual differences in intelligence in humans. The P-FIT model is consonant with a unitary theory of intelligence, involving general intelligence (*g*), given that "one of the main insights of cognitive neuroscience is that the 'functional units' of higher cognition are networks of brain areas, not single areas" (Gray & Thompson 2004). J&H's important review can serve as a starting point for future research into the correlation of brain structure with intelligence. Neuroimaging technology and analysis procedures have now progressed to the point where a detailed analysis of the correlation of networks of brain activation with cognitive function is feasible. Such an analysis may, as the authors acknowledge, necessitate further, possibly significant, modifications of the P-FIT. Nevertheless, the P-FIT model provides an important basis for future investigations.

The technology and analyses available for neuroimaging research on intelligence have progressed substantially from simple correlations of whole-brain or whole-head volumes. Only a few of the functional studies cited by the authors have investigated the role of functional or effective connectivity, however, which would seem to be critical for evaluating the role of specific functional networks in intelligence. The P-FIT model would seem particularly amenable to the use of techniques such as linear structural equation modeling (SEM) (Buchel & Friston 1997; Karunanayaka et al. 2007; McIntosh et al. 1994), or dynamic causal modeling (DCM) (Friston et al. 2003; Penny et al. 2004), which allow the investigation of effective, as opposed to functional, connectivity. Whereas functional connectivity refers only to a relationship, or association, between brain regions, effective connectivity assesses the degree of influence of one brain region over another (Patel et al. 2006). Other techniques for connectivity analysis have

also been developed, including a Bayesian analysis of functional connectivity (Patel et al. 2006; Schmithorst & Holland 2007) and multivariate autoregressive modeling (MAM; Harrison et al. 2003). Together, these techniques will allow a detailed analysis of how cognitive function related to intelligence relies on an integrated network of several regions of the brain.

The research will further benefit from the incorporation of magnetoencephalography (MEG) or electroencephalography (EEG) studies carried out in conjunction with fMRI, as the much greater temporal resolution afforded by MEG and EEG will allow finer distinction of how the activation of functional networks differs in more-intelligent individuals. Each of the imaging studies cited by the authors employed only a single methodology, whether fMRI, VBM, or DTI. An integrated approach combining these methodologies, possibly also in conjunction with MRS, into a single study would constitute a powerful tool to further unravel present questions about the biological bases of intelligence. An example is the combination of fMRI and DTI in analysis of the properties of the auditory cortex (Upadhyay et al. 2006). For instance, is greater neuronal density in men (Haier et al. 2005) correlating with intelligence, also associated with greater "neural efficiency" (Neubauer et al. 2002) and with greater localization of cognitive function (Schmithorst & Holland 2006)? And is this correlation also possibly associated with differences in white matter anisotropy (Schmithorst et al. 2005) and metabolite concentrations, as measured by MRS (Jung et al. 2005)? A combined methodological approach, using the P-FIT model as an a priori hypothesis, would be a powerful tool to answer these types of questions.

These advanced imaging approaches provide the tools to investigate the P-FIT model in a great deal of detail. There obviously remain several unresolved questions to be answered by future studies, which will likely necessitate significant modification of the P-FIT model. Most of the papers reviewed used adult subjects, hence, it is yet to be determined precisely how the P-FIT develops through childhood and adolescence. The authors propose the *ASPM* and *microcephalin* genes as candidates for a genetic basis behind general intelligence; however, the relationship among these genes, evolution, and cognition has recently been challenged (Balter 2006; Currat et al. 2006) and a significant gene–environment interaction is also likely, further complicating the issue of genetic mechanisms and hereditability. Sex differences may also interact with the P-FIT. Whereas J&H focus on fronto-parietal (presumably intrahemispheric) connections, a recent fMRI study (Schmithorst & Holland 2007) has shown an increasing dependence on interhemispheric functional connectivity with age in girls, and a greater dependence on functional connectivity with Broca's area in boys. Moreover, in boys, a negative correlation of parieto-frontal connectivity with intelligence has been seen to develop with age in the left hemisphere (Schmithorst & Holland 2006), although in that study the superior medial frontal gyrus as well as the left prefrontal cortex were included in the network. It is therefore likely that a characterization of the relevant network merely as "parieto-frontal" lacks sufficient specificity, and a detailed investigation of the contribution of each area in the parietal and frontal lobes will be necessary. Functional segregation has been seen, for instance, in regions including Broca's area (Cannestra et al. 2000), and the P-FIT model will likely need to encompass these differences. How the P-FIT model is consistent with "neural efficiency," where more-intelligent individuals use a more limited set of brain circuits and neurons and fewer neural resources to perform at a given cognitive level (Gray & Thompson 2004), is another issue to resolve in the future, especially since neural efficiency is modulated by task and sex (Neubauer et al. 2002).

In conclusion, the authors provide a convincing motivation for the use of neuroimaging technology in studies of intelligence and a useful model (P-FIT) for further investigation. With current advances in the field of neuroimaging technology and analyses, researchers should now be poised to make substantial advances in our understanding of the biological bases of intelligence.

Right answer to the wrong question: A reply to Jung and Haier

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Abstract: Jung & Haier (J&H) have done an admirable job of solving the wrong problem. Their article does not show "where in the brain is intelligence," because intelligence resides not in the brain but, rather, in the interaction of brain and environment. I describe four reasons why the article does not adequately localize intelligence in the brain.

"Where in the brain is intelligence?" This is the first sentence of Jung & Haier's (J&H's) target article. The article does a very fine job of solving a problem – but, unfortunately, not the problem it sets out to solve with this question.

What problem does it solve? The problem it solves is: "Where in the brain are there functions that, when measured in particular ways, show correlations with scores on conventional IQ-related tests?" This is a problem very different from, and much more limited than, the problem posed in the first sentence of the article. It is not a bad problem to solve, but it is more restricted in scope than the problem of "where in the brain is intelligence?"

Why does the target article not solve the problem of where in the brain intelligence is? There are four reasons.

First, the article assumes that intelligence is "in the brain." Where else, you might ask, could it be? It is, rather, in the interaction between organisms and their environments. Hence, intelligence cannot be localized "in the brain." Intelligence has traditionally been defined as the ability to adapt to the environment (Sternberg & Detterman 1986), so both organisms and the environments to which they must adapt matter for localizing intelligence.

The adaptive demands of different organisms and kinds of organisms are different, and they differ across time and place. Consider, first, the demands of changing times, then of changing places.

As an example with respect to time, mathematical-computation skills were important when I was growing up in the 1950s, and they were a notable part of aptitude and achievement tests, as well as of school success. Today, with the advent of electronic computational devices, these skills are much less important than they once were. This lesser importance is reflected in tests and in school. Conversely, the abilities to deal with computational devices were once unimportant, because the devices did not exist, but today are quite important. Someone who successfully can navigate today's Internet environment is in a much better position to adapt than someone who cannot. Is intelligence today the same as in the 1950s? No. What was once "intelligence" has changed. Attempts to locate intelligence "in the brain" cannot succeed if one assumes that the same areas of the brain will always be relevant to intelligence.

As an example with respect to place, consider that in cultures other than our own, different skills may be relevant to the concept of intelligence (see review in Sternberg 2004). For example, we found, in a study in rural Kenya, IQ actually may be negatively correlated with the skills needed for adaptive success (Sternberg et al. 2001). The reason is that, in this environment, the people identified as "intelligent" in terms of adaptive demands learn practical skills not measured by the tests, such

as knowledge of natural herbal medicines used to combat parasitic illnesses. In Alaska, Yup'ik Eskimo children who are viewed as successfully adaptive are those who have developed the hunting and gathering skills necessary to adaptation, not those who excel in academics (Grigorenko et al. 2004). What matters in rural Alaska may change in the future, but that is my point. Attempts to localize intelligence in the brain need to take into account that different areas of the brain may be differentially important in different places as well as times. The static approach taken by J&H will not work.

Second, from an evolutionary point of view, intelligence as adaptation to an ecological niche does not even require a brain. Hence, we cannot localize intelligence in certain parts of the brain. We humans battle, and, in a sense, have been outsmarted by, organisms that do not even have brains. Consider, for example, a virus such as HIV. It has no brain; so, in terms of the J&H article, it presumably has no intelligence. But it has managed to outwit the many millions of people it has killed and will kill. It also has outwitted some of the world's most brilliant scientists, who have been trying to eradicate it but have, as yet, been much less than fully successful. Ditto for the malaria parasite and any of numerous other organisms with which humans are in competition. In terms of the adaptive niches in which they live, HIV, *Plasmodium falciparum*, and many other species have shown themselves to be quite intelligent, despite the fact that they have no brain.

Are these organisms showing intelligence in outwitting humans? Certainly there are objections that might be posed. One might say that any individual virus or parasite is no match for any one intelligent human. But at the level of a gene pool, they do not seem to be doing badly at all, comparatively speaking. If their gene pool eradicates the human one, what humans counted as "intelligence" may have been a serious misdefinition in terms of biological adaptation that benefited them only so long as they survived as a gene pool.

The same principle applies within, as well as across, species. The Romans probably thought themselves much more intelligent than the "Barbarians" who were knocking at their gates, until their Empire came crashing down in the face of the barbarian onslaught. Once the Romans were almost wiped out, those who were left could repent at leisure their underestimation of the people they considered to be barbarians. Contemporary civilization may find itself with similar challenges. We may someday conclude that we were defeated by the greater viciousness, or birthrate, or brutality of an enemy; but in the end, it will not matter what story glorifying our intelligence we wish to tell, because we will not be around to tell it.

One could argue that a hurricane would pass the above test for intelligence. It would not, because it spreads its destruction equally. It does not target. And it is inanimate. Its genes are not "clever," because it has no genes.

Third, the article assumes that IQ tests measure intelligence. This is a convenient assumption for those who have been brought up on a steady of diet of IQ-like tests (SATs, GREs, LSATs, etc.), and who have done well on them, thereby helping to promote, in their society, their own economic well-being. To a large (although not full) extent, scores on these tests are proxies for socioeconomic and educational status (Ceci 1996; Gardner 1983). Even in our own society, IQ-related indices are far from a complete predictor of either school success (Hedlund et al. 2006; Sternberg & the Rainbow Project Collaborators 2006) or real-life success. Other forms of intelligence – creative, emotional, practical, social – may be needed to supplement the analytical intelligence measured by IQ in order to more accurately predict adaptation to the environment (Kihlstrom & Cantor 2000; Mayer et al. 2000; Sternberg et al. 2000; Wagner 2000).

Fourth, the article assumes some kind of causality whereby brain determines IQ. But research shows that learning affects the brain, which in turn affects IQ-related scores and various kinds of performances (e.g., Greenough & Black 2000). What the studies cited in the article show is a correlational, not causal, relationship.

In sum, IQ helps people solve problems, such as that of identifying correlates of brain and IQ-test functioning. Where it is not so helpful is in making sure that the problem being solved is the optimal one to solve. Scientists therefore need especially to ensure that they are solving the optimal problem, because their training may better prepare them for problem-solving than for problem-finding. And if they find the wrong problem, they may indeed come up with the right solution, but not to the problem they were seeking to solve, and not necessarily to a problem of great importance.

Plasticity in high-order cognition: Evidence of dissociation in aphasia

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Abstract: High-order constructs such as intelligence result from the interaction of numerous processing systems, one of which is language. However, in determining the role of language in intelligence, attention must be paid to evidence from lesion studies and, in particular, evidence of dissociation of functions where high-order cognition can be demonstrated in face of profound aphasia.

Jung & Haier (J&H) present a broad-ranging review of research into the neural bases of intelligence. They synthesize evidence from functional neuroimaging, genetic, and lesion studies. The neuroimaging and lesion research appear to converge on the notion that language and the neural systems that underpin it are an essential component of intelligence. Included in the P-FIT network are left hemisphere Brodmann Areas (BAs) 22, 39, 40, 44, and 45, all of which are central to language function and lesions of which result in aphasia. J&H review mid-twentieth-century research for evidence of decline of intelligence in aphasia. They identify the common theme that people with Broca's aphasia, and lesions in and around BAs 44 and 45, can show no reduction in performance on nonverbal intelligence scales.

This conclusion is supported by more recent research showing that people with severe agrammatic aphasia, and also marked lexical impairment, can still sustain high-level intellectual performances in domains including social, causal, and mathematical reasoning (Varley 2002; Varley & Siegal 2000; Varley et al. 2005). The group of aphasic patients for which there are consistent reports of cognitive decline are those with global aphasia (e.g., van Mourik et al. 1992). However, individuals with global aphasia often have very large left hemisphere lesions, spanning much of J&H's P-FIT network, and it becomes difficult to determine whether cognitive decline in these cases is due to impairment of language or to loss of some other cognitive subsystem that is geographically close to, or overlapping with, the language network. In addition, the extent of disconnection of functional systems that occurs with large lesions might account for cognitive decline, independent of a specific role for language in high-level cognition.

The evidence that some individuals with lesions within the P-FIT network can still sustain high-order intellectual activities presents an apparent contradiction to the results of functional imaging studies that show recruitment of the same zones in a range of intellectual tasks. The behavioral tasks used to

investigate intelligence are varied, but they all represent high-demand cognitive activities. Typical tasks might involve rapid perceptual-motor recoding of information, loading of working memory, deductive and inductive reasoning, and the frequent formation and shifting of strategies. Successful completion of such tasks typically involves the recruitment of a bundle of cognitive mechanisms. Some of these mechanisms will be core to the completion of the task (such as visual perceptual processes in a matrix reasoning test), whereas others represent more fluid "co-opted" mechanisms that scaffold performance (Clark 1998; Siegal & Varley 2002).

The status of language as a "core" versus "co-opted" mechanism is crucial in many debates as to the role of language in thought and high-order cognition. There are aspects of language which make it an excellent candidate for core status in many forms of reasoning. The lexicon provides a set of symbols that permits the encapsulation and manipulation of abstract notions such as spatial relationships or large numerosities (Dehaene et al. 1999; Hermer-Vasquez et al. 1999). Similarly, the grammatical mechanisms of language might be crucial, permitting the capture of relationships between entities. However, the language faculty is also a prime candidate for co-opted status. Language, either in the form of overt verbalization, or as covert inner speech, may appear in many tasks, including ones that involve the manipulation of abstract visuo-spatial information, such as matrix reasoning tests. The breaking down of a complex problem into a series of sub-steps represented in language sentences may represent an important cognitive tool in solving that problem. Similarly, the encoding of information into phonological form permits rehearsal and maintenance in working memory of intermediate products of problem solving.

Functional brain imaging studies allow identification of the neural mechanisms that are associated with the performance of a particular cognitive task. Hence, activation of left hemisphere peri-sylvian zones might indicate that language is a component of the activity under investigation. However, functional imaging data cannot discriminate whether language-related activation corresponds to a core or co-opted component of an activity. To some degree, appropriate linguistic baseline conditions in an imaging study might clarify this issue, and linguistic processing during baseline scanning might permit the subtraction of generalized activity from activity in experimental conditions. However, it is not clear that the language demands of a control condition necessarily equate to those of the active internal dialogue that is ubiquitous in high-demand cognitive activities. Passively viewing sentences or making decisions as to whether first-mentioned nouns are human agents (Goel et al. 1997) does not necessarily match the functional demands of forming a series of natural language sentences during problem solving.

J&H's scholarly synthesis of evidence from diverse domains is to be welcomed. However, in reviewing neuropsychological studies it is important to consider the evidence of dissociation of functions and that high-order cognition can be retained despite large lesions within the P-FIT network. Such evidence suggests flexibility and plasticity in the mechanisms that are recruited to perform a task. The neurobiological substrate of phonological working memory lies within the P-FIT network. However, when the capacity to encode and maintain information in phonological form is impaired, as it invariably is in aphasia, alternative resources such as visuo-spatial working memory can be recruited in order to sustain a performance. Many of the regions identified by J&H may reflect the mechanisms that are ordinarily recruited by healthy participants to complete a demanding intellectual task. For most human participants, language represents a fine resource to support thinking and reasoning. However, the evidence from people with severe aphasia suggests that these regions and the functions that they sustain are not necessary for high-order cognition. Intelligence may be characterized both at the behavioural and neural levels by flexibility and plasticity.

The neuronal basis of intelligence: A riddle, wrapped in a mystery?

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Abstract: "Where in the brain is intelligence?" is an intriguing question, and Jung & Haier (J&H) resist the temptation to provide a simple answer. Their concept tries to integrate and transcend previous findings, and, while omitting the contributions from complementary methods, results seem to converge. Whether similarities or differences in such networks are more important, though, is still open for discussion.

For a long time people have speculated about what makes some human brains "brainier" than others; in the present target article Jung & Haier (J&H) go a bold step beyond speculation. As I think the authors do too, I have a hard time believing that we will find one singular "structural basis of intelligence": Considering the multitude of characteristics that, together, make up intelligence, I would rather expect several collaborating (and competing?) network nodes, with strengths in one (or more) explaining individual performance advantages. Therefore, the proposed model is a step in the right direction, allowing for different emphases within its framework. Considering the numerous studies that contributed to this review, it seems to me that intelligence research using neuroimaging methods has come to a crossroad: Based on the available data, a broad pattern seems to emerge, and now more sophisticated approaches seem warranted, including an exact characterization of the cognitive functions that are under scrutiny.

In that respect, I tend to agree with Thorndike (1921) that intelligence is "that which intelligence tests measure." Correlates of global parameters are likely to give us only so much insight, as the various cognitive functions underlying performance in such tests will likely preclude finding distinct nodes in the to-be-suspected networks. Instead, the correlates of defined and more "pure" cognitive functions as assessed in different ways would seem to be more promising in defining distinct parts within the complex network that must be suspected to underlie "intelligence." Neuroimaging studies of "schizophrenia" may serve as a reminder: there is practically no brain region that has not been implicated in the neurobiology underlying schizophrenia (Honea et al. 2005; McCarley et al. 1999). The explanation for this (apart from different methodological approaches) is likely that schizophrenia, in the neurobiological sense, is not one disease but may rather be a common final path of several disorders, or the result of a variable combination of disturbances caused by (at least) "two hits" (Rapoport et al. 2005). At the least, the clinical variability between subjects severely decreases the chances to find similarities, as the consequently increased variability will make the detection of subtle abnormalities much less likely.

The same may and will be true for finding the neuroanatomical substrate of intelligence, broadly defined: no one region can be expected to underlie such a complex cognitive function, and the challenge for the next years will be to more closely define the different nodes while not forgetting their contribution to the underlying network. Along these lines, we may find that the differences between the nodes tell us more than the similarities.

The omission of results from complementary imaging methods, although necessary for this format, somewhat limits the scope of the model: Processing speed and neuronal regions driving each other on the millisecond time scale are likely important aspects contributing to the efficiency of fast decision-making processes. These are more accurately described using methods such as magnetoencephalography or electroencephalography, as done recently (Thatcher et al.

2007). The lower spatial resolution of these methods is somewhat compensated by the very high time resolution, thereby almost ideally complementing dynamic MRI methods. As J&H pointed out, multi-modal imaging approaches are likely to have the highest yield when assessing such a complex interplay.

There is one point where I would like to urge caution: I would be very careful in drawing inferences on normal neuronal organization from studies on children with severe epilepsy. The pediatric brain has been shown to be highly adaptable when overcoming early neuronal insults (Krägeloh-Mann 2004), and our own group could show the enormous adaptive potential with regard to language (Staudt et al. 2002), as well as the limitations of this potential with regard to the perception of biological motion (Pavlova et al. 2006) and visuospatial functions (Lidzba et al. 2006). Considering this plasticity (which has also been shown in the context of epilepsy; Gleissner et al. 2005; Yuan et al. 2006) it is difficult to establish a cause-and-effect chain: If subjects with severe epilepsy profit when the epileptogenic region is removed, it could be due to the interfering effect of this region on other regions (which are consequently released from the interference and therefore function better). Alternatively, the interfering region itself could be an important network player in the healthy state and might have lost this functionality in favor of another region that has since assumed this role. Or, the epileptogenic region is still a malfunctioning part of the network and only its removal prompts a reorganization, or... Without knowing the sequence of events, the effect of such long-term interference in a more-adaptive neuronal system (i.e., the pediatric brain) is difficult to impossible to predict.

This is not to discount the importance of lesion studies, however. The findings from acute brain lesions in adults, as in the case of the historic missile wound studies, may well be used to supplement and inform the results obtained from healthy individuals (or special patient populations), and may contribute important information (e.g., it was mainly the case of the famous "Monsieur Tan" that lead Paul Broca to formulate and articulate his theory over specific language centers in the brain; cf. Broca 1861).

Winston Churchill is said to have coined the famous "a riddle, wrapped in a mystery" quote (concerning Russia; supposedly he even added "inside an enigma"). Right now, the field of intelligence research may have moved towards stripping away parts of the mystery, but the riddle inside is still unsolved. Overall, I believe this to be an important contribution, hopefully sparking interesting and fruitful discussions within the intelligence research community.

Overall intelligence and localized brain damage

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Abstract: Overall mean performance on intelligence tests by brain-damaged patients with focal lesions can be misleading in regard to localization of intelligence. The widely used WAIS has many subtests that together recruit spatially distant neural "centers," but individually the subtests reveal localized functions. Moreover, there are kinds of intelligence that defy the localizationist approach inferred from brain damage.

Brain damage fragments cognition into numerous perceptual and cognitive units that can then be examined with an eye toward their functional localization in the brain. The 14 subtests of the Wechsler Adult Intelligence Scale (WAIS) are commonly employed to assess the effects of the damage on different aspects of intelligence. Each subtest relies on separate or overlapping brain functions, but together all subtests need the computational powers of the entire brain, not just the frontal-parietal axis. For example, what is required at the very minimum for performing the Information subtest of the WAIS test is intact auditory comprehension, namely Wernicke's Area complex in the left temporal lobe, as well as verbal output, namely Broca's Area complex in the left frontal lobe, together with long-term semantic memory, which includes the left hippocampus, the temporal and parietal lobes. To use another example, consider the Block Design, a subtest that measures spatial abilities: The frontal lobes in both the left and right hemispheres are required for foresight, the right parietal lobe for translating the two-dimensional diagrams of the blocks into three-dimensional construction of the blocks, not to mention sustained attention on the task by the left parietal lobe. But what specific brain regions control performance in the Picture Arrangement subtest (arranging individual pictures so they tell a unified story) besides the occipital lobes, the parietal lobes, commissural fibers, both hemispheres or only one hemisphere, is not known. All four lobes, in each hemisphere, and possibly subcortical regions, would be expected to contribute to intelligence as measured by the widely employed intelligence tests.

In section 7.1, Jung & Haier (J&H) cite studies that did not reveal striking alterations in overall IQ, or intelligence in general, or just verbal intelligence following localized brain damage, and they use the results as supporting evidence for their main thesis. However, such empirical outcomes should not be surprising considering the following: Performance on several subtests can compensate for the reduction on only one or two. It is not informative to declare that overall intelligence as measured by the WAIS or a similar test is reduced or not following focal damage. Likewise, with brain-damaged patients, reporting whether or not the Verbal Scale or the Performance Scale of the WAIS is affected, masks the compensatory contribution of intact regions. What is potentially meaningful in the context of brain lesions is the breakdown of scores in individual subtests, and, in tests such as the Raven's Progressive Matrices where subtest breakdown is not possible, the clustering of failed versus successful items, or item analysis results. Finally, the cognition measured by intelligence tests reflects the combined effects of diseased and healthy tissue. The effects of focal and lateralized damage could go against a large regional involvement such as the frontal-parietal axis.

Moreover, localized specialized brain regions form pathways and networks connected to each other in selective interactive ways, as J&H point out. However, the extent of their interconnectedness could be critical for optimal performance on intelligence tests. The issue of high intelligence versus average or low intelligence has not been fully addressed in the target article as a function of the interconnectivity. Number of functional axonal fibers and their myelin is a neglected issue in assessing effects of neural injury. Abundant connectivity among widely localized neuronal centers would be expected for above-average performance on intelligence tests, whereas for average intelligence only limited connectivity may be sufficient.

Further, there are kinds of intelligence that traditionally have not been subjected to many decades of scrutiny as the WAIS or the Raven's Progressive Matrices (Gardner 1993b; Sternberg 1985). These kinds are complex and cannot be measured easily, and consequently brain damage cannot illuminate their components sufficiently to provide clues to their localization, nor can functional magnetic resonance imaging (fMRI), positron emission tomography (PET), or Single Photon Emission Computerized Tomography (SPECT) help here.

One need only think of social intelligence, emotional intelligence, athletic intelligence, and artistic intelligence to realize

their enormous complexity and their unamenability to numerical, analytic measures. There are other types of "intelligences" not defined yet in terms of cognitive units, and no neuronal "centers" or specific neural pathways have been uncovered for them (Rose 2004). Artistic intelligence, for example, relies heavily on specialized cognition, skill, practice, and talent, and is extremely resistant to a wide variety of brain-damage etiology (Zaidel 2005). To apply the frontal-parietal axis to this type of intelligence is wholly inadequate.

Authors' Response*

Beautiful minds (i.e., brains) and the neural basis of intelligence

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Abstract: The commentaries address conceptual issues ranging from our narrow focus on neuroimaging to the various definitions of intelligence. The integration of the P-FIT and data from cognitive neuroscience is particularly important and considerable consistency is found. Overall, the commentaries affirm that advances in neuroscience techniques have caused intelligence research to enter a new phase. The P-FIT is recognized as a reasonable empirical framework to test hypotheses about the relationship of brain structure and function with intelligence and reasoning.

So, where in the brain is intelligence? The commentators provide us with a wide range of insights about our interpretation of neuroimaging studies that speak to this deceptively simple question. Happily and unhappily, the criticisms are relatively mild. On one hand, intelligence research has matured to a point past earlier vehement arguments about whether or not intelligence is a proper subject for scientific investigation. On the other hand, perhaps our parieto-frontal integration theory (P-FIT) model is too tame to invoke strong criticism, at least from other intelligence researchers. Hence, we attempt to be a bit more provocative here for the sake of discussion.

R1. Not a pretty picture

The 19 commentaries generally fall into three categories: Most of them question aspects of our conceptual framework, others focus on specific discussion of P-FIT details, and a few seek to generalize the P-FIT to other theories and domains. Within these categories, most of the commentaries are quite disparate in their emphasis. Therefore, we will discuss each in turn, but first we wish to offer our own pointed criticism of the P-FIT. At best, the P-FIT is a rather bland listing of the brain areas which may be related to intelligence. The important points of our review are that such areas can be identified empirically (after 20 years of neuroimaging research) and that there are multiple areas distributed throughout the brain rather than a single region within the frontal lobe. Whether the P-FIT list is fully accurate is addressed in one way or another by most of the commentaries, but only additional research will firmly establish the relevant areas linking brain and intellectual functioning. The P-FIT suggests that integration among the areas is important for intelligence, but the P-FIT is largely silent about how the areas work and how the areas communicate with each other. Until we can address these issues, the P-FIT is only a modest beginning, as noted by many of the commentators. Brains and minds are beautiful and elegant. As it stands, the P-FIT model is not. We are hopeful that these qualities, necessary for a meaningful theory of the neurobiology of intelligence, will emerge with time.

We begin with acknowledging the historical perspective noted by **Hunt,** a pioneer in intelligence research. In some ways, our review marks the end of the first 20-year phase of neuroimaging research related to intelligence. As he notes, the studies we reviewed in the target article move well beyond earlier controversies about whether or not there is a neurobiological basis for intelligence, and well past behaviorist dogma that the brain is an unknowable black box. As Hunt suggests, we can now address specific sources of individual differences in intelligence by studying individual differences in brain structure and function. Surely, if Binet or Terman were alive today, they would be avidly applying neuroimaging to move beyond the inherent limitations of psychometrics. The next phase of neuroimaging studies should focus more on multiple measures of intelligence (from psychometrics) and cognition (from cognitive psychology) in using large samples stratified across the range of intellectual ability, gender, and age. Several research groups are doing just this, and are incorporating experimental manipulations of brain areas with drugs, and electrical/magnetic stimulation, to test the role of specific brain regions and networks on intellectual ability. This experimental phase will be more challenging, it will take some time, and it might depend upon imaging, analysis, or data fusion techniques currently unavailable; however, this phase is now poised to begin in earnest based on the progress of the last 20 years. Hunt also reminds us that understanding the genetic aspects of intelligence remains a long and arduous task. Since we wrote our review and described relatively new work on the specific *ASPM* and *Microcephalin* genes, new results have been published which dampen enthusiasm that these genes might underlie the relationship between whole brain size and intelligence (Woods et al. 2006), although whether these genes or others (Meyer-Lindenberg et al. 2007) are related to the size or functioning of specific P-FIT areas remains to be determined.

R2. Some conceptual clouds – why study the brain?

Sternberg's commentary focuses on the importance of interactions between brain biology and environmental factors. He chastises us for asking the wrong question because he doubts that intelligence resides in the brain, and he provides examples of nonhuman intelligence in

the absence of any brain at all. Sternberg credits us with answering instead the question, "Where in the brain are there functions that, when measured in particular ways, show correlations with scores on conventional IQ-related tests?" Two issues are entangled here: the relationship between intelligence test performance and real world adaptation/intelligence, and how to formulate questions about the localization of complex abilities in the brain. Regarding the first point, there is considerable evidence that intelligence test performance and many life adaptations are highly related (Gottfredson 2003; Jensen 1998). Regarding the second point, consider the question, "Where in the brain is vision?" Surely the eyes are important and there can be no vision without something to see. Nonetheless, we have been able to investigate how vision works by studying the brain. We take Sternberg's point that knowledge about brain structure and function alone may not be sufficient to answer all questions of interest to intelligence researchers, but we believe that our question is not ill put, and is one of many legitimate questions. The P-FIT is based solely on our review of existing neuroimaging studies, all of which are correlational and use "conventional" tests including but not limited to IQ tests. New neurobiology studies will surely expand the type of measures and research designs used to study intelligence beyond current neuroimaging approaches, but we do not share Sternberg's assertion that there is an "optimal problem" about intelligence and that we should focus only on solving it, whatever it may be. We know of no other scientific field where "optimal problems" are agreed upon and all other problems are deemed "wrong."

Norgate & Richardson similarly question both the empirical and conceptual basis for a brain-based theory of intelligence, asserting that inconsistencies among studies reviewed show that the correlational basis of the P-FIT must be unreliable. We based the P-FIT on consistencies among the studies as we saw them and ignored many obvious inconsistencies – a necessary step in reviewing a nascent literature. Some questions about the nature of *g* or IQ are still open in the psychometric domain and the P-FIT bridges psychometric research on these issues with brain research. The alternative explanation of the positive manifold underlying *g* (van der Maas et al. 2006), for example, is helping to define more possibilities for brain relationships to intelligence and cognitive measures, not fewer. The P-FIT will evolve as we follow these new observations.

Norgate & Richardson also raise an important point about socioeconomic status (SES). Only one of the neuroimaging studies we reviewed included SES measures (Shaw et al. 2006). This study did not relate SES to brain measures, but rather found that SES was significantly correlated with IQ in their sample of young people ($r = -.35$, $p < .01$). Some simple empirical questions that need attention are: In predicting scores on intelligence measures from neuroimaging data, how much variance would be accounted for by adding a measure of SES? Would this be the same amount of variance at all ages or more in younger individuals? Is there a correlation between SES and regional brain volume, especially in P-FIT areas? Along these lines, Noble and colleagues recently reported that fMRI results on a reading-related task differed in children as a function of SES (Noble et al. 2006). The inclusion of SES measures can enrich neuroimaging studies to the extent that they can establish unique sources of variance.

As noted in **Hunt**'s commentary, the P-FIT focuses on brain relationships to intelligence and not on the other aspects noted by **Norgate & Richardson**. A focus on brain structure and function does not diminish the importance of other factors, nor the importance of interactions between the domains. Researchers working on the cognitive and social aspects of intelligence do not need to diminish the contributions of brain research (or psychometric) perspectives to advance the importance of their theoretical focus. Most research on intelligence is correlational. As we have noted earlier, brain imaging opens the potential for new experimental approaches to a variety of questions about intelligence.

Rae points out that the P-FIT focus on the neuroimaging aspects of intelligence is, in fact, not focused enough because data from molecular and systems biology are not yet available. She notes some of the conceptual difficulties inherent in neuroimaging studies of intelligence, acknowledges that we must nonetheless start somewhere, and remarks that we have been suitably cautious in "sieving the data down to groups of mutually inclusive spots." She notes that the P-FIT is silent about how effective integration among brains areas happens, a key point. Indeed, our very first PET (positron-emission tomography) imaging study, for example, found inverse correlations between cerebral glucose metabolic rate and scores on the Raven's Advanced Progressive Matrices (RAPM; a high *g* test of nonverbal abstract reasoning) taken during the PET procedure (Haier et al. 1988). We interpreted this as showing that the less hard a brain was working, the better it solved the test problems which became known as the brain efficiency hypothesis. A number of studies have examined "brain efficiency" in various ways and generally support a role for efficient allocation of cognitive resources in intelligent individuals (see Neubauer & Fink 2003; Neubauer et al. 2002; 2004; Rypma et al. 2006). We also note our recent study in which performance on intelligence tests was *positively* correlated with parietal and *inversely* correlated with frontal brain N-acetylaspartate (NAA), particularly in women, suggesting some level of sex-mediated biochemical optimization across the brain as underlying intellectual capacity (Jung et al. 2005). As Rae notes, new imaging technology using diffusion tensor imaging (DTI) and connectivity analyses will help determine how effective communication occurs among brain areas; molecular and systems biology surely play important roles, as demonstrated by the work she cites on bioenergetic capacity. We have proposed that neuronal mitochondria function (or even the number of mitochondria and variation in their structure) may be important in understanding how brain energy is created and consumed during cognition (Haier 2003).

Rae also properly cautions that the P-FIT may characterize some but not all groups; we completely agree. We see the P-FIT areas somewhat like a tool kit. Some people have more, different, or better tools to apply to cognition and problem solving, forming the basis for individual differences in intelligence. Which subsets of the P-FIT areas work best for which individuals in which cognitive domains are open questions. Even studies of this kind, however, fall short of Rae's warning: we critically need more research on molecular and systems levels, in addition

to investigating the location of "spots" in the brain. Here we have the full range of conceptual comment on the P-FIT's focus, from too much brain biology (**Sternberg** and **Norgate & Richardson**) to not enough.

Like Rae, **Schmithorst** notes the central importance of the concept of connectivity among brain areas implied in the P-FIT and the paucity of data available to test hypotheses about relationships among areas, despite the availability of sophisticated statistical methods to do so. He details an important conceptual distinction between effective connectivity and functional connectivity. The former refers to how much one brain area influences another area; the latter refers only to there being a connection or relationship between areas (i.e., "correlation"). Both can be studied effectively, especially in large samples. Schmithorst also points out that each of the neuroimaging studies we reviewed used a single imaging method. He notes the importance of using a combination of imaging techniques in the same sample in future studies. We know of several projects where this is under way and we completely agree that this will provide powerful data for understanding intelligence. We also agree that, in its current form, the P-FIT lacks sufficient specificity for how each area might contribute to intelligence, and the likely interactions of age and sex to such contributions. Again, we are partial to thinking about the P-FIT from the analogy of a tool kit. The current state of imaging research reviewed in the target article provides a tentative listing of brain "tools," but additional research and analysis techniques of increasing sophistication, as nicely summarized by Schmithorst, will provide the empirical basis for detailing how, when, and for whom specific "tools" are applied.

R3. Darker conceptual clouds – What is "intelligence"?

Blair raises the most challenging conceptual critique of the P-FIT, simply and starkly: "general intelligence is a mathematical abstraction, not a thing in itself." In early schizophrenia research, a claim was made that schizophrenia was a myth based on an abstract social construct of normality and not a medical illness or disease. A psychiatrist involved in adoption studies once remarked that if schizophrenia was a myth, it was a myth with a genetic component. However intelligence is defined, there is a genetic and, therefore, a biological component which is evident in neuroimaging studies. Blair's challenge (Blair 2006) is based upon a careful distinction between general intelligence and fluid intelligence. **Lee, Choi, & Gray** (**Lee et al.**) also point out that the P-FIT may be more related to fluid intelligence than to general or crystallized intelligence. Both commentaries note that fluid intelligence refers to what some researchers think of as fundamentally "working memory/executive cognitive abilities."

Blair's skepticism, however, is focused more on whether there is a neural basis of "general intelligence" to discover. He argues that theories of general intelligence must include consideration of experience and development. We have no argument with his position. The P-FIT is based on existing neuroimaging studies which have the limitations enumerated by us and other commentators. Chief among these is the reliance on single measures of intelligence rather than on a standard battery, which could provide analyses testing models of the general factor of intelligence (i.e., *g*) and on models of general intelligence (as we defined in our review; see also **Colom**'s commentary). Early on, we attempted to incorporate test difficulty and/or levels of intelligence among subjects into our neuroimaging paradigms (e.g., Haier et al. 2003b; Larson et al. 1995), but much more needs to be done in studying these interactions (see Lee et al. 2006). As indicated previously in this response, we will not be surprised if some subset of the P-FIT are more relevant than others, depending on what the tasks are and who the subjects are. Moreover, the subsets may also depend on which definition of intelligence is applied. How P-FIT areas develop and how sensitive they may be to experience or training are open questions central to evolving more detailed neural theories. In our view, it is still too early to rule out a neural basis for a general factor of intelligence independent of a neural basis for specific cognitive abilities.

Noveck & Prado also address fundamental questions of definition and caution us specifically that intelligence and reasoning are not the same thing. They argue that there is no advantage to study a "large" domain like intelligence over a subset domain like "reasoning," and that a correlational-based individual difference approach, especially one dependent upon Wechsler Adult Intelligence Scale (WAIS) subtests, does not have any advantage over the investigation of component parts of reasoning as studied in the cognitive neuroscience tradition. However, as we noted in response to **Sternberg**'s concept of an "optimal" problem, we are dubious that any one approach, either philosophical or experimental, is so superior over another in all instances that research should be limited to that approach alone. The potential merging of traditional psychometric research on individual differences with traditional cognitive psychology based on neuroimaging is welcome and exciting, and it is unlikely that either approach will subsume or diminish the other. Both will evolve to explain different aspects of higher cognitive function. For example, teachers are interested in why one child reasons better than another. Empirical investigations of this question may well require several well-integrated approaches, and perhaps the answer will have something to do with general intelligence, the *g* factor, and/or the P-FIT. Would it not be interesting, for instance, to know if cognitive imaging experiments designed to study components of reasoning show the identical results in subjects selected for high or low intelligence? What non-intuitive insights and conjectures might emerge if the results differed for men and women?

Going further than **Noveck & Prado**, commentators **Cohen Kadosh, Walsh, & Henik** (**Cohen Kadosh et al.**) focus on a single cognitive component in their commentary. This component is response selection and they make a strong case for its central role in any definition of intelligence. They note that response selection is the "interface between perception and action that allows one to choose the most adequate response among alternatives." They are concerned that the parietal-frontal network is not specific to intelligence, but rather to the response selection problem they see as common to all intelligence measures (see our remarks on **Naghavi & Nyberg**'s commentary further on). We are intrigued

with Cohen Kadosh et al.'s notion but we find it unlikely that this single component alone is the cognitive key to intelligence. Separating out response selection from other components of cognition (e.g., reasoning) should be a problem amenable to neuroimaging research.

Colom calls attention to the inconsistencies in P-FIT areas derived from different imaging modalities, as well as the problem of defining the construct of human intelligence. He concludes that many of the inconsistencies among the neuroimaging studies we reviewed have their basis in that every measure used in these studies comprises several cognitive abilities along with some amount of the *g* factor, producing heterogeneous imaging results. One might conclude, therefore, that the component abilities should be studied separately, but Colom instead approaches the problem by focusing on the *g* factor. The practical implication of this approach is that future neuroimaging studies would do well to include a diverse battery of cognitive tests so that *g* can be extracted.

The commentary by **Wilke** bridges the disparate arguments made by **Colom** favoring focus on a general factor and the arguments by **Noveck & Prado** and **Cohen Kadosh et al.** favoring a focus on component abilities. Wilke understands that the P-FIT provides a framework of "several collaborating (and competing?) network nodes, with strengths in one (or more) explaining individual performance advantages." This is consistent with the tool kit analogy for the P-FIT that we discussed earlier. Moreover, like Colom, Wilke takes the view that the P-FIT has identified a broad pattern based on available data, and that it is time to apply more sophisticated approaches both to global definitions of intelligence and to a possibly more promising effort for "an exact characterization of the cognitive functions" underlying performance on such intelligence tests. (Noveck & Prado also suggest this.) Wilke's caution about generalizing from cases of pediatric brain injury is particularly important (see our remarks on the **Varley** and **Zaidel** commentaries below).

The definition of intelligence continues to be a major concern, as these commentaries demonstrate. Psychometric approaches to definition issues may be reaching an inherent limit because no intelligence measures are based on a ratio scale with an actual zero point. Jensen has proposed shifting away from psychometrics to a focus on mental speed assessed with reaction time (RT) measures to overcome this problem (Jensen 2006), an approach he calls mental chronometry. Many studies show that higher intelligence scores are associated with faster reaction times. Jensen makes the following observation as a general rule: "The lower the grade of measurement used to represent the variables of interest, the more their quantitative description and analysis must depend upon complex statistical methods" (Jensen 2006, p. ix). He further notes that the lowest grade of measurement is typical in the behavioral and social sciences because it is based on ordinal scales. Chronometry, however, is based on a true ratio scale. Moreover, he notes that a chronometric *g* can be extracted from RT batteries and this is related both to psychometric *g* and to biological variables. Therefore, it will be important for future imaging studies of intelligence to include RT measures on a variety of tasks as well as psychometric batteries. The use of RT also bridges intelligence and cognitive research even more closely (see Thoma et al. [2006] for an excellent example).

R4. Some rays of light on the P-FIT spots

As we began to characterize the results of our review, we realized that the P-FIT areas also appear regularly in cognitive neuroimaging studies. A comprehensive review of this literature by **Naghavi & Nyberg** was particularly helpful (Naghavi & Nyberg 2005). As they point out in their commentary, cognitive studies have revealed a robust frontal-parietal network involved in several fundamental functions, including attention, working memory, and episodic memory. Our model, which is based solely on imaging studies of higher-order, global measures of intelligence, shows essentially the same brain network. Naghavi & Nyberg argue that the apparent multifunctionality of this network may be understood conceptually as a framework for integration and control of information. They regard the frontal-parietal network as uniquely suited for these functions, and this is consistent with the P-FIT role for intelligence. However, they caution us that this system may well be a more general backbone for bringing order to diverse brain functions rather than a more specific neural basis for intelligence. We are inclined to propose that intelligence may be defined as the degree to which the frontal-parietal network integrates and controls the flow of information throughout the brain. The sequence of flow through these areas and the efficiency of the flow at various points may be parameters that can be measured with neuroimaging methods, and correlated to measures of intelligence (*g* or otherwise). This data-driven conceptual merging of two empirical traditions, the psychometric and the cognitive, will advance our understanding of the neural basis of intelligence.

Prabhakaran & Rypma summarize some of their results from fMRI studies, which are more or less consistent with the P-FIT, but with some distinctions. They are inclined to see a more general posterior interaction with the prefrontal cortex than one focused on the parietal lobe. They argue that posterior brain areas are recruited for separate and varying task demands while the prefrontal cortex generally integrates among component task demands. When they divide subjects on the basis of fast or slow reaction time to a visual search task, they find that the slower group shows stronger evidence of frontal-parietal connection. For the faster (more efficient?) group, there is more independence between frontal and posterior areas. They also report evidence that efficient brain function was a key variable in that poor performers during a word generation task showed increased activity in frontal areas; a rest condition showed increased activity in parietal areas. Thus, Prabhakaran & Rypma are already working with the next generation of neuroimaging research designs described earlier, and more investigations of this type will be of obvious consequence to the P-FIT model.

Two commentaries, in addition to **Wilke**'s, advise caution in the interpretation of neuropsychological data from brain-damaged individuals to support the

neuroimaging findings in normal individuals which form the basis for the P-FIT. **Varley** notes that damage can cause reorganization of brain functions so that cognitive performance can be sustained, citing examples about language and aphasia. Intelligence, she notes, may be characterized by neural (and behavioral) flexibility and plasticity. We know very little yet about the dynamic cognitive reorganization manifested within brain tissue as a patient regains or improves a behavioral or cognitive skill. Sequential neuroimaging in brain damaged patients, soon after the injury and periodically during recovery (in tandem with cognitive rehabilitation as specific functions improve), could be quite informative in articulating the constraints that the P-FIT might place on how and where such skills are integrated into a larger cognitive framework. **Zaidel** makes a similar point and discusses examples based on performance of WAIS subtests, which she notes are difficult to link with specific brain areas. We tried to find support for the P-FIT in the lesion literature and concede that this is more complex than it may appear at face value. We favor Zaidel's hypothesis that, consistent with discussions above, "Abundant connectivity among widely localized neuronal centers would be expected for above-average performance on intelligence tests, whereas for average intelligence only limited connectivity may be sufficient." It would seem that the P-FIT areas would be places to start connectivity analyses (see commentaries by **Rae** and **Schmithorst**). Whether the P-FIT applies to the other "intelligences" as listed by Zaidel depends on issues of definition discussed above and remains an open question.

R5. New fronts to consider

Three commentaries address how the P-FIT may generalize to other domains. **Roring, Nandagopal, & Ericsson** (**Roring et al.**) provide an interesting commentary on skilled and expert performance. They review studies which show that expert and skilled performance generally is unrelated to individual differences on traditional intelligence tests. We have no issue with their conclusion that future neuroimaging studies of intelligence and mental ability should address skill development in beginners and experts, especially over time. In fact, we were among the first to use neuroimaging to study brain changes associated with the development of visuospatial skill (Haier et al. 1992a) and how those changes related to intelligence (Haier et al. 1992b), so we are quite interested in this perspective. Currently, we are undertaking a new multimodal neuroimaging study to track network connectivity changes associated with making the transition from novice to expert.

Kirov's commentary calls attention to the role that sleep and consciousness may play in intelligence. His summary of the sleep data is intriguing, but we need more data to determine if all the subcortical areas implicated in sleep are also implicated in intelligence. The lack of subcortical areas in the P-FIT has troubled us, although we do make reference to the "mission critical" nature of these subcortical structures as compared to the individual differences manifested in the cerebral cortex. Subcortical areas allow interesting inferences about neurotransmitter systems, which surely must be implicated in neural theories of intelligence. We have published several studies which use anesthetic drugs to manipulate states of consciousness during neuroimaging in the hope of identifying the subcortical areas, and the neurotransmitter systems, relevant for consciousness (Alkire & Haier 2001; Alkire et al. 1999). As far as we are aware, there is not yet any confirmation that the brain systems relevant for consciousness studies are also implicated in intelligence studies.

Demetriou & Mouyi compare the P-FIT to a model of intelligence based on psychometrics and development (i.e., the PSY-DEVO model). After noting some conceptual points of agreement between the two models, they apply the "So what?" test. Overall, their commentary challenges whether the areas identified in the P-FIT could be the only areas necessary for intelligence, since so many cognitive processes and networks must be involved. For us, this is an empirical as opposed to a rhetorical question. It may be that the list of P-FIT areas will expand as future neuroimaging studies of intelligence become available. Existing studies, however, support the idea that some brain areas are more relevant than others for the components underlying higher-order cognition and these areas are consistent with the P-FIT (see **Naghavi & Nyberg**'s commentary). Undoubtedly, many networks are necessary even for much simpler brain functions than those active during reasoning and problem solving. Each of the P-FIT areas easily could be part of multiple networks, but it should be possible to address which networks and areas define a core for intelligence.

R6. Conclusion

Although we have expressed our view in favor of parsimonious, elegant approaches at this early stage of neuroimaging studies of intelligence, **Nyborg** finally reminds us that the world is exceedingly complex. We admire his attempt at integrating findings across multiple domains at different levels of analysis. His commentary tantalizes us with a possible approach to resolving the persistent dualist dilemma, but we cannot relate his large-scale conceptual model to the relatively small-scale empirically based P-FIT. We are of a mind that a deep understanding of brain/mind relationships will come when we can describe the underlying complexities with elegant clarity. We are inspired by those who study the first few nanoseconds of the Big Bang at the creation of the universe billions of years ago. If they can seek to describe this unseen moment with precision and clarity, surely we have a chance to capture the essence of a neural basis of intelligence.

NOTE

*__Editorial Note:__ As per the target authors' request and specification, Richard J. Haier is the first author and Rex E. Jung the second author for this coauthored Response article.

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[The letters "a" and "r" before author's initials stand for target article and response references, respectively.]

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