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How similar are fluid cognition and general intelligence? A developmental neuroscience perspective on fluid cognition as an aspect of human cognitive ability

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Abstract: This target article considers the relation of fluid cognitive functioning to general intelligence. A neurobiological model differentiating working memory/executive function cognitive processes of the prefrontal cortex from aspects of psychometrically defined general intelligence is presented. Work examining the rise in mean intelligence-test performance between normative cohorts, the neuropsychology and neuroscience of cognitive function in typically and atypically developing human populations, and stress, brain development, and corticolimbic connectivity in human and nonhuman animal models is reviewed and found to provide evidence of mechanisms through which early experience affects the development of an aspect of cognition closely related to, but distinct from, general intelligence. Particular emphasis is placed on the role of emotion in fluid cognition and on research indicating fluid cognitive deficits associated with early hippocampal pathology and with dysregulation of the hypothalamic-pituitary-adrenal axis stress-response system. Findings are seen to be consistent with the idea of an independent fluid cognitive construct and to assist with the interpretation of findings from the study of early compensatory education for children facing psychosocial adversity and from behavior genetic research on intelligence. It is concluded that ongoing development of neurobiologically grounded measures of fluid cognitive skills appropriate for young children will play a key role in understanding early mental development and the adaptive success to which it is related, particularly for young children facing social and economic disadvantage. Specifically, in the evaluation of the efficacy of compensatory education efforts such as Head Start and the readiness for school of children from diverse backgrounds, it is important to distinguish fluid cognition from psychometrically defined general intelligence.

Keywords: cognition; cognition-emotion reciprocity; developmental disorders; emotion; fluid cognition; Flynn effect; general intelligence; limbic system; neuroscience; phenylketonuria; prefrontal cortex; psychometrics; schizophrenia

1. Introduction

1.1. What is general intelligence?

Historically, theories of intelligence have focused on the identification of a single factor, referred to as *psychometric g*, that has been shown to underlie performance on tests of mental abilities (Spearman 1927). The single-factor theory reflects the fact that the various subtests of IQ measures correlate positively. Although several alternative interpretations exist as to just what this positive manifold among tests means, it is beyond question that a single mathematically derived factor can be extracted from tests of diverse mental abilities (Carroll 1993; Jensen 1998; see the edited volume by Sternberg & Grigorenko 2002). Jensen (1998) provides a comprehensive review of research on *g*, detailing the evidence for *g* and the relation of *g* to various real-world outcomes by using the method of correlated vectors. There are, however, numerous questions about *g* that are the subject of ongoing research and scientific exchange. In particular, questions about the unitary nature of *g*, the biological bases of *g*, and the extent to which *g* is itself reducible to known, theoretically tractable cognitive processes, are interrelated, overarching questions high on the priority list for intelligence researchers.

As a mathematically defined entity with large explanatory power, the general factor has been pervasive in the psychological literature for over one hundred years. However, it is important to keep in mind that

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psychometric *g* is not a thing in itself but a manifestation of some as yet undefined properties of brain structure and function. In fact, it is only in the last several decades that the underlying processes and functions through which *g* may be manifest have begun to be worked out in any detail, albeit with only limited success. For example, a general speed-of-processing hypothesis has been examined using measures of inspection time and reaction time. Although the conceptual relation of these measures to *g* is sound, a number of studies have shown that their empirical relation to *g* tends to be small (Crawford et al. 1998; Luciano et al. 2004). Similarly, a conceptually sound general synaptic plasticity thesis has been proposed as an underlying basis for *g* (Garlick 2002). However, although perhaps promising, the synaptic plasticity argument lacks specificity as to a clear relation between brain plasticity and intelligence and at present offers no way of measuring individual differences in plasticity that might correlate with psychometric *g*.

In apparent contrast to general speediness and plasticity explanations for *g*, work on fluid cognitive functions – those associated with general reasoning and problem-solving processes and referred to primarily as *working memory* (WM), *executive function* (EF), or *fluid intelligence* (gF) – seems to have shown some early and substantial promise in indicating that both the conceptual basis and neural structural basis for *g* may be close at hand. However, as is argued in section 3 and the sections that follow, this promise is perhaps more apparent than real. Given psychometric evidence for a relation between fluid cognition and psychometric *g* and the increasingly well-established neural basis for this relation, what has yet to be thoroughly examined is the growing body of evidence indicating that fluid cognitive functions are in some instances clearly dissociated from general intelligence. Evidence indicating dissociation of fluid cognitive functions from other aspects of *g* is something of a problem for research on human cognitive abilities because it calls into question some earlier conclusions and prior thinking about the general factor. In particular, dissociation of fluid cognitive functions from other indicators of mental abilities through which *g* is manifest suggests that some reconceptualization of human cognitive competence is needed and may indicate instances in which *g* has reached or exceeded the limits of its explanatory power.

Plainly stated, the central thesis of this target article is that currently available evidence indicates that, although fluid cognition appears highly similar to general intelligence in many instances, the association between fluid function and general intelligence is limited in ways that are important for understanding the development of cognitive competence in humans and its application across the lifespan. Furthermore, once the limits of the association between fluid cognition and *g* are recognized, the independent fluid cognitive construct can be seen to have a relevance to human behavior that may be as far reaching in its explanatory power, if not more so, than that associated with psychometric *g*. However, the limits of the association between fluid cognition and general intelligence may be most pronounced in populations in which specific environmental and/or genetic background factors are distinct from those of normative or typically developing populations. These instances help to "pull apart" fluid cognition and *g*, whereas ordinarily these two aspects of functioning covary to an extent that they appear to be unitary. Overall, the available evidence suggests that fluid cognition is an aspect of cognitive functioning that can be under considerable environmental influence both cumulatively over time and interactively within context in a way that indicates it to be a highly salient influence on behavior, but one that is distinct from general intelligence, psychometrically defined.

Several sources of evidence indicate dissociation of fluid cognition from *g*, and the purpose of this target article is to review this evidence and to consider its implications for understanding cognition and human behavior. The first source of evidence is psychometric and at the population level of analysis and concerns the worldwide rise in the mean level of mental test performance known as the *Flynn effect*. The second is neuroscientific and at the individual level and concerns evidence indicating fluid cognitive and learning impairments in humans and in animals with damage to a neural network integrating areas of the prefrontal cortex with structures of the brain's limbic region. A third source of evidence is neuropsychological and concerns the extent to which cognitive impairments in identified developmental disorders are consistent with a pattern of dissociation between fluid cognitive functions and general intelligence. Having considered this evidence, work examining reciprocal interconnectivity among limbic brain structures associated with emotional reactivity and the stress response and prefrontal cortical structures associated with fluid cognition is reviewed. It is argued that this work indicates potentially large environmental influence on fluid functioning and thereby on aspects of cognition that many have previously taken to be central to general intelligence. In summary, it is suggested that evidence outlining environmental influence on fluid cognition may provide for an important advance in understanding the development of human cognitive ability.

2. Fluid cognition

2.1. What is fluid cognition?

Fluid cognitive functioning can be thought of as all-purpose cognitive processing not necessarily associated with any specific content domain and as involving the active or effortful maintenance of information, whether verbal or visual-spatial in working memory for purposes of planning and executing goal directed behavior (Baddeley 1986; Kane & Engle 2002). As a consequence, fluid functioning involves the inhibition of irrelevant, competing, or prepotent information likely to interfere with information maintenance and response execution and the alternate shifting and sustaining of attention important for organizing and executing sequential steps or actions. Furthermore, fluid functioning is for the most part distinguishable from cognitive functioning associated with previously acquired knowledge available in long-term store, referred to as *crystallized intelligence* (gC). It is important, however, not to overstate the distinction between fluid processes and other aspects of cognition or the overall unity of the processes that comprise fluid functioning. Fluid functions play some role in encoding and retrieving crystallized knowledge in long-term store (Braver et al. 2001; Ranganath et al. 2003), and although the overlap among information maintenance,

attention shifting, and interference resolution processes in completing complex tasks is considerable, these aspects of fluid cognition are distinguishable (Miyake et al. 2000) and associated to some extent with distinct patterns of brain activation as observed by using brain-imaging techniques (Smith & Jonides 1997; Sylvester et al. 2003). As a unitary entity, however, fluid function has been described in the psychological literature under a variety of terms, including executive function, executive attention, effortful control, and working memory capacity. Although researchers may emphasize one or another aspect of fluid functioning under the various terms, each essentially describes the same overarching construct, and for the remainder of this article the term *fluid cognitive functioning* is utilized as a primary descriptor for these integrated aspects of cognition and is used interchangeably to some extent with the terms working memory and executive function.

2.2. Association between fluid cognition and general intelligence: Psychometric evidence

As domain general indicators of integrated cognitive processes involving information maintenance, attention shifting, and resistance to interference, measures of fluid cognition have not surprisingly demonstrated substantial relations with performance on measures of general intelligence (Embretson 1995; Engle et al. 1999b; Gustafsson 1984; 1988; Kyllonen & Christal 1990). Factor-analytic studies have demonstrated that measures of working memory correlate extremely highly (r's > 0.90) with the general factor extracted from various measures of cognitive ability (Colom et al. 2004; Gustafsson 1988; Kyllonen 1996), and fluid functions have been shown in latent variable models to be essential aspects of general intelligence (Conway et al. 2003; Kane & Engle 2002; Süβ et al. 2002). Tests that directly measure fluid cognitive functions have higher g loadings than do other cognitive measures (i.e., they exhibit larger factor scores on the higher-order g factor extracted from hierarchical analysis of mental test batteries; see Colom et al. 2004; Gustafsson 1984; 1988). And *working memory capacity*, defined as the amount of information that can be actively maintained in the presence of conflicting or distracting information, has been shown to underlie performance on a variety of tests of mental abilities, including measures of general intelligence (Carpenter et al. 1990; Engle et al. 1999b; Kyllonen & Christal 1990).

2.3. Association between fluid cognition and general intelligence: Evidence from brain imaging

Furthermore, not only do psychometric data indicate the centrality of fluid cognition in the study of general intelligence (e.g., Engle et al. 1999b; Süβ et al. 2002), studies examining brain structures and neural interconnectivity that support fluid cognitive functions (Braver et al. 1997; MacDonald et al. 2000; Smith & Jonides 1997) indicate a high degree of overlap within the brain between fluid cognition and general intelligence (Duncan et al. 2000; Prabhakaran et al. 1997; Thompson et al. 2001). Structural magnetic resonance imaging (MRI) has indicated positive correlations between IQ and gray matter in the prefrontal cortex (PFC) and anterior cingulate cortex (ACC) and has shown frontal gray matter, as with IQ, to be highly heritable (Thompson et al. 2001; Wilke et al. 2003; but see Haier et al. 2004 for evidence indicating a more distributed structural neural basis for intelligence). And functional brain imaging has consistently demonstrated activations in dorsolateral areas of the PFC in response to working memory tasks that are highly similar to activations observed in response to measures of general intelligence such as Raven's Progressive Matrices Test (Duncan et al. 2000; Prabhakaran et al. 1997). By demonstrating increasing PFC activation with parametric increase in the working memory load or cognitive control demand of tasks performed during imaging, these studies have linked the PFC to fluid cognition (Braver et al. 1997; MacDonald et al. 2000; Rypma et al. 1999) and present an apparent neurocognitive basis for general intelligence (Duncan et al. 2000; Gray et al. 2003).

Using positron emission tomography, brain activation in dorsolateral PFC, and to some extent ACC, has been selectively associated with high g cognitive tasks (Duncan et al. 2000). Furthermore, PFC activation in response to diverse tasks has indicated that the integration of information in working memory, such as verbal and spatial information, or maintenance of information in working memory while executing subsidiary tasks (i.e., cognitive control functions that would seem to be the hallmark of general intelligence), is associated with greater PFC activation than that associated with either task on its own (Koechlin et al. 1999; Prabhakaran et al. 2000). Furthermore, study of individual differences in intelligence and activation in the PFC by using functional magnetic resonance imaging (fMRI) found performance on Raven's matrices test to be positively correlated with individual level of left lateral PFC activation in response to the 3-back condition of an n-back working memory task (Gray et al. 2003).

The relation between activation in the PFC and performance on working memory tasks and tests of intelligence, however, is not one such that greater activation necessarily equals higher performance. Examinations of individual differences in working memory capacity indicate higher levels of PFC activation at moderate working memory loads in adults with limited working memory capacity relative to adults with greater working memory capacity. Change in activation in the PFC in response to increasing working memory load demonstrates an inverted U shape with increasing activation at initial load levels followed by decreasing activation once a capacity set point is exceeded (Callicott et al. 1999; Goldberg et al. 1998; Rypma et al. 1999). Increased frontal activation in individuals with lower working memory capacity appears to reflect processing inefficiency in the PFC and is similar to the finding of an inverse relation between cerebral glucose metabolism and IQ as reported by Haier (1993; see also Haier et al. 2003).

Increased PFC activation as observed in imaging studies of brain activation in response to measures of general intelligence reflects the curvilinear relation between PFC activation and working memory load, indicating relative activation at high working memory load. For example, in the study by Gray et al. (2003), the relation between change in PFC activation and intelligence was observed only in the high working memory load 3-back condition of the task. Furthermore, this relation was specific to

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trials in which attention and inhibition demand was very high because of the presence of lure stimuli (i.e., recently viewed stimuli in the 2-, 4-, or 5-back position). In the study by Gray et al., individuals exhibiting higher left lateral PFC activation in this highly demanding 3-back "lure trial" condition tended to score higher on Raven's matrices test.

Experimental and brain-imaging research strongly suggests that fluid cognitive processes of the PFC play a prominent role in higher-order cognition and that the brain structures and neural interconnectivity that support fluid functions may serve as the neural substrate for general intelligence. It is important not to map cognitive functions directly onto specific cortical areas, however, but to recognize the distributed nature of certain types of information processing in the brain in which the PFC and ACC may play central roles (Carpenter et al. 2000; Cohen et al. 1997). For example, brain-imaging studies of working memory and fluid intelligence have observed temporal, parietal, occipital, and cerebellar activations in addition to activation in distinct regions of the PFC (Cabeza et al. 2002; Duncan et al. 2000; Gray et al. 2003; Prabhakaran et al. 1997). Structural MRI has also indicated relations between IQ and brain volumes in parietal, occipital, and temporal as well as frontal cortical areas (Haier et al. 2004). Furthermore, studies of cognitive impairment associated with cerebellar dysfunction, in particular, indicate a potentially large role for the cerebellar vermis in coordinating fluid cognitive functions (Teicher et al. 2003), in much the same way that the cerebellum provides a neural foundation for the coordination of balance and movement (Schmahmann 1998). And examinations of the role of limbic structures in fluid cognition, particularly the hippocampus, as reviewed in section 5, but also the thalamus (Van der Werf et al. 2000; 2003), indicate prominent roles for these brain structures in tasks associated with prefrontal cortical activity.

Furthermore, the PFC is not a unitary entity but is composed of distinct areas. Although dorsolateral areas of the PFC have been primarily associated with working memory and general intelligence (Duncan et al. 2000), imaging studies of working memory indicate lateralized activations associated with verbal versus visual-spatial types of information and information updating and more ventral medial activations associated with information maintenance (Cohen et al. 1997; Rypma et al. 1999; Smith et al. 1996). Also, orbitofrontal and ventral medial areas of the PFC are associated with performance on fluid cognitive tasks that involve some reward component or in which some positive or negative emotion is evoked (Davidson 2002). Similarly, studies employing fMRI have demonstrated activation in the ACC to be associated with error detection and performance-monitoring processes (Bush et al. 2000; MacDonald et al. 2000) and, most significantly for present purposes, have demonstrated the ACC to be comprised of cognitive and emotional divisions that interact reciprocally in response to specific types of information (Bush et al. 2000). Overall, evidence for relations between areas of the PFC and ACC and specific aspects of cognition and emotion suggest that a variety of influences, particularly those associated with emotional arousal and the stress response, may impact fluid cognitive functioning and its apparent similarity to general intelligence.

3. Fluid cognition and general intelligence: Evidence for dissociation in adults

3.1. Evidence from the Flynn effect: Rising mean IQ and dissociation of fluid skills and general intelligence

Caveats about whole brain processing and the role of diverse brain structures in studies of working memory and general intelligence are more than just gentle reminders to think broadly about brain function and mental ability. Although brain-imaging and psychometric findings present a striking convergence of evidence seemingly in support of a fluid cognitive basis for general intelligence, a number of sources provide contravening evidence indicating that fluid skills cannot be *g*. Most prominent, perhaps, is the rapid secular rise in IQ over the past century known as the Flynn effect (Flynn 1984; 1987; 1999). Flynn's examinations of IQ gains have indicated that gains are particularly large, in fact, massive, on tests of fluid skills. Most noteworthy is the finding that gains are greatest, upward of 18 points in a single generation, on Raven's Progressive Matrices Test, a test previously thought to be a relatively pure measure of psychometric *g* and, as already noted, one that is highly dependent on fluid cognition and the integrity of the PFC. Mean IQ gains on measures more closely tied to crystallized intelligence, however, are considerably smaller and become increasingly small the closer intelligence subtests come to measuring purely crystallized aspects of cognition. The very rapid and substantial rise in scores on measures of fluid intelligence without a concurrent rise of similar magnitude in crystallized skills suggests dissociation of fluid cognitive functions from *g*.

The indication of change in fluid skills independent of *g* has been further substantiated by analysis of measurement invariance in data from successive normative cohorts on a variety of intelligence tests (Wicherts et al. 2004). Gains in IQ on each of the tests examined could not be accounted for by increases in the common factor, *g*, but were shown to reflect systematic sources of variance between normative cohorts in specific subtests. However, not all observed gains were in the fluid realm of cognition; gains were also observed in crystallized content. And not all fluid subtests demonstrated gains. Furthermore, decreasing scores were observed in some cohorts, although these decreases were primarily among recent cohorts and associated with crystallized knowledge. At the very least, the analysis clearly lends itself to the conclusion that intelligence tests are not measurement invariant between cohorts and that, while some increase in general intelligence appears to have occurred, change associated with rising mean IQ is, by and large, subtest specific.

The historical data on mean increases in IQ strongly suggest the presence of environmental influences on fluid cognitive skills that led to a rise in fluid cognition independent of *g*. As mean increases have occurred too rapidly to be attributable to genetic selection, it is clear that increases in IQ as measured by several widely used tests of intelligence most likely reflect social changes that impacted specific cognitive functions associated with performance on specific measures. As noted by Flynn (1999), if the change were in the general factor, this would indicate a mean level of cognitive functioning in entire

cohorts of prior generations that is in the range of mental retardation. However, this is clearly not the case and indicates that increases in fluid cognitive abilities between generations must have specific determinants and be selectively associated with distinct outcomes. Accordingly, any satisfactory explanation for the rise in fluid skills relative to crystallized skills would seem to need to identify mechanisms that could so greatly affect one aspect of intelligence over the other. While most explanations for rising mean IQ tend to be underspecified on this point (i.e., general increases in parenting skill, education, or nutrition), others that more directly address the types of skills tested for in measures of fluid intelligence (such as increased visual-spatial complexity or selective changes in specific aspects of education associated with fluid-skills development) are perhaps more likely to be shown to account for the phenomenon (Dickens & Flynn 2001b; Williams 1998). Whatever the case, the data on rising mean IQ clearly suggest that conclusions about the relation between fluid cognition and *g* are in need of some revision.

3.2. Clinical evidence: Dissociation of fluid skills and general intelligence

As with the Flynn effect but at the individual rather than population level, findings from clinical neuropsychological work provide further evidence indicating dissociation of prefrontally based fluid cognitive functions from general intelligence. Here, with the emphasis on a decrease rather than a rise in fluid intelligence, adults with damage to the dorsolateral PFC perform very poorly on fluid cognitive tasks but exhibit measured general intelligence within the normal range (Duncan et al. 1995; Waltz et al. 1999). In fact, individuals with damage to the dorsolateral PFC exhibit scores on measures of fluid intelligence that are one to three standard deviations below their scores on measures assessing primarily crystallized intelligence. Such data can easily be taken, and have been previously by many, as support for what would seem to be the erroneous conclusion that prefrontally based fluid skills are unrelated to intelligence! However, adult patients with lesions to the PFC demonstrate intact IQ relative to matched controls as assessed by the Wechsler Intelligence Scale for Adults (WAIS) while simultaneously exhibiting substantial postmorbid fluid-intelligence deficits as measured by the Cattell Culture Fair Test (Duncan et al. 1995). In essence, whereas the crystallized IQ of these individuals is in the normal range, fluid IQ scores are in the range of mental retardation. No such discrepancy is observed among matched controls who, in fact, exhibit fluid-intelligence scores equivalent to or higher than their WAIS scores. Further examination of the deficit displayed on measures of fluid IQ in patients with frontal lesions but intact IQ as assessed by the WAIS indicates that performance is dramatically impaired by the requirement of holding multiple relations in mind simultaneously when attempting to solve problems adapted from Raven's matrices test. Individuals with prefrontal damage exhibit no deficits on problems whose solution requires holding in mind no relations or only one relation, but exhibit a near inability to solve problems involving two or more relations (Waltz et al. 1999).

Although seemingly contradictory, given the apparent relation between fluid cognition and general intelligence in typically developing populations, these fascinating results become remarkably clear in light of the fact that the WAIS, perhaps more than any other widely used measure of intelligence, disproportionately assesses crystallized intelligence (Ashton et al. 2001; McGrew 1997). Implications of the discrepancy observed by Duncan et al. (1995) and Waltz et al. (1999) for understanding intelligence and what it is that intelligence tests measure, however, are far from clear. Duncan et al. reason that perhaps the WAIS represents knowledge already acquired and therefore intact, whereas tests of fluid intelligence represent skills through which crystallized knowledge was acquired in the past and further knowledge would be acquired in the future. However, their data cannot readily address such an interpretation. For one, there would need to be some indication that the ability to acquire new types of crystallized information is dramatically impaired in patients with frontal lesions. Duncan et al.'s interpretation is speculative, and their data are not longitudinal and can offer no insight into the developmental relation between fluid and crystallized skills. However, there are data available to address this important point and the following sections examine the viability of such a developmental hypothesis.

4. Fluid cognition and general intelligence: Evidence for dissociation in children

4.1. Developmental evidence: Typical development

The idea that fluid intelligence (gF) precedes or paves the way for the development of crystallized intelligence (gC) is not new. Cattell and Horn, the originators of the *g*F-*g*C theory of intelligence, proposed several reciprocal developmental relations between fluid and crystallized intelligence (Cattell 1971; Horn & Cattell 1967). Cattell and Horn theorized that gF would be a precursor to gC because fluid skills would facilitate and enhance the acquisition of crystallized knowledge. Limited examinations of this investment hypothesis, however, have failed to provide strong support for a directional relation between gF and gC. Similarly, the authors hypothesized that the gF-gC distinction would not be prominent in young children. As with the body of research examining change in diverse cognitive abilities in the study of cognitive aging, however, the gF-gC distinction is present early in the life span and the developmental course of diverse cognitive abilities remains distinct (Horn & Hofer 1992; Horn & Noll 1997; McArdle et al. 2002). Analysis of intellectual abilities from age 2 to 95 years in an accelerated longitudinal design with the Woodcock-Johnson Psycho-Educational Battery–Revised (WJ-R) found that "the functions describable as broad fluid reasoning (gF) and acculturated crystallized knowledge (gC) are separable entities that have different growth patterns" (McArdle et al. 2002, p. 134). Distinct patterns hold for several distinguishable aspects of cognitive ability across the life span. Furthermore, rates of change noted by McArdle et al. (2002) are particularly rapid in early childhood such that change in fluid skills over a single year in childhood is equivalent to change over an 11-year span in adulthood. For crystallized skills, change over a single year in

childhood is equivalent to change over the entire adult life span.

The gF-gC distinction has also been prominent in the study of cognitive aging for some time as evidenced by the relatively greater stability in crystallized as opposed to fluid function (Schaie 1994). Neurobiological evidence suggests that fluid decline with age is associated with alterations in the neurobiology of the PFC and reduced efficiency in processing of information in the PFC (Braver & Barch 2002; Cabeza et al. 2002; West 1996). As with neurobiological evidence in research on cognitive aging, it is likely that influences on the neurobiology of the PFC also play some role in the development of fluid cognition independent of general intelligence early in the life span. However, life-span analysis examining differentiation of cognitive abilities at different ages, while indicating general differentiation in all age groups, indicates that gF-gC correlation is somewhat larger among the very young and the very old (Li et al. 2004), perhaps suggesting some directional relation of gF to gC at the extremes of the life span. Alternatively, it may be that fluid cognition plays a particularly important role in intelligence-test performance in the very young and the very old and, for this reason, gF and gC appear more highly related in these age groups.

In contrast to research on cognitive aging, however, the examination of the gF-gC distinction in children has not been extensive. The reason could be that relations between IQ and fluid cognition labeled as executive function (EF) or working memory are not strong given the limited assessment of gF currently available in many widely used intelligence tests (Woodcock 1990). The study of fluid function under the label of EF in children, however, is a rapidly growing area of research in which the definition of EF employed is essentially identical to that used by individuals studying working memory and intelligence in adults. Specifically, when cognitive researchers working with child populations define EF as the maintenance of an appropriate problem-solving set involving mental representation of a given task and goal state within a limited-capacity central processing system (Welsh & Pennington 1988), they are describing cognitive processes that are being studied under the name of working memory in adults (e.g., Carpenter et al. 1990; Conway et al. 2002; Prabhakaran et al. 1997; 2000). The few studies examining the relation of measures of working memory and EF to measures of intelligence in typically developing children have indicated some overlap between fluid skills and intelligence as well as unique variance in school achievement associated with each. For example, whereas one study identified substantial overlap between measures of working memory and *g*F measured by Raven's matrices test (de Jong & Das-Smaal 1995), a finding highly similar to the adult literature (Engle et al. 1999b), another found that EF tasks predicted unique variance in math achievement over and above that associated with a widely used estimate of Wechsler full-scale IQ (Bull & Scerif 2001). Here again, because of the underrepresentation of fluid skills in the Wechsler batteries, use of the Wechsler would be expected to result in unexplained variance associated with EF measures. Furthermore, and perhaps most interesting for present purposes, factor-analytic examinations of various EF tasks have demonstrated that the tasks are largely unrelated to performance on measures of intelligence assessing primarily crystallized knowledge (Espy et al. 1999; Krikorian & Bartok 1998; Pennington 1997; Welsh et al. 1991).

4.2. Developmental disorders in children

A further source of evidence relevant to the developmental differentiation of fluid skills from *g* is provided by the study of cognitive impairment among individuals with specific developmental disorders. Studies examining a variety of developmental disorders of childhood indicate that children with attention deficit hyperactivity disorder (ADHD), early and continuously treated phenylketonuria (PKU), and specific learning disabilities (LDs) exhibit impaired performance on measures of EF but general intelligence in the normal range (Barkeley 1997; Berlin 2003; Diamond et al. 1997; McLean & Hitch 1999; Stanovich et al. 1997; Swanson 1999). Furthermore, some studies have identified specific patterns of fluid deficits associated with different disorders. In an examination of four developmental disorders, ADHD, autism, conduct disorder (CD), and Tourette syndrome (TS), consistent EF deficits were identified in ADHD and autism but not CD and TS. More severe deficits relative to IQ-matched controls were observed in autism compared with ADHD. In contrast, children with ADHD exhibited greater deficits in inhibitory processes relative to autism (Pennington & Ozonoff 1996).

Prima facie developmental evidence for the distinction between fluid cognitive functions and measures of *g* is provided by work on specific LDs, as defined in the United States. In LD as defined in the United States, deficits in fluid cognition impair learning and academic achievement, but general intelligence is in the normal range. Examination of EF in studies of both reading and math disability have indicated fluid cognitive impairments in comparisons with age-matched and, to some extent, ability-matched (i.e., younger) controls. Differences in the maintenance of information in working memory and in executive control, but also in speed of processing, have been noted in the presence of measured intelligence in the normal range (Bull & Scerif 2001; McLean & Hitch 1999; Pennington 1997; Sikora et al. 2002; Swanson & Sachse-Lee 2001; Willcutt et al. 2001).

Although fluid cognitive deficits are certainly not the only problem that children with LD as defined in the United States face, these problems can be substantial and would appear to contribute to the observed discrepancy between measured intelligence and academic achievement for these individuals. In reading disability, for example, difficulty with word identification has been related by using fMRI to decreased brain activation in two posterior left hemisphere systems associated with phonological processing (McCandliss & Noble 2003; Pugh et al. 2001). However, young impaired readers also exhibit lesser PFC activation on some phonological tasks than do non-impaired readers, suggesting some fluid cognitive involvement in reading impairment. Most interesting, older dyslexic readers demonstrate larger frontal activations in response to phonological tasks than do non-impaired readers (Shaywitz et al. 2002). Such a pattern of activation may suggest a compensatory effort whereby poor readers come to draw more heavily on fluid functions when engaged in a reading task.

Additionally, such increased activation may also indicate reduced processing efficiency in the PFC of impaired readers. Here, frontal activations in comparisons of non-impaired and dyslexic readers suggest that fluid cognitive deficits will impair reading progress both for non-impaired readers and for individuals with dyslexia and that the severity of reading difficulty will be greatest among individuals exhibiting fluid-function deficits in combination with posterior phonological processing-system deficits.

Given fluid cognitive deficits and the demonstrated interrelation of anterior and posterior brain function in the study of reading and reading disability, it is interesting to ask whether there might be a developmental relation between fluid cognitive deficits and intelligence in children with LD. Do problems with fluid cognition and with crystallized processes associated with phonological processing and word recognition lead developmentally to lower IQ for these children? In a particularly powerful design for examining this question, twin pairs in which one of the twins had a reading disability but the other did not were assessed using Wechsler full-scale IQ and measures of fluid cognition (Pennington 1997). Although IQ was in the normal range for all participants, twins with reading disability exhibited lower full-scale IQ than did unaffected co-twins, and both affected and unaffected twins exhibited lower full-scale IQ than did a matched control sample of twins in which neither twin had a reading disability. Furthermore, both affected and unaffected twins in the reading-disability twin pairs exhibited reduced EF in comparison with the matched control twin pairs. Overall, the control twins were found to have higher IQ and EF than both the typically developing twin and the reading disabled twin in a linear pattern of results that would seem to indicate that cognitive deficits associated with reading impairment lead to delayed development of general intelligence. However, the absence of IQ subscale information on performance and verbal IQ components of the Wechsler battery, which are generally associated with fluid and crystallized aspects of intelligence, respectively, limits inference. It may be that some proportion of the full-scale IQ difference both within and between the reading-impaired and non-impaired twin pairs is attributable specifically to reduced performance or verbal IQ.

4.3. Research on schizophrenia and phenylketonuria

Findings indicating a relative performance IQ or verbal IQ deficit in the measurement of intelligence in reading disability would be of some interest given evidence for fluid cognitive impairments and performance IQ deficits in the presence of full-scale IQ and verbal IQ in the normal range in schizophrenia (Egan et al. 2001). Although examinations of premorbid and postmorbid IQ among schizophrenics suggest full-scale IQ decline with disease onset, estimation of premorbid full-scale IQ has been based on postmorbid reading and language scores and, for this reason, inference regarding premorbid to postmorbid IQ change should be viewed with caution. The performance IQ subscales of the Wechsler battery have higher fluid cognitive demand than do the verbal intelligence scales, and patients with schizophrenia exhibit deficits in abstraction and attention greater than would be expected from postmorbid verbal and full-scale IQ. In fact, performance IQ decrements appear in some instances to account for most, if not all, of the full-scale IQ discrepancy observed between patients and matched controls (Kremen et al. 2001). Estimation of premorbid full-scale IQ by relying on reading ability and academic achievement would therefore be invalid to the extent that premorbid performance IQ may have been significantly lower than premorbid verbal IQ. Evidence for just such a discrepancy is provided by two studies, one a prospective cohort study and the other a case-control design. Both indicate substantial increase in risk for schizophrenia associated with premorbid fluid-skills deficits and with significantly low premorbid performance IQ relative to verbal IQ in individuals developing the disorder (Amminger et al. 2000; Gunnell et al. 2002).

However, population-based cohort data from the Israeli Draft Board indicate that adolescents diagnosed as suffering from schizophrenia and adolescents identified as having schizotypal personality disorder (SPD) score lower than do healthy adolescents not only on fluid intelligence as measured by Raven's matrices test but also on measures of crystallized intelligence as assessed by the WAIS-R arithmetic subtest and by a modified Otis-type verbal intelligence test (Weiser et al. 2003). It is important to note that adolescents with schizophrenia and those with SPD in this population had significantly fewer years of education than did normal controls. Controls had on average 11.23 years of education (SD = 1.65) at the time of draft-board assessment while individuals with SPD had 9.06 (SD = 3.35) and those with schizophrenia 7.38 (SD = 3.74) years of education. The authors of this study elected not to control for years of education in analyses of differences in cognitive function between groups, citing Meehl's description of the matching fallacy that "disease in an individual both impedes education and impairs cognitive abilities measured in intelligence tests" (Weiser et al. 2003, p. 37). Although not controlling for years of education in this context is certainly a defensible choice in analysis, it is plausible that doing so would have indicated levels of crystallized ability appropriate for level of education in the SPD and schizophrenic groups but deficits in fluid function.

Further support for the idea that early fluid-skills deficits may be characteristic of risk for schizophrenia and responsible for observed low-normal full-scale IQ in individuals with schizophrenia is provided by examinations of neuropsychological profiles among adult patients, their unaffected siblings, and matched controls. These studies indicate that cognitive differences among the groups are primarily observed in tests of fluid skills. Comparison of patients with controls has indicated substantial deficits in neuropsychological tasks requiring abstraction and attention and has demonstrated that these deficits are most pronounced in patients with lower full-scale IQ (Kremen et al. 2001). Of further interest, studies of patients, siblings, and controls indicate that fluid-skills deficits relative to matched controls are present in the siblings of schizophrenic patients, suggesting an underlying fluid cognitive liability for the disorder (Egan et al. 2001). It is important to note, however, that measures of achievement and full-scale IQ as assessed by the WAIS discriminate patients from siblings and from matched controls, but do not discriminate patients' siblings from matched controls. In contrast, measures of fluid skills do tend to discriminate all

three groups, with discrimination between siblings and matched controls being largest for siblings of probands exhibiting impaired cognition on the particular measure being examined. As with the findings of Duncan et al. (1995) and Waltz et al. (1999) in the study of adults with lesions of the PFC, normal full-scale IQ as measured by the WAIS is observed in the presence of fluid-skills deficits in adults with schizophrenia and their unaffected siblings. These studies identify normal to low-normal crystallized IQ and achievement in schizophrenic patients and their siblings in the presence of deficits in types of fluid abilities that are highly correlated with general intelligence.

It is important to point out, however, that intelligence in schizophrenia has been of necessity studied almost exclusively with adult samples. Bedwell et al. (1999) provide perhaps the only developmental data on schizophrenia in childhood. Although their study sample is small, reflecting the rarity of childhood-onset schizophrenia, findings indicated a lack of raw-score change with age on the information subtest of the Wechsler Intelligence Scale for Children (WISC), an aspect of crystallized intelligence, in addition to deficits in subtests with a fluid component, namely, picture arrangement and block design. The lack of raw-score change indicates a failure to demonstrate developmentally normative increases in general knowledge and would seem to be at variance with the literature on intelligence in schizophrenia in adulthood, which suggests little crystallized deficit. Furthermore, the lack of raw-score change in the information subtest was correlated with post-schizophrenic hippocampal volume. Given findings discussed in section 5.2 indicating a strong relation between hippocampal volume and fluid cognition in schizophrenia (Weinberger et al. 1992), these data lend themselves to the interpretation that the fluid deficits of patients with childhood-onset schizophrenia impair the acquisition of new information and that this, in part, contributes to observed full-scale IQ declines. Such an association would be consistent with a developmental relation between fluid and crystallized intelligence, and perhaps the study by Bedwell et al. (1999) provides one source of data supporting this relation in childhood.

A second source of evidence regarding the developmental relation between fluid and crystallized ability is provided by the study of the cognitive development of children with phenylketonuria (PKU). Children with the inborn error of metabolism that limits the synthesis of phenylalanine (Phe) develop severe mental retardation if levels of Phe are not controlled through a strict dietary regimen. The buildup of Phe reflects the failure of the synthesis of Phe into Tyrosine (Tyr), a dopamine precursor. Given the predominant role of dopamine in the function of the prefrontal cortex (Sawaguchi & Goldman-Rakic 1991), also described in section 5.2 and the sections that follow, reduced levels of Tyr are associated with fluid cognitive impairments in children treated early and continuously for PKU (Diamond et al. 1997; Welsh et al. 1990). Specifically, although reduction of Phe prevents severe mental retardation, it results in lower levels of Tyr and reduced dopaminergic function in the PFC, leading to impaired ability on measures of fluid skills in children treated early and continuously for PKU (Diamond & Herzberg 1996; Diamond et al. 1997; Puglisi-Allegra et al. 2000).

Given the presence of fluid cognitive deficits in PKU, it is of some interest that individuals with PKU tend to exhibit IQ and academic achievement in the low-normal range. Although it is not certain that fluid cognitive impairment is responsible for the low-normal full-scale IQ of children with PKU, this may be the case, as the cognitive abilities of children with PKU on a variety of other tasks associated with intelligence do not appear to be impaired (Diamond et al. 1997). In one of the few studies, if not the only one, to examine the performance versus verbal IQ distinction in children with PKU, a significant decrement in performance IQ relative to verbal IQ was observed at age eight years (Griffiths et al. 2000). Deficits relative to the population norm were observed in all performance IQ subtests, including the block design, object assembly, picture completion, picture arrangement, and coding subtests. Interestingly, a deficit was also noted in one verbal IQ subtest – the information subtest – but not in the similarities, arithmetic, vocabulary, and comprehension subtests. The pattern of results involving performance IQ deficits and a deficit in only the information subtest of the verbal IQ subscales is striking in its similarity to that of Bedwell et al. (1999) in the study of intelligence in childhood-onset schizophrenia and provides further evidence of specific dissociation of fluid and crystallized cognitive abilities early in the life span.

5. Developmental neuroscience of cognition and emotion

5.1. Neuroscience of developing fluid cognition

The evidence reviewed to this point offers little support for a close association between fluid cognition and general intelligence. Evidence for the unity of working memory and *g* notwithstanding, a number of studies suggest dissociation of fluid cognitive functions from *g*. On the one hand, it would seem without question that the ability to integrate diverse information in working memory is central to human reasoning and problem-solving ability and thereby to general intelligence (Duncan 2001; Miller & Cohen 2001; Prabhakaran et al. 2000). But given the discrepant evidence outlined in sections 3 and 4, what exactly is the relation between fluid functioning and general intelligence? If fluid cognitive functions are somehow less central to *g* than was once thought, then what do we know about the development of fluid cognition and how can this knowledge shed light on the idea that fluid functions can appear so central to intelligence in one instance and yet so distinct in another? Furthermore, what are the implications of dissociation of fluid cognition and *g* for understanding cognitive development and the assessment of human cognitive abilities and what is the state of measurement available for this assessment? These are central questions, relevant to both basic and applied science study of human cognitive function; relevant to basic science understanding of brain-behavior relations in the study of cognitive ability and relevant to applied science understanding of how to best measure and support mental development and the real-world functioning to which it is related.

Fortunately, neuroscientific study of fluid cognition offers some insight into why fluid functions are to some extent distinct from *g* and what this means for the relation of fluid cognition to real-world competence. Specifically, it is well established that areas of the PFC and ACC known

to be important for fluid cognitive functions and performance on tests of fluid intelligence (Braver et al. 1997; Duncan et al. 2000; Gray et al. 2003; Prabhakaran et al. 2000) are extensively and reciprocally interconnected with limbic and brain-stem structures associated with emotional reactivity, the stress response, and autonomic function (Allman et al. 2001; Bush et al. 2000; Diorio et al. 1993; Drevets & Raichle 1998; LeDoux 1989; Paus 2001; see the edited volume by Uylings et al. 2000). In combination, prefrontal, limbic, and brain-stem structures integrate cognitive, emotional, and autonomic responses to stimulation with the primary implication of such reciprocal innervation and regulation being that prefrontally mediated fluid cognitive processes directly influence *and, most important for present purposes, are influenced by emotional and autonomic responses to stimulation* (Erickson et al. 2003; de Kloet et al. 1999; Groenewegen & Uylings 2000; Kaufman & Charney 2001). A traditional view of reasoning ability as distinct from or liable only to disruption from emotional arousal has been replaced by a model in which cognitive, emotional, and autonomic responses work in concert to organize patterns of behavior (Davidson 2002; Van Eden & Buijs 2000).

5.2. A neural basis for cognition-emotion reciprocity in fluid cognition

The integration of cognitive, emotional, and autonomic responses to stimulation in the PFC is directly relevant to understanding fluid cognition and its distinction from psychometric *g*. What this integration means is that in order to understand fluid cognition it is important to understand that the prefrontal cortical structures and functions thought to closely reflect *g* are dependant to some extent on brain structures and functions that underlie emotional reactivity and the stress response. Brain structures that subserve working memory, attention shifting, and inhibitory control, all aspects of fluid cognition, and those that subserve emotional and stress reactivity are integrated in what is referred to as a *corticolimbic circuit*, that is, a circuit of reciprocal neural interconnectivity among dorsolateral, ventromedial, and orbitofrontal areas of the PFC, the ACC, and amygdaloid and hippocampal structures of the limbic system. The functioning of this neural interconnectivity in part underlies performance on fluid cognitive tasks such that dysfunction in one component of the system is likely to lead to difficulty in the self-regulation of cognition, emotion, and behavior (Davidson 2002; Posner & Rothbart 2000).

Brain-imaging studies of the processing of attention- and emotion-related information in the PFC and ACC indicate the integrated and reciprocal relation between affect and cognition in the brain. Distinct regions of the ACC are activated in response to cognitive tasks and to stimuli eliciting emotional arousal (Bush et al. 2000; Drevets & Raichle 1998). Similarly, examinations of intentional reappraisal of emotional arousal and of changes in emotional state associated with emotionally arousing stimuli have indicated reciprocal prefrontal cortical-limbic activation (Mayberg et al. 1999; Ochsner et al. 2002). With reappraisal of negative emotion and recovery from sadness and depression, prefrontal and cognitive ACC activation is increased and limbic and emotional ACC activation is decreased. During periods of negative affect without reappraisal, however, limbic and emotional ACC activation is increased and prefrontal and cognitive ACC activation is decreased. Such reciprocal interconnectivity of emotion and cognition in the brain is highly consistent with the idea that fluid cognitive functioning is goal directed. Working memory and cognitive control processes are utilized in the service of specific goals related to problem solving and learning. However, at high levels of emotional arousal, fluid cognitive functions become inhibited, and impairments in the control of attention, working memory, and inhibitory control are more likely to occur.

In the study of emotion-cognition reciprocity in the brain, the amygdala has been shown to play a central role in threat detection and fear reactivity (LeDoux 1995; 1996), directing attention to ambiguity and enhancing vigilance in response to uncertainty (Whalen 1998). Such a role is in keeping with evidence that the amygdala directs cognitive and autonomic responses to sources of potential threat (Davidson 2002). Very high levels of threat or fear are thought to activate a relatively automatic link between the amygdala and the "fight/flight" response of the sympathetic branch of the autonomic nervous system that essentially bypasses or inhibits higher-order fluid cognitive appraisal and response processing of threat-related stimuli (LeDoux 1996). Such an automatic response to threat would confer a substantial evolutionary advantage and, as such, would tend to be highly conserved across species. Electrophysiological and brain-imaging evidence in human and nonhuman animal models attests to the reciprocal modulation of activity between the amygdala and the PFC in response to fear-evoking stimuli. Direct electrical recording of brain activity in rats through electrodes implanted in dorsolateral PFC and amygdala has demonstrated that decreased activity in the PFC in response to fear-evoking stimulation is attributable to increased amygdala activity (Garcia et al. 1999). Similarly, brain imaging in humans has demonstrated that perceptual processing of fear-evoking stimuli is associated with amygdala activation whereas cognitive evaluation of these stimuli is associated with increased PFC activation and decreased amygdala activation (Hariri et al. 2003).

Furthermore, amygdala activation plays an important role in the formation of highly stable long-term memories associated with stressful and highly emotionally arousing events (McGaugh et al. 1996; Roozendaal 2000). The mechanism through which the amygdala performs this function is modulation of stress hormones known to be important for memory storage. Such a system is highly adaptive in unpredictable environments, serving to promote survival by instantiating relatively automatic sympathetic responsivity to indicators of impending threat or harm. However, in the instance of extreme trauma, the relative automaticity associated with this memory system, as an aspect of corticolimbic connectivity, appears to be highly detrimental to the effortful cognitive regulation of emotion, cognition, and behavior, as in the occurrence of post-traumatic stress disorder.

Effortful cognitive control by the PFC of negative emotion and stress reactivity associated with the amygdala would seem to be the norm rather than the exception and to occur through reciprocal connectivity of the ventromedial and orbitofrontal regions of the PFC, the hippocampus, and the amygdala (Davidson 2002; Davidson et al. 2000). Ventromedial PFC appears to be central in

representing the emotional valence of stimuli, and its integrity is essential for holding in mind and acting on information of motivational significance to the organism. Disruption of the ventromedial PFC results in difficulty in the regulation of emotion and is associated with anomalous decision-making in response to information regarding the likely reward or penalty associated with a given choice (Bechara et al. 1996; 1999). In individuals sustaining damage to ventromedial PFC, negative consequences associated with aversive contingencies appear not to be marked with somatic or autonomic responses that serve to signal the individual not to engage in a particular behavior (Bechara 2004; Damasio 1994). The absence of an anticipatory autonomic response to perceived penalty and adverse decision-making associated with this absence have been observed in several studies (Bechara et al. 1996). As well, laterality in this system has been observed such that the right ventral medial PFC appears to play the central role within the corticolimbic system in reactions to stressful or aversive contingencies (Sullivan & Gratton 2002). Such laterality is consistent with the relative right-sided electroencephalographic PFC activation (left hypofrontality) observed in individuals with affective disorders (Davidson 2002; Sutton & Davidson 1997).

The hippocampus is understood to be integral to the information maintenance and cognitive control functions of the PFC through the rapid encoding of spatial and temporal context. Through relations with the amygdala and ventral and dorsolateral PFC, the hippocampus plays a pivotal role in cognition-emotion interaction. Studies of hippocampal function in rats and monkeys and in computational neural network models indicate that the hippocampus plays this role in part by modulating the action of dopamine in the PFC. Hippocampal damage in rats and monkeys has been shown to impair working memory functions by disrupting the responsivity of PFC neurons to dopamine (Bertolino et al. 1997; 2002; Lipska et al. 2002a; 2002b). In contrast, increased hippocampal synaptogenesis in rats has been associated with increased spatial learning and memory (Lee & Kessner 2002; Liu et al. 2000). Similarly, hippocampal representation of context has been demonstrated using computational modeling to facilitate the maintenance of competing sets of representations and the emphasis of task-relevant and inhibition of task-irrelevant processes and information (Cohen & O'Reilly 1996). Disruption of hippocampally dependent representation of contextual information in a neural component corresponding to neuromodulatory effects of dopamine in the PFC has also been suggested to account for fluid cognitive deficits in schizophrenia (Cohen & Servan-Schreiber 1992). This computational model is consistent with the study of cognition in schizophrenic patients which indicates that cognitive function and cerebral blood flow in the dorsolateral PFC in response to the Wisconsin Card-Sorting Task (WCST), a well-known and widely used measure of fluid functioning, are highly related to hippocampal volume (Weinberger et al. 1992). In a sample of monozygotic twins discordant for schizophrenia, difference in hippocampal volume between affected and unaffected twins was strongly related to physiological activation in the dorsolateral PFC during the WCST. Particularly impressive in this study is the finding that the greater the within-twin-pair difference in hippocampal volume, the greater the reduction of physiological activation in the PFC in response to the WCST.

5.3. Fluid functioning and the integrity of corticolimbic connectivity

Although brief, the foregoing examination of some of the behavioral and psychological implications of prefrontal corticolimbic connectivity serves to emphasize that the fluid cognitive functions of the PFC are dependent, perhaps to a large extent, upon the integrity of this connectivity. Accordingly, a further point central to the overall thesis of this target article is that the integrity of the corticolimbic system that underlies fluid cognition depends upon the activity of the hypothalamic-pituitary-adrenal (HPA) axis, the physiological stress-response system. As detailed in many comprehensive reviews, the HPA axis regulates the glucocorticoid hormone response to stress and does so through positive-feedback and negative-feedback mechanisms involving the amygdala, hippocampus, and PFC (Kaufman & Charney 2001; Lopez et al. 1999; Vazquez 1998). In the stress response, levels of circulating glucocorticoids are controlled by the activity of the paraventricular nucleus of the hypothalamus through cascading effects on the pituitary and adrenal glands. Glucocorticoids stimulate activity of the central nucleus of the amygdala and work to maintain a state of arousal in response to threat. The PFC and the hippocampus, in turn, respond to glucocorticoid increase with negative feedback on the central nucleus of the amygdala and structures involved in glucocorticoid response to stress to down-regulate levels of glucocorticoids (Francis et al. 1999a).

A notable consequence of the bidirectionality of the HPA system is that high levels of stress early in life influence its development. The homeostatic balance of the system in its ability to regulate the neuroendocrine response to stress appears to be established early on. The primary mechanism of this early experience effect as demonstrated in rodents involves tactile stimulation associated with maternal care (Caldji et al. 2000a; 2000b; Francis et al. 1999b). In rats, high levels of maternal licking and grooming of pups and the occurrence of a nursing style known as *arched-back nursing* are associated with high levels of cognitive and behavioral competence. The effect of this maternal rearing style has been shown to be associated with increased synaptogenesis in the hippocampus, increased benzodiazepine and gamma-amino-butyric acid receptor binding within structures of the corticolimbic circuit including the PFC that allows for increased down-regulation of circulating glucocorticoids, and enhanced cognitive function as assessed by learning and spatial memory tasks (Francis et al. 1999a; Liu et al. 2000). However, high levels of stress early in life that result from prenatal or postnatal stress and/or disruptions to maternal care are associated with the opposite of this pattern. Rats experiencing stress prenatally or extended maternal separation in the neonatal period exhibit reduced ability to regulate the activity of the HPA axis, higher levels of circulating glucocorticoids, and reduced hippocampal synaptogenesis (Gould & Tanapat 1999; Liu et al. 2000).

One consequence of this poor regulation of HPA activity and reduced hippocampal synaptogenesis is

disrupted dopaminergic innervation of the PFC. In rats experiencing extended maternal separation and social deprivation as neonates, several regions of the PFC exhibited reduced dopaminergic innervation by age 45 days (Braun et al. 1999). As noted in section 4.3, there is clear evidence that dopamine plays a prominent role in regulating the fluid cognitive functions of the PFC (Brozoski et al. 1979; Diamond et al. 1997; Goldman-Rakic 1999; Lewis et al. 1999). Computational, lesion, and transient inactivation models provide considerable evidence of disrupted dopaminergic activity in the PFC and impaired functioning of prefrontal neurons associated with early hippocampal pathology and high levels of circulating glucocorticoids (Bertolino et al. 1997; 2002; Kinnunen et al. 2003; Lindley et al. 2002; Lipska & Weinberger 2000a; Meyer-Lindenberg et al. 2002; Saunders et al. 1998; Seamans et al. 1998; Weinberger et al. 2001). That the effect appears to be a developmental one is indicated by the demonstration that neonatal but not adult lesions of the ventral hippocampus in rats and monkeys are associated with impaired performance on a variety of working memory and learning tasks dependent upon dopamine function in the PFC (Chambers et al. 1996; Le Pen et al. 2000; Lipska et al. 2002).

The foregoing suggests that fluid-skills deficits are likely to be associated with adverse rearing conditions and may be partially mediated through stress-related disruptions of hippocampally modulated dopaminergic innervation of the PFC and stress-related disruption of the responsiveness of prefrontal cortical neurons to multiple neurotransmitter systems. Given the principle of use-dependent synaptic plasticity and the fact that the PFC is relatively slow in maturing (Gogtay et al. 2004), it may be that patterns of limbic-prefrontal reciprocity become biased toward either emotional-reactive or cognitive-regulatory types of responding fairly early in life. High levels of stress or threat might lead to patterns of primarily autonomic reactive responses to stimulation rather than effortful fluid cognitive responses. Lifelong patterns of reciprocity are almost certainly not established by early experience, but, in young children, the development of fluid cognition and the many aspects of behavior to which fluid cognition is related, may be driven to some extent by early experience and its effect on emotional reactivity and regulation. Individuals with a lower threshold for emotional reactivity and stress responding associated with the amygdala and related limbic structures may experience difficulty with fluid cognitive functioning, particularly when reared in high-stress environments.

However, the extent of stress required to bring about fluid cognitive deficits and the applicability of animal models to human populations are open to question. As well, the exact mechanisms through which dopamine and other neurotransmitter functions in the PFC are disrupted by early hippocampal pathology remain uncertain (Lipska & Weinberger 2000a; Lipska et al. 2002). Interactions of dopamine with glutamatergic and GABAergic systems in the PFC indicate both inhibitory and excitatory roles for dopamine (Lewis et al. 1999; Yang et al. 1999), suggesting that dopaminergic tuning of prefrontal pyramidal neurons may underlie both inhibitory control and information maintenance functions of working memory (Braver et al. 1999; Cohen & Servan-Schreiber 1992; Miller & Cohen 2001). However, the specific role of dopamine in the prefrontal cortex is complex and elucidation of its specific and selective effects remains a work in progress (Durstewitz & Seamans 2002).

6. Implications of developing corticolimbic circuitry for intelligence in human populations

6.1. Stress and early experience

Neurobiological evidence relating corticolimbic connectivity to fluid cognitive skills and demonstrations of the effects of stress-related HPA activity on the integrity of this circuit suggest plausible mechanisms through which early chronic rearing stress affects the development of one aspect of what has generally been regarded as intelligence in human populations. In the neuroscience literature, neonatal hippocampal damage has been referred to as an animal model of schizophrenia (Lipska & Weinberger 2000b). This is largely due to the fact that some of the effects of neonatal hippocampal manipulations on specific schizophrenic-like phenotypic traits emerge after the pubertal period in affected rats. Effects of hippocampal disruption on aspects of learning and working memory, however, appear prior to puberty (Chambers et al. 1996), in itself a phenotypic trait consistent with early risk for schizophrenia in human populations (Amminger et al. 2000; Gunnell et al. 2002). In particular, as already noted, neonatal but not adult lesion of the hippocampal formation is associated with working memory deficits both prior to puberty and in adulthood in rodents and nonhuman primates. In contrast, working memory deficits associated with PFC lesions are seen only when the lesions are made in adulthood and not in the neonatal period (Bachevalier et al. 1999; Lipska et al. 2002; Malkova et al. 2000; Weinberger et al. 2001).

Of similar interest regarding fluid cognitive deficits as seen in PKU is evidence indicating that high concentrations of phenylalanine attenuate synaptic plasticity in the rat hippocampus (Glushakov et al. 2002). As synaptic plasticity in the hippocampus is known to be associated with aspects of fluid cognition (Liu et al. 2000), these results suggest fluid cognitive impairment associated with PKU results from disruption to the integrity of the corticolimbic circuit similar to that observed in schizophrenia and in animal models of the effect of stress on developing fluid cognitive skills. However, it is important to note that moderate concentrations of Phe, such as those observed by Diamond et al. (1997) in individuals treated early and continuously for PKU, may have lesser effects on synaptic plasticity. It may be that the effect of moderate levels of Phe on hippocampal synaptogenesis combined with reduced levels of Tyr is sufficient to produce the reduced dopaminergic function and working memory deficits in individuals with early and continuously treated PKU (Diamond & Herzberg 1996; Diamond et al. 1997), but such a mechanism remains to be determined.

In light of research on fluid cognition in schizophrenia and PKU, evidence relating rearing stress to reduced hippocampal synaptogenesis and to working memory deficits in nonhuman animal models provides perhaps one plausible neurobiological model for the effects of environmental disadvantage and disrupted early rearing experience on the development of one aspect of intelligence in humans. Nonhuman animal models of the development of working

memory indicate that chronic early rearing stress affects the activity of the HPA axis with attendant negative consequences for hippocampal function and aspects of fluid cognition dependent upon the corticolimbic circuitry of the PFC. As a result, early life stress would be expected to attenuate fluid cognitive functions in human populations in ways that might appear to underlie deficits in general intelligence. Given a large number of studies demonstrating moderate to high heritability for general intelligence but also considerable environmental influence on intelligence, particularly early in the life span (Gottlieb et al. 1998; Wahlsten 1997), developmental neuroscience work on the role of chronic stress in the development of corticolimbic connectivity and the integrity of the PFC provides evidence of a putative mechanism through which early rearing stress, and conversely early education and care intervention, would appear to influence one prominent aspect of developing cognition in humans.

Such a relation among early stress, enriched early experience, and later developmental competence has been demonstrated in rats. Specifically, Francis et al. (2002) and Bredy et al. (2003) demonstrate reversal of the effect of chronic early stress on later stress responsivity and behavior among rats receiving environmental enrichment during the post-weaning period. As with prior studies, these studies suggest a functional reversal of the effects of life stress by compensatory mechanisms that alter the phenotypic expression of the underlying stress reactivity associated with antenatal or early postnatal stress (Maccari et al. 1995; Whimbey & Dennenberg 1967). In humans, it is well known that inconsistent or inadequate caregiving and disruption to the early rearing environment are aspects of risk for poor developmental outcomes in children growing up in low socioeconomic status (SES) environments (McLoyd 1998). As is also well known, early compensatory caregiving interventions such as the Abecedarian Project (Ramey & Campbell 1991; Ramey et al. 1998) have demonstrated effects on IQ and on multiple aspects of developmental competence from birth through adulthood in randomized designs involving children at high risk for low IQ as a result of low SES. Presumably one of the mechanisms through which compensatory education and care among humans leads to enhanced competence is through the attenuation of early stress and adverse neurobiological consequences associated with chronic rearing stress. Therefore, one important future direction for work on early intervention will be the identification of specific stress mechanisms and demonstrations of the ways in which early intervention reduces rearing stress and affects neurobiological development and cognitive functioning.

6.2. Stress, early intervention, and intelligence in human populations

Work in developmental neuroscience indicates that chronic early rearing stress can lead to disruptions in essential neural systems underlying fluid cognitive skills with nonhuman animal models providing evidence that developing corticolimbic connectivity underlies the integrity of functioning of the PFC. But could environmental influences on developing corticolimbic connectivity really underlie the development of general intelligence? Even though evidence for disrupted fluid skills associated with the effects of early chronic stress on developing corticolimbic connectivity in nonhuman animal models may be compelling, the relation of developing fluid functions to the development of intelligence and to estimates of general intelligence in human populations remains unclear. Would general intelligence really be affected by high levels of rearing stress and/or by programs designed to eliminate that stress? Jensen (1998) examines the early intervention literature and declares that no study, with the possible exception of the Abecedarian Project, actually changed *g*. However, given the previously established relation of fluid skills to *g* (Gustafsson 1988), it would be expected that programs that could promote fluid-skills functioning through the enhancement of corticolimbic connectivity would at least appear to influence general intelligence. Certainly findings from imaging studies and single-cell-recording studies indicate a highly flexible and adaptive role for the PFC in coordinating diverse information streams and attest to the centrality of fluid skills in any conceptualization of intelligence (Duncan 2001). However, given the aforementioned evidence suggesting dissociation of fluid cognitive functions from intelligence as measured by standard assessments, it may be the case that early environment affects specific aspects of cognition – namely, fluid functions – that closely resemble but are distinct from psychometrically defined general intelligence. Of course, whether such a mechanism related to fluid cognition is actually present in early intervention for children in poverty and whether such a mechanism would be associated with enhanced corticolimbic functioning and lead to the appearance of increased general intelligence are open questions. In investigating such questions, however, it is necessary to keep in mind that the effects of poverty and, conversely, environmental enrichment on child development are quite diverse and perhaps have as much or more to do with the promotion of crystallized knowledge or the diminution of the adverse effects of poor nutrition and inadequate health care on child outcomes as with anything associated with stress and fluid cognition.

6.3. Genetic and environmental influences on developing cognitive abilities

Although the study of early intervention for children facing psychosocial disadvantage may shed potentially valuable light on relations between stress and cognitive development, another approach to questions about environmental influences on fluid cognition and their relation to general intelligence is found in behavior genetics research. For some time now, it has been well established within the framework of behavior genetic twin and adoption study designs that both genetic and environmental influences act on general intelligence and that some substantial proportion of variance in general intelligence is accounted for by genetic variation. If fluid cognition is similar to but distinct from general intelligence and more liable to environmental influence, it should be possible to demonstrate this by using the variance-partitioning methods of behavior genetics research. Indeed, although behavior genetic examinations of working memory and general cognitive ability are somewhat rare, those that do exist indicate that working memory is distinguishable from general intelligence both genetically and environmentally.

Specifically, for the working memory measures that have been examined, common genetic variance is not particularly large, and both genetic and nonshared environmental loadings on the measures are distinct from those associated with general intelligence (Ando et al. 2001; Luciano et al. 2001). However, these studies are limited by relatively low phenotypic correlation between working memory and general intelligence and have been conducted only with adult samples.

Although in need of replication, both with adults and children, findings indicating moderate to small common genetic variance in working memory are perhaps consistent with heritability estimates for *g* in childhood. Specifically, heritability estimates of *g* in young children are small, at about 20%, but increase to about 60% in adult samples (Plomin & Spinath 2002). Always something of a puzzle as to why heritability would increase with age, if environmental influences on fluid function are relatively large, and if fluid function is particularly relevant to IQ test performance in early childhood, then the noted change in heritability with age may be more apparent than real. Furthermore, if fluid function in the guise of the general factor is highly liable to environmental influence early in the life span, then heritability estimates of IQ would also be smaller for children from lower SES backgrounds. This is in fact the case, as estimates of environmental influence on measures of cognitive functioning in children increase and estimates of heritability decrease as a function of SES (Rowe et al. 1999; Turkheimer et al. 2003). Of particular note, in early childhood this modification of the heritability of IQ has been observed at age seven years on measures of full-scale and performance IQ but not verbal IQ as assessed by the Wechsler Intelligence Scale for Children (WISC) (Turkheimer et al. 2003). In an adolescent sample, however, modification of the heritability of IQ by SES was observed for a version of the Peabody Picture Vocabulary Test, a measure of crystallized knowledge (Rowe et al. 1999).

7. Measurement

7.1. Limits to the measurement of a single factor of intelligence

Although the available evidence does not as yet render a definitive conclusion regarding dissociation of fluid cognitive function and *g*, the psychometric, developmental, clinical, and behavior genetic data outlined in this target article do suggest a distinction between fluid cognitive function as examined in the cognitive and neuropsychological literatures and general intelligence as defined by researchers working within the psychometric tradition. This is very interesting because, as noted at the outset of this review, psychometric examinations of typically developing populations have found measures of fluid function to be essentially identical to general intelligence. Based upon evidence presented in this review, however, it would seem reasonable to conclude that fluid function is to some extent an indicator of the integrity of a corticolimbic brain system that reflects the interdependence of cognition and emotion in a way that renders it amenable to the influence of early environment and distinct from psychometric *g*. Differentiation of fluid cognition from general intelligence would appear to be an important measurement goal for research on cognitive development.

Evidence for a distinct developmental trajectory for fluid cognition in the study of human cognitive abilities that is particularly rapid in early childhood calls into question the specific utility of measures of general intelligence, particularly for young children. The explicit measurement of a single factor may in many instances not be particularly informative regarding individual cognitive growth and the relation of that growth to adaptive functioning. Unfortunately, several widely used measures of mental abilities, including those frequently used with young children, excel as measures of general intelligence but are weaker as measures of specific cognitive ability factors (Caruso 2001; Laurent et al. 1992; Woodcock 1990). Perhaps of most immediate concern, as already noted, widely used measures of intelligence disproportionately assess crystallized skills and domains of intelligence associated with opportunity for learning (Woodcock 1990). In extensive factor analyses of the most widely used intelligence batteries for children, including the Wechsler batteries, the Stanford-Binet IV, and the WJ-R among others, Woodcock (1990) and McGrew (1997) have shown that approximately one-third of the batteries' subtests measure crystallized skills and an additional quarter focus on quantitative knowledge and reading/writing skills that directly assess instruction and opportunity for learning – crystallized skills broadly defined. Only approximately 7% of subtests directly assess fluid skills and perhaps another 10% assess processes and memory skills that have a fluid-intelligence component. Furthermore, nearly all of the fluid subtests were found on the WJ-R, the only measure explicitly grounded in gF-gC theory. The Wechsler batteries contain no explicit measure of fluid skills, and the Stanford-Binet IV was found to contain only one explicit measure of fluid skills. As noted by McGrew (1997), the underrepresentation of measures of fluid skills in widely used assessments of intelligence is considerable.

Given that many commonly used measures of IQ disproportionately assess crystallized mental abilities, intelligence as tested by these measures must be seen to be limited in specific ways. However, it may be that for typically developing children in typical environments, discrepancies between fluid and crystallized aspects of cognition are small or perhaps not particularly meaningful. This could be due to the fact that nurturing, low-stress environments also tend to provide high levels of educational stimulation. However, for children from chaotic or dysfunctional homes or otherwise facing some experiential or developmental disadvantage, the poor representation of fluid cognitive assessment on currently available measures of intelligence is perhaps particularly disadvantageous. As measures of crystallized skills, currently available assessment batteries will provide a limited perspective on the cognitive abilities of children. Furthermore, as has been already outlined in detail, chaotic rearing environments are likely to have distinct adverse effects on fluid aspects of cognition. Currently available measures, however, will not really be able to address these effects. From a single-factor perspective on the measurement of intelligence, the underrepresentation of fluid skills on most measures of intelligence would be of minimal concern. However, such an approach to measurement would not appear to be justified, as evidence from

a number of sources indicates that increased precision in the assessment of developing fluid cognition in young children is needed.

7.2. Measuring fluid cognition

Given the presence of fluid-skills deficits in a wide variety of developmental and learning disorders, increased attention to the measurement of fluid cognitive functions, referred to primarily as executive function in the study of young children, and their relation to widely used measures of intelligence and achievement is a high priority. It may be that identification of fluid cognitive deficits in the presence of typically developing crystallized abilities could prove to be an indicator of increased risk for developing psychopathology or learning disorder. Several cross-sectional studies examining normative developmental changes in aspects of EF provide an increasing knowledge base on fluid cognition in children. Findings indicate a general age-related progression on various EF tasks and differences among tasks in the age at which adult-level performance is reached (Krikorian & Bartok 1998; Luciana & Nelson 1998; Pennington 1997; Welsh et al. 1991). These studies have also demonstrated distinct information maintenance and cognitive control factors underlying EF task batteries (e.g., Pennington 1997). What is needed, however, is research within an individual-differences perspective relating differential performance at specific ages and developmental time periods to various outcomes and competencies. Although further work on normative levels of performance on EF tasks is needed, an equal priority is the need for cross-sectional and longitudinal research examining correlates of individual differences in task performance in both typically and atypically developing populations of children.

The need for the differentiation of fluid skills from *g* early in the life span would also seem pressing given evidence for the relation of fluid cognitive skills to academic achievement and to social competence in typically developing young children. Studies of achievement and behavior indicate broad influence of fluid cognitive functions on achievement in both reading and math and in social and emotional competencies known to be important for the adjustment to school (see Blair 2002 for a review). Examination of the relation of WJ-R measures of cognitive ability to WJ-R measures of academic achievement indicates distinct developmental relations of fluid and crystallized intelligence to progress in both reading and math. As expected, fluid skills show a predominant influence on achievement in early and middle childhood that declines by adolescence. In contrast, the relation between crystallized intelligence and reading and math achievement rises rapidly in late childhood and adolescence and remains very high in adulthood (Evans et al. 2001; McGrew & Hessler 1995). Furthermore, a relevant example for achievement in math concerns brain-imaging findings indicating bilateral PFC activation occurring during reasoning on math problems. While simple calculation processes have been associated with parietal and parieto-occipital regional activation, problems requiring multiple operations, that is, multiple calculations with intermediate steps, demonstrate PFC activation (Burbaud et al. 1995; Prabhakaran et al. 2001). Such prefrontal activation in response to multiple-operation problems is consistent with imaging findings observed by Waltz et al. (1999) in the examination of brain activation occurring in response to increased relational complexity in problems adapted from Raven's Progressive Matrices Test.

Whether through facilitation of the acquisition of crystallized skills or as a separate influence on academic achievement in specific subject areas during early and middle childhood, fluid functions play a clear role in academic achievement early in the life course. Continuing attention to influences on and the measurement of fluid aspects of cognitive function in young children should prove particularly valuable for educational and social policy decision making. Perspectives on the development of intelligence and its relation to academic achievement that rely on the measurement of a single factor may be particularly disadvantageous. If children are having difficulty in learning, measures that conflate fluid and crystallized functions cannot differentiate whether children have limited opportunity to acquire the types of knowledge assessed by measures of crystallized intelligence or difficulty with the fluid skills associated with learning unfamiliar material, or both. There is an increasing emphasis on accountability in education; on the need to ensure that children acquire the crystallized skills that schooling can provide. In contrast, the development and application of knowledge about fluid skills and their perhaps unique role in early learning and development are currently inadequate. Particularly in the evaluation of the efficacy and effectiveness of preschool and early school readiness initiatives such as Head Start, emphasis on children's acquisition of crystallized skills such as those associated with early reading would be well served by an equal and complementary emphasis on the development of fluid cognitive abilities.

7.3. Differentiating fluid cognition from general intelligence

If available evidence indicates the need to differentiate fluid cognition from general intelligence, an important next step is to ask how separable the constructs may be in typically developing populations. Here, the lead of Gustafsson (1988) may prove useful in a somewhat unexpected way. Specifically, having examined a number of hierarchical factor models of cognitive abilities, Gustafsson (1988) determined that the relation between gF and *g* was so strong as to indicate unity. Having arrived at this conclusion, he then made the insightful suggestion that it would be desirable to set *g*F identical to *g* and to purge the remaining second-order factors of their *g* variance. Doing so would enable one to study aspects of cognition on their own, independent of variation in them attributable to *g*. Purging gC of its *g* variance would result in a gC residual, gC′, that would represent crystallized intelligence independent of *g*. Similarly, with the other second-order factors, *g* variance could be removed, and differences among individuals in the residual variance examined.

Following Gustafsson's logic, evidence presented in this target article would suggest that there must also exist some gF residual, gF′, that can be purged of *g* variance and studied independently of *g*. The near unity of the relation between gF and *g* in the psychometric study of intelligence would seem to render this problematic; however,

in light of the evidence presented in this article, it would seem that measures of working memory and EF have important sources of variance independent of *g*. The need for such measurement would seem to be indicated and be in keeping with Carroll's (1996) call for increased experimental work examining the identity of gF relative to *g*. While acknowledging that Gustafsson (1988) may be correct in setting gF equal to *g*, Carroll speculated that "it is possible that measures of *g*F feature attributes that require specific skills in inductive and deductive reasoning that are not necessarily present in other measures of *g*" (Carroll 1996, p. 15).

Considering the possibility of removing *g* variance from gF raises the interesting question of whether the resulting indicator would in fact continue to resemble *g* in certain respects. Would gF′, defined as fluid cognition independent of *g*, function as something like a pseudo-*g*, accounting for variance in a number of aspects of human functioning much like psychometrically defined general intelligence? That is, could some of the predictive power of the real *g* be due to its close association with fluid function? One source of evidence to examine this possibility might be analysis of patterns of test-score gains between cohorts on measures of intelligence to see whether variation in increases in crystallized scores could be accounted for by non-*g* fluid cognitive gains. It may be that gains on crystallized aspects of cognition are attributable to non-*g*-related gains in fluid function. Alternatively, it may be that all cognitive gains are highly compartmentalized and related to changes in specific aspects of experience. Evidence supporting this latter possibility is provided by studies that offer intensive training on fluid skills. Preliminary findings from two short-term but intensive working memory training studies with young children indicate that the training is associated with fluid cognitive gains as measured by Raven's matrices test (Klingberg et al. 2002) and the matrices section of the Kaufman Brief Intelligence Test (Posner & Rothbart 2004) but not on other aspects of cognition.

An additional or alternative explanation for any relation of non-*g* fluid gains to gains in other aspects of intelligence, should they exist, however, would be that they represent processes related to motivation. Improvements in test scores associated with fluid skills could be indicative of enhanced motivation and engagement in testing situations. The role of motivational factors in cognitive test performance has been acknowledged for some time, particularly with children from low-income backgrounds and children and adults with IQ in the range of mental retardation (Zigler 1999; Zigler et al. 1973). Given evidence outlined early in this review indicating reciprocal relations among prefrontally based fluid cognitive functions and stress and emotion-related processes of the limbic system, it would not be surprising if positive relations between fluid cognition and performance on a variety of cognitive measures were mediated through greater engagement and reduced anxiety in testing situations.

Fluid cognition independent of *g* may be wide ranging in its influence. It may, for example, be relevant to the concept of successful intelligence as defined by Sternberg (1996). Successful intelligence refers to an individual's adaptability and persistence in response to new environments in ways that enable or promote the individual's propensity to demonstrate competence – sometimes very high levels of competence. Measurement of gF′ in the study of successful intelligence could prove informative, as the construct of successful intelligence has face validity but its relation to psychometrically defined intelligence is perhaps unclear. Support for the role of gF′ in the study of human cognitive abilities could also add further empirical weight to Jensen's caution to readers of his 1998 book that *g* should not be seen as an all-encompassing variable; that it is only one among many factors that contribute to what passes for success in life. Evidence reviewed here indicates that gF′ may very well be one of these other factors – one that is important to differentiate from *g*.

Of course, further work on measurement is needed in the delineation of fluid cognition from *g*. Studies measuring IQ in the presence of fluid-skills deficits have approached the problem from either a neuropsychological or psychometric framework, and rarely are the two combined to examine possible dissociations between the two types of measures. Further work using diverse measures with both typically developing and atypically developing populations could help to develop the measurement of gF′. This would be particularly valuable in the study of children for whom diverse aspects of cognition are developing rapidly. For instance, studies employing Raven's matrices test, an age-appropriate Wechsler battery, and a number of EF tasks might provide useful descriptive data on variations in performance. Such an approach would likely be of considerable diagnostic utility in addressing learning and/or behavior problems in children. A theoretically sound multi-measure assessment of this type is referred to as a *cross-battery approach* in the psychometric literature. Here, intelligence researchers, recognizing limits to the diagnostic utility of the general factor and of specific IQ measures, advocate for the use of subtests from diverse measures to explicitly examine variation in patterns of cognitive performance (Flanagan et al. 2000; McGrew 1997). Such a cross-battery approach to the differentiation of fluid functions from general intelligence and other second-order factors such as speed of processing would be valuable in the study of developmental disabilities and for designing innovative curricula and teaching approaches to meet the needs of diverse groups of children. It might also prove valuable in mental retardation research in further refining and defining the adaptive behavior construct. Here, fluid cognitive performance higher or lower than expected from estimates of *g* derived from a Wechsler battery would be expected to be a robust indicator of adaptive functioning.

Multi-measure studies could perhaps reveal something fundamental about fluid-cognition development and its relation to intelligence and behavior. One of the important points of such an approach is that expectations regarding dissociation among different cognitive measures be theoretically grounded and clearly specified a priori. The evidence reviewed in this article provides some conceptual and empirical basis for expected dissociation among aspects of intelligence. However, this does not by any means imply that fluid functions or other second-order factors typically lack *g* variance. On the contrary, the psychometric data clearly indicate that, in typical brains in typical environments, fluid functions may tend to go hand in glove with crystallized and other aspects of intelligence. However, in atypical brains in typical environments

or typical brains in atypical environments, dissociation is not only possible but also perhaps likely.

8. Summary and conclusion

8.1. Fluid cognition as an independent construct

This review has presented evidence indicating fluid cognition to be a distinct neurobiologically grounded aspect of cognitive function, amenable to the effects of experience both cumulatively in terms of life stress/life opportunity and situationally in terms of the reciprocity between emotion and fluid cognition. Furthermore, the review has suggested that environmental stressors acting on PFC and limbic brain structures and functions may contribute to individual differences in fluid cognition and account to some extent for long-standing associations among low general intelligence, psychosocial and socioeconomic adversity, and risk for developmental disorder and psychopathology. As a corollary of this suggestion, the observation has also been made that the enhancement of fluid cognition may be an important aspect of compensatory education programs for young children facing early adversity and that the promotion of fluid cognitive ability through the disruption of stress-related processes by early intervention may prove to be one mechanism through which intervention effects occur. Accordingly, it is recommended that an increased emphasis be placed on normative and individual-differences research in the development of fluid cognition in young children, and the idea is proposed that fluid cognitive ability might account for some of the broad explanatory power of general intelligence. In particular, one of the seemingly unshakeable but continually disputed aspects of research on general intelligence has been the breadth of the construct's reach – the extent to which it has been shown to account for variation in so many aspects of human functioning. However, given evidence for an independent fluid-function construct outlined in this target article, it may be that some of this breadth can be accounted for by fluid cognitive skills. Specifically, the magnitude of positive correlations between measures of human cognitive abilities and life outcomes increases in proportion to the cognitive measures' loadings on *g*. For example, cognitive ability measures with high *g* loadings, such as measures of fluid skills, have higher correlations than do low *g* measures with column vectors extracted from scores measuring such things as performance on learning tasks, performance on elementary cognitive tasks, and nerve conduction velocity – all robust indicators of *g* (Jensen 1998). However, it may be that some of the relation between cognitive measures with high *g* loadings and life outcomes, particularly indicators of learning, job success, and other aspects of real world competence, is attributable to gF′ as much as to *g*. If gF′ were somehow partialled from these analyses, as it is not really *g*, some of the evidence supporting the broad explanatory power of *g* for life outcomes might be reduced, perhaps substantially.

By focusing on fluid cognition in thinking beyond the general factor, one might also question noted racial differences in general intelligence. Differences in mental abilities between blacks and whites increase with the size of the g loadings of various tests, being smaller on measures of crystallized intelligence but more substantial on measures with high *g* loadings such as fluid skills. Here, at the population level, one might ask whether black-white differences have more to do with fluid cognition independent of *g* than with *g* itself and whether evidence regarding the gF′ construct might to some extent support the idea that black-white intelligence differences have more to do with differences in the typical environments in which blacks and whites function in American society than with anything else. As already noted, fluid skills independent of *g* are liable to environmental influence in a number of ways. Identification of gF′ might suggest that the intelligence of black Americans as well as ethnic groups the world over living in circumstances either less advantaged than or simply substantially different from that of the average white American, differs not so much as a function of *g* loadings of given cognitive measures as with a culturally loaded *g*, in which measures purported to be the best measures of general intelligence are those on which some groups may be least likely to do well. Certainly the idea that the intelligence deck is culturally stacked against some groups is not a new one. However, understanding the relation of fluid cognition and brain function to intelligence and to intelligence-test performance helps to illuminate cross-cultural differences in performance with an alternative, neurobiologically based experiential rather than narrowly defined hereditary explanation for that difference.

Furthermore, cultural loading not only in what is being tested, but in the testing process itself, could be informed by the gF′ construct. It is well known that scores from specific cognitive test batteries should not be used to evaluate cognitive ability for individuals whose cultural and experiential background differs substantially from that of normative samples (Flanagan et al. 2000; Greenfield 1997). A more theoretically defensible assessment strategy for cross-cultural comparison, and one in keeping with the relation between fluid cognition and human behavior outlined in this target article, is a dynamic testing approach. In the dynamic approach, the emphasis is on the measurement of learning and test-score change during the assessment process, reflecting the ability of the examinee to incorporate feedback when attempting to complete a given cognitive task successfully. Empirical examination of such an assessment approach has indicated that scores obtained through a dynamic testing procedure are better indicators of school achievement in a rural African sample than are scores obtained from static testing procedures and that measures of fluid cognitive functions correlate positively with test-score increases in response to dynamic testing (Sternberg et al. 2002).

Although more work is needed, if ongoing investigation of gF′ were to provide support for the construct, it is likely that many individuals invested in the study of *g* would welcome the opportunity to remove extraneous variance from its measurement and definition. It is, after all, the goal of factor analysis to get to the distillate of the various measures, factoring out aspects of cognition that are unrelated to *g* itself. However, proponents of the *g*-based understanding of human development and behavior (also described through clever word play as the "*g*-ocentric worldview"), in which general intelligence possesses enormous explanatory power, would likely protest, some vehemently. Some of the explanatory

power of *g* would likely be attributable to gF′. However, while such an end point would perhaps seem a blow to proponents of psychometric *g*, it would really represent a considerable advance for cognitive psychology and developmental neuroscience. Studies demonstrating influences on fluid cognitive functioning that are distinct from *g* provide an important source of information for the study of relations between mental ability and behavior. In particular, developmental neuroscience work on fluid cognition provides a valid neural architecture for clearly defined cognitive functions and processes that would seem to have brought the study of intelligence very, very close to a neurobiologically grounded explanation for individual differences in *g*. Such a unification of psychometric, componential, and neuroscientific approaches to the study of intelligence has for long been desired, and research relating prefrontal corticolimbic circuitry to working memory and to psychometric *g* would seem to have come as close as possible to filling the bill for the identification of a neural basis for general intelligence (e.g., Duncan et al. 2000). In fact, were it not for the dissociation data outlined in this target article, one might really craft a compelling story regarding individual differences in the neurobiology of the prefrontal cortex and general intelligence. However, it would seem that such an explanation would really amount to nothing more than a crafty story and that *g* remains as inscrutable as ever.

Open Peer Commentary

What we need is better theory, not more data

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Abstract: Although I find Blair's case for arguing for the distinction between fluid cognitive functions and general intelligence less than compelling, I believe him. However, I also believe that what is required next is a theory of both general intelligence and fluid cognitive functions that articulates the distinction. In the absence of this, more data, particularly of the neuroscience variety, is likely to stall rather than advance progress.

I was pretty much on board with the first third of Blair's target article. He does a good job of summarizing a body of research that at least opens the possibility that there is a case for dissociating "fluid cognitive functions" from psychometric *g*. However, the case is not overwhelming, and the road that Blair subsequently takes – to argue that the structure of the brain supports the dissociation – if anything, weakens his case. What the article cries out for is the development of a theory that justifies the dissociation. Such a theory would say something like this: Psychometric *g* maps onto cognitive parameters "a, b, c," whereas fluid cognitive functions map onto a different set ("x, y, z"). In the absence of such a theory we are thrown back on the state of the evidence – which is actually rather poor. Let me unpack this a bit.

Nearly all the evidence in favour of a dissociation between psychometric *g* and fluid cognitive functions boils down to their less than perfect correlation. I am prepared to suspend disbelief that the psychometric measures of *g* really measure *g* (as theoretically unhelpful as that is) because there is a hundred years of convention to go by. But what of the measures of fluid cognitive functions? The first problem is that they are psychometrically much more unreliable. It is little wonder that many studies find that fluid cognitive functions are not perfectly correlated with measures of *g*. "Big deal," I hear my psychometrician friends say, "it is just another example of how cognitive/experimental/neuro/developmental psychologists do not know how to develop useful tests – when they get good at it they will find the correlations high enough to support the case that fluid cognitive functions and *g* are indistinguishable." But this brings me to the more fundamental problem. How do we know that they are measures of fluid cognitive functions, in the absence of a theory of what those functions are? For example, what does a Stroop task, in its many instantiations, measure (if you care to, substitute your favourite "frontal" task)? Is it a measure of (a) resistance to interference or (b) task switching, or (c) working memory capacity, or maybe even (d) speed of processing? The unhelpful answer is, very likely, all of them. But even leaving that aside, each of these constructs are themselves nearly always free-floating in current research. The constructs usually amount to nothing much more than the operationalization of performance on some tasks and are the subject of a "theory" that contains but one reference – and that is itself (a theory of speed of processing, a theory of working memory capacity, or whatever). I suspect that few other commentators will address this issue. Like the blind spot on our collective retinae, we have become so used to it that it is noticed only by those who specially look out for it. Rarely are such constructs pitted against each other for their explanatory value, and almost never do they feature in a wider theory of the structure of the mind/brain.

Sensing that the distinction, if it is real, might be important, Blair then takes two steps. One is a look for corroboration in neuroscience data, and the other is to argue for a new set of measurements of this distinctive construct (fluid cognitive functions). This reminds me of the very strategy that Arthur Jensen has used in his advocacy of psychometric *g* itself (see Anderson [2000], Barrett [2000]; and Jensen [2000a; 2000b] for a discussion). Without knowing what it is that we are looking for, we can either make little sense of some arbitrary data (e.g., positive correlations between IQ and gray matter – how exactly does this speak to the dissociation?), or we resort to forgetting what psychometric *g* is supposed to be about. For example, the claim that data from studies of the amygdala, or whatever, show that emotion and stress are important determinants of fluid cognitive functions is relevant only to the dissociation of fluid cognitive functions and psychometric *g* if we are discussing the presumed cognitive overlap – for by definition there is no emotion or stress content to psychometric *g*. Consequently, this line of evidence and reasoning renders the dissociation vacuous. Further, although new measures of a different construct are a necessary step for science, the new measures that Blair wants to develop seem to be alternative predictors of various real-life behaviours. Therein lies fool's gold – psychometric *g* has already cornered the market.

I do believe Blair's central claim (that fluid cognitive functions show some independence of *g*), but I believe this because I have a theory of cognitive functioning that says it is so (see Anderson 2001). Briefly, this theory says that there are two dimensions to *g* – one related to individual differences in IQ and dependent on variation in speed of processing, and the other developmental, related to mental age and dependent on the maturation of modular functions, some of which are intrinsically related to "executive functioning" (see Anderson 2005). So I find myself in general agreement with Blair's manifesto and in wholehearted agreement that evidence from psychopathology, neuropsychology (where the studies are driven by theory-based hypotheses), and in particular the study of atypical