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The Cognitive Differentiation-Integration Effort Hypothesis: A Synthesis Between the Fitness Indicator and Life History Models of Human Intelligence

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This article presents a potential synthesis between the fitness indicator and life history models of human intelligence through consideration of the phenomena of ability differentiation and integration. The cognitive differentiation-integration effort hypothesis proposes that these effects result from a life history tradeoff between cognitive integration effort, a mating effort component associated with strengthening the positive manifold amongst abilities; and cognitive differentiation effort, a somatic effort component associated with the cultivation of specific abilities. This represents one of two largely independent sources of genetic variance in intelligence; the other is mediated by general fitness and mutation load and is associated with individual differences in levels of 'genetic *g*'. These two sources (along with a common source of environmental variance) combine to give rise to a variety of cognitive phenotypes characterized by different combinations of high or low levels of 'genetic *g*' and cognitive specialism or generalism. Fundamental to this model is the assumption that measures of life history speed (*K*) and *g* are essentially independent, which is demonstrated via meta-analysis of 10 studies reporting correlations between the variables ($\rho = .023$, *ns*, $n = 2056$). The implications of the model are discussed in an evolutionary, ecological, and developmental context. Seven key predictions are made in the discussion which if tested could provide definitive evidence for the hypothesis.

Keywords: cognitive differentiation-integration effort hypothesis, fitness indicators, life history, manifold inconstancy

There exist two major evolutionary theories on the origins of individual differences in intelligence, which have thus far traveled on largely separate paths. The first is the fitness indicator theory, which is predicated upon the idea that new deleterious mutations introduced into each generation contribute to a mutation load. These mutations are pleiotropic, meaning that they can affect multiple traits through their influence on developmental stability (the capacity for a phenotype to resist genetic and environmental factors that perturb normal development [Van Valen, 1962]). As a consequence the quality of one trait (e.g. intelligence) can be reflective of the quality of other traits (e.g. fluctuating asymmetry) (G. Miller, 1998, 2000a, 2000b; Prokosch, Yeo, & G. Miller, 2005). These traits can therefore function as fitness indicators and the positive manifold amongst these has been termed the *F* or general fitness factor. This dimension captures individual differences in genetic quality or mutation load, and its existence may increase the efficiency of social and sexual selection (Furlow, Armijo-Prewitt, Gangestad, & Thornhill, 1997; Houle, 2000; G. Miller, 1998, 2000a, 2000b, 2000c).

The second is Rushton's (1985, 2000, 2004) life history differential K theory, which holds that highly stable environments such as those found in more northerly or easterly regions of the globe facilitated the evolution of mechanisms to deal with novel adaptive problems associated with the need to plan ahead and improvise. These mechanisms combine to give rise to a coherent life history strategy characterized by high intelligence, high parental investment, and high covitality (i.e., good mental and physical health, longevity etc.). Conversely, low stability environments (such as those that were more evolutionarily familiar to *H. sapiens*) are thought to have selected for a less differentially K (faster) life history strategy, as humans would have been less able to plan for contingencies; hence they aimed to exceed the carrying capacity to compensate for higher infant mortality. In addition to undergirding population-level differences in intelligence, differential K is also predicted to be at the root of individual differences in intelligence (Rushton, 1985); paradoxically, however, attempts to determine whether *g* correlates with measures of 'differential K-ness' (life history speed) at this scale have failed to yield consistent results, with the majority of published studies reporting no correlations between the two (Bogaert & Rushton, 1989 [female sample]; Gladden, Figueredo, & Jacobs, 2008; Sefcek & Figueredo, 2010). It must be noted that Rushton's theory has proven controversial (e.g., J. L. Anderson, 1991; Brand, 1995a; Flynn, 1989; Graves Jr, 2002; Leslie, 1990; M. Lynn, 1989; Roberts & Gabor, 1990; Silverman, 1990; Weizmann, Wiener, Wiesenthal, & Ziegler, 1990; Zuckerman, 1991; E. Miller, 1993). Moreover alternative

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theories to differential K have also been presented which purport to be able to explain population differences with references to other mechanisms, such as E. Miller's (1994a) paternal investment theory, which holds that warmer climates selected for mating success whereas colder climates selected for paternal provisioning. This has been countered with the observation that the paternal investment and differential K theories are in fact fundamentally similar however (Rushton & Ankney, 1993).

Presented here is a novel evolutionary hypothesis, which aims to integrate the fitness indicator and life history theories through consideration of an often overlooked phenomenon associated with human intelligence, namely Spearman's law of diminishing returns (SLODR) and related effects, which describe the tendency for the positive manifold among test scores to vary in strength as a function of increasing age and ability (Jensen, 1998). The hypothesis is termed the cognitive differentiation-integration effort (CD-IE) hypothesis and is based on the idea that genes and environmental factors regulating life history speed control the degree to which either cognitive differentiation effort (a specialized form of somatic effort) is invested into the development of separate abilities, or cognitive integration effort (a specialized form of mating effort) is invested into strengthening the positive manifold. It is argued that this represents one of two independent sources of genetic variance in intelligence; the other involves factors that give rise to individual differences in general fitness and is associated with individual differences in levels of *g*. These two sources combine to give rise to a variety of cognitive phenotypes characterized by different combinations of high or low levels of *g* and cognitive specialism or generalism, the existence of which has significant implications for the evolution, ecology and development of intelligence.

This article is organized as follows. First, SLODR and related effects (collectively referred to as "manifold inconstancy" effects) are introduced. This is followed by an introduction to life history theory along with a discussion of what is currently known of the relationship between intelligence and components of life history. In this section the results of a meta-analysis involving all known correlations between *g* and *K* (both published and unpublished) will also be presented demonstrating the independence of these variables. The CD-IE hypothesis is then discussed, along with evolutionary and ecological frameworks. In the discussion the merits of the CD-IE hypothesis are evaluated in light of other proposed developmental models of manifold inconstancy. This is presented along with major predictions stemming from the hypothesis.

Manifold Inconstancy Effects

IQ is principally a measure of a dimension of individual differences in cognitive functioning called *g* or general intelligence. This factor arises from the tendency for diverse tests of cognitive ability to correlate with one another giving rise to a positive manifold (Jensen, 1998; Spearman, 1904). The *g* factor sits at the apex of a hierarchy of cognitive abilities with the lower levels containing successively less heritable, more diverse and more domain specific abilities (examples would include the verbal and visuospatial abilities) (Carroll, 1993). Abilities further down the hierarchy also contain larger amounts of non-*g* variance unique to the abilities—what Spearman (1904) referred to as *s*. An interesting observation relating to this is that the *g* factor appears to account for a larger fraction of the ability variance among samples exhibiting lower intelligence (as measured by IQ or mental age), than among samples exhibiting higher intelligence. Jensen (1998) observed that *g* becomes less important in the variety of abilities that individual's posses at high levels of intelligence, as those individuals will tend to exhibit a greater diversity of abilities, with more of the variance existing in non-*g* factors such as the group factors and specializations (i.e., abilities that are lower down in the hierarchy such as verbal or visuospatial ability). This tendency was first observed by Spearman (1927) who posited that it resulted from incremental gains in *g* having diminishing effects across the full range of cognitive abilities. Spearman's law of diminishing returns (SLODR), as it became widely known, also predicts that the correlations between abilities are more equal throughout the full range of *g* earlier in life, before the effects of developmentally induced differentiation. This has led some researchers (e.g., M. Anderson, 1992; Deary et al., 1996) to connect SLODR with the differentiation hypothesis of Garrett (1946), who observed that abstract or symbol intelligence becomes less unified and general and more loosely organized as age increases. Detterman (1991) has argued that diminishing returns cannot explain ability differentiation, as adding constants to either or both members of pairs of observations does not affect the resulting correlation, which means that differences in levels of *g* do not produce differences in correlation strength. SLODR might therefore be an inappropriate descriptor of the effect. In addition to SLODR, there appear to be other similar effects which have also been reported such as integration (the tendency for *g* to strengthen with age or ability) and differentiation followed by dedifferentiation (integration) as a function of age (Balinsky, 1941; Reinert, 1970; McArdle, Ferrer-Caja, Hamagami, & Woodcock, 2002). On the basis of this a new term is proposed to collectively describe SLODR and related phenomena in the form of the manifold inconstancy effect, which describes any tendency toward a change in the strength of the positive manifold.

In total there exists a considerable literature on the ability differentiation effect in particular, comprising numerous independent studies conducted over 75 years, which based on meta-analysis support small differences in *g* saturation across ability groups (with a reported effect magnitude of $r \approx .1$ across an ability span of 1.5-2 SD) (Hartmann & Nyborg, 2004; te Nijenhuis & Hartmann, 2006). Empirically rigorous studies tend to be supportive of the phenomenon (e.g., Brand, Constales, & Kane, 2003; Carlstedt, 2001; Deary et al., 1996; Detterman & Daniel, 1989; Evans, 1999; Jensen, 2003; Legree, Pifer, & Grafton, 1995; Reynolds & Keith, 2007), whereas a few studies in which either sample size, type, or subtests were insufficient have failed to find evidence for the effect (e.g., Arden & Plomin, 2007; Fogarty & Stankov, 1995; Hartmann & Teasdale, 2004, for a full discussion see: Reynolds, 2008). Van der Maas and coworkers (2006) have suggested that manifold inconstancy (specifically differentiation) has not been replicated consistently; however, they note that this is probably truer of age differentiation than ability differentiation. Recent studies by Molenaar, Dolan, Wicherts, & van der Maas (2010) and Reynolds, Keith, and Beretvas (2010) have found that differentiation with respect to ability is robust to the use of diverse psychometric tools such as moderated factor analysis and factor mixture modeling. Taken as a whole the data would appear to indicate that although apparently small in magnitude, differentiation with respect to ability in particular is now a well replicated phenomenon, albeit one currently in need of a coherent explanation (Facon, 2006).

Proposed Explanations for Manifold Inconstancy

Psychologists are divided as to the causes of manifold inconstancy, and a number of potential explanations have been proposed over the decades. Some psychologists have argued that manifold inconstancy is a consequence of biology, with the strength of *g* functioning as a limiting factor preventing ability differentiation in those with low IQ's (M. Anderson, 1992; Brand, Constales, & Kane, 2003; Detterman, 1987; Detterman, 1993; Detterman, 1994). Others have suggested that manifold inconstancy results from a testing artifact associated with small sample sizes or inadequacies in the capacity for certain cognitive ability tests to sufficiently challenge those with the highest IQ's, which results in measured *g* saturation appearing to diminish (Carlstedt, 2001; Curtis, 1949; Detterman, 1993; Fogarty & Stankov, 1995). Environmental causes have also been hypothesized, such as the idea that increased levels of education facilitate changes in ability structure (Abad, Colom, Juan-Espinoza, & García, 2003; Anastasi, 1970; Colom, Abad, García, & Juan-Espinosa, 2002; Ferguson, 1954). The "mutualism model" purports to be able to account for both integration and differentiation through the idea that mutualistic reinforcement between distinct cognitive processes leads to an initial strengthening of the positive manifold (integration) early on in development, which then undergoes a change in complexity as a result of specific patterns of interactions being reinforced at the expense of others (differentiation) as a function of aging (van der Maas et al., 2006). Another theory is the investment model of intelligence (Cattell, 1957), which is based on the idea that the development of specific abilities associated with crystallized intelligence results from the investment of fluid intelligence into the acquisition of domain-specific knowledge. Ability differentiation may also be driven by personality as trait complexes (i.e., abilities and predispositions) give rise to interests, which coalesce around patterns of reinforcement, directing the allocation of cognitive effort (Ackerman, 1996; Ackerman & Beier, 2003; Hunt, 2005, see also: Bouchard Jr, 1997).

The fitness indicator theory presents a potential evolutionary explanation for the effect, where it has been hypothesized that deleterious pleiotropic mutations (small genetic changes which result in large phenotypic effects) are not only characteristic of low IQ, but are also characteristic of the positive manifold strength which defines the *g* factor in low IQ samples. These mutations might uniformly increase the strength and number of genetic correlations between initially unrelated abilities by harming them in parallel (Arden, Gottfredson, G. Miller, & Pierce, 2009; G. Miller, 2000a, 2000b; Prokosch, Yeo, & G. Miller, 2005). G. Miller (2000b) has further argued that ability differentiation might represent a fitness advertisement indicating specialization with respect to different preferred types of mental fitness displays.

Intelligence and Life History

Life History: An Overview

Life history is a midlevel evolutionary theory, which explains the selective tradeoffs associated with the ways in which limited bioenergetic and material resources (effort) are allocated for survival and reproduction by organisms. Originally developed in the ecological literature as a means of comparing species, life history theory uses a continuum characterized by K-strategist species at one end, whose populations exist at or near the carrying capacity (K) of their environments, and r-strategist species at the other, whose populations frequently exceed the carrying capacity through high reproductive rates (r) (MacArthur & Wilson, 1967). K-strategists allocate bioenergetic resources to somatic effort (organismal survival, maintenance, and development) in preference to reproductive effort (the generation of new organisms). Furthermore, K-strategists are specialized in terms of how they allocate reproductive effort, as they preferentially invest in ensuring offspring survival (parental effort) and ensuring the survival of kin (nepotistic effort) over obtaining mates (mating effort). This is in contrast with r-strategists, which invest preferentially in mating effort.

Figure 1 illustrates the hierarchy of tradeoffs that characterize life history. r-strategist species tend to be behaviorally and structurally simple, which permits them to boost their organismal fitness by producing larger numbers of more rapidly maturing young, requiring less care. This short termist reproductive strategy evolved to cope with unstable and unpredictable environments, where exceeding the carrying capacity buffers against high infant mortality. K-strategists, on the other hand, are more behaviorally and structurally complex and will tend to boost their genetic fitness through the production of smaller numbers of more slowly maturing young and through the formation of cooperative and inclusive fitness boosting social arrangements. This strategy evolved in the context of a stable and predictable ecology, where long term investments would have paid-off. (Figueredo, Vásquez, Brumbach, & Schneider, 2007; MacArthur & Wilson, 1967; Pianka, 1970).

A number of studies have investigated the patterning of life history traits within a variety of taxa including *H. sapiens*. Although *H. sapiens* exhibits a generally slower life history than many other mammalian taxa, some individuals and populations appear to have faster life histories than others (Rushton, 1985, 2000, 2004). This is associated with the existence of both heritable and environmental intraspecific individual differences in life history speed (Figueredo, Vásquez, Brumbach, & Schneider, 2004; Rowe, 2000). Indicators of individual differences in life history speed, such as measures of adult attachment to romantic partners, parental attachment to and investments from father figures, Machiavellianism, attitudes towards risk and mating effort have all been found to exhibit a common variance stemming from a unifying factor termed the *K*-factor (Figueredo, Vásquez, Brumbach, Sefcek, Kirsner, & Jacobs, 2005). Similarly indicators of an organism's phenotypic quality combine to give rise to a covitality factor (Rushton, 1985, 2000; Thornhill & Palmer, 2004), which is an indicator of general health (Weiss, King, & Enns, 2002) and is considered to be largely analogous to the general fitness factor (Sefcek & Figeredo, 2010). Another significant life history component is the general factor of personality (GFP), which exists in

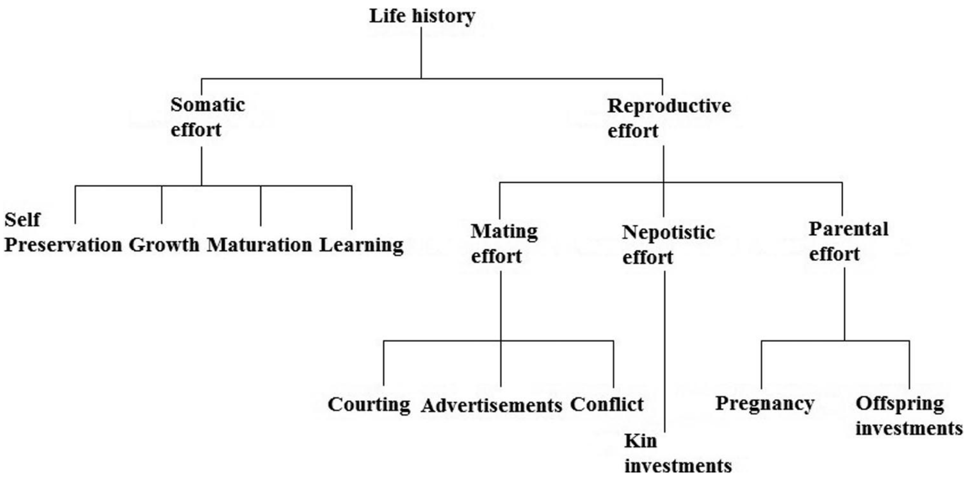

Figure 1. Hierarchical model of life history illustrating the relationships between the major and minor tradeoff domains.

the intercorrelations between various personality factors (Rushton, Bons, & Hur, 2008) and may function as a life history speed signaling mechanism (Vásquez, 2004). It must be noted, however, that this construct is considered controversial (see: Just, 2011). The superordination of these three factors gives rise to another, more fundamental life history factor termed *Super-K*. This single, unifying life history dimension has been shown to capture the majority of the variance in the lower order factors, and has been interpreted as evidence that higher levels of physical and mental health are predictive of high levels of somatic and parental effort (Figueredo, Vásquez, Brumbach, & Schneider, 2007).

The Relationship Between Life History and Intelligence: A Meta-Analysis

Intelligence is predicted to be a significant life history variable for *H. sapiens*, in addition to its evolutionary antecedents (e.g., *Homo erectus*), phylogenetic neighbors (e.g., chimpanzees) and other animal taxa (Kaplan, Hill, Lancaster, & Hurtado, 2000; J. Lee, 2007; Rushton, 1985, 2000, 2004). Cross-taxa associations between factors such as encephalization quotient and life history indicators such as longevity and maturation speed seem supportive of the prediction that higher *g* is generally linked with slow life history speed (Rushton, 2004), as are ecological scale studies aimed at identifying latent life history superfactors in the cross-cultural data (Templer, 2008). Furthermore, there is evidence of correlations between *g* and apparent covitality indicators, such as fluctuating asymmetry (Banks, Batchelor, & McDaniel, 2010) and medical symptoms such as cardiovascular disease and cancer proneness (Batty, Deary, & Gottfredson, 2007; Deary & Der, 2005; Gottfredson & Deary, 2004; Hart et al., 2005; Johnson, Deary, McGue, & Christensen, 2009; Kuh, Richards, Hardy, Butterworth, & Wadsworth, 2004; Martin & Kubzansky, 2005; van Oort, van Lenthe, Mackenbach, 2005). Modest magnitude but significant correlations between *g* and the GFP have also recently been reported (Schermer & Vernon, 2010). There is every indication therefore that *g* and direct measures of life history speed should correlate at individual differences scales, as was predicted by Rushton (1985). Thus far, attempts at determining whether this is the case have produced inconsistent results, however. The study of Gladden and coworkers (2008), for example, found that *g* only correlated .03 (disattenuated $r = .05$ – in both cases nonsignificant) with the *K*-factor; similarly, the study of Sefcek and Figeredo (2010) found that *g* correlated $-.09$ (*ns*) with *K*. Thus far only two published studies (Bogaert & Rushton, 1989; Rushton, Vernon, & Bons, 2007) have reported significant correlations between *g* and *K*-factors. In the case of the former study an (uncertainty corrected) correlation of $r = .29$ was found between a *K*-factor (constructed from 16 different measures of life history) and *g* among the male sample; among the female sample *g* and *K* were found not to correlate ($r = -.05$). In the latter study a significant correlation of $r = .23$ was found between *g* and *K* among a demographically diverse sample of 182 individuals (although among a larger sample of 239, the correlation was weakened but still significant). Presented in Table 1 are the results of a basic meta-analysis involving all known correlations between measures of *g* and *K*. In a number of cases the correlations have not been published but have instead been presented at various scientific conferences. Help was provided in tracking down these correlations by the Figueredo lab at the University of Arizona. Wherever possible the most sophisticated measure of *K* was used in preference to simpler ones. For example, a study reporting the results of the Arizona Life History Battery (Sefcek, 2007) was used in preference to a study using the same sample, but a less comprehensive measure of *K* (the Mini-*K*) (Sefcek & Figueredo, 2010).

Based on Table 1, it appears that *g* and *K* cannot be made to correlate consistently. The population correlation (ρ) is of very low magnitude (.023) and is nonsignificant. Furthermore, the correlations exhibit significantly high heterogeneity ($\chi^2 = 37.26$; $p < .01$).

Given this finding, why then do there exist much stronger and much more consistent cross-taxa, cross-cultural, and bivariate associations between apparent indicators of *g* and life history speed? At cross-taxa scales, the principal cognitive corollary of life history speed is encephalization quotient, which is an indirect endophenotypic measure of *g* in taxa where the factor might be a

Table 1

A Meta-Analysis Involving 12 Correlations Between Measures of g and K Reported in 10 Different Studies

R	*n*	*p*	Author(s)	IQ test used	Measure of *K* used
.29	116 (Male)	<.05	Bogaert & Rushton (1989)	WAIS	LHQ
−.05	100 (Female)	ns	Bogaert & Rushton (1989)	WAIS	LHQ
−.06	193	ns	MacDonald, Vásquez, & Figueredo (2006)	APM18	Mini-K
−.14	143	ns	Wenner, Figueredo, Rushton, & Jacobs (2007)	SILS	ALHB
−.18	110	ns	Figueredo, MacDonald, Wenner, & Howrigan (2007)	WPT	Mini-K
−.01	211	ns	MacDonald, Figueredo, & Wenner (2007)	SILS	ALHB
.18	239	<.05	Rushton, Vernon, & Bons (2007)	MAB	Mini-K
.19	239	<.05	Ruston, Vernon, & Bons (2007)	WPT	Mini-K
−.06	194	ns	Sefcek (2007)	APM18	ALHB
.05	192	ns	Gladden, Figueredo, & Jacobs (2008)	APM18	ALHB
.06	121	ns	Ross & Figueredo (2009)	SILS	ALHB
−.12	198	ns	Brown, Ross, Figueredo, Young, & G. Miller (2010)	APM18	TRIFECTA
$\rho = .023$	Total $n = 2056$	$p_{\text{(Non-directional)}}$ ns			

Note. ALHB = Arizona Life History Battery; APM-18 = An 18-item short form of the Raven's Advanced Progressive Matrices; LHQ = Life History Questionnaire; MAB = Multidimensional Aptitude Battery; Mini-K = A 20-item short form measure of life history speed; SILS = Shipley Institute of Living Scale; TRIFECTA = A common factor of the Mini-K, HKSS, and SF-36 scales; WAIS = Wechsler Adult Intelligence Scale; WPT = Wonderlic Personnel Test (now Wonderlic Cognitive Ability Test).

component of their cognition. Brain size is by no means a perfect correlate of *g* within human populations (the population correlation is .33 [McDaniel, 2005]), which suggests that measurement error might to some extent account for it's apparent association with life history (Sefcek & Figueredo, 2010). The coefficient of additive genetic variance for brain size is also low, suggesting that (unlike *g*) the trait has been under strong recent stabilizing selection. This additionally reduces the appropriateness of using brain size as an evolutionary genetic proxy for *g* (G. Miller & Penke, 2007). Furthermore, inter-specific comparisons are not a sound basis for inferring individual differences within a species, as life history traits can be organized very differently at different scales. A good example of this is body size, which is positively associated with higher-K traits (such as greater brain weight) between taxa, but is negatively correlated with slow life history between individuals within a species as it is associated with larger litters and higher reproductive rates (Altmann & Alberts, 2003; Sefcek & Figueredo, 2010). At cross-cultural scales, it has been theorized that environmental factors simultaneously affecting a population's life history speed and *g* may create environmentally mediated extrinsic correlations between the variables where there are no true intrinsic genetic correlations between them (Figueredo, 2009). In considering the existence of bivariate correlations between *g* and apparent covitality indicators it is necessary to note the fact that *g* and *K* are higher order constructs comprised of diverse intercorrelated variables, therefore their failure to correlate constitutes more definitive evidence of their true association than do bivariate associations between supposed single indicators of life history and *g* (Sefcek & Figueredo, 2010). Furthermore, it is unclear what fraction of the variance in these correlations might be attributable to individual differences in general fitness (*F*) independent of *K*. While *F* and *K* have been found to modestly positively correlate (Sefcek & Figueredo, 2010), there is still much variance that is unique to each trait complex, suggesting the operation of different sources of genetic variance. This is further reinforced by the observation that traits related to general fitness such as mental health, physical health, and physical attractiveness have exclusively positive effects on fitness, suggesting that variance in *F* is maintained by mutation selection balance (which results from the fact that large numbers of deleterious mutations with small effects on a trait will persist in a population for long periods of time) rather than frequency dependent or balancing selection, where the variance in a trait is maintained as a result of different manifestations of the trait having variable effects on fitness in different environments, such as is likely the case for life history related traits, such as personality factors (Penke, Denissen, & G. Miller, 2007a, 2007b; Penke, 2010). Whilst the literature on the relationship between *g* and *K* is generally unremarkable, there exist tantalizing indications that general fitness might mediate the relationship between *g* and fitness indicators (Arden, Gottfredson, & G. Miller, 2009; Arden, Gottfredson, G. Miller, & Pierce, 2009; Prokosch et al., 2005; Silventoinen, Posthuma, van Beijsterveldt, Bartels, & Boomsma, 2006; Sundet, Tambs, Harris, Magnus, & Torjussen, 2005; Yeo, Gangestad, Liu, Calhoun, & Hutchison, 2011). Covitality is likely therefore a broad factor, which encompasses elements relevant to both general fitness (i.e., mutation load) and life history (i.e., maintenance effort). The distinction between potential sources of genetic variance unique to *F* and *K* is an important potential component of any fully evolutionarily informed model of intelligence, as will be demonstrated in the subsequent section.

A Two-Source Model of Genetic Variance in Intelligence

As was discussed in the previous section, indicators of genetic quality may be largely separate (share little genetic correlation) from indicators of life history speed. As a consequence, these may give rise to two largely independent and distinct sources of genetic variation in intelligence characterized by different selective dynamics. These sources may be labeled as G1 and G2, respectively. G1 includes pleiotropic mutation load and is associated with individual differences in levels of 'genetic *g*' identifiable via a Jensen effect on the heritability of *g* (Rushton & Jensen, 2010). Jensen effects are associated with the tendency for the vector of a test's *g*-loadings to function as the best predictor of the vector of any other given variable (such as test heritabilities) (Jensen, 1998; Rushton, 1998). It must be noted however that the Jensen effect is controversial (see: Ashton & K. Lee, 2005). "Genetic *g*" corresponds to basic properties of the brain such as neural plasticity—individual differences in the capacity to adapt neural connections to differential environmental demands (Garlick, 2002) and information processing or neural efficiency (Chiang et al., 2009; Eysenck, 1994a; Haier, 1993; Jensen, 1998; E. Miller, 1994b; Vernon, 1992). "Genetic *g*" is therefore associated with what could be termed "vertical variance" in intelligence, that is, individual differences in the levels of plasticity coupled with neural and processing efficiency.

As was demonstrated in the meta-analysis, *g* and *K* are effectively independent. Despite this the possibility exists that individual differences in life history speed might be associated with manifold inconstancy effects—this being the G2 source. Evidence for this comes from three main sources:

i) It has been observed that slower life history populations such as Ashkenazi Jews (MacDonald, 1994) and East Asians (Rushton, 2000) exhibit less evenly balanced abilities (in terms of verbal vs. visuospatial) than relatively faster life history populations, such as non-Jewish Caucasians (Cochran, Hardy, & Harpending, 2006; MacDonald, 1994; R. Lynn, 1987, 1990, 2004; Vernon, 1990).

ii) Studies have shown that while Neuroticism and *g* negatively correlate only very weakly in meta-analysis ($r = -.15$, $p < .05$) (Ackerman & Heggestad, 1997), with the distinct possibility that this is an artifact of test anxiety (Hembree, 1988; Zeider, 1998), high levels of Neuroticism nonetheless appear to be associated in some studies with a significantly stronger *g*-factor than low levels (Austin, Deary & Gibson, 1997; Austin, Hoffer, Deary & Eber, 2000; Austin et al., 2002; Brand, 1995b; Eysenck, 1994b; Eysenck & White, 1964). Neuroticism exhibits a consistently stronger negative correlation with the *K*-factor ($r = -.24$, $p < .01$) (Figueredo, Vásquez, Brumbach, Sefcek, Kirsner, & Jacobs, 2005), suggesting that slower life history (lower Neuroticism) is associated with a weaker *g* than faster life history (higher Neuroticism).

iii) Autistic-like personality appears to be associated with both slower life history and uneven ability profiles with a distinct bias toward visuospatial ability (Del Giudice, Angeleri, Brizio, & Elena, 2010). Furthermore, aspects of autistic-like personality in children are known to predict the development of specialized talents (Happé & Vital, 2009).

These lines of evidence converge to suggest that the change in the variance proportion between *g* and the non-*g* variance unique to abilities might be a life history tradeoff, associated with two hypothetical forms of effort. These could be termed cognitive differentiation effort and cognitive integration effort, respectively. The former represents the fraction of resources invested into the development of specialized domains of cognition (i.e., abilities) rather than into the more cognitively generalized positive manifold and is associated with ability differentiation, whereas the latter represents the inverse of the former and is associated with ability integration. This G2 source might therefore include life history-related polymorphisms maintained via frequency dependent or balancing selection (this will be further elaborated upon in the subsequent section) at a number of loci, which essentially function as developmental "switches" setting the balance between positive manifold strength and abilities. It has been argued that for frequency dependent selection to have shaped a coordinating hierarchical life history construct such as *K*, it would have to have favored the evolution of a highly asymmetric genetic architecture characterized by the presence of only a handful of 'major effects' polymorphisms. The absence of evidence for these has been used to argue against the plausibility of the *K*-factor (Penke, Denissen, & G. Miller, 2007a, 2007b). This can be countered with the observation that *K* could still arise from the interplay of multiple neural and physiological systems which will buffer against any one gene coming to dominate the phenotype (Bürger, 2002a, 2002b; Kopp & Hermisson, 2006), thus multiple polymorphisms of moderate effect size associated with a variety of loci and maintained by frequency dependent selection constitute a plausible genetic basis for the existence of *K* and dependent traits (Figueredo & Gladden, 2007). This source therefore controls what could be termed "horizontal variance" in intelligence, that is, individual differences in the composition of the trait as reflected in the evenness versus the unevenness of ability profiles. It must be noted that the two-source model has been anticipated to an extent by Penke (2010), who suggested that while frequency dependent (balancing) selection cannot account for individual differences in the level of *g*, it may be a viable mechanism for maintaining genetic variance in lower order abilities once *g* has been controlled for.

Finally, there also exists a source of environmental variation, which could be labeled E. This would include factors that disturb developmental stability such as infections and poor nutrition, which might also simultaneously affect life history speed thus shifting the balance between manifold strength and specialized abilities.

The two-source model can be represented hierarchically (see Figure 2). Integration effort and differentiation effort are here conceptualized as components of mating effort and somatic effort respectively. Levels of 'genetic *g*' are here connected with general fitness and are associated with neuro-developmental stability (Sefcek & Figueredo, 2010).

Figure 3 indicates that distinctions can be drawn between a typology of four primary alternate cognitive phenotypes (labelled 'α' through to 'δ') which can emerge from combinations of integration effort and differentiation effort with either low or high levels of 'genetic *g*'.[1] These are the high-IQ cognitive generalist or 'α' phenotype, which emerges from high levels of 'genetic *g*' coupled with large investments of integration effort into manifold strength congruent with fast life history speed. The high-IQ cognitive specialist or 'β' phenotype, which emerges from high levels of 'genetic *g*' coupled with large investments of differentiation effort into abilities. The low-IQ cognitive generalist or 'γ' phenotype, among which manifold strength results from integration effort investment coupled with the handicapping effects of pleiotropic mutations on the development of 'genetic *g*'. This phenotype will be associated with 'obligate generalism,' which would reflect in low developmental stability and a fast life history. The

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[1] It is important to note that no attempt is being made here to establish a hierarchy amongst cognitive phenotypes-greek letters are commonly used in science to differentiate between phenomena such as in the case of classifying types of radiation.

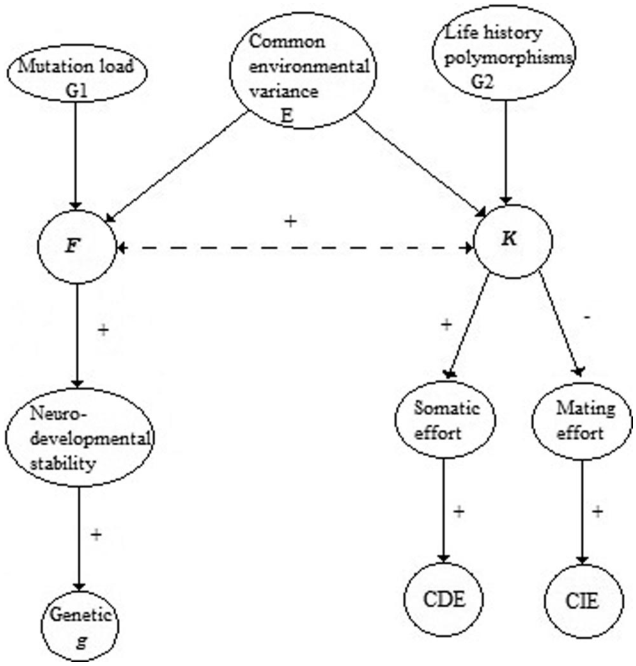

Figure 2. A hierarchical representation of the CD-IE hypothesis. G1 (mutation load) and G2 (life history polymorphisms) represent sources of genetic variance in intelligence unique to general fitness (*F*) and life history (*K*), respectively. *E* represents sources of environmental variance that may be common to both pathways. Neuro-developmental stability mediates the relationship between *F* and individual differences in levels of 'genetic *g*,' whereas somatic effort and mating effort mediate the effects of *K* on differentiation effort (CDE) and integration effort (CIE), respectively. + indicates a positive relationship between variables, − indicates a negative relationship.

low-IQ cognitive specialist or 'δ' phenotype, which is associated with developmental abnormalities of a sort that prevent the normal establishment of general intelligence. In this instance the compensatory overdevelopment of specific narrow abilities via constrained investments of differentiation effort may occur. The result would be a phenotype, which would tend to possess an overall low level of *g* but would exhibit high levels of competence with respect to one or more very narrow abilities. This profile might be associated with "obligate specialism" reflected in an overall slow life history speed. Examples of the 'δ' phenotype might be found in the case of those with savant syndrome, about half of whom are also autistic (Treffert, 2009). Such "obligate specialist" cognitive phenotypes would be expected to be relative rare however owing to the possibility that low general fitness might attenuate life expectancy such that the development of a short termist condition-dependent reproductive strategy may be more likely to raise fitness than a long termist one (but see also Gangestad & Simpson, 2000). It is worth noting that on average people will be intermediary of these four phenotypes, as they will possess intermediary levels of 'genetic *g*' and will be neither excessively differentiated nor integrated in terms of ability structure.

An interesting implication of the two-source model is that as a life history effect, manifold inconstancy should be relatively independent of levels of *g*. This suggests that differentiation with respect to abilities may largely be an artifact simply reflecting the greater diversity of cognitive phenotypes ('α', 'β' and "intermediary") among those with high levels of 'genetic *g*,' relative to those with low levels (primarily 'γ'). This may account for the apparent weakness of the effect in meta-analysis (Hartmann & Nyborg, 2004; te Nijenhuis & Hartmann, 2006), and also for the fact that Jensen (2003) found that *g*-loadings were more variable (not uniformly low) among those with high ability when compared with those of low ability. Furthermore the possibility that high-*g* individuals are to be found throughout the full range of *K* relative to those with low-*g* (predominantly low-*K*), may be associated with small differences in the *g*-means between those with fast and slow life histories, thus giving rise to a positive but *extrinsically mediated* correlation between *g* and *K* which should be visible in a sufficiently large sample derestricted for range in the variables. This could account for the finding of weak but significant positive correlations between *g* and *K* in the study of Rushton, Vernon, and Bons (2007), as these researchers used a fairly large and demographically representative sample.

Evolutionary and Ecological Implications of the CD-IE Tradeoff

A potentially important component of human life history is ecological generalism versus specialism, which is essentially a measure of niche breadth. Within insects for example it is known that generalist r-strategist species tend to occupy broad niches in that they utilize a wide array of resource gradients. Specialist *K*-selected species on the other hand tend to occupy narrower niches (Matthews & Matthews, 1978; Matthews & Kitching, 1984). The generalism–specialism continuum as a component of the human life history matrix may therefore provide the evolutionary ecological basis for the CD-IE tradeoff.

Two environmental risk dimensions that are believed to be important for the evolution and development of life history strategy are unpredictability and harshness. The former is associated with factors that impose a high variance in adult mortality, whereas the latter is associated with factors that impose high absolute adult mortality (such factors would include pathogen outbreaks, famines and droughts). High levels of harshness and unpredictability facilitate the development of fast life history speed, where individuals attempt to overshoot the carrying capacity through the production of large numbers of offspring as a means of buffering against high infant mortality. Low levels of harshness and unpredictability or conversely high levels of predictable harshness facilitate the development of slow life history speed, as ecological stability affords individuals the ability to mature more slowly and to consolidate resources into fewer offspring (Ellis, Figueredo, Brumbach, & Schlomer, 2009).

Cognitive generalism and specialism translate into ecological generalism and specialism within human populations, as cognitive generalists can occupy much broader sociocultural niches than cognitive specialists. Early in human evolution, being able to occupy a broad sociocultural niche would have been a good means of buffering against harshness and unpredictability, as the integration of basic cognitive processes would have conferred the ability to acquire skill sets that could be transferred across ecological domains, therefore permitting ancestral humans to effectively cope with domain general problems containing large situational com-

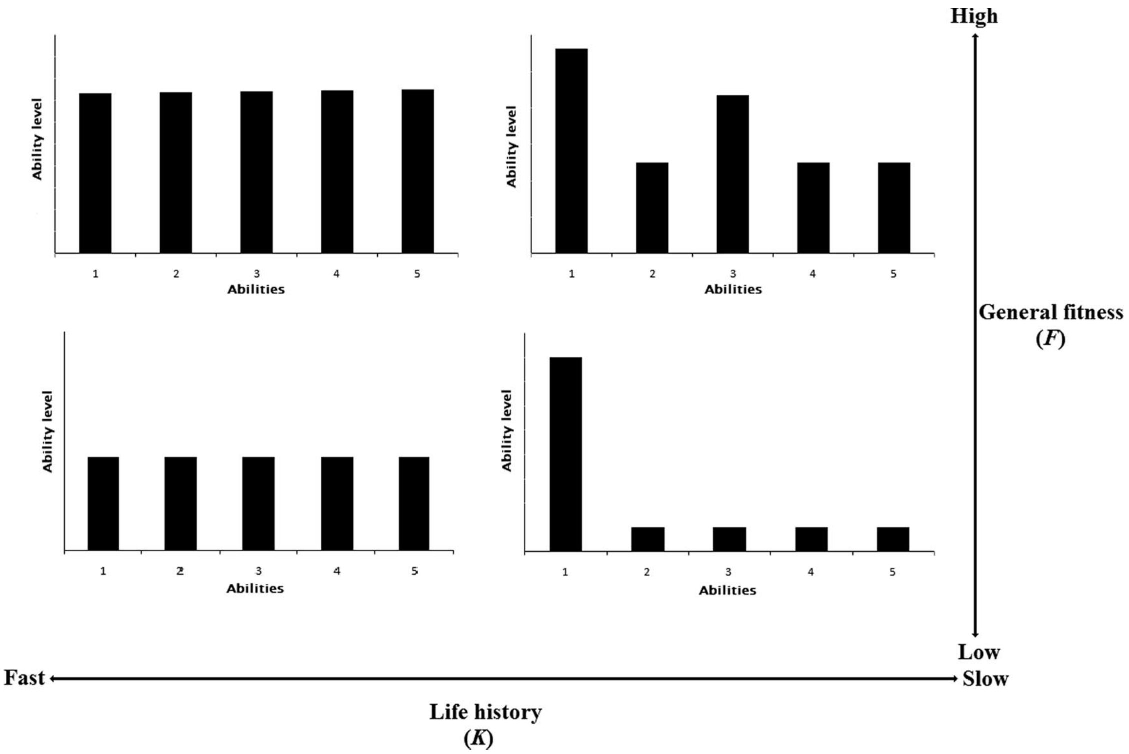

Figure 3. Hypothetical ability profiles (ability level vs. ability type numbered one through five) for four principal cognitive phenotypes, which emerge from different combinations of general fitness (vertical axis) and life history speed (horizontal axis). 'α' top left, 'β' top right, 'γ' bottom left, 'δ' bottom right.

ponents (Geary, 2005). This advantage would have persisted into historical times also as a farmer who can retrain as a soldier or a laborer is far more robust against unpredictability and harshness, such as crop failure, than a farmer who is capable of little other than farming, for example.

An even ability profile might not be such an asset in the context of a stable ecology, however, as faster life history generalists would find themselves in competition with one another. This may have been the case among ancestral human populations living through particularly ecologically stable periods. The advantage of the CD-IE tradeoff therefore results from the fact that it would have allowed for 'cognitive polymorphism' (i.e., the emergence of different combinations of abilities) among those possessing slower life histories. Individuals thus endowed would have had the capacity to diversify into and exploit specialized and narrow sociocultural niches. This would have led to multilevel selection, where frequency dependent selection operates at the individual level to favor those possessing uneven ability profiles as they would have experienced competitive release, which would compensate for the cost of deviation away from species-typical norms (i.e., the even ability profile). Individual differences in personality traits may be maintained in this manner, as it has been suggested that the existence of these permit a diversification of social and sexual strategies, which in turn reduces the intensity of competition (Rushton, 1985; Figueredo, et al., 2011; Figueredo, Sefcek, Vásquez, Brumbach, King, & Jacobs, 2005; MacDonald, 1995; Nettle, 2001; Penke, Denissen, & G. Miller, 2007a, 2007b). Furthermore, the existence of divisions of cognitive labor within a population might result in group selection based on higher aggregate economic efficiency through factors such as gains from trade (G. Miller, pers. comm).

For much of human evolution cognitive and ecological generalism would have been the favored strategy owing to the influence of sources of harshness and unpredictability, however expansion into more northerly and easterly latitudes might have reduced the influence of these factors on human mortality (pathogen prevalence, e.g., is negative correlated with latitude [Eppig, Fincher, & Thornhill, 2010]). Rushton (2000) has argued that this ecological stability was key to the evolution of population level differences in average life history speed. Another significant point made by Cochran and Harpending (2009) is that civilization has had an accelerating effect on human evolution, enhancing traits such as intelligence over the last 10000 years through the provision and creation of new sociocultural niches bought about through innovations such as agriculture and through changes in social dynamics. A potentially important and overlooked factor driving this acceleration might be associated with the fact that new sociocultural niches would have provided opportunities for those possessing slow life history speed and uneven ability profiles, which in turn might have potentiated group selection for gains in aggregate efficiency associated with enhanced divisions of labor.

Life history strategy has a heritability of around .65 (Figueredo, Vásquez, Brumbach, & Schneider, 2004), which suggest significant plasticity to environmental factors. Modernity is associated with the mitigation of many sources of harshness and unpredictability such as disease, drought, and famine, which were a problem in some parts of the developed world up until fairly recently and are still significant problems in much of the developing world. One possibility is that in industrialized nations where these factors have been eliminated and where life history speed has historically been slowing (as evidenced by diminishing family size and declining fertility), divisions of labor continued to increase as a consequence of the emergence of increasing numbers of individuals possessing the potential to develop specialized and uneven ability profiles. Perhaps this is the driving force behind the Flynn effect, which appears to be associated with both a weakening of the strength of Spearman's *g* and differential gains in the non-*g* variance unique to abilities (Juan-Espinosa, Cuevas, Escorial, & García, 2006; R. Lynn & Cooper, 1993, 1994; Kane, 2000; Kane & Oakland, 2000; for a fuller exposition of this hypothesis see Woodley, in press).

As balancing selection currently favors a heterogeneity of life history phenotypes amongst those with above average levels of 'genetic *g*' in modern societies, the tendency towards either cognitive generalism or specialism is likely a significant and overlooked determinant of occupational preferences amongst this demographic. Connell, Sheridan and Gardner (2003; see also Gardner, 2006) have investigated the implications of the cognitive generalism/specialism divide in ability profiles for occupations and have proposed two broad categories of problems that undergird different occupational demands. These are modular tasks and integrative situations. The former encompasses targeted assignments that draw on specific abilities, whereas the latter encompasses complex sets of problems requiring the orchestration of various abilities. These researchers further suggest that those who are differentiated with respect to specific abilities tend to be attracted to and excel in what they term targeted task areas, such as political speechwriting or mechanical engineering, whereas those with strong integrative capacities stemming from a more even ability profile are more likely to be attracted to and to excel in areas requiring what they term situational competencies, such as being a CEO or a politician. An implication of this is that occupations containing a large modular task component might be more attractive to those with slow life histories, whereas occupations containing a large integrative situational component may be more attractive to those with somewhat faster life histories. This is not to say that CEO's and politicians have especially fast life history speeds, it is simply suggested that they might have faster life histories than academics and those capable of 'deep specialization.' Those with the very fastest life histories are likely to be found in the arts and creative writing domains such as poetry, where moderate psychoticism (Simonton, 2009) and possibly also high integrative complexity—the capacity to coherently combine diverse elements into a complex interconnected schema (which would seem to necessitate a strong manifold) may be characteristic of creativity. Studies have shown that artists tend to appear during times of social instability, whereas scientists tend to appear during times of stability (Simonton, 1975, 1997, 2009), strongly evidencing a life history connection. As high-*g* creativity is clearly manifested at both extremes of the life history spectrum, frequency-dependent selection for creativity and its societal benefits (Simonton, 1999) would therefore explain the absence of any kind of extrinsic correlation between *g* and *K* amongst those with above average *g*, as those with both fast and slow life histories may assortatively mate for high-*g* creativity. This is especially important given the fact that spatio-temporally heterogeneous environments varying in terms of their relative stability and instability, may be somewhat less variable in terms of the presence of certain 'evolutionarily novel' problems (Sefcek & Figueredo, 2010). The absence of an extrinsic correlation may therefore have permitted the creative solving of these problems irrespective of the levels of environmental stability.

It must also be noted that integrative situational demands are likely not restricted to high-*g* professions. Returning to the example of the premodern farmer, a requirement for integrative situational competency is likely characteristic of many low-*g* professions also, where during periods of ecological and social instability limited skills can essentially be transferred from one occupation to another. This makes sense given the likely dominance of the fast life history 'γ' cognitive phenotype among low-*g* professions.

Differentiation Effort and Integration Effort as Somatic and Mating Effort, Respectively

An issue that has yet to be comprehensively addressed concerns the exact nature of differentiation effort and integration effort. As they are associated with opposing life history strategies, differentiation effort may constitute a form of somatic effort whereas integration effort may constitute a form of mating effort. The process of cognitive specialization is associated with the cultivation of lower order abilities containing large amounts of non-*g* variance. Lower order abilities possess lower heritabilities than the highest order factor – *g* (Carroll, 1993), therefore the cultivation of abilities may involve the allocation of time as a primary resource. Slow life history is likely therefore associated with a strong proclivity toward learning. This is certainly true of those with autistic-like personalities, who are characterized by both very slow life histories and a strong drive to acquire knowledge, often in highly specific and technical domains (Del Giudice, Angeleri, Brizio, & Elena, 2010; Happé & Vital, 2009). The capacity to allocate time as a resource therefore constitutes a form of somatic effort, as it would be associated with competition avoidance (i.e., the development of sociocultural specialization), slower maturity, and the desire to learn. Time allocation is therefore a "luxury" that is contingent upon ecological stability, as individuals would be unable to afford to allocate this resource in the context of an unpredictable environment. Other resources that could be allocated to the cultivation of specific abilities include calories, which would be needed to run distinct cortical networks and cortical real estate (i.e., gray matter), which could be allocated to the implementation of specific abilities (G. Miller, pers. comm). Although the focus here has been on somatic effort, it must be noted that parental effort could also conceivably play a role in both directing and reinforcing the allocation of effort into the development of cognitive abilities amongst offspring.

Integration effort, on the other hand, is not nearly as significantly associated with time allocation, as those with fast life histories mature much more rapidly and so would be unable to afford to allocate such a resource to an extent greater than that needed to acquire a very general set of competencies. This is evidenced by the fact that eminent individuals exhibiting fast life history creativity (i.e., creative writers and artists) are much more likely *not* to have undergone long periods of formal education relative to those exhibiting slow life history creativity (i.e., scientists) (Raskin, 1936; Simonton, 1986, 2009). Where those high on integration effort might differ from those high on differentiation effort is in the existence of a developmental preference constraining calorie, cognitive real estate, and even time investments such that they occur globally throughout the cortical networks and brain regions undergirding intelligence. This creates either a uniformly efficient or inefficient intelligence depending on the disruptive effects downstream of pleiotropic mutations on factors such as neural plasticity and processing efficiency.

One environment in which having high situational competency might be significantly advantageous is the short-term mating market. An example of a situation in the short-term mating market might be male–male competition over a prospective female mate. Using Connell, Sheridan, and Gardner's (2003) schema, responding appropriately to this situation might require the identification of the relevance of the situation, followed by a determination of which cognitive tasks need to be carried out in order to achieve the goal (in this instance the acquisition of a short-term mate might be contingent upon using/detecting deception, choosing an appropriate fitness display, assessing the competition, etc.), which in turn would be followed by integration of the separate tasks resulting in the creation of a coordinated response to the situation, that is, the development of a context appropriate "courtship display" for acquiring the desired short term mates. Integration effort investments may therefore constitute a form of mating effort, as in addition to conferring an ability to better cope with ecological instability, short-term mating goals may also be facilitated through situational competence. A case could also be made for short-term mating markets being ecologically unstable, as they will be dominated by "here and now" oriented individuals who have developed an unpredictability schema characterized by "a pervasive belief that people are unpredictable and the world is chaotic" (Ross & Hill, 2002, p. 458). This schema in turn orients individuals toward risk-taking behaviors such as early sexual activity, risky sexual behavior, and adolescent pregnancy and childbirth (Ellis, Figueredo, Brumbach, & Schlomer, 2009; Ross & Hill, 2002).

Situational competence, while a necessary criterion for the acquisition of short-term mates, is not in and of itself sufficient for success in a short-term mating market however, as success will be very much contingent upon general fitness (Gangestad & Simpson, 2000). Sexual selection will therefore principally operate on the quality of specific indicators of 'genetic *g*' and other fitness indicators that individuals can chose to deploy as part of a coordinated strategy. 'α' type high-IQ cognitive generalists might therefore opt into situational competence demanding professions on the basis that they permit the effective advertisement of diverse mental fitness indicators. Stand-up comedy might constitute an example of such a profession, where situational demands require the exhibition of *g*-loaded (and therefore fitness indicating) cognitive abilities such as vocabulary size, abstract reasoning, fast reaction times, and working memory. It also requires a keen sense of humor, which is an indicator of both intelligence and general fitness (Greengross & G. Miller, 2011; Kaufman, Kozbelt, Bromley, & G. Miller, 2007; Howrigan & MacDonald, 2008; G. Miller, 2000c). Artists and creative writers might use their medium of creativity to exhibit similar fitness indicators (Miller, 2001), albeit ones deployed in a manner consistent with the idiosyncratic situational demands of these fast life history professions. The capacity to formulate and to coordinate an appropriate courtship display in an unstable ecological context (i.e., one in which situational demands are high) may therefore form an important and overlooked component of fast life history manifestations of mating intelligence—the combination and coordination of both cognitive and noncognitive psychological mechanisms for the purposes of acquiring mates (Geher & Kaufman, 2011). It is important to finally note that under the current regime of mutation selection balance for *g*, variability in the trait might also aid in the sexual selection of more 'generally fit' long term mates amongst those with with slow life histories.

Discussion

The CD-IE Hypothesis Versus Other Theories of the Manifold Inconstancy Effect

A variety of proximate level (nonevolutionary) theories have been posited to explain the manifold inconstancy effect, some of which were briefly discussed in an earlier section. The CD-IE hypothesis is effectively an investment model of intelligence, similar to that first proposed by Cattell (1957). It incorporates some of the same conceptual elements, such as the idea that "cognitive effort" can be differentially invested into the cultivation of specific abilities. Furthermore it is likely that interests, personality (as a component of life history) and abilities combine to drive differentiation effort investment, perhaps in a manner akin to that described by the four-factor PPIK (intelligence-as-Process, Personality, Interests and intelligence-as-Knowledge) model of Ackerman (1996), and Ackerman & Beier, (2003), which extends Cattell's investment model by positing a role for personality and interest domains in the acquisition of crystallized knowledge. A discussion of the possible intersections between the CD-IE and PPIK models will not be attempted here, however it is worth noting that future investigation into the relationship between the PPIK trait complexes (social, science/math and intellectual/cultural), manifold inconstancy and life history may be fruitful.

Where the CD-IE hypothesis differs markedly from proximate investment models is in its incorporation of a model of ability integration. Proximate investment models have been curiously silent on this process, which must be characteristic of the development of situational competencies and cognitive generalism (Connell, Sheridan, & Gardner, 2003; Gardner, 2006). An even ability profile must therefore be the result of factors that constrain the cultivation of specific abilities and instead ensure that effort is globally distributed throughout the cortical networks and brain regions undergirding intelligence.

Another key difference concerns the use of life history theory, which gives the CD-IE hypothesis ultimate (evolutionary) rather than simply proximate explanatory power. The manifold inconstancy effect has been largely ignored by those studying the evolution of human intelligence and/or *g*, possibly because of the apparent weakness of the effect across studies, the presence of "contradictory" findings (e.g., differentiation vs. integration vs. null results etc.), or the belief that the effect results from methodological constraints such as measurement error and therefore doesn't constitute a genuine phenomenon. One exception to this is the fitness indicator theory, which attributes ability differentiation to the cultivation of preferred mental fitness displays (G. Miller, 2000b). The CD-IE hypothesis suggests that the cultivation of abilities is primarily a slow life history response to competition, which permits the carrying capacity of an environment to be raised via divisions of labor. It is associated with somatic effort investments of time, calories, and cognitive real estate into specific cortical networks and brain regions over a longer than average period of development. Mental fitness displays are characteristic of cognitive generalists whose heightened situational competence gives them the ability to cope with unstable environments and to select and mobilize an array of fitness indicators to aid in acquiring short term mates. The capacity to specialize in a creative role (i.e., to develop a unique mental fitness display) is therefore not necessarily the same thing as having a specialized ability profile.

A proximate model in need of more detailed discussion is the mutualism or reciprocal causation model proposed by van der Maas and coworkers (2006). This model posits the existence of a positive manifold, resulting purely from positive beneficial interactions between cognitive processes during development. It basically rejects the need for an independent common source of variance stemming from the *g* factor. As was mentioned in an earlier section, the mutualism model attempts to account for the manifold inconstancy effect through the idea that early in life, mutualistic reinforcement between distinct cognitive processes generates the positive manifold (integration), which then changes in complexity with age as a result of the reinforcement of specific patterns of interactions (differentiation). The existence of a Jensen effect on the heritability of *g* would appear to render the mutualism model implausible, however, as this indicates that *g* constitutes a real genetic and developmental entity rather than simply being a purely statistical phenomenon (Rushton & Jensen, 2010). Van der Maas and coworkers (2006) concede that the Jensen effect requires the assumption of some baseline level of initial intercorrelation between distinct cognitive processes, which does somewhat undermine the fundamental premise of their model. The CD-IE hypothesis presents an alternative model of the development of intelligence. The positive manifold among children possessing high levels of 'genetic *g*' may initially be present, due to a combination of baseline interconnectivity and low mutation load, but is weaker than is commonly assumed. Instead of mutualism, it is proposed that the strength of the initial manifold varies as a function of the operation of G2 and E (developmental cues), based on the investment of integration effort into strengthening the positive manifold congruent with fast life history (i.e., the development of an 'α' type cognitive phenotype), or conversely through the investment of differentiation effort into abilities and cognitive specialism congruent with slow life history (i.e., the development of a 'β' type cognitive phenotype).

Among children possessing low levels of *g*, the initial manifold strength is predicted to be higher owing to the effects of larger numbers of pleiotropic mutations and environmental stressors (i.e., the G1 and E sources), which operate by encouraging faster life history, and therefore the allocation of integration effort into manifold strength such that a strong but inefficient manifold will emerge, hence the tendency of the 'γ' type cognitive phenotype toward "obligate" cognitive generalism. Among this demographic, manifold strength will tend to be invariant throughout the life span, whereas among "obligate" cognitive specialists like savants (i.e., those with the 'δ' type cognitive phenotype), the manifold would weaken fairly early in development as developmental constraints would result in significant compensatory differentiation effort investments into the cultivation of a specific narrow ability (such as long term memory).

The CD-IE hypothesis can also account for another manifold inconstancy phenomenon, namely the age related differentiation followed by dedifferentiation effect, which has been observed in several studies (Balinsky, 1941; Reinert, 1970; McArdle, Ferrer-Caja, Hamagami, & Woodcock, 2002). It is predicted that this effect manifests itself among those with slow life histories, who initially invest differentiation effort into abilities (hence an initial phase of differentiation is observed); however, as they age, damage to the brain (stemming from both environmental and organic sources) increases the manifold strength by reducing overdeveloped abilities while simultaneously lowering overall levels of *g*. An important implication of the CD-IE hypothesis is the idea that the suite of effects reported in studies examining manifold inconstancy by age and ability (differentiation, integration, and differentiation-dedifferentiation) are all plausible effects associated with individual differences in general fitness and life history speed. Future researchers studying manifold inconstancy would therefore do well to consider the potential interplay of these variables when convening samples or interpreting data.

Major Predictions

Seven novel testable predictions result from the CD-IE hypothesis, these are grouped on the basis of the nature of the studies required to test them.

Individual Differences

i) The overall *g*-loadedness of tasks would be expected to vary in samples possessing similar levels of IQ but pronounced individual differences in life history speed. Those with slow life history speeds would be predicted to exhibit more differentiated abilities coupled with lower *g* variance than those with fast life history speeds.

This should be detectable using both direct measures of life history speed (*K*) and proxies such as personality. Interestingly, studies investigating manifold inconstancy as a function of levels of the Big Five or Eysenck's Big Three personality factors have only found evidence of an effect from Neuroticism (Austin, Deary & Gibson, 1997; Austin, Hoffer, Deary & Eber, 2000; Austin et al., 2002; Brand, 1995b; Eysenck, 1994b; Eysenck & White, 1964), with some studies failing to replicate this (Bonaccio & Reeve, 2006; Escorial, García, Cuevas & Juan-Espinoza, 2006). There are two possibilities which should inform future investigations. Firstly, it may be the case that intellectual investment traits existing in the personality space around intelligence and outside of conventional personality taxonomies, such as Typical Intellectual Engagement (Ackerman & Goff, 1994) and Need for Cognition (Cacioppo & Petty, 1982) regulate manifold inconstancy (von Stumm, Chamorro-Premuzic & Ackerman, 2011). This would be consistent with the idea that time allocation and a desire to learn are somatic effort components. In this instance it is predicted that these constructs should strongly positively correlate with *K* in addition to predicting cognitive differentiation vs, integration. A second possibility is that higher order personality constructs that share more variance with life history (such as the GFP) might better capture the CD-IE tradeoff. This could be tested via the reanalysis of datasets in which manifold inconstancy has been investigated as a function of the levels of diverse personality traits (e.g., Austin et al., 2002; Escorial, García, Cuevas & Juan-Espinoza, 2006).

ii) It is predicted that amongst large and demographically representative samples derestricted for range in measures of intelligence and life history speed, the observation that those with above average g are more likely to be found throughout the full range of K than those with below average g, should give rise to an extrinsically mediated, low-magnitude correlation (around .2) between the *g* and *K*. Therefore in addition to there being small differences in the IQ means between the fast and slow life history groups, favoring the latter, the fast life history group should also exhibit a larger variance in IQ scores relative to the slow life history group.

Group Differences

Sex differences should exist in the level of manifold inconstancy owing to the sex difference in the variance of life-history speed. Women have a slower average life history speed than men (Del Giudice, 2009; Geary, 2002), however they also have a lower variance in life history (Del Giudice, Angeleri, Brizio, & Elena, 2010). As the proliferation of professions and specialized cognitive niches during social evolution has been a primarily male phenomenon until very recently, manifold inconstancy effects (both differentiation and integration) should be considerably stronger in males; this should hold even controlling for sex differences in IQ (e.g., by excluding extremely high male scores outside the female range). Consistent with this prediction is the study of Escorial and coworkers (2008), who found no evidence of ability differentiation among their female sample.

Longitudinal Studies

i) It is predicted that the ability differentiation–dedifferentiation effect is associated with slow life history. Studies examining the effect have produced mixed results (e.g., Balinsky, 1941; Tucker-Drob, 2009). One possibility is that the samples comprise both fast and slow life history individuals. Characteristic of the cognitive development of fast life history individuals would be ability integration and the development of an even ability profile, therefore despite a predicted decline in the level of *g* later in life, there will be no dedifferentiation with age. Controlling for the effects of life history speed in longitudinal samples should therefore permit the effect to be consistently identified.

ii) It is predicted that low mutation load would be associated with an initially weaker 'genetic *g*,' which among those with high IQs could be strengthened or weakened based on either integration effort or differentiation effort investments. Among those with a higher mutation load and fast life histories, manifold strength would be higher earlier in life. This suggests that childhood IQ should be more heritable (it will be more predictive of adult IQ) at the low ability end than at the high end. While there is some evidence for this prediction, it must be noted that studies in which the heritability of *g* has been investigated as a function of level of ability are contradictory in their findings (Bailey & Revelle, 1991; Cherny, Cardon, Fulker, & SeFries, 1992; Detterman, Thompson, & Plomin, 1990; Jensen, 1997), therefore more research is needed.

Neurology

It is predicted that the presence of extensive white matter tracts is a characteristic of the brains of both 'β' type high-*g* specialists and 'α' type generalists (more white matter implies a better connected, more efficient and more plastic cortex—i.e., higher *g*), where those high on differentiation effort might differ from those high on integration effort is in the degree to which gray matter (cognitive real estate) is allocated disproportionately to specific brain regions associated with abilities, which makes sense of Johnson, Jung, Colom, and Haier's (2008) finding of a tradeoff associated with the overdevelopment of brain regions associated with rotation-verbal abilities relative to the underdevelopment of brain regions associated with focus-diffusion abilities, which consistent with the CD-IE hypothesis, occurs independently of the level of *g*. Integration effort might instead be associated with the homogenization of gray matter allocation, such that diverse brain regions can develop equally, and cognitive integration can occur.

Twin Studies

As life history speed is independent of individual differences in the levels of *g*, heritable intelligence should show no genetic correlations with heritable life history indicators, such as *K* or the GFP when analyzed in a cross-twin cross-trait multivariate genetic analysis.

Conclusions

The CD-IE hypothesis represents a potential synthesis between the fitness indicator and life history models of human intelligence, which, as was noted in the introduction, appear to have traveled largely separate paths until now. Needless to say the hypothesis is likely to prove controversial on a number of fronts. The results of the meta-analysis presented here strongly affirm the intrinsic independence of *K* and *g*, which stands in direct contrast to the predictions of the differential K theory (Rushton, 1985, 2000, 2004). This finding should not come as a surprise, however, given the fact that balancing selection, while a plausible mechanism for maintaining variance in life history traits (such as personality factors) *and* abilities is not capable of maintaining variance in *g*, which like other components of general fitness is likely to result from mutation selection balance (Penke, Denissen, & G. Miller, 2007a, 2007b; Penke, 2010). As has been discussed elsewhere, there appear to be a variety of evolutionary advantages to the decoupling of *g* and *K* amongst those with above average *g*, such as the idea that 'creative' solutions to evolutionarily novel problems can manifest irrespective of the levels of environmental stability, and also the idea that as a fitness indicator, individual differences in *g* can function to guide mate choice in both the short term (fast life history) and long term (slow life history) mating markets. There may however exist small positive extrinsically mediated correlations between *g* and *K* amongst large samples derestricted for range in these variables.

The idea that there are two largely distinct sources of genetic variance in intelligence and that ability integration and differentiation are associated with a life history tradeoff therefore provides a fertile theoretical framework within which the potential contributions of both general fitness and life history to intelligence can be reconciled. A related issue concerns the current state of life history theory, which is predicated upon the idea that the general fitness factor and covitality are essentially isomorphic, and that general fitness constitutes part of life history (Sefcek & Figueredo, 2010). Once again general fitness is unlikely to be a part of life history as indicators of general fitness (such as *g*) are maintained via mutation selection balance rather than through frequency dependent selection, as is likely the case for life history traits. It is possible that the correlation between the two is extrinsically mediated. As individuals with low general fitness may be more likely to exhibit conditionally-dependent fast as opposed to slow life history speed, whereas a diversity of life history phenotypes are likely to exist amongst those with high general fitness. This has significant implications for future research into covitality, as care must be taken to disentangle the influences of fitness-relevant components on factors such as longevity from life history-relevant ones.

Another point that will undoubtedly prove controversial is the idea that manifold inconstancy effects are primarily dependent upon life history speed rather than on ability level or age. The last couple of decades has seen the rise of a “cottage industry” in studies examining manifold inconstancy, yet the most comprehensively studied of these effects (ability differentiation) appears to be only very weak (Hartmann & Nyborg, 2004; te Nijenhuis & Hartmann, 2006). Furthermore, there appear to be strange regularities associated with the effect such as the observation that *g*-loadings are more variable among high-IQ subjects and that the effect diminishes on tests with high *g*-loadings (Jensen, 2003). The CD-IE hypothesis makes sense of these observations through the observation that any test which strongly taps ‘genetic *g*’ is going to be primarily measuring individual differences in neural processing efficiency and plasticity, which is likely to swamp the effects of differences in ability structure on test scores (Johnson, Jung, Colom, & Haier, 2008). The heterogeneity of *g*-loadings among those with higher *g* is likely the result of the greater diversity of cognitive phenotypes among this demographic relative to those with lower *g*.

Testing the predictions of this hypothesis could allow these controversies to be effectively addressed and resolved. This in turn may give rise to fundamentally novel insights into the nature of human intelligence and may finally permit human intelligence to be properly situated in an evolutionary and ecological context.

In terms of general directions for future research, the two-source model of genetic variance developed here may shed light on a fascinating yet critically understudied issue in personality psychology, namely the observation that personality appears to differentiate as a function of increasing *g* in a manner somewhat analogous to the ability differentiation effect (Austin, Deary, & Gibson, 1997; Austin et al., 2002; Austin, Hofer, Deary, & Eber, 2000; Brand, Egan, & Deary, 1994; Harris, Vernon, & Jang, 2005; Harris, Steinmayr, & Amelang, 2006). Unlike *g*, the GFP is known to strongly correlate with *K* (Figueredo, Vásquez, Brumbach, & Schneider, 2007); an interesting implication of this phenomenon, assuming that it is not an artifact (Mõttus, 2006), is that mutation selection balance might regulate individual differences in the diversity of personality traits (perhaps having a more multifaceted or “deeper” personality functions as an honest signal of neurodevelopmental stability), while the “level” of GFP, as a life history trait, is maintained by balancing selection. Congruent with this preliminary hypothesis, individual differences in levels of GFP do not appear to be associated with measures of fluctuating asymmetry (Hope et al., 2011); however, contrary to the premise of this hypothesis is the finding that the GFP exhibits a modest correlation with *g* (Schermer & Vernon, 2010), although this finding has not been replicated in all studies (e.g., Rushton et al., 2009). One possible reason for this correlation is that measures of Openness to Experience are not “pure” measures of the Openness domain, and are in fact contaminated with measures of *g* (captured by Intellect) (Brand, 1994; DeYoung, Shamosh, Green, Braver, & Gray, 2009; Nusbaum & Silvia, in press). This might account for why Openness to Experience frequently exhibits the lowest GFP loading of the Big Five (e.g., Barrick & Mount, 1991). Controlling for measures of *g* in Openness to Experience might therefore result in the creation of GFPs that are purer measures of life history and do not correlate with *g*. The diversification of personality implies a more general diversification of life history also, with those higher on general fitness possibly being able to manifest more polymorphic life history strategies (both at the fast and slow poles) than those with low general fitness, who may be restricted instead to “obligate” manifestations of fast or slow life history.

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