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Abstract

To further knowledge concerning the nature and nurture of intelligence, we scrutinized how heritability coefficients vary across specific cognitive abilities both theoretically and empirically. Data from 23 twin studies (combined $N = 7,852$) showed that (a) in adult samples, culture-loaded subtests tend to demonstrate greater heritability coefficients than do culture-reduced subtests; and (b) in samples of both adults and children, a subtest's proportion of variance shared with general intelligence is a function of its cultural load. These findings require an explanation because they do not follow from mainstream theories of intelligence. The findings are consistent with our hypothesis that heritability coefficients differ across cognitive abilities as a result of differences in the contribution of genotype-environment covariance. The counterintuitive finding that the most heritable abilities are the most culture-dependent abilities sheds a new light on the long-standing nature-nurture debate of intelligence.

Keywords

intelligence, behavior genetics, cognitive ability, environmental effects, individual differences

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Whether intelligence depends more on nature or on nurture is a long-standing issue dating back to 17th-century rationalism and empiricism and with roots in the ancient Greek philosophies of Plato and Aristotle (Fancher, 1996). With the emergence of psychometrics and behavioral genetics in the 20th century, it became possible to address this issue empirically—in terms of individual differences—through the decomposition of variance in psychometric intelligence into genetic and environmental variance components (Plomin, DeFries, McClearn, & McGuffin, 2008). At first sight, the results seem to favor nature: In samples of adults, on average, the genetic variance components account for up to 80% of the variance in full-scale IQ and general intelligence (Plomin et al., 2008). However, the results on which this average is based were often derived under assumptions that may not have been met. For example, in behavior-genetic models of intelligence, genotype and environment are commonly assumed to be independent and, hence, do

not covary, whereas genotype-environment covariance is presumably present and might account for as much as 30% of the variance in adult IQ (Johnson, Penke, & Spinath, 2011).

Our aim in the present research was to further knowledge concerning the nature and nurture of intelligence by scrutinizing how heritability coefficients vary across specific cognitive abilities, both theoretically and empirically. We evaluated the implications of the empirical findings for theories of intelligence, notably, the mainstream *g* theory (Jensen, 1998; Spearman, 1927) and fluid-crystallized theory (Cattell, 1971).

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How Do Heritability Coefficients Differ Across Cognitive Abilities?

Theory

In both *g* theory and fluid-crystallized theory, intelligence is conceptualized as a major, largely genetically fixed source of individual differences in IQ (referred to as *g*, for general intelligence, in *g* theory; as *Gf*, for fluid intelligence, in fluid-crystallized theory; and henceforth in this article, as *g*). On the basis of these theories, cognitive abilities and IQ subtests are often categorized as fluid or crystallized. IQ subtests are further viewed as being—to varying degrees—culture reduced or culture loaded (Jensen, 2012).

Fluid abilities are assessed by subtests that minimize the role of individual differences in prior knowledge (henceforth, *fluid tests*), and crystallized abilities by subtests that maximize it (henceforth, *crystallized tests*). Individual differences in fluid-test scores thus reflect primarily the sources of individual differences in on-the-spot cognitive processing (e.g., reasoning or memorizing), whereas individual differences in crystallized-test scores reflect primarily the sources of individual differences in previously acquired knowledge and skills. Because knowledge and individual and group differences in knowledge are strongly culturally influenced, crystallized tests require relatively many adjustments to adapt them from one language or culture to the next (Georgas, van de Vijver, Weiss, & Saklofske, 2003). In this sense, crystallized tests are typically more culture loaded than are fluid tests.

From both *g* theory and fluid-crystallized theory, it follows that heritability coefficients differ across specific cognitive abilities and IQ subtests. In *g* theory, this can be deduced from the following assumptions (Jensen, 1987, 1998). First, individual differences in IQ scores reflect the sources of individual differences in cognitive processing, either directly (in fluid tests) or indirectly (in crystallized tests). Second, among these sources, *g* is the most heritable source. Third, individual differences in IQ-subtest scores reflect individual differences in *g* to different degrees: The more complex an IQ test is (i.e., the more cognitively demanding solving its items is), the more individual differences in subtest scores reflect the relative contribution of *g*. From this it follows that, compared with noncomplex fluid tests (e.g., forward digit-span tests), complex fluid tests (e.g., abstract-reasoning tests) have relatively strong relations to *g*, as indicated by their *g* loadings, and thus display relatively high heritability coefficients.

The level of cognitive demand required to solve the items of crystallized tests is considered to be relatively low (Jensen, 2012). Hence, to account for the substantial

g loadings of crystallized tests, theorists must invoke one or more additional assumptions. In this regard, it is common for *g* theorists (Jensen, 1998) to adapt the *investment hypothesis*, as formulated in fluid-crystallized theory (Cattell, 1971), from which it also follows that heritability coefficients differ across abilities and subtests.

The investment hypothesis holds that the acquisition of knowledge depends strongly on cognitive processing, such that individual differences in acquired knowledge largely reflect fluid abilities and, thus, the underlying sources of individual differences therein, notably, *g*. Ultimately, individual differences in crystallized abilities and crystallized-test scores largely reflect the same genetic and environmental variables as individual differences in fluid abilities. However, given that additional (non-*g*) influences (e.g., education) play a role during the acquisition of knowledge, the investment hypothesis holds that in the general population, the heritability coefficients of crystallized abilities will be lower than those of fluid abilities (Cattell, 1971). Yet if the variance in the additional influences is small—for example, in culturally homogenous samples—the heritability coefficients of crystallized abilities are expected to approach the heritability coefficients of fluid abilities (Jensen, 1998).

In the absence of other hypotheses and, hence, on the basis of the subtest-complexity and investment hypotheses alone, heritability coefficients of crystallized abilities are expected not to exceed those of fluid abilities (see the left panel of Fig. 1). Whether empirical findings (e.g., Pedersen, Plomin, Nesselrode, & McClearn, 1992) support this expectation has been questioned (e.g., Horn, 1985; Mackintosh, 1998), but to date, definite results are scarce. Moreover, the consideration of the role of genotype-environment covariance (e.g., Scarr & McCartney, 1983) in the development of intelligence may call for a revision of this expectation, as we outline next.

Heritabilities of IQ and *g* increase gradually over the course of the life span (Haworth et al., 2010). This phenomenon has been attributed to a gradual increase in active genotype-environment covariance (Haworth et al., 2010; Johnson et al., 2011), which is thought to arise because people with relatively high levels of cognitive ability increasingly actively seek out and, therefore, are exposed to cognitively stimulating environments (Dickens & Flynn, 2001; Haworth et al., 2010; Johnson et al., 2011; Scarr & McCartney, 1983).

The relative contribution of genotype-environment covariance may differ across abilities. If stimulating environments foster societally valued knowledge and skills more than cognitive processing per se, we expect, on the basis of computer simulations with dynamical models (Dickens, 2008; van der Maas et al., 2006), that (a) individual differences in culture-loaded tests should be relatively strongly related to *g* and (b) heritability estimates of

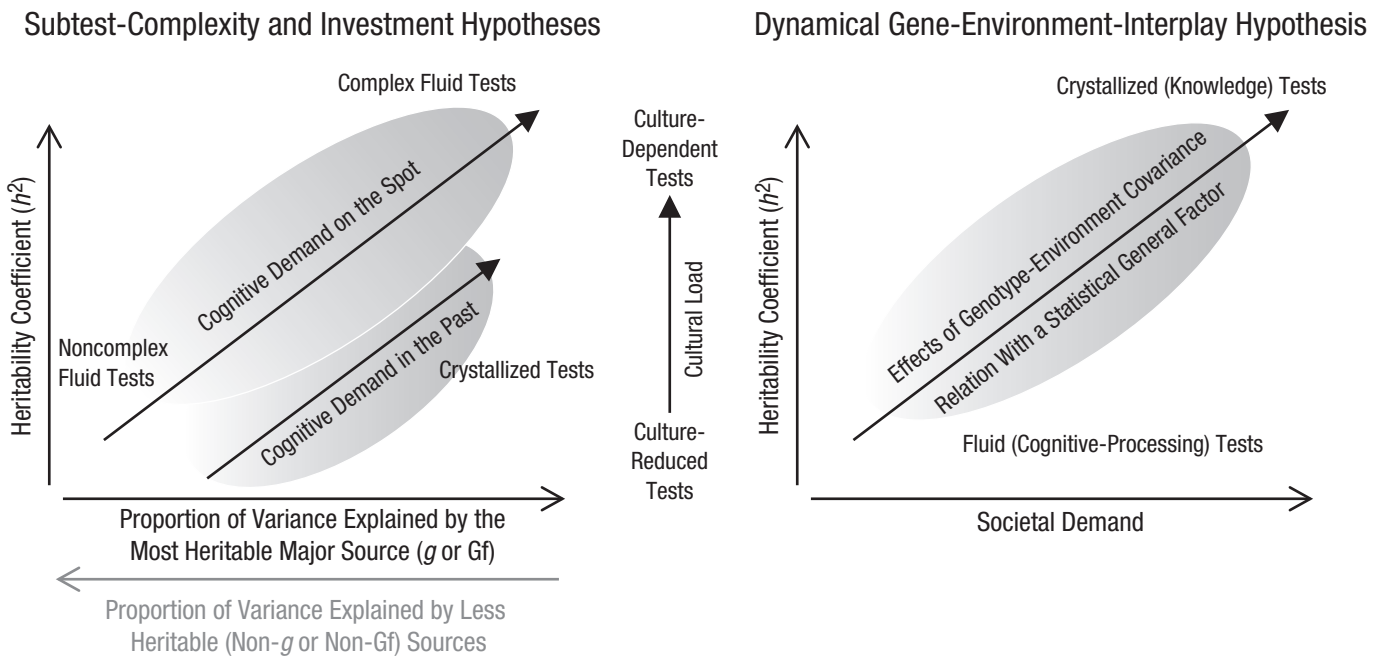


Fig. 1. Schematic illustration of the subtest-complexity and investment hypotheses from mainstream theories of intelligence, which predict that heritability coefficients of culture-loaded crystallized abilities do not exceed those of culture-reduced fluid abilities (left panel), and our dynamical gene-environment-interplay hypothesis, which predicts relatively high heritability coefficients of culture-loaded crystallized tests (right panel). g = general intelligence; G_f = fluid intelligence.

culture-loaded knowledge tests should be affected relatively strongly by genotype-environment covariance, which should ultimately result in the heritability coefficients of culture-loaded knowledge tests exceeding those of tests that measure cognitive-processing abilities (see right panel of Fig. 1).

The way in which heritability coefficients empirically vary across specific cognitive abilities can be used to evaluate the explanatory power of theories of intelligence (e.g., Rushton & Jensen, 2010). Toward this end, we performed a meta-analysis of relevant empirical findings from 23 independent twin studies conducted with representative samples (combined $N = 7,852$).

Empirical Data

Method. We first gathered data from previous research on the relation between subtest g loadings and subtest heritability coefficients in the Wechsler scales of intelligence (Jensen, 1987, 1998; Rijdsdijk, Vernon, & Boomsma, 2002). Next, we conducted a comprehensive search to locate all studies that involved the Wechsler Intelligence Scale for Children (WISC), the Wechsler Adult Intelligence Scale (WAIS), or revisions of either one that provided sufficient information to obtain heritability coefficients on IQ-subtest level.

From WISC and WAIS manuals (Wechsler, 1949, 1955, 1974, 1981, 1991, 1992, 1997, 2002, 2005), we obtained subtest loadings on the first principal component (see Tables S1 and S2 in the Supplemental Material available online). The subtest reliability coefficients are provided in Tables S3 and S4 in the Supplemental Material. The squared loadings served as approximations of the subtests' proportions of variance shared with general intelligence. Cultural load was operationalized as the average proportion of items that were adjusted in each subtest of the WAIS-III when the scale was adapted for use in 13 countries (Georgas et al., 2003). Because the Wechsler Verbal IQ (VIQ) and Performance IQ (PIQ) subscales mapped well on cultural load (see Table 1), we also searched for all WISC and WAIS studies that reported heritability coefficients of VIQ and PIQ.

In the analyses, we assumed that tests were independently and randomly sampled from a population of tests to which the associations generalize. Because this assumption may be incorrect, inferences may pertain to the Wechsler scales only. Other limitations concerning the analyses are addressed in the Conclusion and Discussion sections.

Analysis 1. Our first analysis involved six WISC (Jacobs et al., 2001; LaBuda, DeFries, & Fulker, 1987; Luo, Petrill,

Table 1. Cultural Load of the Wechsler Intelligence Test Subtests on the Verbal IQ (VIQ) and Performance IQ (PIQ) Subscales

Subtest	Cultural load (percentage of adapted items)	Scale
Vocabulary	35	VIQ
Information	22	VIQ
Comprehension	15	VIQ
Similarities	9	VIQ
Arithmetic	8	VIQ
Picture Completion	3	PIQ
Picture Arrangement	2	PIQ
Block Design	1	PIQ
Coding	0	PIQ
Digit Span	0	VIQ
Object Assembly	0	PIQ

Note: Subtest cultural load was obtained from Georgas, van de Vijver, Weiss, and Saklofske (2003, Table 18.1), except for the Coding subtest cultural load, which was obtained from F. J. R. van de Vijver (personal communication, November 30, 2011).

& Thompson, 1994; Owen & Sines, 1970; Segal, 1985; Williams, 1975) and four WAIS studies (Block, 1965; Friedman et al., 2008; Rijdsdijk, et al., 2002; Tambs, Sundet, & Magnus, 1984) from which we obtained subtest-level heritability coefficients (see Tables S5 and S6 in the Supplemental Material). Figure 2 presents these coefficients and each subtest's proportion of variance shared with general intelligence, ranked according to the subtests' cultural load. Proportion of variance was clearly a function of cultural load: The greater the cultural load, the greater the squared loading on the first principal component. In the WAIS results, the subtest heritability coefficient also appeared to be a function of cultural load: The greater the cultural load, the greater the heritability coefficient. This relation did not appear in the WISC results.

To test the relationships statistically, and to rule out the possibility that the relationships were due to differences in subtest reliability, we examined the WISC and WAIS data separately, taking the following steps.

1. We first computed each subtest's mean loading on the first principal component and mean reliability coefficient.
2. We squared these loadings, which resulted in proportions of variance shared with general intelligence.
3. We divided these proportions by the corresponding mean reliability coefficient, which resulted in corrected proportions of variance shared with general intelligence.
4. We computed the Pearson correlation between these corrected proportions and the subtests' cultural loadings and obtained the corresponding (one-tailed) p value.
5. We divided, within each of the studies from which we obtained heritability coefficients, each subtest's heritability coefficient by the corresponding mean reliability coefficient, which resulted in heritability coefficients corrected for attenuation.
6. We computed, within each of these studies, the Pearson correlation between the subtests' corrected heritability coefficients (b^2) and corrected proportions of variance shared with general intelligence (gl^2).
7. We pooled (weighted averaged) these correlations, whereby the square root of the studies' sample sizes constituted the weights.
8. We calculated a combined p value using the Stouffer method (Rosenthal, 1991; i.e., we transformed each one-tailed p value into a z value, multiplied each z value by the square root of the corresponding study sample size, summed the outcomes, divided this sum by the number of studies, back-transformed the outcome into a one-tailed p value, and doubled this one-tailed p value to obtain a two-tailed p value).
9. Finally, we repeated Steps 7 and 8 with the correlations between heritability coefficient and cultural load (cl^2).

The correlation between cl^2 and gl^2 was positive, high, and clearly significant in both the WISC ($r = .82, p < .001$) and WAIS ($r = .83, p < .001$) studies. In the WAIS studies, the pooled correlations between cl^2 and b^2 ($r = .40, z = 2.65$, combined $p = .01$) and between gl^2 and b^2 ($r = .34, z = 2.42$, combined $p = .02$) were also positive and significant. In the WISC studies, the pooled correlations between cl^2 and b^2 ($r = .30, z = 1.50$, combined $p = .15$) and between gl^2 and b^2 ($r = .27, z = 1.34$, combined $p = .18$) were in the same direction, but they did not differ significantly from 0.

Analysis 2. Our second analysis involved five WISC and seven WAIS studies that reported heritability coefficients on VIQ and PIQ subscale levels (respectively b^2_{VIQ} and b^2_{PIQ} ; see Table S7 in the Supplemental Material). Corroborating the findings presented in the Analysis 1 section, results from a one-tailed, paired Wilcoxon test showed that in the WAIS studies, b^2_{VIQ} was greater than b^2_{PIQ} (median of the differences = 0.07, $W = 19, p = .047$). In the WISC studies, there was no such effect (median of the differences = 0.00, $V = 5, p = .5724$). Results from the only longitudinal study in our meta-analysis showed that the increase in b^2_{VIQ} ($.84 - .46 = .38$) was significant,

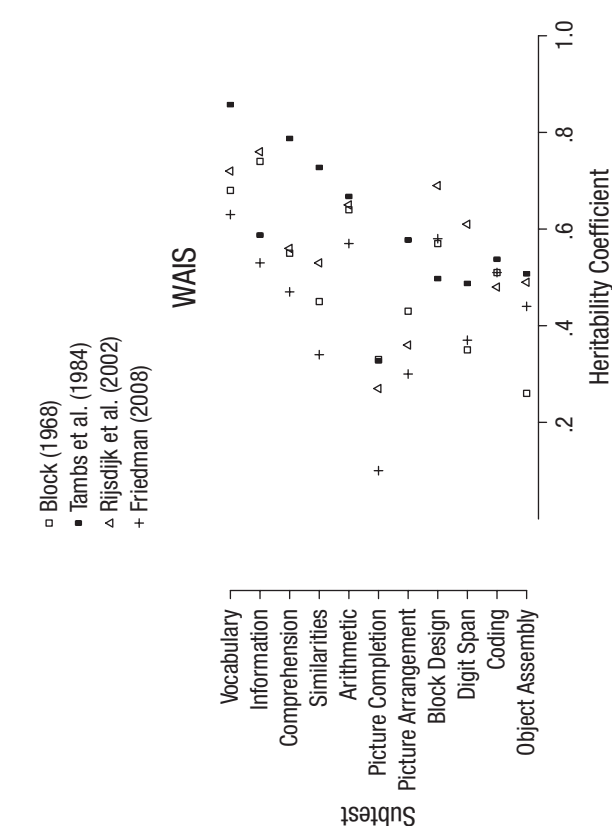
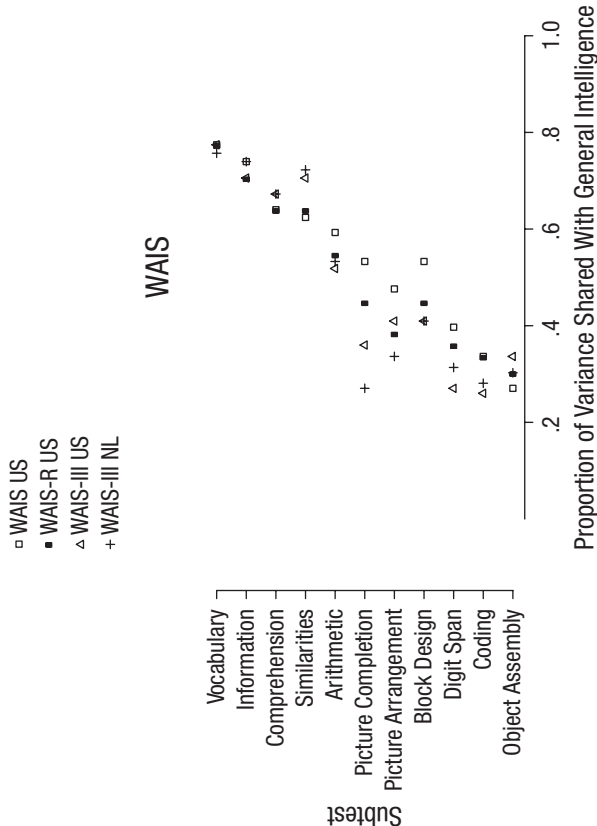


Fig. 2. Subtests' proportion of variance shared with general intelligence (upper panels) and heritability coefficients (lower panels) of the subtests of the Wechsler Intelligence Scale for Children (WISC; left panels) and Wechsler Adult Intelligence Scale (WAIS; right panels). Subtests are ranked according to their cultural load (see Table 1). WISC US = Wechsler (1949); WAIS US = Wechsler (1955); WISC-R US = Wechsler (1974); WAIS-R US = Wechsler (1981); WISC-III US = Wechsler (1991); WISC-III UK = Wechsler (1992); WAIS-III US = Wechsler (1997); WISC-III NL = Wechsler (2002); WAIS-III NL = Wechsler (2005). Additional data were drawn from the following studies: Block (1965); Friedman et al. (2008); Jacobs et al. (2001); LaBuda, DeFries, and Fulker (1987); Luo, Pettrill, and Thompson (1994); Owen and Sines (1970); Rijdsdijk, Vernon, and Boomsma (2002); Segal (1985); Tambs, Sundet, and Magnus (1984); and Williams (1975).

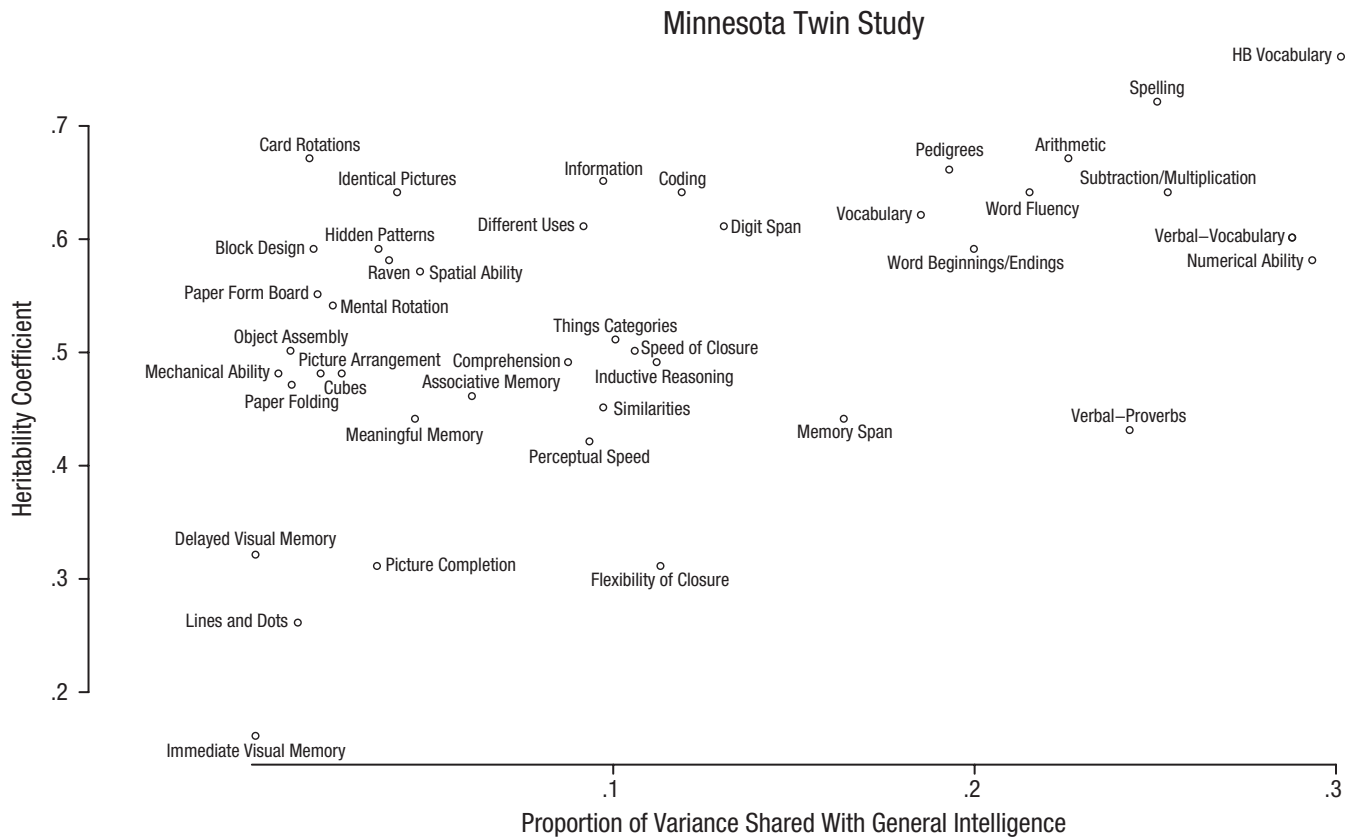


Fig. 3. Heritability coefficients for subtests used in the Minnesota Study of Twins Reared Apart (Johnson et al., 2007) as a function of the proportion of variance shared with general intelligence.

whereas the increase in b^2_{PIQ} ($.74 - .64 = .10$) was not (see Hoekstra, Bartels, & Boomsma, 2007).

Analysis 3. Our third analysis involved data from the Minnesota Study of Twins Reared Apart (Johnson et al., 2007), in which 126 adult twin pairs completed 42 cognitive subtests from diverse batteries, including the WAIS. We gathered the subtests' heritability coefficients (b^2) and computed—on the basis of Johnson et al.'s (2007) factor analytical results—the subtests' proportions of variance explained by the highest-order factor (gl^2). The Pearson correlation between b^2 and gl^2 was positive, of medium-to-large effect size, and significant ($r = .50, p < .001$).

Figure 3 shows b^2 set out against gl^2 . The highly culturally loaded Wechsler Arithmetic, Information, and Vocabulary subtests had relatively large b^2 and gl^2 values, and the same applied to similar tests from other batteries, such as those involving multiplication and subtraction, spelling, and vocabulary.

Statistical testing of the relations between cultural load on the one hand and g loading and heritability on the other hand required the operationalization of the cultural

load of each subtest. We investigated various operationalizations, but they all were based on Jensen's (1980) definition of *culture-reduced tests*, which are "those that are nonlanguage and nonscholastic and do not call for any specific prior information for a plus scored [i.e., correct] response" (p. 374). For example, in one operationalization, subtests were categorized as culture loaded if the first-order verbal and scholastic factors in combination explained more variance in the subtest than did all other first-order factors together. Otherwise, subtests were categorized as culture reduced. In another operationalization, subtests were categorized as culture loaded if they loaded positively on the second-order verbal factor (on which the first-order factors verbal, scholastic, fluency, and number loaded). In a third operationalization, subtests were categorized as culture loaded if, on the basis of subtest descriptions, it was reasonable to assume that the completion of the items involved language (as in, e.g., the Vocabulary and Verbal-Proverbs subtests), that scholastic skills were measured (as in, e.g., the Arithmetic and Spelling subtests), or that completion of the items depended strongly on prior information (as in, e.g., the

Information subtest). Table S8 in the Supplemental Material shows this information at the subtest level.

Across the different operationalizations of cultural load (cl^2), the point-biserial correlations between dichotomous cl^2 and continuous gl^2 and b^2 were always positive and of medium-to-large effect size. Moreover, they were almost always significant.

Conclusion

Each subtest's proportion of variance in IQ shared with general intelligence was a function of cultural load: The more culture loaded, the higher this proportion. In addition, in adult samples, culture-loaded tests tended to have greater heritability coefficients than did culture-reduced tests, and there was a relationship between subtest's proportion of variance shared with general intelligence and heritability. In child samples, these relationships were in the same direction, but correlations were small and insignificant.

The interpretation of these results is complicated for at least two reasons. First, on the one hand, the distribution of the standard errors of g loadings, heritability estimates, and cultural loadings are unknown, and data points may be clustered, which makes the standard errors of the correlations not completely trustworthy. On the other hand, the power to test the correlations is low, and the risk of making a Type II error is high, which is one of the reasons alpha levels of .10 are also often considered in these kinds of analyses (Jensen, 1998).

Second, a correlation between, for instance, g loading and heritability coefficient is in line with the hypothesis that the g factor is the most heritable factor (Jensen, 1998), but a test of the significance of this correlation does not provide the means to test whether the g factor is indeed the most heritable factor¹ (Dolan & Hamaker, 2001). The method merely serves to evaluate competing theories of intelligence (Rushton & Jensen, 2009): A significant correlation denotes that a phenomenon exists that is in need of theoretical explanation. Theories that account for the correlation are stronger (with respect to this correlation) than are theories that do not account for it or are silent about it. The same line of reasoning holds for the correlations of cultural load with g loadings and heritability coefficients. In light of these observations, we discuss the implications of our results.

Discussion

Our result showing that culture-loaded knowledge tests (crystallized tests) are more strongly related to general intelligence than are culture-reduced cognitive-processing tests (fluid tests) fits better with the idea that g loadings reflect societal demands (Dickens, 2008) than

that they reflect cognitive demands (Jensen, 1987). Furthermore, in adult samples, our finding that the heritability coefficients of culture-loaded tests tend to be larger than those of culture-reduced tests calls for an explanation, given that this result does not follow from the subtest-complexity and investment hypotheses of g theory and fluid-crystallized theory.

One way to account for the relatively high heritability coefficients of culture-loaded tests is to assume an equal genetic effect on cognitive abilities when environmental variance in highly culturally dependent knowledge is lower than in less culturally dependent cognitive-processing abilities (e.g., because society creates a homogenous environment for these abilities). This assumption comes closer to constituting a reformulation of the effect than to constituting a theoretical explanation, however (e.g., both the nature of g and the way cognitive abilities are related to this factor therefore still require explanation). We also doubt that our Western society creates a homogeneous learning environment, given that schools and school systems differ strongly.

Another way to account for the relation between heritability coefficient and cultural load, formulated within g theory (including the investment hypothesis), is to assume that the acquisition of crystallized abilities is considerably more cognitively demanding than is the solving of items from even the most complex fluid subtests, such that crystallized-test performance eventually depends more strongly on g than does fluid-test performance. This assumption leaves unanswered the degree of cognitive demand required in the acquisition of crystallized abilities, such as vocabulary. In addition, the assumption does not automatically provide an account for the increase in heritability of IQ (Haworth et al., 2010).

We believe our findings are best understood in terms of genotype-environment covariance. Because the acquisition of knowledge depends on cognitive processing, individuals who develop relatively high levels of cognitive-processing abilities tend to achieve relatively high levels of knowledge. High achievers are more likely to end up in cognitively demanding environments that encourage and facilitate the further development of a wide range of knowledge and skills. The contents and organization of these environments largely reflect societal demands. These societal demands thus influence the degree of dynamical interaction among cognitive processes and knowledge and, hence, their intercorrelations. In this way, the societal demands determine IQ-subtest loadings on the general factor of intelligence and, eventually, the degree to which broad-sense heritability coefficients of IQ subtests include the effects of (growing) genotype-environment covariance. In view of theoretical parsimony, we conclude that the assumption of a true causal g can be incorporated but that this is not required.

Although we were not able to test the different hypotheses above on the basis of the data presented here, we maintain that our results are difficult to understand, especially without appreciating the role of culture, education, and experience in the development of heritable intelligence, if only because of the relationship between heritability and cultural dependence—the more heritable, the more culture dependent. This relationship sheds new light on the long-standing nature-versus-nurture debate. We hope that in future behavior-genetic studies, researchers will model the effects of genotype-environment covariance to test our hypothesis that heritability coefficients differ across cognitive abilities as a result of differences in the contribution of genotype-environment covariance, such that genotype-environment effects are larger on culture-loaded than on culture-reduced cognitive processing abilities.

Author Contributions

K.-J. Kan, J. M. Wicherts, and H. L. J. van der Maas developed the study concept, and all authors contributed to the study design. K.-J. Kan and J. M. Wicherts collected the data. K.-J. Kan analyzed and interpreted the data under the supervision of H. L. J. van der Maas and C. V. Dolan. K.-J. Kan and J. M. Wicherts drafted the manuscript, and C. V. Dolan and H. L. J. van der Maas provided critical revisions. All authors approved the final version of the manuscript for submission.

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Supplemental Material

Additional supporting information may be found at <http://pss.sagepub.com/content/by/supplemental-data>

Note

1. To test this, one can employ structural equation modeling.

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