



Intelligence tests with higher *g*-loadings show higher correlations with body symmetry: Evidence for a general fitness factor mediated by developmental stability

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Abstract

Just as body symmetry reveals developmental stability at the morphological level, general intelligence may reveal developmental stability at the level of brain development and cognitive functioning. These two forms of developmental stability may overlap by tapping into a “general fitness factor.” If so, then intellectual tests with higher *g*-loadings should show higher correlations with a composite measure of body symmetry. We tested this prediction in 78 young males by measuring their left–right symmetry at 10 body points, and by administering five cognitive tests with diverse *g*-loadings. As predicted, we found a significant ($z=3.64$, $p<0.003$) relationship between each test’s rank order *g*-loading and its body symmetry association. We also found a substantial correlation ($r=0.39$, $p<0.01$) between body symmetry and our most highly *g*-loaded test (Ravens Advanced Progressive Matrices). General intelligence is apparently a valid indicator of general developmental stability and heritable fitness, which may partly explain its social and sexual attractiveness.

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1. Introduction

Developmental stability refers to an organism’s ability to develop the appropriate species-specific phenotype, despite genetic and environmental perturbations that tend to disrupt development, such as

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mutations, inbreeding, toxins, pathogens, parasites, injuries, and starvation (Møller & Swaddle, 1997; Yeo & Gangestad, 1998). Prenatal environmental factors, such as audiogenic stress, extreme temperature, and infection, can also reduce developmental stability, although such influences may be trait- and species-dependent (Møller & Swaddle, 1997; see Chap. 6). Developmental stability is analogous to a builder's ability to turn a blueprint (the genotype) into a well-constructed house (the phenotype). A major discovery in biology and evolutionary psychology has been that individuals show differences in developmental stability: Some individuals grow adaptive phenotypes under almost any conditions, whereas others show disrupted development given the slightest perturbations (Gangestad & Thornhill, 1999). These individual differences show moderate heritability in some studies (see Møller & Thornhill, 1997 for a meta-analysis and associated commentaries for discussion).

At the level of morphological development, one key manifestation of developmental stability is body symmetry. Confusingly, this is usually operationalized as the converse of developmental stability, called developmental *instability*, which is indexed by a measure called fluctuating asymmetry (FA). FA refers to deviation from perfect symmetry in bilateral traits that are symmetrical at the population level (Møller & Swaddle, 1997; Yeo & Gangestad, 1998). FA negatively predicts (i.e., body symmetry positively predicts): health, fecundity, quality of fitness-related traits, social dominance, and mating success across many species, including humans (Gangestad & Simpson, 2000; Johnstone, 1995; Leung & Forbes, 1996; Møller, 1999; Rhodes et al., 2001; Zebrowitz, Hall, Murphy, & Rhodes, 2002), although there is substantial variability in the strengths of associations across studies, and the reasons for this remain poorly understood.

The question naturally arises for psychologists: If developmental stability is central to an organism's biological functioning, is there some manifestation of it at the level of brain development and cognitive functioning? We propose that general intelligence (the *g* factor) basically reflects developmental stability at this psychological level of description. A century of research supports the *g* factor's reliability, validity, and heritability: It emerges robustly from any diverse set of cognitive tests in any representative population; it predicts educational, occupational, economic, and social success more powerfully than any other psychological construct; and it has the highest adult heritability of any psychological trait (e.g., Carroll, 1993; Deary, 2000; Jensen, 1983; Plomin, DeFries, McClearn, & McGuffin, 2001).

Specifically, we hypothesize that there is substantial genetic and phenotypic overlap between developmental stability at the morphological level (which we will call "morphodevelopmental stability"), as manifest in body symmetry, and developmental stability at the neuro-psychological level (which we will call "neurodevelopmental stability"), as manifest in general intelligence. Similar reasoning motivated the study by Furlow, Armijo-Prewitt, Gangestad, and Thornhill (1997), which found a positive correlation ($r=0.23$) between a composite index of body symmetry and general intelligence as measured by Cattell's Culture Fair Intelligence Test. Indeed, they estimated that 17–50% of the genetic variation in intelligence might reflect overlap with morphodevelopmental stability.

Our research goes beyond that study to investigate whether the *g* factor itself is responsible for the correlation between cognitive test performance and body symmetry. An alternative could be that some group factor subordinate to *g*, such as spatial or verbal intelligence, may show a high correlation with body symmetry, but that other group factors may not—if so, then *g* could not be interpreted as a direct index of neurodevelopmental stability. To test the hypothesis that the *g* factor itself mediates the correlations found between morphodevelopmental stability and psychological functioning, we decided to assess correlations between body symmetry and scores on multiple cognitive tests with diverse *g*-loadings. If morphodevelopmental stability and neurodevelopmental stability overlap by tapping into a

general fitness factor, then cognitive tests with higher *g*-loadings should show higher correlations with body symmetry.

2. Methods

2.1. Participants

Seventy-eight male undergraduate volunteers were recruited from various psychology courses at the University of New Mexico (UNM). Mean age was 21.5 years (S.D.=6.13 years, range 18–52 years). All participants signed consent forms after being introduced to the general nature of the study and the methodology used. Participants were screened to ensure that none carried neurological diagnoses or had suffered a concussion producing a loss of consciousness. Participants were compensated by earning research credit toward the completion of their psychology course.

2.2. Procedures

2.2.1. Measurement of FA

For each participant, we used electronic calipers to measure the right and left sides of 10 body features (foot width, ankle width, wrist width, elbow width, ear width, ear length, index finger length, middle finger length, third finger length, and little finger length) to the nearest 0.01 mm. As is usual in FA studies, each side of each body feature was measured twice and then averaged to give a reliable measure. FA was then calculated by taking the absolute value of the right–left difference, and dividing that by the right–left average (trait $FA = |R - L| / [0.5 \times (R + L)]$) (Palmer, 1994). FA scores were calculated for each of the 10 individual body measurements, standardized, and summed to derive a composite FA score for each subject. Participants were asked if they had suffered any significant injury to each body part measures (i.e., ankle sprain or broken finger). If they had, that measurement was not included in their composite FA score.

2.2.2. Cognitive tests

Estimates of a given test's *g*-loading will depend on the other tests in the same principle component analysis as well as unique sample characteristics. Yet, there is a general consensus about the rank ordering of common tests' abilities to tap *g*. Our rank ordering of tests in terms of *g*-loading was based on analyses performed by Marshalek, Lohman, and Snow (1983) and Snow, Kyllonen, and Marshalek (1982); for convenience, figures representing *g*-loadings from both of these studies may be found in Fig. 1 of Carpenter, Just, and Shell's (1990, p. 406) review of the cognitive skills underlying the Raven Progressive Matrices Test (RPMT). In each of these figures, the RPMT stands at the center, representing the prototypical *g*-loaded test. Vocabulary definition (as required on the Wechsler scales) is more *g*-loaded than vocabulary recognition, and each is more *g*-loaded than the Digit Span tests, with Digits Backwards having approximately twice the *g*-loading of Digits Forward (Jensen, 1985).

Half of the participants received the tests in the order listed below (i.e., the most *g*-loaded first), while for the other half the order was reversed:

- (1) Ravens Advanced Progressive Matrices (40-min timed version) (Raven, Court, & Raven, 1994) assessed general nonverbal reasoning. The internal consistency reliability of Ravens is estimated at

- 0.90 (Raven et al., 1994). Although a recent study found a sex difference favoring males (Colom & Garcia-Lopez, 2002), no sex difference was noted in the standardization sample (Raven et al., 1994).
- (2) The WAIS III Vocabulary subtest (Wechsler, 1997) assessed the ability to give concise, accurate oral definitions of words. Due to its ability to tap active recall and definition abilities, the WAIS III Vocabulary is a highly *g*-loaded verbal test. The internal consistency reliability of the WAIS III Vocabulary is estimated at 0.93 (Wechsler, 1997).
 - (3) The Shipley Vocabulary test measures vocabulary recognition in a multiple-choice format ($\sigma=0.87$; Shipley, 1946). The Shipley Vocabulary is probably less cognitively complex, accounting for its lower *g*-loading than the WAIS III Vocabulary.
 - (4) The WAIS III Digit Span Backward subtest assesses complex working memory by requiring individuals to repeat an orally presented digit sequence in backward order ($\sigma=0.90$; Wechsler, 1997). The WAIS III Digit Span Backward was combined with the WISC-R Digit Span Backward (Wechsler, 1991), which is identical in structure except for the actual digits presented, to double the number of items and hence increase the reliability of the measure.
 - (5) The WAIS III Digit Span Forward subtest tests simple auditory working memory capacity by requiring individuals to repeat an orally presented digit sequence in forward order ($\sigma=0.90$; Wechsler, 1997). The WAIS III Digit Span Forward was also combined with the WISC-R Digit Span Forward (Wechsler, 1991) to increase the number of items and the reliability of the measure.

3. Results

Data from each subject included their 10-trait composite FA score and their scores on the five cognitive tests. No tests were compromised by floor or ceiling effects. We first examined the correlations of body symmetry (the negative of our composite FA measure) with each of the five cognitive tests. The Pearson product–moment correlations (with all significance levels two-tailed) between body symmetry and each of the cognitive tests were: $r=0.39$ ($p<0.01$) for Ravens Advanced Progressive Matrices (see Fig. 1 for scatterplot); $r=0.27$ ($p=0.02$) for Wais III Vocabulary; $r=0.25$ ($p=0.03$) for Shipley Vocabulary; $r=0.07$ ($p=0.55$, n.s.) for Backward Digit Span; and $r=-0.05$ ($p=0.70$, n.s.) for Forward Digit Span. As predicted, the relative magnitude of each test's correlation with body symmetry followed the rank order of each test's *g*-loading. The correlation matrix of all tests and FA is provided in Table 1.

Second, we tested the statistical significance of this relationship between each test's *g*-loading and its correlation with body symmetry. Based on the typical *g*-loadings of our cognitive tests found in previous psychometric research, we assigned *g*-loading contrast scores of 5, 4, 3, 2, and 1, respectively, to Ravens, WAIS II Vocabulary, Shipley Vocabulary, Digit Span Backward, and Digit Span Forward. We applied the method of Olkin and Finn (1990) for testing correlated correlations, and found a significant monotonic trend for each test's body symmetry correlation in relation to its estimated *g*-loading ($z=3.64$, $p<0.0003$). Thus, there is a significant association between the extent to which a cognitive test indexes morphodevelopmental stability (as revealed by its correlation with body symmetry) and the extent to which it indexes neurodevelopmental stability (as revealed by its *g*-loading).

Third, we estimated the “true” disattenuated overlap between morphodevelopmental stability and neurodevelopmental stability. As reported above, we found a 0.39 raw correlation between our index of

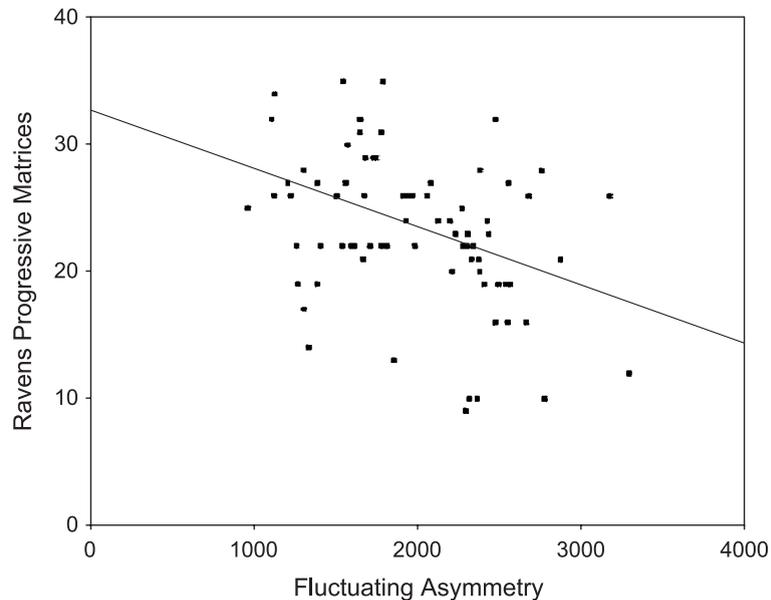


Fig. 1. Relationship between FA and Ravens scores ($r=-0.39$). Line is the best fit least squares regression line.

morphodevelopmental stability (the 10-trait composite score of body symmetry) and our best index of neurodevelopmental stability (i.e., our most highly g -loaded test, Raven Advanced Progressive Matrices). However, neither of these indexes is a perfect measure of the underlying constructs, so to estimate the true magnitude of the relationships between morphodevelopmental stability and neurodevelopmental stability, we must correct the raw correlation ($r=0.39$) for attenuation in each variable. With regard to neurodevelopmental stability, the validity coefficient for Ravens' ability to tap g is estimated at 0.80 (Raven et al., 1994). With regard to morphodevelopmental stability, we can estimate the validity of our 10-trait composite measure given data on the repeatable variance of single-trait asymmetries. Based on a large sample of participants drawn from the same population as the current study, Gangestad, Bennett, and Thornhill (2001) estimated that single-trait asymmetries have approximately 7.8% repeatable variance (see Gangestad & Thornhill, 1999; Van Dongen, 1998;

Table 1

Pearson correlation coefficients between all cognitive tests and total FA score

	FA	Ravens Matrices	WAIS III Vocabulary	ShIPLEY Vocabulary	Digits Backwards	Digits Forward
FA	–	–0.39**	–0.27*	–0.24*	–0.07	0.04
Ravens Matrices	–0.39**	–	0.20	0.21	0.35**	0.25*
WAIS III Vocabulary	–0.27*	0.20	–	0.72**	0.14	0.17
ShIPLEY Vocabulary	–0.24*	0.21	0.72**	–	0.14	0.09
Digits Backwards	–0.07	0.35**	0.14	0.14	–	0.68**
Digits Forwards	0.04	0.25*	0.17	0.09	0.68**	–

* $p < 0.05$.

** $p < 0.01$.

Whitlock, 1998 for procedures for estimating this value). If all traits are independent indicators of developmental instability (as they appear to be; Gangestad & Thornhill, 1999), a 10-trait composite should have an estimated validity coefficient of 0.68. Estimated validity using Cronbach's α yielded a slightly lower value of 0.56. Using standard psychometric procedures (Anastasi & Urbina, 1997) to divide our raw $r=0.39$ correlation (between Ravens and 10-trait composite body symmetry) by these estimated validities (0.80 for Ravens as a g measure, and 0.56–0.68 for our composite as a morphodevelopmental stability measure) leads to an estimated correlation of 0.72–0.87 between the g factor and morphodevelopmental stability, which suggests a substantial and theoretically meaningful relationship.

As a supplementary analysis, we computed the principle components of our cognitive test battery and related these to our FA score. However, given the relatively small number of tests administered and the fact that all except one were verbal, the first PC may be somewhat different than those emerging from more large-scale analyses. Two PCs with eigenvalues greater than one emerged, accounting for 43.78% and 28.89% of variance, respectively. Loadings on the first PC were: Ravens Matrices=0.58, Shipley Vocabulary=0.65, Digits Backwards=0.72, Digits Forward=0.68, and WAIS III Vocabulary=0.68. Loadings on the second PC were: Ravens Matrices=-0.15, Shipley Vocabulary=0.66, Digits Backwards=-0.55, Digits Forward=-0.55, and WAIS III Vocabulary=0.62. The total FA score correlated with the first PC ($r=-0.27$, $p=0.018$), but not with the second PC ($r=-0.18$, n.s.).

4. Discussion

The results confirm our prediction that there is substantial overlap between morphodevelopmental stability (as manifest in body symmetry) and neurodevelopmental stability (as manifest in the g factor, and as measured by g -loaded cognitive tests). The current results extend those of Furlow et al. (1997) by demonstrating that g -loading determines a cognitive test's relationship with morphodevelopmental stability, rather than some other test characteristic. The correlations we observed between our cognitive tests and body symmetry may appear modest, but three of the five (i.e., the RPMT and both vocabulary tests) are larger than the $r=0.23$ correlation found by Furlow et al. (1997) between body symmetry and Cattell's Culture Fair Intelligence Test. Indeed, our $r=0.39$ ($p<0.01$) correlation between body symmetry and Ravens Advanced Progressive Matrices is larger than many correlations reported between general intelligence and key neurobiological variables such as brain size, nerve conduction velocity, and the reaction time reliability of elementary cognitive task performance (see Jensen, 1993; Deary, 2000).

One alternative interpretation could be that if our cognitive tests had widely different reliabilities, the more reliable ones might have shown higher g loadings in the psychometric literature, and higher correlations with body symmetry in our data, which would have rendered our results an artifact of differential test reliability. However, the internal consistency reliability was relatively constant across all five cognitive tests (Ravens=0.90; WAIS Vocabulary=0.93; Shipley Vocabulary=0.87; Backward Digit Span=0.90; Forward Digit Span=0.90), so this alternative interpretation does not seem viable.

A parsimonious explanation for our findings is that both neurodevelopmental stability (as manifest in general intelligence) and morphodevelopmental stability (as manifest in body symmetry) tap into an underlying general "fitness factor" (Miller, 2000a,b). In factor-analytic terms, general fitness is superordinate to these two forms of developmental stability. The existence of this superordinate fitness

factor may explain why general intelligence positively correlates with so many fitness-related biological traits such as health, longevity, and physical attractiveness (Jensen & Sinha, 1993; Whalley & Deary, 2001; Zebrowitz et al., 2002). It may also explain several of our previous findings concerning relationships between morphodevelopmental stability and neurodevelopmental stability, such as lower body symmetry predicting: (1) neurodevelopmental disorders (Yeo, Gangestad, Edgar, & Thoma, 1999); (2) atypical functional brain asymmetry (Yeo, Gangestad, Thoma, Shaw, & Repa, 1997); and (3) atypical anatomical brain asymmetry (Thoma, Yeo, Gangestad, Lewine & Davis, 2002).

The sexual attractiveness of intelligence has traditionally been interpreted as due to the high survival and parenting payoffs of intelligence in long-term sexual relationships (e.g., Buss, 1989; Li, Bailey, Kenrick, & Linsenmeier, 2002; Zebrowitz et al., 2002). Our alternative interpretation is that intelligence is highly valued as a “good genes” indicator that advertises general heritable fitness, apart from any direct survival or parenting payoffs (Miller, 2000a,b,c; Miller & Todd, 1998). This “good genes” interpretation is consistent with the phenomenon of inbreeding depression on intelligence (e.g., Agrawal, Sinha, & Jensen, 1984; Bashi, 1977; Jensen, 1983), which illustrates the role of recessive mutations in the heritability of intelligence.

In our view, general intelligence is a highly valid cue of general biological fitness, and this may partly explain why intelligence is so salient, and so easily and accurately assessed in human social relationships (Bevan and Bansavage, 1958; Bryan, Hunt, & Walker, 1966; Cook, 1939; Fuhrman, Bodenhausen, & Lichtenstein, 1989; Reynolds & Gifford, 2001; Solomon & Saxe, 1977; Zebrowitz et al., 2002). This may also explain why intelligence is so highly valued in human sexual selection, as shown by:

- (1) evolutionary psychology studies on mate choice for intelligence (e.g., Buss, 1989; Buunk, Dijkstra, Fetchenhauer, & Kenrick, 2002; Feingold, 1992; Kenrick Sadalla, Groth, & Trost, 1990; Li et al., 2002; Regan & Joshi, 2003)
- (2) behavior genetics studies on assortative mating for intelligence (e.g., Mascie-Taylor & Vandenberg, 1988; Phillips, Fulker, Carey, & Nagoshi, 1988; Reynolds, Baker, & Pedersen, 2000)
- (3) neuroanatomical and neurogenetic studies of sexual selection's effects on the human brain (Goldstein et al., 2001; Nopoulos, Flaum, O'Leary, & Andreasen, 2000; Sawaguchi, 1997; Zechner et al., 2001).

Thus, our results support the hypothesis (Miller, 2000a) that intelligence functions as a “fitness indicator,” like the peacock's tail, that reveals genetic and phenotypic qualities. Two auxiliary arguments support this view. First, the more genes a trait depends upon, the better a fitness indicator it makes (Rowe & Houle, 1996). Insofar as a substantial proportion of the human genome is involved in brain development, the human brain's functional efficiency (i.e., general intelligence) gives outside observers a pretty good estimate of an individual's overall genetic quality (e.g., the individual's “mutation load”). Second, the higher the marginal costs (e.g., energy costs) of a trait, the better a fitness indicator it makes, as predicted by costly signaling theory (Johnstone, 1995). The human brain constitutes only about 2% of an adult's body weight, but it requires about 15% of the body's blood, 20% of its oxygen, and 40% of its glucose (Cottrell & Smith, 1994; Miller, 2000b). This disproportionately high metabolic cost reinforces the human brain's value as an honest fitness indicator.

We investigated an all-male sample because there are theoretical and empirical reasons to expect that FA will correlate more strongly with other fitness indicators in males than in females. Theoretically, sexual selection almost always acts more strongly on males because variance in reproductive success is almost

always greater in males than in females (Andersson, 1994), so we would expect higher functional variance in the fitness indicators of the most sexually selected sex. Also, insofar as males are under selection to invest more phenotypic resources in growing high-quality fitness indicators, they may typically be closer to the upper limits of their overall phenotypic “budget,” resulting in more consistent correlations between fitness indicators such as FA and intelligence. Empirically, a few studies have found higher correlations between FA and other traits in males than in females. For example, lower FA (implying higher general fitness) correlates more strongly in males than in females with: (1) facial attractiveness (Gangestad, Thornhill, & Yeo, 1994; Thornhill & Gangestad, 1994), (2) number of sexual partners (Gangestad & Thornhill, 1999), (3) lower levels of depression (Martin, Manning, & Dowrick, 1999), (3) lower levels of schizotypy (Rosa et al., 2000), and (5) lower resting metabolic rate, implying a more energy-efficient phenotype (Manning, Koukourakis, & Brodie, 1997). For these reasons, we expected that use of an all-male sample would maximize our likelihood of finding a clear result in this study. Of course, future studies should investigate whether our results generalize to female samples.

5. Conclusion

If general intelligence is a fitness indicator, then the high genetic variance (and substantial heritability) of general intelligence in humans is really a special case of the high genetic variance of general fitness in most species. Biologists recently have focused on the importance of mutation–selection balance in maintaining heritable variation in general fitness (e.g., Crow, 1999; Houle, 2000; Lynch et al., 1999; Rowe & Houle, 1996). For example, Eyre-Walker and Keightley (1999) estimated that over most of human evolution, an average individual has had 1.6 new, harmful, phenotypically expressed mutations that neither parent had; Crow (1999) argues that the number should be closer to three new mutations per individual. With mutations accumulating at this rate, selective pressures appear too modest to reduce the heritability of general ability below its frequently observed levels.

Such research suggests that most heritable variation in general fitness, and hence in morphodevelopmental and neurodevelopmental stability, is due to individual differences in mutation load. Moreover, since most genetic loci have pleiotropic effects on multiple phenotypic traits, most deleterious mutations will disrupt the developmental stability of multiple traits, creating positive correlations between the efficiencies of these multiple traits (Houle, 2000). Miller (2000a) and Anderson (2001) have argued that this “pleiotropic mutation” effect is responsible for the existence of the *g* factor. More generally, it may be responsible for the existence of individual differences in neurodevelopmental stability, morphodevelopmental stability, and general heritable fitness.

If pleiotropic mutations do create much of the heritable variation in general fitness, morphodevelopmental stability, neurodevelopmental stability, and general intelligence, then this has several important implications for psychology. First, it suggests that the *g* factor is best understood at the genetic level as an index of mutation load, rather than at the psychological level as a distinctive “cognitive capacity” that might be localized in some brain area or identified with some distinctive set of information processing operations (Miller, 2000a). The different *g*-loadings of different psychological adaptations simply reflect the susceptibility of those functions (and their underlying neural mechanisms) to disruption by deleterious mutations, and need not be given any cognitive interpretation. Second, there is no theoretical conflict between the existence of a unitary *g* factor at the level of individual differences in psychological functioning (e.g., Jensen, 1998), and the existence of many psychological adaptations at the level of

species-typical cognitive architecture, as advocated in the “massive modularity” view of evolutionary psychology (e.g., Pinker, 1997). Third, the importance of possible “intelligence-boosting genes” (i.e., alleles at specific genetic loci that increase intelligence above the population average; e.g., Chorney et al., 1997; cf. Hill, Chorney, Lubinski, Thompson, & Plomin, 2002) will need to be considered in the context of variation in intelligence maintained by fitness-reducing (and hence intelligence-reducing) mutations.

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