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The more *g*-loaded, the more heritable, evolvable, and phenotypically variable: Homology with humans in chimpanzee cognitive abilities

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Abstract

Expanding on a recent study that identified a heritable general intelligence factor (*g*) among individual chimpanzees from a battery of cognitive tasks, we hypothesized that the cognitive abilities that are more *g*-loaded would be more heritable and would present more additive genetic variance, in addition to showing more phenotypic variability. This pattern was confirmed, and is comparable to that found in humans, indicating fundamental homology. Finally, tool use presented the highest heritability, the largest amount of additive genetic variance and of phenotypic variance, consistent with previous findings indicating that it is associated with high interspecies variance and evolutionary rates in comparative primate studies.

Keywords

general intelligence; primate intelligence; heritability; CVA; chimpanzee

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1. Introduction

1.1 Jensen effects

Many studies with humans have demonstrated that the vector of g loadings of cognitive tests is a strong positive predictor of the tests' correlation with a variety of variables, such as brain size, reaction time, scholastic and workplace performance, and also of phenotypic and genetic characteristics associated with performance on the tests, such as the magnitude of population differences in cognitive performance and inbreeding depression effects (Jensen, 1980; Jensen, 1998; Rushton & Jensen, 2010). The affinity that many biologically significant variables exhibit for g are known as 'Jensen effects' (Rushton, 1999). This effect demonstrates that g is a biologically grounded variable rather than purely a statistical regularity amongst test scores (Rushton, 1999; Rushton & Jensen, 2010). Importantly, however, examination of possible Jensen effects in non-human animals is almost non-existent, even though there are many studies of non-human general intelligence (Galsworthy, Arden, & Chabris, 2014; Reader, Hager, & Laland, 2011).

Various studies in humans have found that the heritability of cognitive abilities measured by intelligence batteries is associated with the g loadings of the respective abilities. In Western samples, correlations between the vector of subtest g loadings and heritability values range in magnitude from .27 to .77 across studies (Jensen, 1997; Kan, Wicherts, Dolan & van der Maas, 2013; Pedersen, Plomin, Nesselroade, & McClearn, 1992; Rijdsdijk, Vernon, & Boomsma, 2002; Rushton & Jensen, 2010), reaching unity if psychometric meta-analytical corrections are applied (Rushton & Jensen, 2010). In a bare-bones meta-analysis of six Japanese samples a correlation of .38 was found (te Nijenhuis, Kura, & Hur, 2014).

Humans are not the only species for which g loading estimates and heritability data exist on cognitive ability measures. A recent study (Hopkins, Russell, & Schaeffer, 2014) found that among a sample of 99 chimpanzees tested using a broad intelligence battery, the results of employing several analytical methods converged on the existence of a g factor, with g loadings ranging from .054 to .723, while heritabilities ranged from .00 to .74 across the 13 subtests. Heritability was evaluated using the program SOLAR (Sequential Oligogenic Linkage Analysis Routines; Almasy & Blangero, 1998), which uses a variance-components approach to estimate the additive genetic variance. One strength is that this approach employs all kinship information, including full sibship, half sibship, parent-offspring and more distant relationships. With SOLAR, maximum-likelihood estimation can be applied to a mixed-effects model that incorporates additive genetic effects (matrix of genetic relationships among all subject pairs in the pedigree times the proportion of phenotypic variance attributable to genetic variation), the shared environmental effects (matrix of shared environmental variables times the proportion of variation attributable to those shared environmental effects), and a term for the unique environment variation and error.

One Jensen effect that has been identified both in humans and more recently in non-human primates is the strong correlation between g loadings and the size of differences in cognitive abilities among populations (or among species, in non-human primates), a phenomenon known as Spearman's hypothesis (Jensen, 1998). Many studies have corroborated that effect in humans (for a review see Fernandes, Woodley, & te Nijenhuis, 2014). An analysis of 69

primate species with five cognitive abilities has shown almost perfect correlations between *g* loadings and the size of the differences among species (Fernandes et al., 2014).

1.2. Genetic and phenotypic diversity

An underexplored question in the intelligence literature is whether the magnitude of the heritability and the amount of additive genetic variance in cognitive abilities are predictors of their phenotypic diversity. As they are indicators of *genetic diversity* (Hughes, Inouye, Johnson, Underwood, & Vellend, 2010), heritability and the amount of additive genetic variance should be positively associated with the magnitude of the *phenotypic diversity* of the cognitive abilities in animals, and this appears to be the case with humans (Spitz, 1988). Additionally, traits closely related to fitness (such as *g* is hypothesized to be) are associated with larger mutational target sizes, and this increases their sensitivity to *de novo* pleiotropic mutation which in turn increases the genetic variability associated with these traits, and also the evolutionary responsiveness of the trait to selection (Houle, 2000; Miller, 2000; Penke, Denissen, & Miller, 2007; see Stearns, 1992, for other putative causes leading to high genetic variability in traits that are importantly connected to fitness). It has been also tentatively demonstrated that new heritable phenotypic variation can be produced in response to directional selection (e.g. Pavlicev, Cheverud, & Wagner, 2010). As more *g*-loaded abilities appear to be under stronger selection in the primate phylogeny (Fernandes et al., 2014), we expect that *g* loadings are positively correlated with not only genetic diversity but also with phenotypic diversity.

1.3. Aims and predictions

Following on from previous research, in which Spearman's hypothesis was demonstrated to generalize to comparisons involving primate species (Fernandes et al., 2014), here we reanalyse the data from Hopkins et al. (2014) in an effort to determine whether the finding that heritability is a Jensen effect generalizes to chimpanzees, and whether individual chimpanzees differ from one another to a greater degree on more *g*-loaded abilities. We also expand on these previous two studies and examine phenomena that are still unexplored in studies of Jensen effects in human intelligence: it is possible to calculate coefficients of additive genetic variance (CVA) using the database from Hopkins et al. (2014), which constitute a mean-standardized and scale-invariant index of genetic variance in a trait (Houle, 1992). Unlike heritabilities, CVAs are independent of environmental variation effects upon individuals, and they are evolutionarily informative as high CVAs are typical of fitness-related traits, especially those under directional selection and those influenced by many genes (Miller & Penke, 2007). Thus, we predict that there should *also* be a Jensen effect on CVA, which would indicate that more *g*-loaded abilities have been subjected to stronger and more recent selection pressures than more specific and modularized cognitive abilities. A positive and strong association between *g* loadings and the CVAs of the respective cognitive abilities would be consistent with the findings of Fernandes et al. (2014) in the primate phylogeny, and with the tentative demonstration that *g* has undergone positive selection in the genus *Pan* (Reader et al., 2011). Finally, we expect that heritabilities and CVAs will be positively associated with phenotypic variability in Hopkins et al.'s (2014) chimpanzee sample, for the reasons outlined in Section 1.2.

Examining whether g loadings, heritability, additive genetic variance, and phenotypic variance are positively interrelated in chimpanzees is an important step towards determining whether the human g -nexus (i.e. the nomological net of psychological findings indicating the centrality of g in predicting phenotypic and genetic characteristics associated with cognitive abilities; Jensen, 1998) generalizes to other primates. Additionally, further studies on g in chimpanzees would provide invaluable data and test many contemporary theories stemming from ethologists and also evolutionary psychologists who propose that humans and other animals are essentially different in ways that make the organization of their cognitions incomparable (e.g. Barkow, Cosmides, & Tooby, 1992; Herrmann & Tomasello, 2012; Macphail, 1985).

2. Methods

The subjects and the collected data used here are the same as those reported in Hopkins et al. (2014). There were 99 captive chimpanzees (*Pan troglodytes*) housed at the Yerkes National Primate Research Center. Each chimpanzee was tested on 13 tasks designed to broadly assess social and physical cognition (see Table 1). Normal probability plots (a special case of Q-Q probability plots; Chambers, Cleveland, Kleiner, & Tukey, 1983) and skewness and kurtosis tests (Kim, 2013; Lewis-Beck, Bryman, & Liao, 2013) indicated that the distribution of performance on the 13 tasks did not deviate from normality assumptions. In this study, we used a different technique to assess g in the chimpanzee sample than that employed in Hopkins et al. (2014), we calculated the additive genetic variance and the phenotypic variance for performance on each cognitive task, and then proceeded to test the several predictions regarding Jensen effects proposed in Section 1.3 within the chimpanzee sample.

First, Principal Axis Factor analysis (PAF) eliminates error variance and retains only truly shared variance among traits (Costello & Osborne, 2005). Thus, we reanalyzed using PAF the raw data from Hopkins et al. (2014) in order to obtain a purer set of g loadings for the analyses. Similarly to Hopkins et al. (2014) and to general practice (Jensen & Weng, 1994), we used the loadings of cognitive abilities on the first unrotated factor as the g loadings, as rotations are designed to break general factors into specific components (Darton, 1980). Heritabilities of the cognitive abilities were directly obtained from supplemental Figure S1 in Hopkins et al. (2014).

Second, as in other primate intelligence studies in which performance on tasks was compared within and between species (e.g. Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007), to compare the phenotypic variability (i.e. the dispersion) of different cognitive abilities, we computed the coefficient of (phenotypic) variation (usually referred to as CV or CVP, which is the standard deviation/mean ratio, multiplied by 100; Sokal & Rohlf, 1995) for each ability. This is because CVs are a mean-standardized and scale-invariant measure of trait variability, and are thus ideal for comparing the variability of different traits, especially if their means are considerably different, such as the means of performance in the 13 cognitive tasks employed in this study (see Table 1). The CVAs were also computed for each cognitive task, by computing the product of its CV and the square root of its heritability (Houle, 1992).

Third, the method of correlated vectors (MCV; Jensen, 1998) was employed in testing all predictions, as is common practice in studies in humans investigating the relationship between g loading and heritability (e.g. Rushton & Jensen, 2010). This involves calculating the Pearson product-moment correlation between (a) the column vector of a property of the cognitive tasks (such as their g loadings), and (b) the column vector of a second property of the respective cognitive tasks (such as heritability estimates or CVAs).

Finally, we subjected the variables to multivariate MCV, which involves taking the common factor amongst the four vectors (g loadings, heritabilities, CVs and CVAs), and then correlating each vector with the common factor (Rushton, 1998). Such a “multivector common factor” represents the common-factor variance among the g vector in addition to the vectors of other biological/genetic variables (Woodley, te Nijenhuis, & Murphy, 2014). The factor loading of the multivector common factor upon each of its vectors represents an omnibus test of the Jensen effect for a given variable, as it constitutes the correlation between that vector and the set of all vectors.

With four indicators, and an N of 13 datapoints apiece, it is impossible to recover a meaningful factor structure for the multivector common factor using conventional factor analysis, unless the factor structure is defined *a priori* (Figueredo, Cox, & Rhine, 1995; Gorsuch, 1983). This is because factor loadings produced with Principal Axis Factoring and Principal Components Analysis (PCA) in small samples are less reliable than those computed with unit-weighted factoring, as increasing standard errors of PCA or PAF factor loadings with decreasing sample size prevents one from discriminating between the factor loadings of the different variables (Bobko, Roth, & Buster, 2007; Figueredo, Cox, & Rhine, 1995; Gorsuch, 1983; Schmidt, 1971). To that end, we constructed a *unit-weighted factor* by simply standardizing each indicator (i.e. computing its z -score) and then summing across the vectors in order to generate a composite score, as is recommended (Figueredo et al., 1995; Gorsuch, 1983). The unit-weighted factor loadings were then obtained by correlating each indicator with the common factor.

3. Results

The descriptive statistics for each cognitive measure used in the analyses are presented in Table 1. The g loading scores varied from .048 to .607 (see Supplement 1 for correlations and covariances among the tasks, which also indicate a positive manifold), and parallel analysis (Horn, 1965) indicated that only one factor was extracted in this PAF analysis, as in Hopkins et al.'s (2014) Principal Components Analysis (PCA) results. The heritability estimates ranged from 0 to .740. The coefficients of additive genetic variance ranged from 0 to 263.80 and the phenotypic variability ranged from 46.38 to 306.66.

The results for the vector analyses are presented in Table 2. As can be seen, correlations among g loading, heritability, CVA and CV ranged from $r=.26$ to $r=.94$, and were statistically significant.

Lastly, the multivector MCV analysis confirmed that these vectors were strongly and significantly related to one another, sharing variance with the multivector common factor

(see Table 3). The factor loadings ranged from .67 to .95. Reproducing this MCV analysis with PAF produces similar loadings for all vectors (.94 for h^2 , .97 for CVA, .94 for CV, all significant) except for the loading of the vector of g loadings (.46, $p > .05$). As mentioned above, however, PAF loadings are known to present large standard errors in small samples, and thus unit-weighted factor loadings are to be preferred due to their reliability in such cases (Bobko, Roth, & Buster, 2007; Figueredo, Cox, & Rhine, 1995; Gorsuch, 1983; Schmidt, 1971).

For comparability, the statistical effects presented in Tables 2 and 3 were also examined using the g loadings reported by Hopkins et al. (2014), based on a PCA. As that set of g loadings and the set presented here in Table 1 (based on a PAF) correlate at $r = .99$ ($p < .05$), the vector correlations displayed on Table 2 involving the vector of g loadings were reduced only by .00–.04 when using the PCA-based g loadings. The multivector common factor loading upon the vector of PCA-based g loadings was reduced by .03 compared to the multivector common factor loading upon the vector of PAF-based g loadings.

5. Discussion

This study examined whether in chimpanzees the g loadings of cognitive abilities, their heritabilities, CVAs, and CVs are positively interrelated. Several predictions were tested: more g -loaded cognitive abilities should be more heritable in chimpanzees as has been found in multiple studies with humans, individual chimpanzees were expected to differ more among themselves in more g -loaded abilities as is the case with humans, and heritability and additive genetic variance should be positively associated with phenotypic diversity (as they are indicators of genetic diversity). Moreover, CVA should be higher in more g -loaded traits, as g has been tentatively demonstrated to have undergone positive selection in *Pan*. The correlations among those vectors were moderate to strong (see: Cohen, 1988; Kotrlik & Williams, 2003) and were all positive (Table 2). Moreover, the loadings of the multivector common common factor (comprising g loadings, heritabilities, CVAs and CVs) on each indicator were of high magnitude (Table 3), thus in agreement with the bivariate correlations, and corroborating all predictions for the specified Jensen effects.

The observed relationship between g loadings and CVs (.26; Table 2) however was smaller than expected (i.e. .46) if trait heritability were a complete mediator of the relationship and also smaller than expected (i.e. .40) if CVA were a complete mediator of the relationship, suggesting that environmental influences on the ontogenetic development of cognitive abilities may attenuate the relationship between g loading and phenotypic variability.

Additionally, it should be observed that, with regard to the multivector common factor, stronger factor loadings were found on the indicators of genetic diversity than on the phenotypic properties of the cognitive tasks. This replicates recent findings with humans (Woodley et al., 2014) and reinforces the proposal that genetic components are central to the g -nexus.

It is also important to note that tool use exhibited the highest interspecies variance and g loading in recent comparative (i.e. cross-species) studies with primates (Fernandes et al.,

2014; Reader et al., 2011), while in the present analysis it was also found to exhibit the highest heritability, phenotypic variability (CV), and CVA of the thirteen abilities, in addition to presenting a high *g* loading. This is consistent with the theory developed by Fernandes et al. (2014) that the need for ecological control is among the most domain-general, and therefore *g*-loaded classes of cognitive problems. Being able to manipulate ecology furthermore has the potential to generate positive evolutionary feedback operating on *g* via niche construction (Odling-Smee, Laland & Feldman, 2003). There are more than 370 independently observed instances of tool-using behavior in chimpanzees (Reader et al., 2011), far more than in any other non-human primate; it is therefore likely that, just as in humans (e.g. Cochran & Harpending, 2009), selection for highly *g*-loaded and highly heritable tool-using behaviors might have been an instrumental driving force in the evolution of chimpanzees.

Thus findings from the study of human intelligence, non-human intelligence at the individual level, and comparative intelligence between taxa continue to be largely comparable, consistent with the prediction that the *g*-nexus should generalize to all taxa for which *g* is a central component of cognition.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Highlights

- We computed g -loadings for 13 cognitive tasks in chimps to test Jensen effects
- We calculated phenotypic and additive genetic variance for each task
- We obtained h^2 of cognitive abilities from the same sample of chimpanzees as Hopkins et al. (2014)
- The four variables were positively, strongly related, expanding on studies in humans
- Tool use showed signs of strong selection pressures in line with Primata-wide studies

Table 1

g loading, heritability (h^2), coefficient of additive genetic variance (CVA), and phenotypic variability (CV) of the 13 cognitive tasks.

Cognitive task	<i>g</i> loading	h^2	CVA	CV	Mean performance (SD)
Spatial memory	.270	.268	45.474	87.841	.623 (.547)
Object permanence	.659	.295	31.635	58.244	.615 (.358)
Rotation	.466	.000	0.000	75.441	.488 (.368)
Transposition	.538	.479	48.965	70.749	.661 (.468)
Relative numbers	.472	.000	0.000	46.383	.665 (.308)
Causality-noise	.203	.000	0.000	54.972	.543 (.299)
Causality-visual	.237	.000	0.000	50.701	.628 (.318)
Tool use	.516	.740	263.795	306.656	.305 (.935)
Tool properties	.191	.105	18.398	56.776	.701 (.398)
Comprehension	.468	.268	74.991	144.857	.419 (.607)
Production	.607	.501	150.058	212.003	.352 (.746)
Attention state	.515	.314	73.773	131.654	.393 (.517)
Gaze following	.048	.020	20.484	144.842	.474 (.687)

Table 2Correlations between *g* loadings, heritabilities, CVAs, and CVs of cognitive tasks.

	(1)	(2)	(3)
(1) <i>g</i> loading	–		
(2) Heritability (h^2)	.61 *	–	
(3) CVA	.43	.90 *	–
(4) Phenotypic variability (CV)	.26	.75 *	.94 *

Note.

* Significant correlations ($p < .05$; $N=13$).

Table 3

Loadings of the vectors of *g* loadings, heritabilities, CVAs and CVs on the multivector common factor using unit-weight factor analysis.

Indicator	Factor loadings
<i>g</i> loading	.67 [*]
Heritability (h^2)	.95 [*]
CVA	.95 [*]
Phenotypic variability (CV)	.86 [*]

Note.

^{*} Significant factor loadings ($p < .05$; $N = 13$).