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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 more *g*-loaded cognitive abilities would also be more heritable addition to presenting greater additive genetic variance and interindividual phenotypic variability. This pattern was confirmed with multiple analytical approaches, 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 phenotypic variance, consistent with previous findings indicating that it is associated with high interspecies variance and has evolved rapidly in comparative primate studies.

1. Introduction

1.1. Jensen effects

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

Various studies involving humans have found Jensen effects on subtest heritabilities. In Western samples, correlations between the vector of subtest *g* loadings and heritability values range in magnitude from .27 to .77 across studies (Jensen, 1987; Kan, Wicherts, Dolan, & van der Maas, 2013; Pedersen, Plomin, Nesselroade, & McClearn, 1992; Rijsdijk, 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).

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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 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 environmental variation and error.

One Jensen effect that has been identified both in humans and more recently in nonhuman primates is the strong correlation between *g* loadings and the size of differences in cognitive abilities among populations (or among species, in nonhuman 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, 2008), 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. This appears to be the case with humans (Spitz, 1988). Additionally, traits closely related to fitness, as is hypothesized to be be case for g, are associated with larger mutational target sizes, which increase their sensitivity to *de novo* pleiotropic mutations which in turn increase 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 Pavlicev, Cheverud, & Wagner, 2010; Stearns, 1992, for other putative causes leading to high genetic variability in traits that are importantly connected to fitness). As more *g*-loaded abilities appear to be under stronger selection in the primate phylogeny (Fernandes et al., 2014), we expect that *g* loadings will correlate positively not only with 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 data from Hopkins et al. (2014) in an effort to examine 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. Therefore we attempt to investigate whether these properties are *homologous* (i.e. features common to different species that are derived from common ancestry) between humans and chimpanzees. We also expand on these previous two studies via examination of phenomena that are still unexplored in studies of Jensen effects in human intelligence: using the database from Hopkins et al. (2014) it is possible to calculate coefficients of additive genetic variance (CVA), 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 for 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 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;