Please cite this article in press as: Hopkins et al., Chimpanzee Intelligence Is Heritable, Current Biology (2014), http://dx.doi.org/10.1016/j.cub.2014.05.076

Current Biology 24, 1–4, July 21, 2014 ©2014 Elsevier Ltd All rights reserved http://dx.doi.org/10.1016/j.cub.2014.05.076

Report

Chimpanzee Intelligence Is Heritable

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Summary

The role that genes play in human intelligence or IQ has remained a point of significant scientific debate dating back to the time of Galton [1]. It has now become increasingly clear that IQ is heritable in humans, but these effects can be modified by nongenetic mechanisms [2–4]. In contrast to human IQ, until recently, views of learning and cognition in animals have largely been dominated by the behaviorist school of thought, originally championed by Watson [5] and Skinner [6]. A large body of accumulated research now demonstrates a variety of cognitive abilities in nonhuman animals and challenges traditional behaviorist interpretations of performance [7, 8]. This, in turn, has led to a renewed interest in the role that social and biological factors might play in explaining individual and phylogenetic differences in cognition [9]. Specifically, aside from early attempts to selectively breed for learning skills in rodents [10–12], studies examining the role that genetic factors might play in individual variation in cognitive abilities in nonhuman animals, particularly nonhuman primates, are scarce. Here, we utilized a modified Primate Cognitive Test Battery [13] in conjunction with quantitative genetic analyses to examine whether cognitive performance is heritable in chimpanzees. We found that some but not all cognitive traits were significantly heritable in chimpanzees. We further found significant genetic correlations between different dimensions of cognitive functioning, suggesting that the genes that explain the variability of one cognitive trait might also explain that of other cognitive traits.

Results and Discussion

Principal-Component Analysis

Cognitive performance was assessed on 13 tasks from the Primate Cognition Test Battery (PCTB) task originally developed by Herrmann and colleagues [13, 14]. The 13 tasks are designed to assess a variety of cognitive abilities, broadly defined as nonsocial and social cognition. To assess the structure and heritability in cognitive performance in the chimpanzees, we performed principal-component analysis (PCA) on their accuracy for individual PCTB tasks. PCA allowed us to derive unbiased component-performance constructs based on item loadings of the different tasks. Component scores with eigenvalues greater than 1.0 were considered significant, and item-component coefficients greater than 0.55 (absolute value) were considered salient items. We also computed a single measure of cognitive performance by deriving a composite factor score from the first unrotated component from a separate PCA analysis (this measure is referred to as the "g" factor). Descriptive data and heritability analyses of the raw performance data can be found in Table S1 and Figure S1.

The PCA with varimax rotation revealed four components with eigenvalues >1.0, and these accounted for 54.20 percent of variance (Table 1). Performance on the tasks involving spatial memory, object permanence, rotation, and transposition loaded on component 1. The causality-visual task and tool use loaded on component 2, while communication production, attention state, and gaze following loaded on component 3. Finally, causality-noise was the single task to load on component 4. Each of the four significant component scores was saved, and we compared these scores between sexes and rearing groups by using multivariate analysis of variance (MANOVA). No significant main effects or interactions were found between sex and rearing conditions on the component scores (Table S1).

Quantitative Genetics

As has been done in previous studies in primates [15, 16], we used the program SOLAR (Sequential Oligogenic Linkage Analysis Routines) to estimate heritability [17]. The overall "g" factor score as well the scores for each of the four components derived from the PCA served as the variables of interest in the heritability analyses. Age, sex and rearing history served as covariates. Significant heritability was found for the overall "g" factor score as well as components 1 and 3 but not 2 and 4 (see Figure 1). Recall that the four tasks spatial memory, object permanence, rotation, and transposition loaded on component 1, while communication production, attention state, and gaze following loaded on component 3 (see Table 1). None of the covariates accounted for a significant proportion of variance in the PCA components.

Genetic Correlations

To determine the extent to which any two traits might have the same set of genes that account for their variation, we performed genetic correlations between the component 1 and 3 scores. This analysis revealed a significant genetic correlation between these two components (r_g = 0.992, SE = 0.522, $p < 0.05$), suggesting that the same set of genes explains variability in performance on the tasks loaded onto components 1 and 3 (see Table 1).

PCA analysis with varimax rotation of performance measures on 13 cognitive tasks revealed four factors. Two of these components (1 and 3), as well as the overall "g" factor, were found to be significantly heritable. Significant genetic correlations were found between factors 1 and 3, suggesting that common genes might underlie their heritability. Lastly, neither sex nor rearing history accounted for a significant proportion of variance in cognitive performance.

A significant proportion of variance in overall chimpanzee cognitive performance was found to be heritable. The overall "g" factor and two (1 and 3) of the four components were significantly heritable, suggesting that genetic factors contribute to individual differences in chimpanzee cognition. The proportion of variance accounted for by genetic factors was moderate to large [18], whereas nongenetic factors, including sex

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Table 1. Component Scores and Item Loadings for the PCTB Tasks

Item	C1	C2	C3	C4
Eigenvalue	3.066	1.513	1.404	1.063
Percent variance	23.59	11.68	10.80	8.18
Spatial memory	.648*	−.473	−.014	.029
Object permanence	.621*	.243	.265	.148
Rotation	.665*	.157	−.088	−.002
Transposition	.729*	.046	−.027	.102
Relative numbers	.260	.392	.122	.432
Causality-noise	.038	.084	−.008	.776*
Causality-visual	−.064	.711*	−.062	.114
Tool use	.218	.667*	.224	.063
Tool properties	.265	.449	−.479	.040
Comprehension	.424	.400	.339	−.356
Production	.458	.095	.587*	.150
Attention state	.173	.084	.669*	.397
Gaze following	−.163	.062	.584*	−.239

Entries marked with an asterisk indicate significant item loading. C = component.

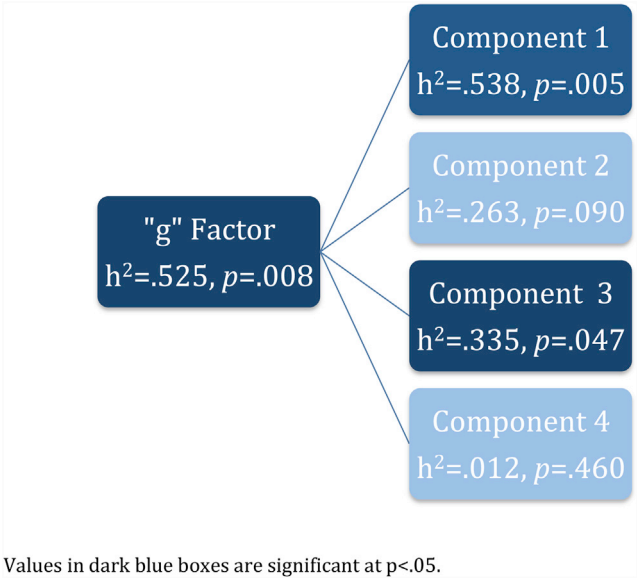

Figure 1. Hierarchical Representation of PCA Results and Associated Heritability Estimates for the Overall "g" Factor and Each of the Four Components Derived from the Analysis

and rearing history, were not significant. Furthermore, for the spatial-cognition and communication components, significant genetic correlations were found, suggesting that common genes might explain individual differences in performance on these two measures.

Although we found significant genetic correlations between the communication and spatial-cognition components, it is important to emphasize that the overall "g" factor score was also significantly heritable. Thus, even though some cognitive constructs (components 1 and 3) were heritable and others (components 2 and 4) were not, we believe the general findings reported here reflect heritability in overall cognitive performance rather than distinct aptitudes for two reasons. First, although we used eigenvalues >1.0 to derive specific components, examination of the spree plot does not show a sharp drop off between any of the components; such a drop off is more commonly observed when robust distinct components are evident from PCA. Furthermore, it has been suggested that using eigenvalues >1.0 as the criteria for determining relevance in PCA can lead to overextraction [19]. Parallel analysis, which evaluates what minimum eigenvalues are needed to reject the null hypothesis when it is adjusted for sample size and the number of tasks or items, has been proposed as a solution to this problem [20]. When parallel analysis was applied to this study, only component 1 had an eigenvalue that would be considered significant. Second, the composite scores for the individual components were positively and significantly correlated with the first unrotated factor (or "g" factor score). Thus, individual differences in the derived "g" factor score correlated with scores for components 1 (r = 0.771, p < 0.001), 2 (r = 0.457, p < 0.001), 3 (r = 0.363, p < 0.001), and 4 (r = 0.256, p < 0.02), suggesting substantial overlap in the underlying or latent cognitive ability [21].

In terms of the structure of the performance measures on the PCTB tasks, the PCA findings are not entirely consistent with the a priori structure originally proposed by Herrmann et al. [13]. In previous studies in human children, chimpanzees, and orangutans, the individual tasks comprising the PCTB were broadly defined into a two-construct structure including nonsocial and social cognition [13]. The nonsocial cognition construct was further broken down into three subcomponents, including spatial cognition, understanding causality, and number discrimination, whereas social cognition was divided into two constructs, communication and theory-of-mind [13]. The two-construct structure of PCTB performance in chimpanzees (i.e., nonsocial versus social constructs) has been validated with confirmatory factor analysis [22], but the five-construct structure has not been found and was likewise not demonstrated in this study. Thus, the a priori structure of social and nonsocial cognition as measured by the PCTB task does not appear to be entirely valid, at least on the basis of the data and PCA analysis used in this study.

There are at least two limitations of this study. First, although this is one of the largest studies of cognition performed on chimpanzees, compared to other quantitative genetic studies in humans, it was relatively small. A replication of this study in a larger cohort of chimpanzees would be useful and allow for increased statistical power. One advantage of the PCTB is that it is relatively simple to administer, and therefore data could be obtained from a larger sample of apes without too much effort and expense. Nonetheless, we do believe the findings presented here are stable and valid. For instance, over a two-year period, we re-tested 86 of the original 99 chimpanzees in this study on the 13 PCTB tasks. For the most part, performance was stable over time, although the chimpanzees did significantly better on the retest of the object permanence, rotation, transposition, and relative number tasks, whereas performance was significantly lower for gaze following (Table S2). A PCA on the retest data constrained the number of components to four and revealed a pattern of item loadings similar to that found in the original analysis (Table S3). The only differences in the item loadings for the components between tests were that gaze following loaded on component 4 instead of 3 and the visual-causality task failed to load on any component. Importantly, heritability for the "g" factor based on the retest data was significant (h^2 = 0.624, SE = 0.242, p < 0.005) and quite similar to the values from the original analysis (see Figure 1). Thus, within our sample, the structure and heritability in cognitive performance was consistent over time.

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Second, it is important to recognize that the findings of this study are limited to a discussion of heritability in cognition for a specific set of tasks assessed at a given point in time. We did not measure the acquisition and learning of the tasks comprising the PCTB; therefore, we are not estimating heritability in chimpanzee learning abilities per se. To estimate heritability in learning ability would require assessment of the acquisition of novel problem-solving tasks, as has been reported in mice [23]. This could be a novel and alternative approach to comparative heritability studies of cognition in human and nonhuman primates in the future.

Finally, from an evolutionary standpoint, the results reported here suggest that genetic factors play a significant role in determining individual variation in cognitive abilities, particularly for spatial cognition and communication skills. Presumably, these attributes would have conferred advantages to some individuals, perhaps in terms of enhanced foraging skills or increased social skills, leading to increased opportunities for access to food or mating [24, 25]. These individuals would have then potentially had increased survival and fitness, traits that would have become increasingly selected upon during primate evolution, as has been postulated by a number of theorists, going all the way back to Darwin [26–30].

Experimental Procedures

Subjects

This study involved 99 chimpanzees, including 29 males and 70 females. Subjects ranged in age from 9 to 54 years (mean = 24.55, SD = 10.67). Ninety-five of the subjects were residing at the Yerkes National Primate Research Center (YNPRC) of Emory University, and four were housed at the Language Research Center (LRC) of Georgia State University. Within the sample, there were 44 mother-reared (35 female, 9 male), 43 human-reared (24 female, 19 male), and 12 wild-caught individuals (11 female, 1 male). The 40 human-reared YNPRC chimpanzees had been separated from their mothers within the first 30 days of life as a result of unresponsive care, injury, or illness [31, 32]. These chimpanzees were placed in incubators, fed standard human infant formula (nonsupplemented), and cared for by humans until they could sufficiently care for themselves, at which time they were placed with other infants of the same age until they were 3 years of age [31, 32]. At 3 years of age, human-reared chimpanzees were integrated into larger social groups of adult and subadult chimpanzees. The rearing of the three human-raised LRC chimpanzees has been described extensively elsewhere [33–37]. Mother-reared chimpanzees were not separated from their mother for at least 2.5 years of life and were raised in nuclear family groups ranging from 4 to 20 individuals. Wild-born chimpanzees were individuals who had been captured in the wild and subsequently brought to research facilities within the United States prior to 1974, when the importation of chimpanzees was banned. Within the mother-reared cohort of 44 chimpanzees, offspring from 29 different females were represented, and the 43 human-reared offspring were born to 30 different females. Thus, the range in genetic variation, at least from the standpoint of the dams, was comparable between the cohorts. The average related coefficient of the sample was 0.0178 and did not differ between mother- (mean = 0.017) and human-reared (mean = 0.0185) individuals [$t(97) = -1.18$, $p = 0.240$]. All procedures used with the chimpanzees were approved by the local institutional animal care and use committee.

Procedures

Subjects were tested on a modified version of the PCTB originally developed by Hermann et al. [13, 14] and described elsewhere [38]. The PCTB attempts to assess subjects' abilities in various areas of nonsocial and social cognition. We followed the previously published procedures as closely as possible, but we modified some tasks to better address the questions at hand given the past experience and environmental constraints of our subjects. The nine nonsocial and four social cognition tasks are described in the Supplemental Experimental Procedures (S1), and we have indicated when procedures differed from those described by Herrmann et al. [13]. Testing was completed over three to five testing sessions, depending on the motivation and attention of the subject.

Quantitative Genetic Analysis

Heritability (h^2) is the proportion of total phenotypic variance that is attributable to all genetic sources. Total phenotypic variance is constrained to a value of 1; therefore, all nongenetic contributions to the phenotype are equal to $1 - h^2$. The analytic approach we took takes into consideration all relationships within a sample and allows for an analysis of heritability via quantitative genetics based on the entire pedigree. To estimate heritability in PCTB performance, we used the software package SOLAR [17], which uses a variance-components approach to estimate the polygenic component of variance when the entire pedigree is considered. SOLAR has been previously used for estimating heritability in various behavioral and temperament traits, as well as different aspects of cortical organization in extended pedigrees of baboons, vervet, and rhesus monkeys (see [39–44]).

Supplemental Information

Supplemental Information includes one figure, three tables, and Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.05.076.

Acknowledgments

This research was supported by NIH grants MH-92923, NS-42867, NS-73134, and HD-60563 to W.D.H. and National Center for Research Resources grant P51RR165 to YNPRC, which is currently supported by the Office of Research Infrastructure Programs under OD P51OD11132). We appreciate the helpful comments of the four reviewers and Alex Weiss for bringing to our attention the use of parallel analysis in determining the number of components to extract with PCA.

Received: August 7, 2013
Revised: March 18, 2014
Accepted: May 30, 2014
Published: July 10, 2014

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