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Abstract

Most studies of animal cognition focus on group performance and neglect individual differences and the correlational structure of cognitive abilities. Moreover, no previous studies have compared the correlational structure of cognitive abilities in nonhuman animals and humans. We compared the structure of individual differences of 106 chimpanzees and 105 two-year-old human children using 15 cognitive tasks that posed problems about the physical or social world. We found a similar factor of spatial cognition for the two species. But whereas the chimpanzees had only a single factor in addition to spatial cognition, the children had two distinct additional factors: one for physical cognition and one for social cognition. These findings, in combination with previous research, support the proposal that humans share many cognitive skills with nonhuman apes, especially for dealing with the physical world, but in addition have evolved some specialized skills of social cognition.

Keywords

individual differences, chimpanzees, human children, social cognition, physical cognition

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The main approach in studying both animal and human cognition is to compare experimentally constituted groups on some cognitive task, with individual differences serving as “error variance” only. There is a second approach to human cognition, however—one that is based on the analysis of individual differences and their intercorrelations (for overviews, see Sternberg, 1999, 2004). In this approach, one looks for underlying factors that might be responsible for individual variation in cognitive performance on multiple cognitive tasks.

There has been very little work on the cognition of nonhuman animals from the perspective of individual differences. A few animal studies have found positive correlations across various types of spatial orientation (maze) tasks (e.g., Crinella & Yu, 1995; Davenport, Hagquist, & Rankin, 1970; Thorndike, 1935), and a few other studies, mostly with mice and rats, have used a somewhat broader range of tasks and also found positive correlations (e.g., Thompson, Crinella, & Yu, 1987). In some of these studies, however, the underlying motivational system was the same across tasks, and therefore the positive correlations could have been due to motivational rather than cognitive commonalities (Anderson, 1993; Locurto & Scanlon, 1998). More diverse batteries of cognitive tasks with different motivational demands have yielded mixed

results (e.g., Galsworthy et al., 2005; Locurto, Benoit, Crowley, & Miele, 2006; Locurto, Fortin, & Sullivan, 2003; Matzel et al., 2003). Almost all nonhuman studies have focused on tasks of physical problem solving, usually emphasizing spatial abilities, without examining performance on social tasks at all.

No studies of nonhuman primates have used the individual differences approach systematically, and there have been no comparisons of humans and other animal species from this perspective. In a meta-analysis, Deaner, van Schaik, and Johnson (2006) proposed a domain-general explanation of intelligence in primates, but this analysis was based on a general comparison across different genera, not on individual variability (see also Lee, 2007). Based on previous research, one hypothesis would be that humans have some factor of social intelligence not possessed by their nearest primate relatives—as humans are specifically adapted for living in and exchanging information in cultural groups. In a previous study comparing the cognitive performance of chimpanzees, orangutans, and 2-year-old

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human children on a wide-ranging battery of cognitive tasks, we found that all species had the same basic cognitive skills in the physical domain (tasks involving space, quantities, and causality), but that the children showed more skills in the social domain (tasks involving communication, social learning, and theory of mind; Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007). But this finding of species differences in the social domain does not speak to the issue of the internal structure of the cognitive abilities underlying task performance for the different species.

In the current study, therefore, we investigated individual differences in the cognitive abilities of human children and chimpanzees, with the goal of uncovering the factor structure underlying those individual differences. This investigation was based on an especially broad array of cognitive tasks (15 tasks from six categories) given to a large number of individuals of the two species (more than 100 of each). This study is the first systematic comparison of the individual differences in cognitive abilities of humans and one of their two closest living relatives. Based on previous research (Herrmann et al., 2007; see Tomasello, Carpenter, Call, Behne, & Moll, 2005, for a review), our hypothesis was that the children would show a distinct factor for social intelligence, whereas the chimpanzees would not.

Method

Participants

Subjects for this study were 106 chimpanzees (*Pan troglodytes*) and 105 human children (*Homo sapiens*) from our previous study (Herrmann et al., 2007). Thirty-six chimpanzees lived at the Ngamba Island chimpanzee sanctuary, Lake Victoria, Uganda, and 70 lived at Tchimpounga chimpanzee sanctuary, Republic of Congo. The chimpanzees' ages ranged from 3 to 21 years, and there were equal numbers of females and males. All of the chimpanzees came to the sanctuaries as orphans as a result of the illegal bush-meat trade, were raised by humans together with peers, and at the time of testing lived in social groups with access to outdoor forest areas during the day and dormitories at night. The human subjects included 53 female and 52 male 2.5-year-olds (± 2 months), mostly from middle-class German homes; they were recruited by telephone from an existing database.

Tasks and administration

In the original study (Herrmann et al., 2007), we developed and administered a large battery of cognitive tasks (the Primate Cognition Test Battery, or PCTB), which consisted of 15 different tasks of several items each (Table 1 describes the tasks briefly, and more information is available in Methodological Details and Additional Analysis, part of the Supplementary Material available on-line). Both the human children and the chimpanzees had never previously participated in

similar studies; therefore, the test situation and all test items were novel for both species.

Participants were tested individually by a human experimenter, with the same experimenter testing a given subject throughout the entire battery. Each participant completed all tasks in the PCTB, which took from 3 to 5 hr altogether, across several days of testing. The same basic task order was used for both species. The chimpanzees were tested in a familiar room, and the human children were tested in a child laboratory, accompanied by a parent who was told not to influence or help in any way.

For most of the tasks, a human experimenter sat behind a table facing the subject; a Plexiglas window (children and some apes) or a mesh panel (apes only) separated the experimenter and the subject. At different positions, the window had three holes, through which subjects could insert a finger to indicate their choice when necessary. The experimenter always waited until the subject was facing her before beginning a trial. For trials requiring a choice, the position of the reward was counterbalanced across either two or three locations, but the reward was never hidden in the same place for more than two consecutive trials. In a few tasks, such as those requiring subjects to follow gaze direction or gesture to the experimenter, subjects were tested in other setups.

All testing was videotaped. Subjects' responses were initially coded live by the experimenter, except in the case of gaze-following trials, which the experimenter coded from videotape after the test. A second observer independently scored (from videotape) 100% of the trials from each task for both species. The interobserver agreement for all tasks combined was 99% for the chimpanzees and 99% for the human children.

Data analysis

To test the factor structure of the PCTB for the human children and chimpanzees, we used confirmatory factor analysis (CFA). For each species, we tested one-, two-, and three-factor structures (see Fig. 1).

We combined the alternative-models, or *competing-models*, approach with a *specification-search* approach (Jöreskog & Sörbom, 1996), in which modifications of the initially specified model are added—that is, the model is respecified in order to obtain a model that fits better or is more parsimonious than the original model. We tested these models with LISREL 8.80 (Jöreskog & Sörbom, 2006), fixing each factor's variance to 1.00 in order to identify the models. The analysis was computed from covariance matrices. The LISREL maximum likelihood solution algorithm was used to estimate model parameters, and the assumptions of multivariate normality and linearity were tested with Prelis 2.80 (Jöreskog & Sörbom, 2006). We evaluated the models' goodness of fit with the following indices: the chi-square test, the comparative-fit index, the nonnormed fit index, the standard root-mean-square residual, and the root-mean-square error of approximation

Table 1. Primate Cognition Test Battery: Description of Tasks and Mean Proportion (With Standard Deviation) of Correct Responses by Chimpanzees and Human Children

Scale and task	Description	Chimpanzees		Human children	
		Mean	SD	Mean	SD
Physical domain					
Space					
Spatial Memory (1 item, 3 trials)	Locating a reward	.95	.15	.91	.17
Object Permanence (3 items, 9 trials)	Tracking of a reward after invisible displacement	.64	.18	.79	.17
Rotation (3 items, 9 trials)	Tracking of a reward after a rotation manipulation	.56	.19	.55	.18
Transposition (3 items, 9 trials)	Tracking of a reward after one or more location changes	.70	.23	.57	.26
Quantities					
Relative Numbers (1 item, 13 trials)	Quantity discrimination	.66	.12	.71	.16
Addition Numbers (1 item, 7 trials)	Quantity discrimination with added quantities	.69	.16	.64	.18
Causality					
Noise (2 items, 6 trials)	Causal understanding of noise produced by hidden rewards	.61	.17	.85	.16
Shape (2 items, 6 trials)	Understanding of appearance change caused by a hidden object	.68	.18	.83	.20
Tool Properties (5 items, 15 trials)	Understanding of functional and nonfunctional tool properties	.61	.11	.71	.13
Social domain					
Social learning					
Social Learning (3 items, 3 trials)	Solving a simple but not obvious problem by observing a demonstrated solution	.10	.17	.86	.23
Communication					
Comprehension (3 items, 9 trials)	Understanding communicative cues indicating the location of a hidden reward	.63	.13	.84	.15
Point Cups (1 item, 4 trials)	Production of communicative gestures in order to retrieve a hidden reward	.74	.27	.72	.36
Attentional State (4 items, 4 trials)	Adapting choice of communicative gesture to the attentional state of the recipient	.34	.29	.59	.38
Theory of mind					
Gaze Following (3 items, 9 trials)	Following an actor's direction of gaze to a target	.22	.20	.45	.34
Intentions (2 items, 6 trials)	Understanding what an actor intended to do (unsuccessfully)	.59	.16	.85	.17

Note: Some parts of this table are taken from Herrmann, Call, Hernández-Lloreda, Hare, and Tomasello (2007).

(Mulaik et al., 1989; Schreiber, Stage, King, Nora, & Barlow, 2006).

We calculated the unstandardized estimates and standard errors, as well as standardized estimates, in order to assess the magnitude of the contribution of each latent variable to the dependent variable (see Tables S1 and S2 in the Supplementary Material). The statistical significance of each coefficient was established through an examination of the *t* value (the ratio between the unstandardized coefficient and the standard error); *t* values with an absolute value greater than or equal to 2 indicated statistical significance at the .05 level.

We preceded CFA with exploratory factor analysis (EFA) in order to explore the pattern of the matrix of factor loadings for each of the two species. EFA was performed using the software program FACTOR (Lorenzo-Seva & Ferrando, 2006).

The correlation matrices were used as input data into minimum-rank factor analysis (see, e.g., Shapiro & ten Berge, 2002). After the extraction phase, the solution was rotated using the Promin method (Lorenzo-Seva, 1999) to achieve maximum simplicity and interpretability. We computed the *parallel analysis* (Lattin, Carroll, & Green, 2003) to help us determine the number of factors.

Results

The overall level of performance of the two species on the 15 tasks of the PCTB (as originally reported in Herrmann et al., 2007) is presented in Table 1. The psychometric properties of each task are reported in Tables S3 and S4 of the Supplementary Material.

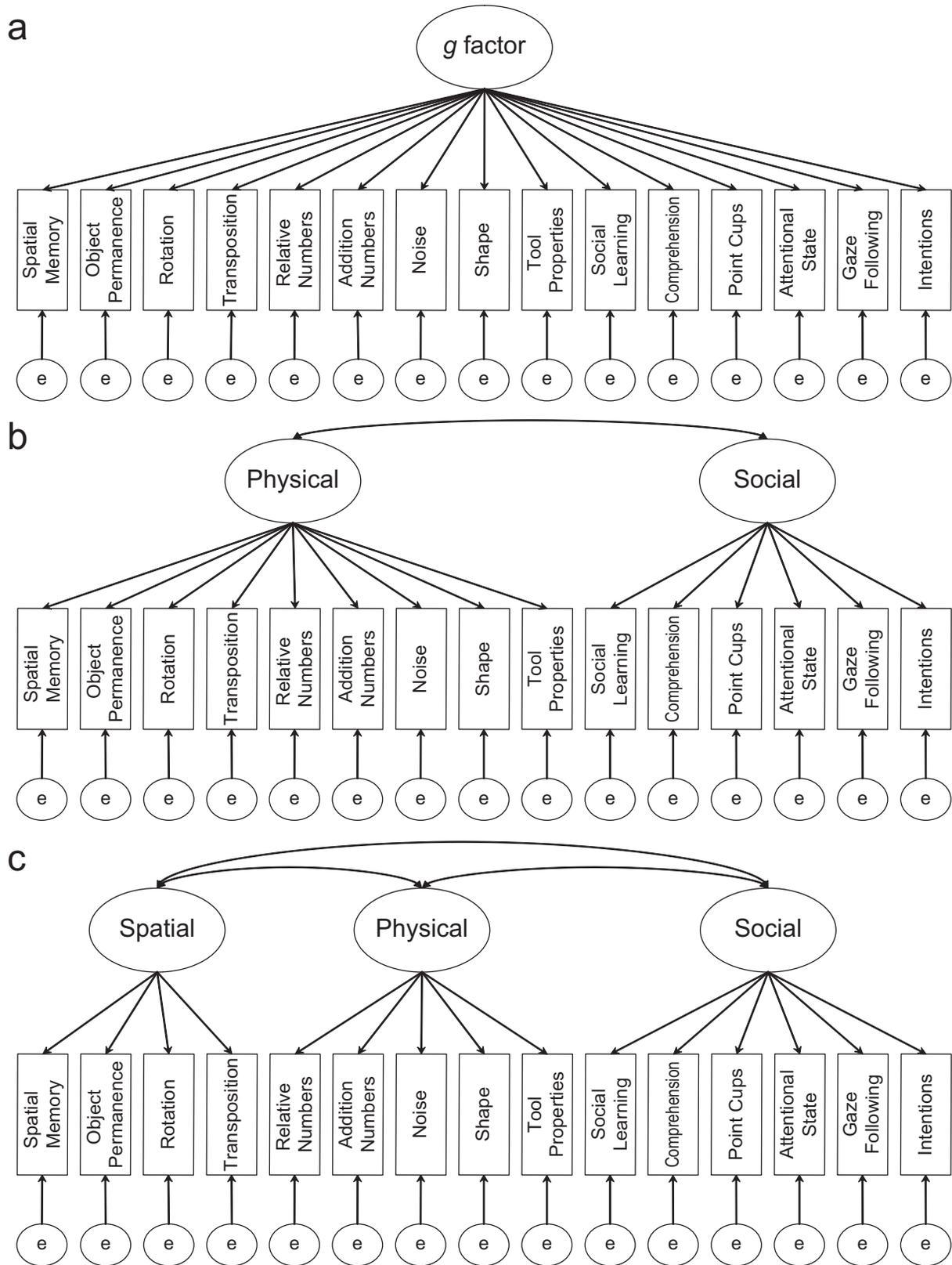


Fig. 1. Theoretical models used in the data analysis: (a) *g*-factor model (general intelligence), (b) two-factor model (physical and social factors), and (c) three-factor model (spatial, physical, and social factors). Observed variables are depicted graphically using rectangles. Unobserved variables are depicted with circles or ovals. The ovals at the top of the models are the unobserved, or latent, variables (latent factors, common factors, or constructs); the circles at the bottom of the models are the unique factors, or measurement errors (*e*), in the observed variables. The straight arrows pointing from a factor to the observed variables indicate the causal effect of the factor on the observed variables. Curved arrows between factors indicate that they are correlated.

Preliminary EFAs suggested a different number of factors for the two species. Consequently, we conducted CFAs for each species separately (Meredith, 1993). The theoretical model underlying the CFAs was derived from Tomasello and Call's (1997) theoretical analysis of primate cognition, on which the PCTB was based. In this analysis, the primary division is between physical cognition and social cognition. Furthermore, the theory posits that physical cognition evolved mainly in response to demands of foraging and comprises skills involving *space* (for finding food), *quantity* (for comparing yields of different foraging locations), and *causality* (for extracting food from difficult places). Social cognition evolved mainly in response to demands of social interaction and comprises skills of *social learning* (for learning important things vicariously), *communication* (for manipulating other individuals), and *theory of mind* (for predicting the behavior of other individuals). The PCTB therefore comprises three scales within each of two domains (i.e., physical and social cognition).

We performed a CFA of the full battery for each species, testing one-, two- and three-factor structures (see Fig. 1). All tasks were expected to load on the single factor (general intelligence, or *g*) in the one-factor model; that is, one factor should account for performance on each task. The two-factor model divided the battery into physical and social domains. We were also interested in investigating a separate spatial factor, given that studies on nonhuman animals have often found a *g* factor based mainly on spatial tasks. Thus, the three-factor model divided the battery into spatial, physical, and social domains.

CFA for human children's performance on the PCTB

There were no missing data for any of the 105 human children, and therefore all human subjects went into the analysis. Results revealed that the best-fitting model for human children was the three-factor model, $\chi^2(54) = 52.68, p = .53$, that is, a model that divided the PCTB into spatial, physical, and social domains. Neither the one- nor the two-factor model fitted the data. The chi-square test for the one-factor model was statistically significant, $\chi^2(44) = 72.31, p = .005$, indicating that the model did not fit. The two-factor model did not fit the data and indeed led to negative estimates of unique variance.

The correlations among the three factors were statistically nonsignificant. Figure 2 presents the results of the CFA for the children's data; it shows the standardized parameter estimates, as well as the squared multiple correlation values (in italics), which represent the lower bounds of the proportion of variance accounted for by the factors. For example, the spatial factor accounted for 7% of the variability in performance on the Spatial Memory and Object Permanence tasks and 37% of the variability in performance on the Transposition task. All the coefficients in the model were statistically significant. The two variables not included in the final model were one that had a nonsignificant coefficient estimate and another whose inclusion led to nonconvergence or improper solution problems (i.e., variables with zero or negative estimates of unique variance; see, e.g., van Driel, 1978). The correlation matrix is included in Table S5 of the Supplementary Material. The goodness-of-fit values indicated a good fit between the model and the observed

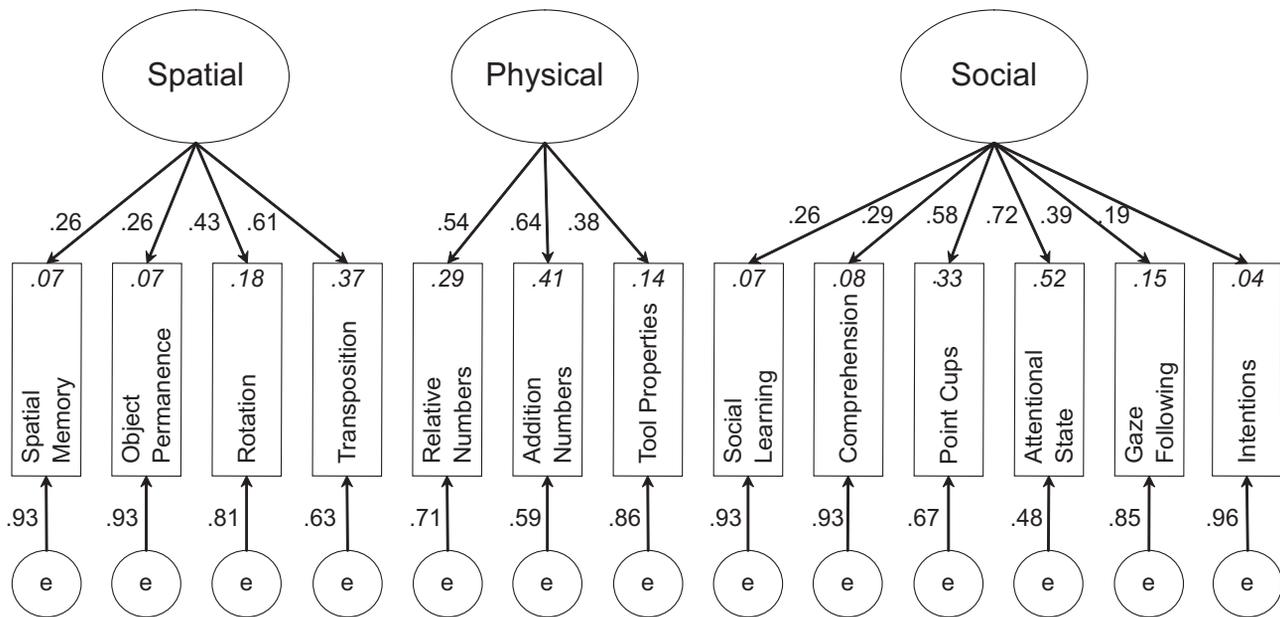


Fig. 2. The best-fitting model from the confirmatory factor analysis of the human children's performance on the Primate Cognition Test Battery. In this model, performance on 13 tasks loaded onto three factors (e = error). The numbers alongside the arrows are standardized parameter estimates. The numbers in italics are the squared multiple correlation values, which represent the lower bounds of the proportion of variance accounted for by the factors.

data: $\chi^2(54) = 52.68, p = .53$; comparative-fit index = .99; root-mean-square error of approximation < .00; nonnormed fit index = .98; standardized root-mean-square residual = .08.

comparative-fit index = .90; root-mean-square error of approximation = .034; nonnormed fit index = .85; standardized root-mean-square residual = .07.

CFA for chimpanzees’ performance on the PCTB

There were no missing data for any of the 106 chimpanzees, and therefore all these subjects went into the analysis. Results revealed that the best-fitting model for chimpanzees was a two-factor model (see Fig. 3); the correlation between the two factors was statistically nonsignificant. The one-factor and three-factor models did not converge. We named the factors Spatial and Physical-Social. The former accounted for individual variability in spatial tasks, and the latter accounted for individual variability in some nonspatial physical and social tasks. There was no factor that seemed to identify specifically social cognition skills apart from physical cognition ones. Again, the variables not included were those with nonsignificant coefficient estimates and those whose inclusion led to nonconvergence or improper solution problems. The correlation matrix is included in Table S5 of the Supplementary Material. The goodness-of-fit values indicated, in general, a good fit between the model and the observed data: $\chi^2(14) = 16.93, p = .26$;

Discussion

We found different factor structures underlying chimpanzees’ and human children’s performance on a battery of cognitive tasks. For chimpanzees, the best-fitting model was a two-factor model, with one factor accounting for performance on spatial tasks and a second factor accounting for performance on two physical and two social-cognitive tasks. For children, in contrast, the best-fitting model was a three-factor model, with one factor again accounting for performance on spatial tasks, and with two separate factors accounting for performance on three physical tasks and six social-cognitive tasks, respectively.

In terms of commonalities, we did not find a *g* factor for either species. This could be because we used an especially wide range of cognitive tasks that included everything from assessing quantities to interpreting social cues; most standardized assessments use a more limited range of tasks. Most important, our test battery had approximately equal representation of physical and social tasks. This is not typical for traditional IQ tests, which are most often based on a very restricted

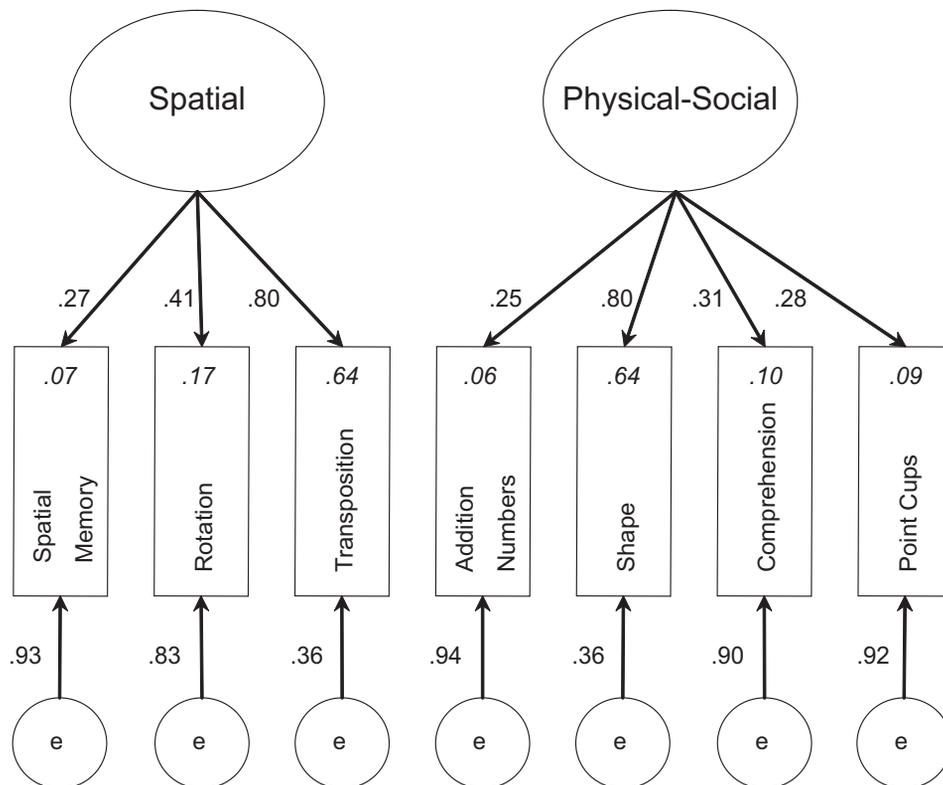


Fig. 3. The best-fitting model from the confirmatory factor analysis of the chimpanzees’ performance on the Primate Cognition Test Battery. In this model, performance on seven tasks loaded onto two factors (*e* = error). The numbers alongside the arrows are standardized parameter estimates. The numbers in italics are the squared multiple correlation values, which represent the lower bounds of the proportion of variance accounted for by the factors.

range of tasks and situations. However, a number of our test items yielded fairly low variabilities in performance, and it is possible that this low variability made it more difficult to find a *g* factor. (Note that this low variability cannot account for the positive patterns we found or the difference in factor structures between the two species.) Further studies are needed to determine with confidence whether chimpanzees and 2-year-old children show a factor of general intelligence when administered a wide array of cognitive tasks.

Another commonality was that both chimpanzees and human children displayed a distinct factor of spatial cognition. In hierarchical analyses of human intelligence, a highly loaded spatial factor emerges consistently. Moreover, in models that do not posit a *g* factor, a spatial factor also typically emerges, as in Thurstone's (1947) primary mental abilities (see review in Plomin, 1988). Within the physical cognitive skills, spatial abilities are obviously among the most critical for survival, as all animals have to locate food and mates and avoid predators. The finding of a separate spatial factor for both species in the current study—as well as findings from mice and rat studies demonstrating that performance on spatial tasks is intercorrelated—suggests a phylogenetically old and coherent underlying skill for solving spatial problems (Plomin, 1988; Upchurch & Wehner, 1989). It has also been shown that brain regions that apparently mediate the expression of spatial performance in rodents and humans may even be homologous (Aggleton, Hunt, & Rawlins, 1986).

The key difference in the current study was that the human children, but not the chimpanzees, showed a separate factor of social cognition. Interestingly, using these same data, we (Herrmann et al., 2007) found that the children scored significantly higher than the chimpanzees on the tasks of social cognition. A given structure of interindividual differences does not necessarily imply an isomorphic structure of intraindividual processes (Borsboom & Dolan, 2006), and different mechanisms can explain the same pattern of correlations (van der Maas et al., 2006). Nevertheless, the findings that children perform better than chimpanzees on tasks of social cognition and also that children's performance on these tasks is more integrated together suggest the possibility that humans have evolved a coherent and specialized set of social-cognitive skills. For dealing with their complex social worlds, chimpanzees have many social-cognitive skills of their own (Call & Tomasello, 2008)—skills that are especially apparent during competition for food and other valued resources (Hare, 2007). But humans may have evolved, in addition, a species-specific “cultural intelligence,” based on even more sophisticated social-cognitive skills, that underlies their unique ways of cooperating and communicating with others in the cultural group (Herrmann et al., 2007; Tomasello et al., 2005). Support for this view comes also from a recent study by Wellman, Lopez-Duran, LaBount, and Hamilton (2008), who found a strong relation between humans' social attention in infancy and their later social-cognitive skills in early childhood—and this continuity was separable from continuities in general information processing.

These results must be viewed with some caution, as it is not really possible for groups from the two different species to be comparable in every respect. Thus, the chimpanzees ranged in age from juveniles to adults, whereas the humans were all young children. But in our previous study (Herrmann et al., 2007), we found no overall effects of age on the chimpanzees' performance, and the human children had to be young because older children or adults would have performed at ceiling on our tasks, and therefore would have produced no variability that could be analyzed. In addition, the chimpanzees and the children had different rearing histories. The chimpanzees we tested were from a special population of orphans put together into social groups as youngsters. At the time of testing, the vast majority of these animals lived in social groups that were allowed to forage socially in a natural environment in Africa on a daily basis. In any case, future research should attempt to determine if our results are widely generalizable to all members of these two species, and, of course, generalization to humans' other closest relative, bonobos, would be important as well. Finally, one might be concerned that children would be more comfortable in our testing situation than apes—given that the experimenter was human and the objects were mostly human artifacts—but in the original study, we measured their comfort level directly and found that the human children were actually shyer than the chimpanzees or less interested than the chimpanzees in the novel items in the test situation. In addition, this temperamental measure did not correlate with performance on the social tasks (Herrmann et al., 2007).

Some classic studies in comparative psychology attempted to identify taxonomic differences in overall intelligence in animals (e.g., Bitterman, 1965; Warden, 1951). But in a modern behavioral ecological approach, the cognitive skills of organisms are studied in relation to the particular ecological problems they are designed to solve, with no assumptions about possible interconnections among different skills (Kamil, 1988; Shettleworth, 1998). This view of the evolution of cognition fits very well with approaches to human intelligence that posit multiple components or multiple intelligences (e.g., Sternberg, 1999; Thurstone, 1938). The current findings thus support the view that different species evolve different cognitive skills for dealing with the ecological and social problems they face, and that humans have evolved special skills of social cognition, presumably for dealing with the complex social-cultural world that they themselves have created. This social-cultural world then supports further development in many different cognitive domains.

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interests with respect to their authorship and/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>

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