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The Role of Socio-Communicative Rearing Environments on the Development of Social and Physical Cognition in Apes

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Abstract

The cultural intelligence hypothesis (CIH) claims that humans' advanced cognition is a direct result of human culture and that children are uniquely specialized to absorb and utilize this cultural experience (Tomasello, 2000). Comparative data demonstrating that 2.5 year old human children outperform apes on measures of social cognition but not on measures of physical cognition support this claim (E. Herrmann, J. Call, M. V. Hernandez-Lloreda, B. Hare, & M. Tomasello, 2007). However, the previous study failed to control for rearing when comparing these two species. Specifically, the human children were raised in a human culture whereas the apes were raised in standard sanctuary settings. To further explore the CIH, here we compared the performance on multiple measures of social and physical cognition in a group of standard reared apes raised in conditions typical of zoo and biomedical laboratory settings to that of apes reared in an enculturated socio-communicatively rich environment. Overall, the enculturated apes significantly outperformed their standard reared counterparts on the cognitive tasks and this was particularly true for measures of communication. Furthermore, the performance of the enculturated apes was very similar to previously reported data from 2.5 year old children. We conclude that apes who are reared in a human-like socio-communicatively rich environment develop superior communicative abilities compared to apes reared in standard laboratory settings, which supports some assumptions of the cultural intelligence hypothesis.

Recently, the cultural intelligence hypothesis (CIH) was put forth by Tomasello (2000) to explain the evolution of the sophisticated cognitive and intellectual abilities of humans compared to nonhuman primates. The CIH claims that human intelligence is dependent on the immersion of human children in a uniquely human culture in which they must learn their native language, learn culturally-specific subsistence skills from community experts and acquire skills in written language and mathematics. The CIH heavily emphasizes the role of social organization and learning in the formation of complex cognition in humans. Tomasello (2000) argues that this dependence on culture for the normal development of species-typical cognitive skills is a uniquely human trait and that human children are uniquely specialized for absorbing and utilizing this cultural knowledge.

From a comparative perspective, the principal data in support of the CIH comes from the recent report by Herrmann, Call, Hernandez-Lloreda, Hare and Tomasello (2007) based on research with human children, orangutans and chimpanzees. Herrmann et al. (2007) used the "Primate Cognitive Test Battery" (PCTB) to measure cognitive abilities in large samples of sanctuary chimpanzees and orangutans and in middle-class German 2.5 year old human

children. The PCTB was designed to test the physical and social cognition abilities of a multitude of primate species, including humans. Herrmann et al. reported that while the chimpanzees and human children did not differ from one another in their performance in the physical cognition domain (although both groups were more skillful than the orangutans), the human children significantly outperformed both ape species in tasks of social cognition. Herrmann et al. (2007) argue that this pattern of results supports the CIH theory and the notion that humans have evolved a specialized set of social cognitive skills which enables them to live in complex cultural groups and facilitates learning through social processes.

While this argument is compelling and the data certainly supported this view, one critical limitation of the previous findings by Herrmann et al. (2007) is the confounding factor of rearing history with species within the context of comparisons between humans and great apes. Specifically, in the study by Herrmann et al., human children raised in a human linguistic and socio-communicative environment were compared to chimpanzees and orangutans raised in sanctuary settings. The claimed evidence of species differences by Herrmann et al. (2007) could arguably be attributable to rearing differences between the human children compared to the great apes. This is particularly significant because the human children would have been raised by humans for 2.5 years whereas the chimpanzees and orangutans would have been raised largely with their conspecifics with only intermittent contact with humans. Recently, Tomasello and Call (2004) reviewed the existing literature focusing on the cognitive abilities of apes reared in different environments and concluded that there are “systematic differences between apes with different rearing histories.” (pp. 214) Ideally, to isolate the role of potential species differences, when controlling for rearing experiences, data from human-raised, enculturated apes are necessary to fully test the CIH.

In this study, we administered a modified version of the PCTB to a sample of enculturated chimpanzees and bonobos and compared the results to a sample of matched-controls who had been raised in standard laboratory or zoo settings. Given the intense focus on communication during the rearing of the enculturated apes, we mainly focused on three social cognition tasks examining communicative abilities in addition to one social cognitive task measuring the apes' propensity to follow gaze. Additionally, we utilized a large set of physical cognitive tasks from the PCTB examining a wide array of abilities including understanding of spatial relationships, spatial memory, numerosity and the properties of tools. If human enculturation has a significant and selective impact on social cognition, then we predicted that human enculturated apes would perform better on social tasks compared to the matched cohorts. Moreover, we hypothesized that enculturated and non-enculturated apes would not differ significantly on physical cognition tasks. Additionally, we compared the performance of the enculturated apes to the results for human children reported by Herrmann and colleagues (2007). If human cultural rearing is a driving force toward social cognitive processes and this effect is not limited to humans, then enculturated apes should perform more similarly to human children than did the standard reared apes used for comparison in Herrmann, et. al.'s study. In contrast, if the CIH is correct and the effects of human cultural rearing on social cognition are species-specific, then enculturation should not mitigate the differences in PCTB performance seen between human children and apes.

Finally, we conducted a large scale study of PCTB performance in a sample of captive chimpanzees that have been differentially reared during the first three years of life. Specifically, we compared PCTB performance in captive born chimpanzees that had been raised by their biological conspecific mothers to those that had been raised by humans for the first three years of life within species-specific peer groups. Our goal in this comparison was to assess whether human rearing per se has a significant impact on PCTB performance or if being raised in a human socio-communicative environment is the critical factor influencing social cognitive processes in great apes.

Method

Subjects

Eighty three chimpanzees (*Pan troglodytes*) and 13 bonobos (*Pan paniscus*) from four different facilities participated in the current study. All available chimpanzees and bonobos who were willing to participate in all aspects of this study were utilized from each facility. The resulting sample included seven bonobos living at the Jacksonville Zoo and Gardens in Jacksonville, Florida (JZG), six bonobos housed at the Great Ape Trust of Iowa in Des Moines, Iowa (GATI), four chimpanzees housed at the Language Research Center in Atlanta, Georgia (LRC) and 79 chimpanzees housed at either the main center or field station of the Yerkes National Primate Research Center in Atlanta, Georgia (YNPRC). It is important to note that all apes voluntarily participated in the current study which meant that they chose to interact with and attend to the experimenter and apparatus. Thus, subjects from all rearing cohorts showed basic motivational and attentional aptitude in order to be included in the study.

Rearing of captive apes is a complex topic and has been done using a variety of methods. However, it can be argued that the rearing environment experienced by most laboratory and zoo apes is drastically different from that of apes reared in the sociocommunicatively rich environments often associated with ape language studies. For our first comparison we distinguished between those apes reared in more traditional captive settings (zoos and laboratories) and those reared in the distinct setting of an ape language project. Thus, for this initial comparison, all apes from JZG and YNPRC were considered “standard reared” while all apes from LRC and GATI were considered “enculturated.” In order to have the most comprehensive subject set possible for this rearing comparison, all apes from GATI and the LRC were included. We then matched each enculturated ape with a standard reared ape based on species, age and sex as closely as possible. Note that one male enculturated bonobo had to be matched to a female standard reared bonobo because there was not an available male for comparison (see Table 1).

Standard reared apes were either raised by their biological mothers or were reared with peers in a nursery setting. For this initial comparison, we do not distinguish between these two rearing methods. In both cases, the apes experienced normal zoological and laboratory rearing environments including the social and physical enrichment typical of these settings. All standard reared apes were housed in groups of 2 to 12 apes and had regular contact with human caregivers. These interactions were typically limited to basic husbandry contexts such as shifting apes between living areas and feeding. The YNPRC chimpanzees have also been involved in a number of behavioral and cognitive testing paradigms (i.e. Hopkins, Dunham, Cantalupo, & Taglialatela, 2007; Hopkins, Russell, & Cantalupo, 2007; Hopkins, Russell, Lambeth, & Schapiro, 2007; Horner & de Waal, 2009; Hostetter, Russell, Freeman, & Hopkins, 2007) thus the apes were familiar with being tested by human experimenters in structured formats. The JZG bonobos had very limited experience as research subjects but regularly participate in positive reinforcement training for basic husbandry behaviors with their caregivers.

The enculturated apes were part of a project at the Language Research Center designed to facilitate intensive social and communicative interaction between humans and apes. Note that our enculturated sample is not limited to the language competent individuals housed at these facilities but also includes the non-language competent “control” subjects. As such, these individuals do not represent a selection bias towards the brightest or most motivated individuals. In fact, some of our enculturated apes actually failed to acquire language competencies despite attempts to teach them and some were selected for the language project simply because they were the first available infant born. In-depth descriptions of the

methodologies utilized in this project have been published extensively elsewhere (Brakke & Savage-Rumbaugh, 1995, 1996; Savage-Rumbaugh, 1986; E. Sue Savage-Rumbaugh & Roger Lewin, 1994; Savage-Rumbaugh, McDonald, Sevcik, Hopkins, & Rupert, 1986; Savage-Rumbaugh et al., 1993; Savage-Rumbaugh, Shanker, & Taylor, 1998). In brief, human caregiver interaction ranged from 8–24 hours daily during rearing of these apes with the majority of that time being engaged in communicative activity. Cognitive testing was performed throughout the day from an early age (initiated between 1–3 years of age). The LRC and GATI apes were in this enriched environment a minimum of 9 years (the age of the youngest bonobo) and a maximum of 30 years (Matata) at the time of testing. In addition, three chimpanzees (Lana, Sherman and Panzee) and three bonobos (Kanzi, Panbanisha and Nyota) are language trained and regularly use a visual lexigram system to communicate with their caregivers. In 2005, the bonobos were moved to the GATI facility, while the four chimpanzees remained at the LRC facility. All eleven of these apes continue to be socially housed and are exposed to high levels of complex communicative interactions with human caregivers.

Note that by our definition, “enculturated” is not synonymous with “language-trained” or with “home reared” which have both been used to define ape enculturation in some previous publications. None of the apes in our sample were reared in an actual human home but rather had close relationships and regular contact with their human caregivers in a non-traditional laboratory setting. Much like human children, these apes spend much of their time engaging with human adults who are actively sharing and teaching about the world around them. While being reared in a laboratory setting, the enculturated apes in our sample are given lots of choices in their daily activities and are given the ability to assert their will and preferences on the social and physical environments in which they live. In terms of language training, three of the GATI bonobos and one of the LRC chimpanzees are classified as enculturated because they regularly interact with humans in a variety of communicative contexts but none of these individuals were trained to use the visual-graphic communication system employed with the other apes.

Furthermore, it is important to note that the enculturated apes in our sample were not “trained” on any of the tasks employed in this study. Instead, they acquired skills in both the physical and social domains in much the same way that human children do, through social interactions with their caregivers and opportunities to interact with objects and peers. They were regularly engaged with their caregivers about the world around them and in the same way that a parent queries a child about the names of objects he sees or helps him count blocks or directs him to objects using point and gaze, the caregivers of the enculturated apes in our study encouraged them to explore their surroundings and to share their experiences with the humans around them. The formalized testing these apes experience parallels the types of experiences human children have being reared in a human culture. In both cases, individuals are given the opportunity to participate in various types of problem solving tasks and are encouraged and reinforced for appropriate responses.

To further explore the impact of human rearing on cognitive development in apes, seventy nine chimpanzees housed at the YNPRC were utilized to compare the effects of mother versus nursery rearing. Thirty eight subjects were mother reared (6 males, 32 females) and 41 were nursery reared (19 males, 22 females). Mother reared individuals remained with their biological mothers from birth and were raised in conspecific social groups. Nursery reared individuals were removed from their mothers within 30 days of birth for a number of reasons including failure to thrive, inadequate maternal care or for experimental purposes. Nursery care consisted of infant chimpanzees being reared in groups of 4–6 peers. Individuals did receive daily interaction with human caregivers who provided necessary health-related care including diaper changing, bottle-feeding, and health checks on a regular

schedule. However, communicative interaction with humans was relegated to these contexts. All nursery and mother reared apes are currently housed in groups of 2 to 12 chimpanzees (with the exception of one chimpanzee who is singly housed for clinical reasons) and have regular contact with human caregivers and researchers. These interactions are typically limited to basic husbandry contexts such as shifting apes between living areas and feeding and to cognitive testing paradigms with no specific emphasis on understanding human communication.

Procedures

Subjects were tested on a modified version of the PCTB originally described by Hermann et al. (2007). The PCTB attempts to assess subjects' abilities in various areas of physical and social cognition. For our study, some aspects of the original PCTB were eliminated due to time and housing constraints. The previously published procedures were followed as similarly as possible but some tasks were modified to better address the questions at hand given the past experience and environmental constraints of our subjects. Each of the eight physical cognition tasks and the four social cognition tasks are described briefly below with notes made when procedures were altered from those described by Herrmann et. al. (2007). Subjects were generally tested in the order that the tasks are presented below and testing was completed over 3 to 5 testing sessions, depending on the motivation and attention of the subject.

Physical Cognition Tasks—Eight tasks were utilized in the “Physical Cognition” portion of our test including tasks exploring the apes' spatial memory and understanding of spatial relationships, ability to differentiate between quantities, understanding of causality in the visual and auditory domains and their understanding of tools. Our test differed from the original PCTB in several ways. We excluded the Addition task as well as certain components of the Tool Properties tasks.

Spatial Memory (3 trials): This test assessed subjects' ability to remember the locations of food rewards. In this task, the subject watched as food was hidden in two of three possible locations. Each subject received all three possible combinations of baited locations. The subject was then allowed to search the locations. The subject was scored as successful if he/she located both food items without searching in the unbaited location.

Object Permanence (9 trials): Here we tested an individuals' ability to follow a food reward after invisible displacement given three different possible displacements. During single displacement trials, only one of three possible locations was manipulated and thus potentially baited. In the double displacement trials, two of three possible locations were manipulated meaning that either location could potentially be baited. Double displacement trials were further divided by whether or not the baited locations were adjacent to one another or not. In order to be considered successful, the subject must locate the hidden food item without searching in the location that was not manipulated.

Rotation (9 trials): In the third task, subjects' ability to track a food reward as it is spatially rotated either 180 or 360 degrees was examined. In this task, subjects watched as one of three possible locations was baited and then as the three locations were rotated as a unit on a horizontal plane. Three different manipulations were employed. In 180 degree middle trials, the middle location was baited and the platform was turned 180 degrees. In 360 degree side and 180 degree side trials, both the left or right location was baited and the platform was then rotated 360 or 180 degrees, respectively. Subjects successfully completed a Rotation trial by tracking and identifying the correct location.

Transposition (9 trials): In this task, subjects watch as a food reward is hidden in one of three possible locations and then as the baited location is changed in one of three ways. In one condition, the baited location is switched with one of the unbaited locations. In the second condition, the baited location is switched with one of the unbaited locations and then the two unbaited locations are switched. In the last condition, the baited location is switched with one of the unbaited locations and then with the other unbaited location. To be considered successful on this task, the subject must track the reward and choose the baited location.

Relative Numbers (13 trials): In the fifth task, subjects were tested for their ability to discriminate between different quantities by being presented with two plates containing different amounts of equally sized food pieces. Each subject received the same set of 13 different quantity pairings as those used in the original PCTB (1:0, 5:1, 6:3, 6:2, 6:4, 4:3, 3:2, 2:1, 4:1, 4:2, 5:2, 3:1 and 5:3). During each trial, the subject was allowed to choose only one plate and received whatever reward was on the chosen plate. A correct response was recorded when the subject chose the plate containing the larger quantity of food. We did not include the task by Herrmann et. al. (2007) referred to as Addition Numbers.

Causality Noise (6 trials): In the sixth task, subjects' understanding of causal relationships based on sound was assessed. In this task, the experimenter placed a hard food reward (i.e. peanut) in one of two metal containers such that the container with the food reward made a sound when shaken while the unbaited container did not. In "Full" trials, the metal container containing the food reward was lifted and shaken and then the unbaited container was lifted. In the "Empty" trials, the empty container was lifted and shaken and then the baited container was lifted. Subjects were then allowed to choose one of the two containers. A correct choice was recorded when the subject chose the baited container.

Causality Visual (6 trials): In the seventh task, subjects were tested for their causal understanding of the physical world in the visual domain. Specifically, in one trial type a food reward was placed underneath one of two boards laying flat on the testing table. The food caused the baited board to be tilted while the unbaited board lay flat. In the second trial type, a food reward was placed underneath one of two pieces of cloth laying flat on the testing table. The reward created a visible bump in the baited cloth while the unbaited cloth lay flat. In both trial types, the subject had to choose the baited item to be considered successful.

Tool Properties: The last Physical Cognition task explored the apes' understanding of the physical properties of tools and how those relate to achieving a goal. In each task, the subject is presented with a choice between two similar tools. However, one tool can be used to obtain a food reward while the other tool is ineffective. For the first task, subjects are presented with two identical pieces of paper. One piece of paper has a food reward sitting on top of the far end while the second piece of paper has a food reward sitting beside it. The subject could pull either piece of paper into their cage, but only by pulling the paper with the food sitting on top of it would they be able to retrieve the food reward. In the second task, one tool was identical to the effective tool in the first task. The second tool consisted of two smaller pieces of paper with a small gap between them, visually emphasizing that they are disconnected. The food reward is placed on the out-of-reach piece of the two disconnected pieces of paper. The subject could pull in the reward using the effective tool but pulling the piece of the disconnected paper is ineffective in obtaining the reward. Note that we did not include three tool properties tasks from the original PCTB including "Bridge", "Broken Wool" and "Tray Circle" (E. Herrmann et al., 2007).

Social Cognition Tasks—The tasks designated as “Social Cognition” in the PCTB that we utilized are four-fold. The first two are designed to test the apes' ability to understand and to produce communicative signals. The third set of tasks assesses their sensitivity to the attentional state of an experimenter and their ability to use appropriate communicative modalities based on this information. The last social cognition task is designed to assess rudimentary aspects of Theory of Mind by testing their ability to follow gaze. Due to housing and time constraints, we excluded the Social Learning tasks done in the original PCTB and made some modifications to several of the other Social Cognition tasks as noted below.

Comprehension (6 trials): For the first task, we chose a slightly different strategy from that of Herrmann et. al. (2007) to assess the apes' abilities to comprehend communicative signals. The original task implemented the same table and cup set-up as used in many of the other physical cognition tasks. However, in our task, a target was placed on the left and right sides of the enclosure while the subject was centered. To accommodate different mesh sizes and available materials at each facility, the object used as the target varied across facilities. However, in all instances, the target object was an item that the apes were familiar with and accustomed to touching. The experimenter then used either gaze (three trials) or gaze combined with a manual point (three trials) to direct the subject to one of the two targets. The subject had to move to and touch the designated target to be considered successful on this task. Note that we did not include the “Mark” condition conducted by Herrmann and colleagues (2007).

Production (4 trials): For the second task, following the established PCTB methods, the apes' ability to produce communicative signals to indicate a hidden food item was tested in four trials (E. Herrmann et al., 2007). In this task, the ape watched as an experimenter baited a location on either the far left or far right side of the enclosure. A second experimenter then approached the cage, centered the subject and waited for the subject to indicate which location contained the hidden food. The subject was given 60 seconds in which to indicate the correct location using an overt communicative signal, such as a manual gesture towards the hidden food.

Attentional State (8 trials): In the third task, we followed the methods outlined by Hermann et al. (2007) but added an additional test. First, an experimenter placed a piece of food on the ground outside of the subject's enclosure. Then a second experimenter approached the cage and altered their attentional state in one of four ways. In the first trial, the experimenter's face and body were directed towards the food item and the subject. In the second trial, the experimenter's body faced the subject but her face was turned away. In the third trial, the experimenter stood with her body facing away from the enclosure but then turned her head to look at the subject. In the last trial, the experimenter's body and face were oriented away from the subject. In order to be successful, the subject had to use a communicative signal in the modality appropriate to the experimenter's attentional state. For example, if the experimenter was looking at the subject, he/she could use a visual signal, such as a manual gesture to indicate the food. However, if the experimenter was facing away from the subject, the subject had to first use an auditory or tactile signal, such as a cage bang or a spit to get the attention of the experimenter and then once the experimenter was looking at him/her, use a visual signal to indicate the food. To further explore this topic, we added an additional set of four trials using the same basic conditions. However, the trials were conducted in a more familiar setting with the experimenter sitting at the testing table, placing a piece of food on the table and then carrying out the four variations of attentional state. The same requirements regarding modality specific communication were required for the subject to be considered successful on any given trial.

Gaze Following (3 trials): For the last Social Cognition test, we examined each ape's ability to follow gaze in three trials. In this task an experimenter sat on a stool approximately one meter from the subject's enclosure. The experimenter captured the subject's attention and centered him/her by offering a piece of food. The experimenter then shifted her head and eyes to gaze at a point directly above her head for a period of 10 seconds. In order to be successful, the subject had to follow the gaze of the experimenter by looking upward. Note that we did not test our subjects on two of the gaze following tasks, "Back" and "Eyes", used in the original PCTB (E. Herrmann et al., 2007).

Data Analysis

The mean proportion of correct trials was calculated for each of the 12 tasks. Mean scores for Spatial Memory, Object Permanence, Rotation, Relative Numbers, Transposition, Noise, Visual Causality and Tool Properties were averaged to create a mean performance score for Physical Cognition. Likewise, mean scores for Comprehension, Production, Attentional State and Gaze Following were averaged to create a mean performance score for Social Cognition. Note that for the comparison of the enculturated apes to the data in 2.5 year old children published by Herrmann, et. al. (E. Herrmann et al., 2007), some modifications to the data sets were made. First, means for the apes on the Attentional State task was limited to the four trials that followed the exact same methodology as that used in the previous study. Second, the human children's data for the Comprehension task was limited to the point and gaze conditions, excluding the "mark" condition (Herrmann, personal communication) so as to make it more comparable to the current data (but see the above methods section for a description of methodological differences between the two studies). Significance is reported with alpha set to $p < .05$.

Results

Zoo vs. Laboratory Reared Comparison

The YNPRC chimpanzees had much more experience in cognitive testing than the JZG bonobos. Therefore, before grouping both groups together in the Standard reared category, we wanted to ensure that this difference in previous testing history did not significantly impact performance on the tasks employed in this study. Given the large difference in sample sizes for the two groups, we used the means of the YNPRC subjects for the Physical Cognition and Social Cognition categories as the test value in two separate one sample t -tests. The JNZ apes did not significantly differ from the YNPRC apes in either the Physical or Social cognitive domains, $t(6) = -.375$, $p > .05$ and $t(6) = -.311$, $p > .05$ respectively. Furthermore, independent samples t -tests were used to evaluate potential differences between the two groups on each of the 12 tasks. Only one task, Tool Properties, revealed significant differences with the YNPRC subjects performing significantly better on this task than the JAX animals, $t(8) = -2.517$, $p < .05$.

Enculturated vs. Standard Reared Comparison

A repeated measures ANOVA with task type (Physical and Social) as the repeated measure and rearing and species serving as between group factors revealed a significant interaction between task type and rearing, $F(1,16) = 5.825$, $p < .05$. Post-hoc analysis using Tukey's HSD revealed several significant differences. First, enculturated apes performed significantly better than standard reared apes in both the Physical and Social Cognition tasks. Second, the standard reared apes performed significantly better in tasks of Physical Cognition than they did on tasks of Social Cognition. On the contrary, there was no significant difference between performance scores for Physical and Social Cognition in the enculturated apes (see Figure 1). Chance levels of performance for the tasks in the different domains varied such that this finding cannot be interpreted to mean that the standard reared apes have more

advanced physical compared to social cognitive skills. However, this analysis is still meaningful as it demonstrates the *relative* difference in performance in the two domains between the two groups of apes. No significant species differences were found so future analysis combined chimpanzees and bonobos in each of the two rearing conditions to increase our statistical power. No other significant main effects or interactions were found.

We next considered the effect of rearing on performance for each task using an independent sample *t*-test. Analysis revealed that the enculturated apes performed significantly better than their standard reared counterparts on three of the eight Physical Cognition tasks (Rotation, Relative Numbers and Causality Noise) and three of the four Social Cognition tasks (Comprehension, Production and Attentional State). Table 2 displays the mean proportion of trials correct, standard errors and *t*-values for each of the 12 specific tasks for the enculturated and standard reared apes.

Comparison between Enculturated Apes and Human Children

The next analysis sought to test whether the performance by the enculturated apes differed significantly from those in human children. Though we did not test children in this study, comparable PCTB test data were available for the 2.5 year old children tested by Herrmann et al. (2007) for ten tasks. Using the reported mean number of trials correct for the human children for each of the different tasks as the test value, we conducted one-sample *t*-tests for each task to determine if performance by the enculturated apes in our study differed significantly from the children's performance in the Herrmann et al. (2007) study. Figure 2 displays the mean proportion of trials correct for the children, enculturated apes and standard reared apes on each of the ten comparison tasks. The enculturated apes did not differ significantly from the human children in six tasks including Spatial Memory, Object Permanence, Rotation, Transposition, Comprehension and Production. Human children outperformed the apes in the causality tasks, (Causality Noise) $t(9)=-4.583, p<.01$ and (Causality Visual) $t(9)=-3.396, p<.01$ while the enculturated apes performed significantly better than the human children on two tasks including Relative Numbers, $t(9)=4.798, p<.01$ and Attentional State, $t(9)=5.098, p<.01$.

Nursery Reared versus Mother Reared Comparison

In the next analysis, we examined whether human rearing per se was the critical factor in determining performance in the PCTB task. This analysis was restricted to the 79 human- and mother-reared captive born chimpanzees residing at the YNPRC. For this analysis, a repeated measures ANOVA with task type (Physical and Social) serving as the repeated variable and rearing serving as the between group factor revealed a significant main effect for task type, $F(1, 77)=31.866, p<.05$ with subjects performing significantly better on tasks of physical cognition than on tasks of social cognition. No significant interaction with rearing was found. In other words, both groups of captive born chimpanzees performed significantly better on the physical cognitive tasks than on the social cognitive tasks but the human-reared subjects did not perform significantly differently from the mother-reared chimpanzees in either the physical or social cognitive domains (see Figure 3).

Discussion

The results of our study are threefold. First, the current data demonstrate that when apes are reared in an environment where social, communicative and exploratory opportunities are greatly enhanced, their cognitive abilities far exceed the abilities of standard reared apes. Specifically, in the physical domain, enculturated apes demonstrated significantly better understanding of rotation, quantities and of causal relationships inferred from sound (Rotation, Relative Numbers and Causality Noise). In the social domain, standard reared

apes performed significantly worse on a task which required them to understand and act on a social cue given by a human, on a task requiring them to gesture to a hidden reward and on a task that called for modality appropriate communication (Comprehension, Production and Attentional State). In contrast to the recent report by Herrmann and colleagues (Herrmann, Hare, Call, & Tomasello, 2010), we found no significant species differences between the chimpanzees and bonobos tested in our sample.

Second, our study demonstrates that when apes are reared in a human-like culture, their performance on a range of cognitive tasks is very similar to that of 2.5 year old human children. The children outperformed the apes on the two tests related to understanding causality which may indicate a greater understanding of physical relationships between objects. However, the enculturated apes significantly outperformed the children in two tasks. The first one tested the subjects' understanding of quantities by asking them to choose the larger of two arrays. The second task tested the subjects' ability to assess the attentional state of an experimenter and then use modality appropriate communicative signals to make a request. One would expect that human adults would have no difficulties in the relative numbers task and likewise, nine of ten of the enculturated apes were correct on over 92% of the trials. Furthermore, the four chimpanzees in the enculturated cohort had a history of extensive testing in the domain of numerosity and delayed gratification using similar paradigms and therefore, may have had an experiential advantage in this task (M. Beran, Taglialatela, & Washburn, 2004; M. J. Beran, Savage-Rumbaugh, Pate, & Rumbaugh, 1999). The exceptional performance of the enculturated apes on the Attentional State task is likely a reflection of their extensive experience communicating with responsive humans. Just like a child reared in a human culture, these apes likely learned the importance of gaining a human's visual attention prior to making a request through repeated experiences in this type of situation. Numerous studies have previously demonstrated that standard reared captive apes are quite sensitive to the visual attentiveness of humans and use a variety of communicative tools such as cage banging and vocalizing when their communicative partner is not looking at them (Hopkins, Taglialatela, & Leavens, 2007; Hostetter, Cantero, & Hopkins, 2001; Hostetter et al., 2007; Kaminski, Call, & Tomasello, 2004; D. A. Leavens, Hostetter, Wesley, & Hopkins, 2004; D. A. Leavens, Russell, & Hopkins, in press; Liebal, Call, & Tomasello, 2004). Captive chimpanzees have also repeatedly been reported to use manual gestures to request items from humans (Hopkins & Leavens, 1998; Hopkins et al., 2005; D. A. Leavens & Hopkins, 1998; D. A. Leavens & Hopkins, 1999; D. A. Leavens, Hopkins, & Bard, 1996; D. A. Leavens, Hopkins, & Bard, 2005). Combining these two well documented skills of using modality appropriate signals to gain the attention of a human and using manual gestures to request a desired object seem to be significantly enhanced in apes by exposure to a rich socio-communicative environment, even to the extent that the apes do as well or exceed the performance of 2.5 year old children on this task.

Our third main finding that standard laboratory nursery-reared chimpanzees and captive chimpanzees reared by their biological mothers do not differ in their cognitive abilities suggests that something more than just human contact is necessary for the development of advanced social cognitive skills. While the nursery-reared apes received basic nutritive and hygienic care from humans during their early development, the contact was limited and did not focus on sociality with people or the emergence of shared joint attention processes or communicative signals. This suggests that immersion in a human socio-communicative culture, not simply human contact, is critical for the development of more sophisticated cognitive skills, particularly in the realm of communication. We would further add that it does not appear that enculturated apes are simply more test-wise than standard raised apes. Recall that many of the standard raised apes have been involved in studies focusing on the cognitive foundation of gestural communication (D. A. Leavens, Hopkins, & Bard, 2008) as well as social learning and therefore had been worked with extensively within the domain of

socio-communication processes (Bonnie, Horner, Whiten, & de Waal, 2007; Whiten, Horner, & de Waal, 2005). Despite these experiences, the standard raised apes' performance was significantly worse than the enculturated apes, reinforcing the argument that there are specific experiences of enculturated apes that facilitates their performance on the PCTB tasks. Tomasello and Call (2004) have offered 4 potential variables that might explain previous reports of rearing effects on imitation. We believe the results reported here are most consistent with the suggestion that the experiences of treating apes as intentional agents early in development is likely a key factor in facilitating performance on the PCTB tasks.

Some but not all of our hypotheses were supported in this study. First, we predicted that given the emphasis on communication experienced by the enculturated apes, they would significantly outperform the standard reared apes on measures of social cognition (which focus heavily on communication) and this was supported by our results. However, we did not predict differences in the physical domain given that most subjects from our standard reared group were raised in outdoor corrals with access to complex climbing structures, natural substrates and other forms of physical enrichment including tool using opportunities. Contrary to our predictions, the enculturated apes also significantly outperformed the standard reared animals on tests of physical cognition despite both having access to similarly complex physical environments. While the performance of the enculturated apes was significantly better in both the physical and social domains, it is interesting to note that when looking at percentage of trials correct, the enculturated apes performed 11% better in the physical domain compared to the standard raised apes. In contrast, the enculturated apes performed 32% better on the social cognition tasks compared to the standard raised apes. Furthermore, when tasks are compared individually, the enculturated apes significantly outperform their standard reared counterparts on only three of eight physical cognition tasks whereas their performance was significantly better in three of the four social cognition tasks. This suggests that while rearing affects cognitive development in many areas, it may have a more profound influence on one's socio-communicative abilities than on understanding of the physical world.

The overall improvement in cognition seen in the enculturated apes in our study adds to the body of evidence suggesting that environmental inputs during development modulate innate intelligence within a species. Whiten and van Schaik (Whiten & van Schaik, 2007) asked the question, "Does culture make you smart?" and our data indicate that yes, immersion in a highly social environment rich with opportunities for social learning does indeed increase intelligence. This supports existing data in both captive and wild primates. Specifically, it is well known from deprivation studies in monkeys, that social isolation results in major cognitive deficits (Sackett, Novak, & Kroeker, 1999). In contrast, previous studies of enculturated apes reared under enriched conditions have revealed increased cognitive capacities, including the ability to comprehend spoken English (E. S. Savage-Rumbaugh & R. Lewin, 1994) and advanced imitation capabilities (Carpenter, Tomasello, & Savage-Rumbaugh, 1995). In the wild, more gregarious apes demonstrate more frequent tool use, arguably as a result of their increased opportunity for social learning (Van Schaik et al., 2003) and more organized food sharing, likely due to increased social tolerance and proximity (Whiten & van Schaik, 2007).

The cultural intelligence hypothesis proposed by Tomasello (2000) argues that it is human children's natural propensity for rapid absorption of the skills and knowledge of their cultural group that allows for the development of uniquely human cognition in adulthood. In some ways, our data showing that the performance of enculturated apes looks very similar to the performance of human children on many cognitive tasks supports this hypothesis. Specifically, if apes are immersed in a human-like culture from a very early age, they too

can develop many of the same advanced cognitive skills seen in developing human children. Therefore, the claim that this sophisticated cognition is directly related to participation in a culture rich with opportunities for social learning and complex communication is supported.

However, Tomasello (2000) and later Herrmann and colleagues (2007) argue that the dependence on culture for the development of general cognitive abilities is limited to humans and that human children are uniquely capable of absorbing this information. Our data demonstrate that our closest living relatives also possess this tie between early rearing experiences and the emergence of complex cognitive abilities later in life. Indeed, the apes in our study that were exposed to a rearing environment most similar to human children's proved to be quite capable of acquiring human-like cognitive abilities in many domains. Perhaps the most interesting area of comparison is the three tasks involving communication (Comprehension, Production and Attention State) given that the enculturated apes' rearing was specifically geared towards encouraging communication between humans and apes. In these three tasks, the apes showed no significant differences from the human children in the first two measures and actually outperformed the children on the third measure. Clearly these apes were sensitive to the highly communicative culture in which they were reared and gleaned the necessary knowledge from their early experiences to develop highly sophisticated communicative capacities. Similar observations of the facilitative effect of enculturation on social learning have been reported in studies of imitation (M. Tomasello, S. Savage-Rumbaugh, & A. C. Kruger, 1993). Thus, the argument that only humans benefit from cultural specific environments that foster social learning are not supported by our findings.

The general findings reported here lead to the inevitable question, what is an "enculturated" ape? We defined enculturated apes as those with extensive rearing experiences within a human socio-communicative environment. However, historically the definition of an "enculturated ape" has often been limited to those with language training (i.e. Carpenter et al., 1995; M. Tomasello, S. Savage-Rumbaugh, & A. K. Kruger, 1993). Though some of our apes had received specific language-training, we do not believe that language-training per se accounts for the overall pattern of results. Based on the available data, Call and Tomasello (2004) concluded that all apes show some level of understanding of intentionality and hypothesize that experience with humans enhances existing social cognitive skills rather than creates new ones. Recent data has demonstrated that all captive apes, regardless of their captive rearing environment, possess impressive social cognitive skills in the domains of understanding intentionality, sensitivity to attentional states and manual gesturing (i.e. Call, Hare, Carpenter, & Tomasello, 2004; Call & Tomasello, 1998; Hostetter et al., 2007; D. A. Leavens et al., 1996; D. A. Leavens, Hopkins, & Thomas, 2004; D. A. Leavens, Hostetter, et al., 2004). However, there is also evidence that different rearing environments can significantly impact performance on several cognitive and communicative tasks (Lyn, Russell, & Hopkins, 2010; Michael Tomasello et al., 1993). The current study begins to answer some of the difficult questions in regards to what elements of exposure to human rearing creates an "enculturated ape" by comparing apes with various rearing histories. Our data demonstrate that human rearing alone, as is the case with laboratory nursery-reared apes, and human contact by itself, as is the case with all captive apes, is fundamentally different in terms of social cognitive development than the socio-communicative cultural rearing typical of ape language laboratories. However, we would argue that the advantages are not limited to language trained animals but also apply to the non-language trained control subjects who share this socially and communicatively rich environment (although larger sample sizes are needed to empirically test this hypothesis). A more in-depth analysis of specific rearing strategies and in a larger cohort of enculturated apes with controlled and varied rearing environments are needed in order to fully understand what components of a socio-communicative culture are key to advanced social cognitive development.

In summary, our collective results suggest that the differences seen between cognitive skills in humans and other apes on the tasks employed in this study is less of a reflection of true biological differences between species, but rather is largely a result of the different socio-communicative cultural environments in which each species is reared. Clearly there are species differences in the cognitive abilities of apes and humans. However one must use caution when drawing conclusions regarding species differences when conducting comparative studies where species variables are confounded with other important subject variables such as rearing. Specifically, in this study apes reared in a human-like culture where communication and sociality between ape and caregiver are highly encouraged develop advanced cognitive abilities when compared to other apes and this was particularly true for socio-communicative processes. Thus, apes raised by humans appear to be able to leverage inherent communicative abilities to their advantage under these rearing circumstances much like human children. What elements of human enculturation specifically account for these results are not clear from this report but this issue warrants consideration in future studies.

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Figure 1.
Mean proportion of trials correct for standard reared and enculturated apes on physical cognitive and social cognitive tasks. * $p < .05$

Figure 2.

Mean proportion of trials correct for human children from Herrmann and colleague's (E. Herrmann et al., 2007) published data and from the enculturated and standard reared apes from the current study for 10 comparable measures. Only differences between the human children and the two categories of apes from the current study are highlighted with asterisks. Data for the Comprehension Task for human children was limited to point and gaze conditions only to match conditions used with enculturated apes (means provided by personal correspondence from Dr. Esther Herrmann). Data for Attention State for the enculturated apes was limited to the four trials that matched the four trials given to the human children. *Either the standard reared apes or the enculturated apes differed significantly from the human children, $p < .05$ **Both the standard reared apes and the enculturated apes differed significantly from the human children, $p < .05$.

Figure 3. Mean proportion of trials correct for both mother-reared and human-reared captive chimpanzees on tasks of physical and social cognition, * $p < .05$.

Table 1

Matched Subject Demographics

Subject Name	Species	Facility	Age (yrs.)	Rear	Sex	Match
<u>Enculturated Apes</u>						
Maisha	Bonobo	GATI	9	E	Male	Lexie
Nyota	Bonobo	GATI	11	E(L)	Male	Jumanji
Elikiya	Bonobo	GATI	12	E	Female	Lily
Panbanisha	Bonobo	GATI	24	E(L)	Female	Kuni
Kanzi	Bonobo	GATI	29	E(L)	Male	Mabruki
Matata	Bonobo	GATI	39	E	Female	Lorel
Mercury	Chimpanzee	LRC	23	E	Male	Winston
Panzee	Chimpanzee	LRC	24	E(L)	Female	Brandy
Sherman	Chimpanzee	LRC	36	E(L)	Male	David
Lana	Chimpanzee	LRC	39	E(L)	Female	Barbara
<u>Standard Reared Apes</u>						
Lexie	Bonobo	JZG	10	N	Female	Maisha
Jumanji	Bonobo	JZG	13	M	Male	Nyota
Lily	Bonobo	JZG	12	N	Female	Elikiya
Kuni	Bonobo	JZG	24	M	Female	Panbanisha
Mabruki	Bonobo	JZG	26	M	Male	Kanzi
Lorel	Bonobo	JZG	40	M	Female	Matata
Winston	Chimpanzee	YNPRC	23	N	Male	Mercury
Brandy	Chimpanzee	YNPRC	25	M	Female	Panzee
David	Chimpanzee	YNPRC	33	N	Male	Sherman
Barbara	Chimpanzee	YNPRC	37	M	Female	Lana

Rear: E=enculturated, E(L)=enculturated+language competent, N=nursery, M=mother

Table 2

Mean Performance by Standard Reared and Enculturated Apes

Task	Standard Reared		Enculturated		t-value
	Mean	Std. Error	Mean	Std. Error	
SpatMem	.60417	.062500	.80000	.088889	-1.854
ObjPerm	.68750	.049916	.78889	.058443	-1.295
Rotation	.47917	.029950	.61111	.084863	-1.726
Transpose	.56944	.066415	.73333	.083148	-1.536
Relative #s	.73077	.035110	.92308	.044412	-3.397*
Causality Noise	.41146	.036853	.67500	.038188	-4.737**
Causality Visual	.67708	.041580	.64286	.055100	.501
Tool Properties	.60417	.054592	.75000	.056928	-1.766
Comprehension	.52083	.087235	.91667	.037268	-.3444*
Production	.31250	.089849	.80000	.104083	-3.472*
Att State	.41406	.055573	.83750	.037500	-5.524**
Gaze	.56250	.078874	.73333	.096864	-1.358

* p < .01

** p < .001