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Differences in the Early Cognitive Development of Children and Great Apes

ABSTRACT: *There is very little research comparing great ape and human cognition developmentally. In the current studies we compared a cross-sectional sample of 2- to 4-year-old human children (n = 48) with a large sample of chimpanzees and bonobos in the same age range (n = 42, hereafter: apes) on a broad array of cognitive tasks. We then followed a group of juvenile apes (n = 44) longitudinally over 3 years to track their cognitive development in greater detail. In skills of physical cognition (space, causality, quantities), children and apes performed comparably at 2 years of age, but by 4 years of age children were more advanced (whereas apes stayed at their 2-year-old performance levels). In skills of social cognition (communication, social learning, theory of mind), children out-performed apes already at 2 years, and increased this difference even more by 4 years. Patterns of development differed more between children and apes in the social domain than the physical domain, with support for these patterns present in both the cross-sectional and longitudinal ape data sets. These results indicate key differences in the pattern and pace of cognitive development between humans and other apes, particularly in the early emergence of specific social cognitive capacities in humans. © 2013 Wiley Periodicals, Inc.* Dev Psychobiol 56: 547–573, 2014.

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INTRODUCTION

Recent research has established many important cognitive similarities and differences between humans and their closest living relatives, the great apes (Lonsdorf, Ross, & Matsuzawa, 2011; Tomasello, 2009; Tomasello & Call, 1997; Whiten et al., 1999). However, most of this research has compared human children to great ape adults, and we know from recent work in developmental biology that many, if not most, important differences between closely related species occur via differences in developmental patterning (Arthur, 2002; Carroll, 2003). What is needed for a fuller and more complete description and explanation, therefore, is a comparison of humans and great apes with respect to their early

cognitive ontogenies (Gomez, 2005; Langer, 2001; Matsuzawa, 2007).

Comparisons of cognitive development between humans and nonhuman apes can test hypotheses regarding shifts in both the *pace* and *pattern* of development. Considering first the pace of development, one possibility is that humans exhibit delayed ontogeny relative to nonhuman apes, developing our cognitive capacities more slowly in line with our prolonged juvenile period and longer period of maternal dependence relative to other ape species (Bjorklund & Green, 1992; Charnov & Berrigan, 1993; Hrdy, 2005; Kaplan, Hill, Lancaster, & Hurtado, 2000). Alternatively, humans and nonhuman apes alike may show consistent ontogeny in their pace of cognitive development, with this pace constrained by the relative complexity of varying skills, predicting that the skills should require similar timing of developmental inputs for any species—as supported by studies showing similarly early emergence of capacities for facial recognition and neonatal imitation in human and chimpanzee infants (Myowa-Yama-

koshi, 2006; Myowa-Yamakoshi, Tomonaga, Tanaka, & Matsuzawa, 2004). Finally, humans might show accelerated ontogeny relative to nonhuman apes, with linguistic or specific social capacities enabling our more rapid development. Indeed, this latter possibility has been supported by comparative developmental data revealing that humans progress more rapidly than nonhuman primate infants in skills of object tracking and certain aspects of sharing and following attention, as well as comparisons of children with adult apes indicating that even at a young age children's social cognitive capacities outstrip those of apes (Gomez, 2005; Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007; Langer, 2006; Tomasello & Carpenter, 2005; Tomonaga, 2006).

Considering potential differences between humans and nonhuman primates in patterns of cognitive development, there are two possible alternatives. First, humans and nonhuman apes may show conserved patterns of cognitive development. This hypothesis would suggest that similar underlying mechanisms shape a given cognitive capacity across species, with a lesser role of species-specific developmental inputs. In support of this possibility, comparative developmental studies have revealed similar patterns in the development of object classification across human, ape, and monkey species, indicating that capacities in this area may be strongly dependent on one another and inflexible in their development (Poti, 1997; Spinozzi, 1993). In contrast, humans and nonhuman apes may show variable patterns of cognitive development. In this case, capacities that might be strongly linked in humans may instead be dissociated from one another during development in other apes, indicating that divergent developmental mechanisms underlie differences in adult behavior. In fact, even observed similarities in adult behavior might derive from differing underlying mechanisms that are revealed by comparative developmental inquiry. For example, comparisons of gaze-following across primate taxa have revealed that nonhuman primates become proficient in gaze-following much more slowly than human infants, strengthening the notion that skills in gaze-following may require a long critical period that is importantly influenced by species-specific developmental inputs (Ferrari, Coude, Gallese, & Fogassi, 2008; Ferrari, Kohler, Fogassi, & Gallese, 2000; Tomasello, Hare, & Fogleman, 2001).

To discriminate among these possibilities regarding the pattern and pace of cognitive development in humans, and how it compares to that of nonhuman apes, we performed a study of humans and our closest living relatives, chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*). We tested individuals between the ages of 2 and 4 years of age in all three species. By testing this age range, we were able to take advantage of an important point revealed by prior comparative developmental studies; namely, that cognitive capacities emerging in the first few months of life appear to be much more similar between humans and nonhuman apes than those emerging later on in development (Langer, 2006; Matsuzawa, Tomonaga, & Tanaka, 2006; Wobber, Rosati, Hughes, & Santos, submitted). This age group therefore allowed us to best elucidate how the pace and pattern of development might differ between humans and other apes throughout juvenility.

We presented young humans, chimpanzees, and bonobos with a broad-scale battery of 14 cognitive tasks assessing a diverse array of skills in social and physical cognition, as well as 3 attentional/motivational control tasks (Herrmann et al., 2007; Herrmann, Hare, Cissewski, & Tomasello, 2011; Tomasello & Carpenter, 2005; Wobber, Wrangham, & Hare, 2010). By using a large test battery, we were able to build on prior comparative developmental studies that have targeted a specific area of cognition in detail (Langer, 2006; Matsuzawa et al., 2006). In particular, this test battery allowed us to examine a wide spectrum of capacities underlying more complex behavior, and to determine the inter-relationships between capacities across domains. In addition, this test battery allowed us to test the predictions of a recent hypothesis, the Cultural Intelligence Hypothesis (Herrmann et al., 2007), that a suite of correlated social cognitive skills emerging earlier in human than in ape development facilitate generalized accelerations in human cognitive development. By testing a larger sample of individuals than available in prior comparative developmental studies, we were able to begin to characterize species-typical patterns of cognitive development independent from potential effects of inter-individual variation.

In Experiment 1, we compared a cross-sectional sample of 48 human children to 49 same-age chimpanzees and bonobos (hereafter referred to by their genus name, *Pan*) in their performance on a broad battery of tasks spanning social and physical cognition validated in previous work (Carpenter, Nagell, & Tomasello, 1998; Herrmann et al., 2007; Tomasello & Carpenter, 2005; Wobber et al., 2010) (Tab. 1). In Experiment 2, we followed a group of 44 *Pan* infants and juveniles longitudinally over the course of 3 years to document their patterns of cognitive development in greater detail. We analyzed data in both studies in terms of the *pace* of cognitive development, using individuals' proficiency across tasks to index their general comprehension of the capacities being investigated, and in terms of the *patterns* of cognitive development, extracting information about the inter-relationships between skills using techniques from prior longitudinal studies

Table 1.   The Comparative Developmental Cognitive Battery (CDCB)

Domain	Task	Description	Number of Trials
Social cognition	Intention–emulation (IE)	Achieve experimenter's goal, seeing only failed attempt	3
	Social obstacle (SO)	Look to experimenter's face after being teased	3
	Gaze-following around barriers (GFB)	Follow experimenter's gaze geometrically	6
	Social inhibition (SI)	Reach selectively during simulated feeding competition	12
	Gaze-following (GF)	Follow experimenter's gaze into space	10
	Social learning (SL)	Copy action demonstrated by experimenter	1
	Point production (PP)	Direct experimenter to a reward out of her view	4
	Goal understanding (GU)	Understand experimenter's goal from failed attempt	12
	Reputation (Rep)	Discriminate between a generous and a stingy experimenter	2 (4)
Physical cognition	Object permanence (OP)	Track invisibly displaced rewards	6
	Transposition (Tra)	Track visibly displaced reward locations	6
	Number (Num)	Discriminate relative quantities	6
	Tool use (TU)	Use tool to obtain out-of-reach reward	1
	Tool properties (TP)	Choose functional over nonfunctional tools	12
Attention and motivation	Risk box	Reach into unknown dark box	1
	Unsolvable task	Motivation to solve previously solvable task	1
	Novel objects	Duration of proximity to novel humans/objects	4

Tasks were divided into three domains: those assessing social cognition (reasoning about other individuals), physical cognition (reasoning about objects), and attention/motivation (control tasks). All tasks had previously been used with nonhuman apes and human infants. Tasks were chosen to represent a diverse subset of the basic cognitive skills utilized for more complex processes in the social and physical cognitive domains. Where trial number differed between children and nonhuman apes, the number of trials presented to apes is indicated in parentheses. Abbreviations for each task that are used in other tables or figures are shown.

of human psychological development (Carpenter et al., 1998; Carpenter, Pennington, & Rogers, 2002).

EXPERIMENT 1

Our first experiment compared a cross-sectional sample of human children to same-age individuals of our closest living relatives, chimpanzees and bonobos (genus *Pan*). We studied an identical age range in both groups, 2–4 years of age, taking advantage of the fact that *Pan* individuals begin to locomote self-sufficiently around 2 years (Doran, 1992; Pontzer & Wrangham, 2006), and can thus be tested in tasks requiring them to independently manipulate objects or move around in space.

Methods

Subjects. Chimpanzees were tested at the Tchimpounga Chimpanzee Sanctuary in the Republic of Congo and bonobos were tested at Lola ya Bonobo in the Democratic Republic of Congo. Apes at these sites are semi free-ranging but can voluntarily participate in cognitive testing in their dormitories (for a full description of these sites see Wobber & Hare, 2011). In

addition, we tested three chimpanzees and one bonobo living at the Wolfgang Koehler Primate Research Center (WKPRC) in Leipzig, Germany. Our sample consisted of chimpanzees ($n = 26$, 15 males) and bonobos ($n = 23$, 12 males) ranging from 1.5 to 4 years of age. For most nonhuman ape subjects we did not know ages to the month, and so here grouped them only by year of age: 2 years ($n = 15$); 3 years ($n = 20$), 4 years ($n = 14$).

Because the majority of nonhuman ape subjects were orphans with unknown birth dates, individuals' ages were estimated to the year using weight and dental emergence both upon arrival at the sanctuary and at the time of testing (see Supplemental Methods). In Experiment 2, our longitudinal data controlled for any remaining uncertainty in subjects' precise age by examining improvements in performance over a known period of time. To ensure that being orphaned did not significantly impact apes' success in the cognitive tasks, we compared the performance of orphans to mother-reared individuals in the test sample (see the Results Section). We also compared the performance of apes living at the sanctuaries to apes living in the WKPRC, to ensure that these differing environments did not significantly impact performance on the cognitive tasks. Critically, we do not wish to argue that apes living at

the sanctuaries are identical in their behavior and cognition to apes living in any other captive facility or in the wild. Instead, we show data that neither maternal rearing nor living environment impacted performance on the tasks presented here (see the Results Section). These findings therefore strengthen our confidence in the reliability of the present test battery. Ape subjects had never taken part in any previous cognitive study of this kind, though a few had taken part in previous tests of inhibitory control (Wobber et al., 2010). Note that the data discussed here does not overlap at all with that reported in this prior article. Subjects were never food or water deprived for testing and all testing was voluntary.

Children ($n = 48$, 24 males) were tested in the Department of Comparative and Developmental Psychology at the Max Planck Institute for Evolutionary Anthropology (MPI-EVA) in Leipzig, Germany. To match the ages of the *Pan* sample, we tested 2-year olds ($n = 16$, range: 19–23 months, mean: 22.2 months), 3-year olds ($n = 16$, range: 33–39 months, mean: 36.4 months), and 4-year olds ($n = 16$, range: 49–53 months, mean: 51.8 months). We targeted age groups that were 14 months apart, rather than 12 months, to provide maximal contrast between age groups. No child subject had previously participated in a similar study; therefore, the test situation and test items were novel to all species.

Design. Nonhuman apes were tested individually in familiar rooms of their dormitories. Children were tested individually in test rooms at the MPI-EVA. All subjects had a caregiver in the testing room or nearby (this caregiver was a human who regularly cared for that individual in the case of the orphan apes, the mother in the case of mother-reared apes, or the mother/father for human children). This caregiver did not participate in the test in any way.

Subjects participated in a battery of 14 cognitive tasks, in addition to 3 attentional/motivational control tasks, over the course of multiple test sessions (Tab. 1). Subjects received one testing session (lasting approximately 30 min) per day, with subjects receiving anywhere from 3 to 10 test sessions in total depending on their relative motivation to participate in multiple tasks on any given day (see Supplemental Methods). Individuals always completed a given task in only one testing session, with breaks between sessions only occurring in between tasks. Two chimpanzees and one bonobo, not included in our sample sizes mentioned above, began but did not complete the test battery because they became unmotivated across repeated days of testing.

The order in which tasks were presented was consistent within-genus. Children received the tasks in

a slightly different order from *Pan* subjects to ensure high motivation throughout the days of task participation in line with our pilot data and previous work (Herrmann et al., 2007) (Supplemental Tab. S1).

Procedure. The same experimenter presented the tests to all nonhuman apes (V. Wobber) and another experimenter presented the tests to all children (A. Loose). Previous analyses have shown that different experimenters can reliably administer these tasks (see supplemental material in Herrmann et al., 2007). Moreover, this procedure ensured that even if there were any slight differences in the experimenters' behaviors, any within-genus age patterns were not a result of these differences since the same experimenter consistently conducted the study within each genus. All tasks utilized human experimenters, since using conspecific ape experimenters would have greatly limited the degree to which experimental stimuli could be presented consistently across a large number of tasks. Critically, previous research has shown that apes are able to perceive humans as social agents in experimental task paradigms (Call & Tomasello, 2008). We elaborate on this point below (see the Discussion Section).

All tasks were videotaped. For 11 of the 14 cognitive tasks and 1 of the 3 attentional/motivational control tasks, results were coded live. Performance on the remaining tasks was scored from video by the first author. For these five tasks, as well as two of the live coding tasks where performance was not simply choice-based, coders blind to the hypotheses of the study scored videos from a random 20% of individuals in each genus. Inter-observer reliability was assessed using Cohen's kappa for tasks where performance was dichotomous (pass/fail) and a Pearson correlation for tasks where performance was continuous (e.g., duration in s), with values for these analyses and their relative significance levels shown below (Tab. 2) (Martin & Bateson, 1986). Reliability across all seven tasks was high, with similar values across both children and *Pan* suggesting that any differences between genera were unlikely to be due to greater measurement error in one group.

Tasks. The 14 cognitive tasks used here were either taken directly from previous work (Herrmann et al., 2007; Wobber et al., 2010) or adapted from prior studies of human-reared infant chimpanzees (Tomasello & Carpenter, 2005) (Tab. 1). Tasks performed identically to previous work are noted below (Herrmann et al., 2007; Wobber et al., 2010). For the other tasks we present short descriptions, with more detailed procedures outlined in the Supplemental Methods.

Table 2.   Analyses of Inter-Observer Reliability

	Children		Pan	
Task	Cohen's Kappa/Pearson Value	*p*-Value	Cohen's Kappa/Pearson Value	*p*-Value
Intention–emulation	1.00	.001	.83	.001
Social obstacle	1.00	.001	.67	.001
Gaze-following around barriers	.94	.001	.82	.001
Gaze following	.95	.001	.77	.001
Social learning	1.00	.001	1.00	.001
Novel objects*	.83	.003	.95	.001
Unsolvable task*	.90	.001	.98	.001

A coder blind to the hypotheses of the study coded a randomly selected 20% of trials in tasks where performance was unambiguous (five cognitive and two attentional/motivational control tasks). Results are shown for each task according to genus (children relative to same-age chimpanzees and bonobos, or genus *Pan*). Cohen's kappa tests were performed for tasks scored dichotomously (0/1) in any given trial (e.g., following gaze or not). Pearson's correlations were performed for tasks scored with continuous measures (e.g., duration in proximity), with these tasks denoted by asterisks.

Procedures were identical for children and *Pan* subjects, except where mentioned below and in that (1) toys served as the reward for children rather than food and (2) in certain tasks, no mesh barriers separated the child from the experimenter. The reward items were chosen as highly desirable items for each species, controlling for motivation to participate rather than for the exact item used as a reward. These rewards were toys to put in a "pling machine" for children, bananas for chimpanzees, and apples for bonobos.

Tasks are divided into the social and physical domain for two main reasons. First, we use this separation of tasks to facilitate comparison between our study and previous publications utilizing a similar task battery with children and adult apes (Herrmann et al., 2007; Herrmann, Hare, Call, & Tomasello, 2010). Secondly, these divisions have empirical support: a factor analysis of performance by 2.5-year-old children and chimpanzees on the Primate Cognition Test Battery revealed that children possess a distinct "social cognition" factor underlying success across the majority of tests listed here as part of the social domain. Meanwhile, both children and chimpanzees were found to possess a factor for "space," encompassing tasks that assess object permanence and transposition as well as spatial rotations (Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2010). We have therefore maintained this classification structure for our discussion of the present test battery.

Social cognition.
Intention–emulation (IE). This test served to measure whether subjects could infer an experimenter's goal, having never seen her complete the goal but seeing only her failed attempts to achieve it (Bellagamba & Tomasello, 1999; A. N. Meltzoff, 1995; Tomasello &

Carpenter, 2005). The experimenter (E1) attempted three times to put together two pieces of PVC pipe, but failed each time. E1 then handed the pieces of PVC pipe to the subject, with the dependent measure for this task the number of trials where the subject successfully put together the two pieces of PVC pipe (Tomasello & Carpenter, 2005). Subjects received three trials of this task (one per day on three subsequent test days) and were rewarded for handing back the PVC pipes regardless of whether they succeeded in putting them together.

Social obstacle (SO). This task was designed to measure a subject's tendency to look to another individual's face as a cue to his or her intentions (Phillips, Baron-Cohen, & Rutter, 1992; Tomasello & Carpenter, 2005). E1 engaged the subject's attention with a toy and then teasingly pulled the toy away, looking straight ahead for 5 s. The dependent measure for this task was whether the subject looked to the experimenter's face in these 5 s (Tomasello & Carpenter, 2005). Three trials were presented in sequence, with a short break between trials to reengage the subject in playing with the toy. Subjects were rewarded after each trial irrespective of their performance in that trial.

Gaze-following around barriers (GFB). This task served to measure whether individuals were able to follow an experimenter's gaze geometrically, requiring the subject to physically move around a barrier to follow this gaze rather than simply reorienting his or her gaze direction (Moll & Tomasello, 2004; Tomasello & Carpenter, 2005). E1 called the subject's name and subsequently looked behind a barrier, alternating her gaze between the subject and this location while calling

the subject's name for 30 s. The dependent measure for this task was whether the subject moved its body to look behind the barrier (Tomasello & Carpenter, 2005). Subjects were rewarded after each trial and given a short break prior to the next trial. Three trials per day were performed on two subsequent test days (resulting in six total trials). Two different barrier setups were utilized (one for the first day, and one for the second) to diminish potential habituation effects (see Supplemental Tab. S1).

Social inhibition (SI). This task was designed to measure individuals' abilities to inhibit their responses in a social situation where they requested rewards from selected human experimenters (Barth & Call, 2006; Herrmann et al., 2007). Procedures were performed identically to the "social response inhibition" test in Experiment 2 of Wobber et al. (2010).

Gaze-following (GF). This test, similar to gaze-following around barriers, measured individuals' abilities to track another's gaze. The experimenter sat across from the subject, called its name, and then looked upwards with her head and eyes for 10 s. The dependent measure was whether the subject also looked upwards (Butterworth & Jarrett, 1991; Herrmann et al., 2007; Tomasello et al., 2001). Ten trials were performed in sequence, with subjects rewarded and given a short break after each trial.

Social learning (SL). In this task, we observed whether subjects imitated the means demonstrated by an experimenter to achieve a goal (Call, Carpenter, & Tomasello, 2005; Gergely, Bekkering, & Kiraly, 2002; Herrmann et al., 2007; A. Meltzoff, 1988; Tomasello & Carpenter, 2005). Procedures were performed identically to the "banana/balloon tube" social learning item in Herrmann et al. (2007), with only this one trial performed (in contrast to the three social learning trials employed by Herrmann and colleagues).

Point production (PP). This task measured whether individuals would signal the location of a reward to an experimenter if that reward were out of her view, reflecting an understanding of the experimenter's attentional state and an ability to communicate gesturally (Herrmann et al., 2007; Tomasello & Camaioni, 1997; Tomasello & Carpenter, 2005). Procedures were performed identically to the "attentional state" task of Herrmann et al. (2007), with two trials of the "away" condition and two trials of the "towards" condition.

Goal understanding (GU). In this task, subjects needed to interpret an experimenter's intentions and goals in

order to find a hidden reward in an object choice paradigm (Braeuer, Kaminski, Riedel, Call, & Tomasello, 2006; Herrmann et al., 2007). Procedures were performed identically to the "intentions" task of Herrmann et al. (2007), with three trials of the "trying" condition followed by three trials of the "reaching" condition, except that two sessions of 6 trials each were presented on two subsequent test days, for a total of 12 trials.

Reputation (Rep). This task measured whether subjects could track other individuals' behavior and base decisions on this information (Hamlin, Wynn, & Bloom, 2007; Herrmann, Keupp, Hare, Vaish, & Tomasello, 2013; Melis, Hare, & Tomasello, 2006). Subjects witnessed a demonstration where one ("nice") experimenter attempted to give a reward to a neutral individual but was prevented from doing so by another ("mean") experimenter. Subjects were then presented with a choice between the "nice" and the "mean" experimenters, both of whom were holding a reward. The dependent measure for this task was whether subjects selectively requested a reward from the nice experimenter. Neither experimenter provided a reward upon the subject's request, to prevent learning from affecting decisions in subsequent trials. Two trials were performed for children whereas four were performed with *Pan* subjects (as children became unmotivated in piloting when using a greater number of trials while *Pan* individuals continued to approach across repeated trials).

Physical cognition.
Object permanence (OP). This task measured subjects' knowledge of object permanence with a Stage 6 invisible displacement task (Barth & Call, 2006; Herrmann et al., 2007; Piaget, 1952). Procedures were performed identically to Herrmann et al. (2007), except that here we used only two trials of three trial types (single, double adjacent, and double nonadjacent displacements), for a total of six trials.

Transposition (Tra). This task also measured individuals' abilities to track hidden rewards, in this case with the reward location being moved in full view of the subject (Barth & Call, 2006; Herrmann et al., 2007; Sophian, 1984). Procedures were performed identically to Herrmann et al. (2007), except that we used only two trials of three trial types (single, double unbaited, and double baited swaps), for a total of six trials.

Relative number (Num). This task measured individuals' ability to discriminate between varying quantities of a reward, with individuals successful if they were able

to choose the option providing the larger reward (Hanus & Call, 2007; Herrmann et al., 2007; Tomonaga, 2008). Procedures were performed identically to Herrmann et al. (2007), except that only six quantity comparison trials were presented, in the following order: 1:0, 6:3, 6:2, 3:2, 2:1, 4:1.

Tool use (TU). In this task, subjects needed to use a tool to obtain an out-of-reach reward (Herrmann et al., 2007). Procedures were performed identically to Herrmann et al. (2007).

Tool properties (TP). To test whether subjects understood the functional properties of tools, beyond simply being able to use tools, we presented them with an object choice task where they needed to choose between a functional and nonfunctional tool, each of which was associated with a reward (Hauser, 1997; Herrmann et al., 2007; Herrmann, Wobber, & Call, 2008). Procedures were performed identically to Herrmann et al. (2007), with three trials of the "side" condition and three trials of the "ripped" condition presented in sequence in each test session. Subjects received two test sessions of this task on subsequent test days, resulting in a total of 12 trials.

Attentional/motivational controls. Three control tasks were conducted to ensure that any species or age patterns reflected differences in subjects' cognitive abilities rather than differences in their motivation to complete the tasks.

Risk box. This task served to measure subjects' interest in novelty, or general willingness to take risks in an unfamiliar situation (Kagan & Snidman, 2004). This task was presented prior to all of the other tasks, making it the first interaction that subjects had with the experimenter and the general test environment. The experimenter presented the subject with a wooden box with a hole on one side, giving the subject 30 s to manipulate the box initially and then placing a reward inside the hole. The dependent measure for this task was whether the subject reached into the hole in the box to obtain the reward, with individuals given 30 s to do so. Only one trial was performed.

Unsolvable task. This task provided an index of how interested subjects were in obtaining a reward and how determined they were to independently solve a problem (Miklosi et al., 2003). The experimenter presented the subject with three trials of a task that was solvable, with a reward placed under an upside-down clear box that could be opened by lifting the box off of its lid. For the unsolvable trial, the experimenter placed a

reward in the box but then fixed the box to its lid (unbeknownst to subjects), making it impossible to open but visually identical to the solvable situation. The dependent measure for this task was how long subjects would manipulate the box in attempting (unsuccessfully) to obtain the reward, with individuals given 1 min to do so.

Novel objects. This task measured subjects' reactivity to novel objects, quantifying their position on a shy–bold continuum and their general interest in objects that might pertain to the test (Herrmann et al., 2007; Kagan & Snidman, 2004). The experimenter sat behind the testing table and placed an object on the table. Two differing objects were used, each of which was presented first as a still object (for 30 s) and then as a moving object (for 30 s). The dependent measure for this task was the time (out of 2 min total) that subjects spent in close proximity to the table. The camera was positioned such that it captured a prespecified area of a certain size (140 cm × 110 cm). Thus in coding, the experimenter could record how many seconds subjects spent in this area as a measure of their interest.

Analysis. We began our analyses by examining differences in the rate of cognitive development between children and young *Pan*, and then examined patterns of development in each group. Chimpanzees and bonobos were combined for the analyses because the sample size of each species in certain age groups was too small ($n < 4$) to compare individually to children (differences in behavior and cognition between the two species appear to emerge in later on in development are discussed elsewhere, see Wobber et al., 2010).

Rate of cognitive development. To assess the rate of cognitive development between the ages of 2 and 4 years, we calculated each subject's average performance for the social and physical domains, as well his or her average performance in the three control tasks. We then performed univariate General Linear Model (GLM) analyses separately for the social domain, the physical domain, and the control tasks with genus (*Homo* vs. *Pan*) and age group (2, 3, or 4 years) as factors. Post hoc analyses were controlled for multiple comparisons using a Bonferroni correction. We used these analyses to determine whether human children showed a delayed, consistent, or accelerated pace of development in comparison to same-age *Pan*, in line with the alternatives outlined in our introduction.

Patterns of cognitive development. We used several measures to analyze patterns of cognitive development in the two genera. First, to determine the age at which

individuals began to succeed in the differing cognitive tasks, we created an emergence criterion for each task (Tab. 3). These emergence criteria were based on previous research where possible (Carpenter et al., 1998; Tomasello and Carpenter, 2005), and represented the minimum level of performance necessary to be considered comprehension for a given task.

We calculated an age of emergence (AOE) for each task as the age group where 50% or more of individuals successfully met the emergence criterion. We then calculated the order of task emergence based on the proportion of individuals meeting the emergence criterion in each task (Carpenter et al., 2002). We ranked the tasks from those where the highest proportion of individuals was successful to those where the lowest proportion was successful within each genus. We then used Green's index of consistency (Green, 1956) to determine the degree to which these rank sequences represented stable patterns, both for the overall sequences and separately within the social and physical domains. Next, we investigated emergence relationships between pairs of tasks using the ordering-theoretic method (Bart & Airasian, 1974), which allowed us to determine which tasks were necessary precursors to one another and which were logically independent. Again, we performed these calculations using the pass/fail emergence data.

Finally, we performed two types of analysis using the continuous data set consisting of percentage correct in each task (rather than the pass/fail emergence measures). We first determined the relative proficiency across tasks in each genus. For this analysis, we ranked tasks *within each individual* based on that individual's relative performance in each (rather than performing these rankings on the group level). We then calculated differences in average within-individual task rank between children and young *Pan*, using Mann–Whitney tests for this analysis since these data were not normally distributed. Note that within-individual task ranks could be biased by tasks where performance was only measured as pass/fail (e.g., success in the single trial of the social learning task would be represented as 100% correct). However, because trial numbers were identical for children and *Pan* (except in the Reputation task), any bias introduced by trial number was held constant in our comparisons of the two genera. Our second analysis in this area examined inter-task correlations in performance, to elucidate the degree to which individuals were consistent in their performance on the whole and to determine whether specific tasks were related in their levels of success. These tests allowed us to determine the degree to which patterns of development in *Pan* mirrored those of human children, and where and how patterns differed between the two

Table 3.   Passing Criteria Used in the Age of Emergence Analysis, Experiment 1 and Experiment 2

Domain	Task	Number of Trials	Forced Choice?	Emergence Criterion
Social cognition	Intention emulation	3		Achieve experimenter's goal on 1 or more trials
	Social obstacle	3		Look to experimenter's face on 1 or more trials
	Gaze-follow barriers	6		Follow gaze around barrier on 1 or more trials
	Social inhibition	12	X	Reach to both correct experimenters on 7 or more trials (chance success 33%)
	Gaze-following	10		Follow gaze on 1 or more trials
	Social learning	1		Copy experimenter's action to obtain reward
	Point production	4		Direct experimenter to reward on 1 or more trials
	Goal understanding	12	X	Choose experimenter's targeted container on 9 or more trials (chance success 50%)
	Reputation	2 (4)		Choose nice experimenter on first participating trial
Physical cognition	Object permanence	6	X	Choose correctly once or more in each potential reward location (left, right, middle)
	Transposition	6	X	Choose correctly once or more in each potential reward location (left, right, middle)
	Number	6	X	Choose correctly once or more on each side (left, right)
	Tool use	1		Use tool to obtain reward
	Tool properties	12	X	Choose functional tool on 9 or more trials (chance success 50%)

To examine patterns of development, we created pass/fail criteria that signified the minimum level of performance in a given task that denoted comprehension of that task. These criteria were defined either from past work or based on statistical relationships. Justifications for the emergence criteria across tasks are provided in the Supplemental Material.

genera, in determining the relative support for models of conserved versus variable patterns of development described in the introduction.

Results

Rate of Cognitive Development. A univariate GLM of average performance in the social domain revealed significant effects of genus and age group, as well as a significant interaction between genus and age (genus: $F(1,94) = 335.20$, $p < .001$; age group: $F(2,94) = 24.51$, $p < .001$; genus $\times$ age group: $F(2,94) = 19.82$, $p < .001$) (Fig. 1a). Post hoc analyses revealed a strong effect of age in humans ($F(2,47) = 33.53$, Bonferroni-corrected $p < .001$) but not in *Pan* (Bonferroni-corrected $p > .8$). Human 3- and 4-year-olds both outperformed human 2-year olds (Bonferroni-corrected p values $<.001$), with 4-year-olds also outperforming 3-year-olds (Bonferroni-corrected $p < .05$), whereas

there were no differences among any age groups in *Pan*. Humans also outperformed *Pan* at every age (2, 3, and 4 years; all Bonferroni-corrected p-values $<.01$). In sum humans were already more skilled than both chimpanzees and bonobos at socio-cognitive tasks by the age of 2 years, and continued improving rapidly until 4 years while *Pan* individuals did not significantly improve in their performance in this age range.

In the physical domain there were also effects of genus and age group on performance, as well as an interaction between the two variables (univariate GLM; genus: $F(1,96) = 62.27$, $p < .001$; age group: $F(2,96) = 23.36$, $p < .001$; genus $\times$ age group: $F(2,96) = 7.52$, $p = .001$) (Fig. 1b). Post hoc analyses again revealed a significant effect of age in humans ($F(2,47) = 30.50$, Bonferroni-corrected $p < .001$) but not in *Pan* (Bonferroni-corrected $p > .1$). Furthermore, 4-year old humans outperformed human 2- and 3-year
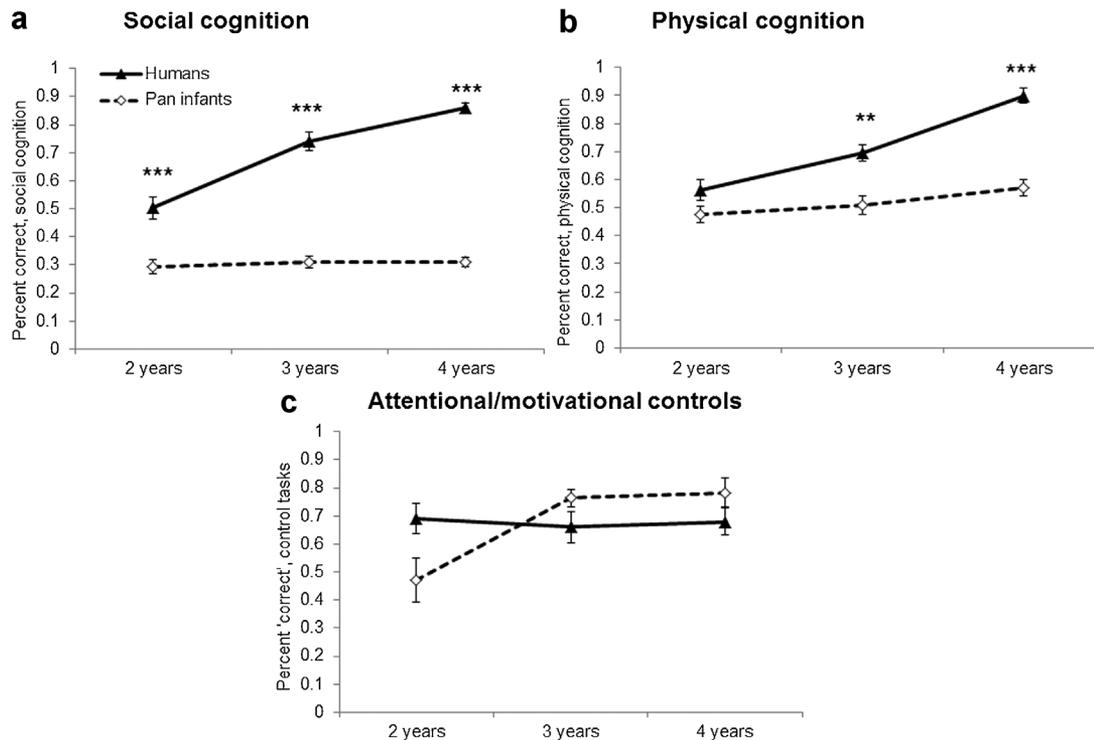

FIGURE 1 Performance in the cross-sectional comparison of human children and *Pan* infants, Experiment 1. The *y*-axis denotes mean percentage correct in (**a**) nine social cognition, (**b**) five physical cognition, and (**c**) three attentional/motivational control tasks, and the *x*-axis denotes the three age groups (children: 2 years, $n = 16$, 3 years, $n = 16$, 4 years, $n = 16$; *Pan* infants: 2 years, $n = 15$, 3 years, $n = 20$, 4 years, $n = 14$). Bars denote standard error. Significant genus differences (adjusted for multiple comparisons using a Bonferroni correction) are denoted as follows: $^*p \leq .05$, $^{**}p \leq .01$, $^{***}p \leq .001$. Children's performance in both domains increased from 2 to 4 years, while performance in *Pan* did not. Children outperformed *Pan* infants in the social, but not the physical, domain at 2 years. There were no significant genus differences in performance on the control tasks either overall or at any age group, nor did performance on these tasks change significantly with age in either genus.

olds (Bonferroni-corrected *p* values <.001), with no differences between age groups in *Pan*. However in contrast to the social domain, humans did not outperform *Pan* in the physical domain at 2 years, becoming detectably more skilled at 3 years (Bonferroni-corrected *p* < .01) and distinctly more skilled at 4 years (Bonferroni-corrected *p* < .001). Thus, humans were comparable to chimpanzees and bonobos in their physical cognition proficiency at 2 years, but they quickly began to outperform the other apes in the next 1–2 years. There were no sex differences in performance in either domain among either humans or *Pan* (univariate GLM analyses with sex as a factor, *p* values >.2).

In the attentional/motivational controls, there were no main effects of genus or age group, nor a significant interaction between the two factors (*p* > .05, with a trend-level interaction between genus and age group given the marginal improvement in *Pan*) (Fig. 1c). Notably, there was no correlation in either genus between performance in these control tasks and performance in the social or physical cognitive domains (linear regressions, *p* values >.05). Thus while *Pan* individuals improved in their performance on the control tasks with age, their increased attention and motivation did not correlate with improved performance in either the social or physical cognitive domain. Meanwhile, children improved in their performance on the social and physical cognitive tasks, but did not change in their performance in the control tasks—suggesting that their improvements in the cognitive tasks did not simply reflect heightened attention or motivation. Finally, since children and same-age *Pan* did not differ in their performance on the control tasks, this indicates that differences between genera were unlikely to have arisen simply from attentional or motivational biases.

Controls for rearing history. Because the majority of our nonhuman ape subjects were orphans, we wanted to ensure that this factor did not account for the observed differences in performance between humans and our *Pan* sample. A comparison of mother-reared apes living in the African ape sanctuaries (*n* = 9) and mother-reared apes living in a zoo population (*n* = 4) in their performance across the cognitive tasks revealed no significant differences between these groups in either social cognition or physical cognition (univariate GLM analyses: physical cognition, *p* > .4, social cognition, *p* = .06 with a trend for sanctuary individuals to perform slightly better than zoo individuals). These results suggest that living environment (zoo versus sanctuary) did not significantly impact performance in the tasks presented. We therefore combined these two mother-reared groups to compare to the orphans living

at the sanctuaries. The sample discussed here differs slightly from the mother-reared sample in our previous article (Wobber & Hare, 2011) because only individuals between 2 and 4 years of age were examined here.

A univariate GLM of performance in the social domain comparing the 13 mother-reared individuals to 13 age- and sex-matched orphans revealed no significant effect of mother-rearing (*p* > .1), suggesting that being orphaned at 2–3 years of age does not significantly affect socio-cognitive abilities in sanctuary individuals. Similarly, there were no differences between mother-reared individuals and orphans in performance on the attentional/motivational control tasks (univariate GLM, *p* > .1). However, mother-reared individuals did significantly outperform orphans in the physical domain (*F*(1,25) = 7.30, *p* = .01). Further investigation revealed no significant differences in performance on any physical cognition task between orphans and mother-reared individuals after correction for multiple comparisons. The only physical cognition task where mother-reared individuals outperformed orphans prior to this correction was object permanence (*t*(24) = 2.05, uncorrected *p* = .05), with a trend towards mother-reared individuals performing more skillfully in tool use ($\chi^2(1)$ = 3.47, *n* = 23, uncorrected *p* = .06) (Fig. 2). These results thus indicate that
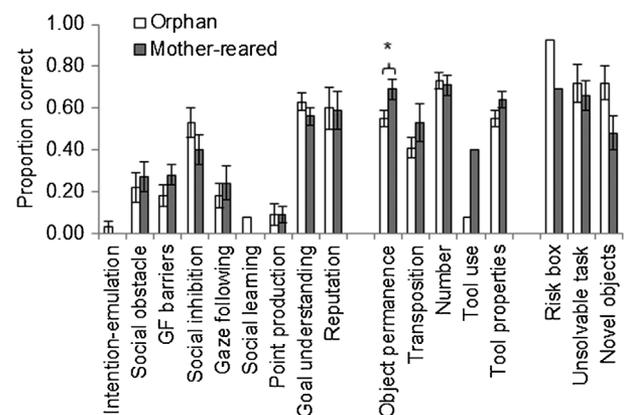

FIGURE 2 Performance across cognitive and attentional/motivational tasks by mother-reared and orphan *Pan* infants, Experiment 1. Average proportion correct is shown for tasks where the dependent measure was continuous, with bars to represent standard error. For tasks where a success/failure measure was used, proportion of individuals correct is shown (and thus there is no standard error for these tasks). Social tasks are on the left, followed by physical tasks, and then the attentional/motivational controls. Comparisons of performance across each task revealed that mother-reared individuals performed comparably to orphans in all tasks. In the object permanence task, there was a significant genus difference in performance prior to correction for multiple comparisons, denoted here by an asterisk.

orphans perform as well as mother-reared infants on the vast majority of cognitive and attentional/motivational tasks, allowing us to group them together with the mother-reared individuals for our analyses. The results also conform to previous findings that adult sanctuary orphans perform just as well or better than mother-reared apes in a zoo population (Hanus & Call, 2008; Vlammings, Hare, & Call, 2010; Wobber & Hare, 2011), indicating that they represent a viable population for nonhuman primate research.

Rate of Cognitive Development—Conclusions. Our analyses comparing the rate of cognitive development between humans and same-age *Pan* supported the accelerated ontogeny hypothesis discussed above. Namely, we found that children improved more rapidly than *Pan* individuals from 2 to 4 years of age in both the social and physical domains. Controls ruled out the possibility that these results reflected mere motivational differences, and our comparisons of mother-reared and orphan apes suggested that these findings did not simply reflect deficits in performance among orphan individuals. In fact, the only area where apes showed significant improvement with age was in the attentional/motivational control tasks, prompting further inquiry into whether these tasks tap into capacities that develop more rapidly in apes. Nevertheless, our finding that 2-year-old children outperformed same-age *Pan* in the

tasks within the social, but not the physical, domain indicated that the two genera showed key differences in their relative proficiencies across tasks. We therefore subsequently analyzed patterns of development in the two genera to examine these differences in more detail.

Patterns of Development.
Age of emergence. Our first analysis investigating patterns of development was to determine the AOE for each of the cognitive tasks in humans and *Pan*. Children met the emergence criteria (described in the Methods Section) for the majority of cognitive tasks (9 of 14) by 2 years of age (Tab. 4). Children also met the emergence criteria for all 14 tasks by the age of 4 years. In contrast, *Pan* individuals had met the emergence criterion for only 4 of the 14 tasks by 2 years of age, and did so in only 8 tasks by the oldest age group tested (Tab. 4). Notably, the physical cognition tasks where young *Pan* had the most difficulty were also those most difficult for children—tool use and tool properties. Moreover, four of the earliest-emerging social tasks in children were also early to emerge in *Pan*—social obstacle, reputation, and the two gaze-following tasks. However, *Pan* individuals struggled with certain social tasks pertaining to understanding others' goals (intention–emulation and goal understanding) and copying their actions (social learning) where children succeeded in these tasks even at

Table 4.   Average Age of Emergence for Each Task in Children and Young Chimpanzees/Bonobos (Genus *Pan*), Using the Cross-Sectional Data From *Pan* in Experiment 1 and the Longitudinal Sample of *Pan* Infants/Juveniles in Experiment 2

Domain	Task	Age of Emergence		
		Humans	*Pan* Cross-Sectional	*Pan* Longitudinal
Social cognition	Intention emulation	2 years	>4 years	Never
	Social obstacle	2 years	2 years	3 years
	Gaze-follow barriers	2 years	2 years	3 years
	Social inhibition	3 years	3 years	3 years
	Gaze-following	2 years	2 years	3 years
	Social learning	3 years	>4 years	Never
	Point production	3 years	4 years	4 years
	Goal understanding	2 years	>4 years	7 years
	Reputation	2 years	2 years	2 years
Physical cognition	Object permanence	2 years	4 years	3 years
	Transposition	2 years	4 years	4 years
	Number	2 years	3 years	3 years
	Tool use	4 years	>4 years	7 years
	Tool properties	3 years	>4 years	7 years

Children's ages are rounded to the closest year (see the Methods Section). Tasks where the average passing criterion was not reached by the oldest age group tested in the cross-sectional sample (4 years) are indicated as emerging ">4 years"; tasks that did not emerge by the oldest age in the longitudinal *Pan* sample (8 years) are indicated as emerging "never." Tasks where *Pan* individuals were least skillful relative to children are highlighted with gray bars—namely, those pertaining to cooperative motivations and understanding others' goals. Ages of emergence were on average later for the longitudinal *Pan* data relative to the cross-sectional *Pan* data owing to the smaller sample of 2-year-old individuals in the longitudinal data set.

the earliest age tested. In Experiment 2, we were able to determine whether these represented consistent differences in skill between children and *Pan* individuals in these tasks or whether proficiency in these areas simply emerged later on in *Pan* development.

Order of emergence. In addition to the later AOE for several tasks in *Pan*, there were also significant differences between children and *Pan* in the overall orders of task emergence (Fig. 3). These differences were present within both the social domain (Supplemental Fig. S1) and, to a lesser extent, the physical domain (Supplemental Fig. S2). Ranking tasks according to relative levels of success, the tasks where children performed most skillfully were overwhelmingly in the social domain, with only one of the five physical cognition tasks present among children's top 50% of skills (Fig. 3). In contrast, three of the five physical cognition tasks were in the top 50% of skills for *Pan* individuals. As is necessary with a test battery approach, it is possible that the precise paradigms chosen influenced individuals' relative levels of success on these tasks (for example, the relative distance between stimuli in the object permanence task might have weakened their performance relative to stimuli placed further apart). Critically however, identical paradigms were presented to both children and same-age *Pan*. Therefore, by comparing relative orders of emergence in these same tasks, we can conclude from this analysis that in the same battery of tasks, *Pan* individuals were relatively

more skilled in the physical tasks than the social, while the reverse was true for children.

Within the social domain, both children and young *Pan* were highly skilled in the gaze-following tasks as well as the social obstacle task, but children's success in comprehending others' goals (measured by the intention–emulation and goal understanding tasks) was not matched by same-age *Pan*. Again, these results highlight differences between humans and other apes in the development of goal understanding that have been demonstrated by prior comparative developmental work as well as comparisons between human infants and adult chimpanzees (Braeuer et al., 2006; Hare, Call, & Tomasello, 2001; Herrmann et al., 2007; Myowa-Yamakoshi, Scola, & Hirata, 2012; Tomasello & Carpenter, 2005; Woodward, 1998).

In looking at the degree to which individuals were consistent in their orders of task emergence, we found that individual patterns of emergence were more consistent in children than they were in *Pan*. Overall, 33.3% of children supported the predominant 14-task pattern of emergence, while only 8.2% of same-age *Pan* supported their respective pattern (though both proportions were significantly greater than the proportion of individuals expected to match these exact patterns by chance, binomial tests, *p* values <.001). No *Pan* individual supported the 14-task pattern found within children, suggesting stronger support for their respective 14-task ordering than that of children (Tab. 5). These patterns were similar in examining
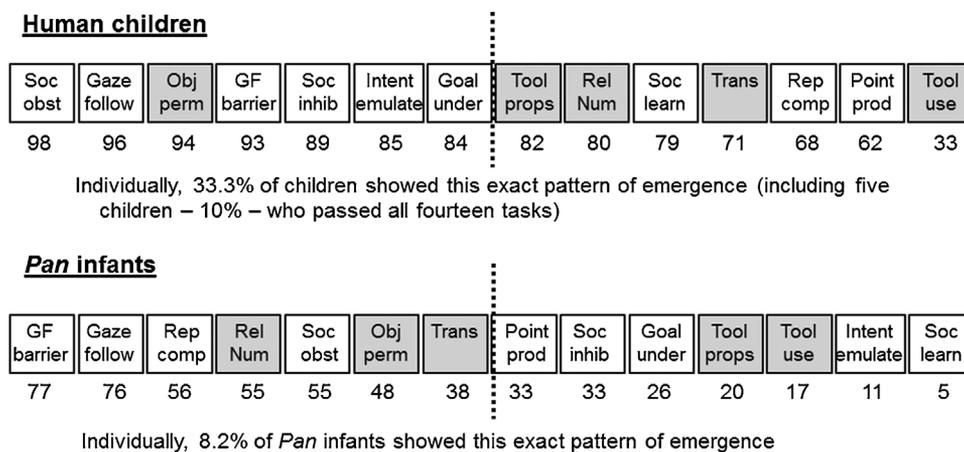

Human children

Soc obst	Gaze follow	Obj perm	GF barrier	Soc inhib	Intent emulate	Goal under	Tool props	Rel Num	Soc learn	Trans	Rep comp	Point prod	Tool use
98	96	94	93	89	85	84	82	80	79	71	68	62	33

Individually, 33.3% of children showed this exact pattern of emergence (including five children — 10% — who passed all fourteen tasks)

***Pan* infants**

GF barrier	Gaze follow	Rep comp	Rel Num	Soc obst	Obj perm	Trans	Point prod	Soc inhib	Goal under	Tool props	Tool use	Intent emulate	Soc learn
77	76	56	55	55	48	38	33	33	26	20	17	11	5

Individually, 8.2% of *Pan* infants showed this exact pattern of emergence

FIGURE 3 Patterns of emergence across cognitive tasks in human children and *Pan* infants, Experiment 1. Each task is represented by its own box; physical cognition tasks are denoted by gray boxes. The percentage of individuals meeting the passing criterion for each task is shown under its respective box. The dotted line denotes the halfway point among the 14 tasks, with skills to the left of this line those where individuals of each genus could be considered most successful. Individual support for patterns of emergence within each genus is also reported. There were numerous differences in order of task emergence between genera, with children overall more successful and more individually consistent in patterns of emergence than *Pan* infants.

Table 5. Levels of Individual Support for Patterns of Task Emergence in Children and Young Chimpanzees/Bonobos (Genus *Pan*), Using the Cross-Sectional Sample of *Pan* in Experimenty 1, and the Longitudinal Sample of *Pan* Infants/Juveniles in Experiment 2

		Domain		
Group	Emergence Sequence	Overall	Social	Physical
Humans	Human pattern	33.3	45.8	81.3
	Pan cross-sectional pattern	12.5	33.3	68.8
	Pan longitudinal pattern	12.5	33.3	45.8
Pan cross-sectional	Human pattern	.0	6.1	30.6
	Pan cross-sectional pattern	8.2	24.5	51.0
	Pan longitudinal pattern	2.0	10.2	42.9
Pan longitudinal	Human pattern	.0	2.3	2.3
	Pan cross-sectional pattern	.0	2.3	22.7
	Pan longitudinal pattern	.0	4.5	31.8

Within each genus, the group-predominant order of task emergence was computed for the 14 tasks overall, as well as separately for the 9-task social domain and the 5-task physical domain. Orders of emergence for *Pan* were calculated separately with both the cross-sectional and longitudinal data. Here, the percentage of individuals that matched their group's predominant sequence of emergence exactly is shown, highlighted in gray. The percentage supporting the predominant patterns of other groups is also shown. Percentage support was on the whole higher among children, but *Pan* individuals better supported their respective emergence patterns than they supported those of children. Note that 10.4% of children passed all 14 cognitive tasks, leading them to support any pattern investigated.

order of task emergence separately by domain (Tab. 5). On the whole, *Pan* subjects showed less individual support for patterns of task emergence than did children, suggesting significant differences between the genera both in overall sequence but also in levels of inter-individual plasticity (Tab. 5).

We next calculated Green's index of consistency (I) (Green, 1956), a measure of scalability that takes chance scaling into account, to determine the degree to which these emergence patterns represented reliable scales. The only reliable scale was in the 5-task pattern of physical cognition task emergence in children, with the overall 14-task sequences and the 9-task social sequences not meeting the criterion for reliable scalability in either children or *Pan* (children: overall, $I = .17$, social cognition, $I = .04$, physical cognition, $I = .50$; Pan: overall, $I = -.03$, social cognition, $I = -.12$, physical cognition, $I = .17$, where values of .50 or above for I indicate a reasonable degree of scaling consistency (Green, 1956)).

We also performed an analysis of the patterns of task emergence using the ordering-theoretic method (Bart & Airasian, 1974) to provide insight into the inter-relationships between specific pairs of tasks. This analysis allowed us to target whether specific task pairs might be inter-dependent in their patterns of emergence in humans but not apes (suggesting differing mechanisms emergence in the two genera) or across both humans and apes (suggesting similar mechanisms underlying performance in the two genera). We set a 0% tolerance level to establish logical prerequisite relationships, as performed in past work (Bart & Airasian, 1974; Carpenter et al., 2002). In children

(Fig. 4), there were a number of task pairs where one skill was found to be a necessary prerequisite to the other, while there were many fewer task pairs in *Pan* meeting the criteria for these logical prerequisite
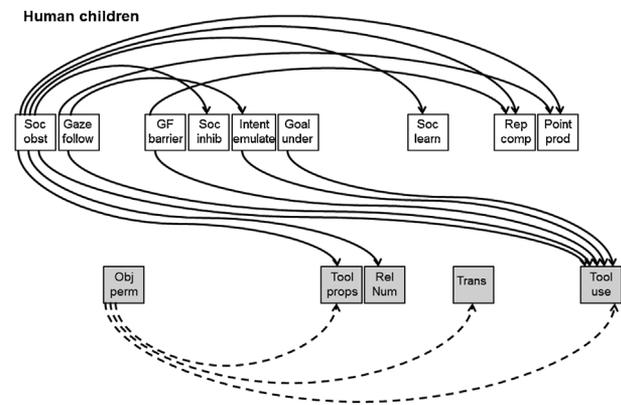

FIGURE 4 Relationships between cognitive tasks in children using the ordering-theoretic method, Experiment 1. We used a 0% tolerance level to determine logical inter-relationships between pairs of tasks. Each of the 14 cognitive tasks is denoted by a box. Physical cognition tasks are shown on the lower part of the diagram, and are denoted by boxes with gray shading. Arrows denote tasks where one was a logical prerequisite to another, with solid arrows denoting a social task that preceded another task, while dotted arrows denote a physical task that preceded another task. Tasks that are not connected by arrows were logically equivalent or independent from one another. A number of social cognitive tasks preceded success in other social and physical cognitive skills among children, where only one physical cognition task preceded success in any other skills.
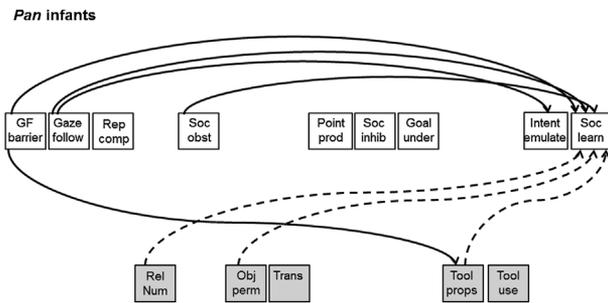
Pan infants

FIGURE 5 Relationships between cognitive tasks in *Pan* infants using the ordering-theoretic method, Experiment 1. We used a 0% tolerance level to determine logical inter-relationships between pairs of tasks. Each of the 14 cognitive tasks is denoted by a box. Physical cognition tasks are shown on the lower part of the diagram, and are denoted by boxes with gray shading. Arrows denote tasks where one was a logical prerequisite to another, with solid arrows denoting a social task that preceded another task, while dotted arrows denote a physical task that preceded another task. Tasks that are not connected by arrows were logically equivalent or independent from one another. Fewer logical prerequisite relationships existed in *Pan* infants than in children, particularly in social cognitive tasks preceding success in other tasks.

relationships (Fig. 5). Among children, there were several social cognition tasks that logically preceded other social skills, but critically also social tasks that logically preceded success in tasks in the physical domain (Fig. 4). In particular, success in the social obstacle task (in looking to the face as a source of another individual's intentions) preceded success in seven other tasks. Only one physical cognition task preceded any others among children: the object permanence task preceded three other physical cognition skills. No physical cognition task preceded any social cognition task in children using this ordering-theoretic analysis.

In contrast, among young *Pan*, few social cognitive tasks preceded other skills. Unlike in children, the social obstacle task, for example, preceded only one other skill in *Pan*. Instead, among *Pan*, a number of physical cognition tasks preceded social cognition tasks, and the task with the highest number of logical prerequisites (six) was the social learning task (Fig. 5). These findings highlight that where social capacities might in fact underlie success across domains in children (where social tasks were found to be logical prerequisites to other skills), success in these same social tasks was not correlated with performance in other skills within young *Pan*. Instead, in *Pan*, physical cognition tasks appear to emerge relatively earlier on, and potentially enable success in later skills. Moreover, these findings provide further support for the notion

that individual patterns of development are more plastic in *Pan* development than in human development, with fewer logical prerequisites and more logical equivalence between tasks in *Pan*. The results also suggest that significant changes in skill inter-relationships during ontogeny are present specifically within the socio-cognitive domain, with the social domain potentially facilitating success in the physical domain among children but not *Pan*.

Despite these broad differences in task inter-relationships, there were two commonalities between children and same-age *Pan* in the logical prerequisite relationships. For both genera, success in social obstacle preceded success in social learning, and success in gaze-following preceded success in intention–emulation (achieving another's failed goal) (Figs. 4 and 5). Mainly, these results stemmed from *Pan* individuals performing fairly poorly on the latter two tasks (social learning and intention emulation). However, it is a compelling suggestion, meriting future inquiry, that *Pan* infants, like human infants, must begin to seek information about others' attention and intention before inferring their goals (Carpenter et al., 1998; Tomasello & Carpenter, 2005).

Relative proficiency. We next used the continuous data set (consisting of percentage correct in a given task rather than pass/fail measures) to examine within-individual ranks of task performance, providing an additional measure of subjects' relative skillfulness across tasks. There were a number of differences in within-individual task ranks between children and same-age *Pan* in the social domain (Fig. 6). Children showed significantly lower (better) ranks than *Pan* individuals in four of the nine social cognition tasks: social obstacle (Mann–Whitney U, $Z = -6.08$, $p < .001$), social learning ($Z = -5.81$, $p < .001$), intention emulation ($Z = -5.68$, $p < .001$), and gaze-following around barriers ($Z = -2.58$, $p = .01$). Meanwhile, *Pan* individuals showed significantly lower (better) within-individual ranks for reputation ($Z = 4.79$, $p < .001$) and gaze-following ($Z = 2.07$, $p = .04$–though the difference in mean rank for gaze-following was minimal, *Pan* subjects' performance was highly consistent and so this led to an overall group-level difference). In contrast, there were no differences in task rank between children and *Pan* within the physical domain. These findings indicate that when controlling for differences in absolute skill level (by comparing individuals to their own average task performance using *relative* ranks), the relative complexities of the physical tasks was similar between children and same-age *Pan* (e.g., the same tasks proved most difficult for both groups). In contrast, the relative
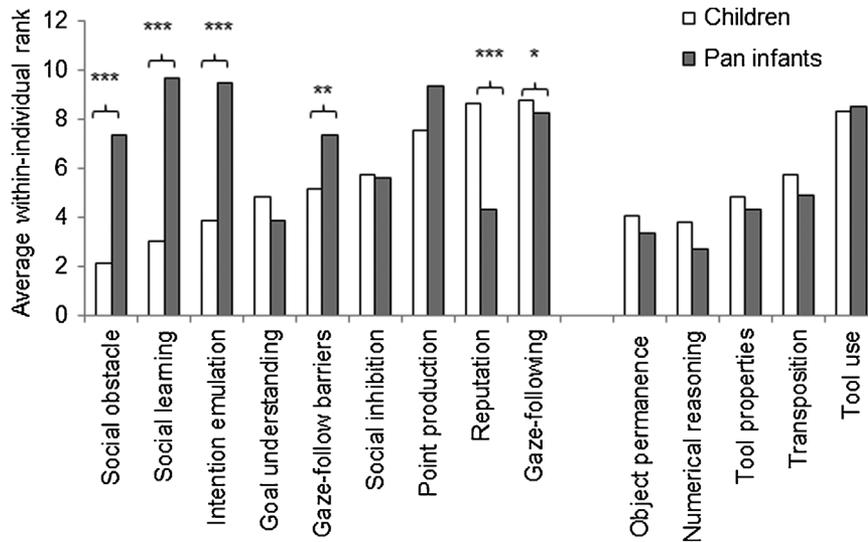
FIGURE 6 Average within-individual task ranks in children and *Pan* infants, Experiment 1. Social tasks are on the left of the graph, and physical tasks are on the right. Lower ranks represent better performance (since a subject's best task would be his or her 1st rank task, while that subject's worst task would be rank 14). There were a number of significant differences in task rank between children and *Pan* juveniles in the social domain, noted on the graph, with the significance values from Mann-Whitney tests denoted as follows: $^*p < .05$, $^{**}p < .01$, and $^{***}p < .001$. Meanwhile, within-individual ranks in the physical domain did not differ between children and *Pan* infants for any task.

rankings of social cognition tasks differed significantly between children and *Pan*. These results further support the notion that the development of socio-cognitive skills has changed more dramatically between humans and our closest living relatives than has the development of physical cognition skills. This provides an open question for future inquiry, in determining the degree to which certain patterns of cognitive development are conserved across species while others (such as in the social domain) are more variable.

Inter-task correlations. Finally, to examine the degree to which individual performance correlated across tasks, we calculated pairwise task correlations using the continuous performance data set. Pearson correlations between each of the 14 tasks in each genus revealed 38 significant ($p < .05$) relationships in children, but only 5 significant relationships in *Pan*. Among these five significant relationships in Pan, one was between two social tasks, two were between two physical tasks, and two were cross-domain. Meanwhile, in children, there were 15 significant correlations solely within the social domain, 7 correlations solely within the physical domain, and 16 cross-domain correlations. Importantly, after correcting for multiple comparisons (by adjusting the *p*-values of these correlations with a Bonferroni

correction), 8 of the 38 inter-task correlations remained significant among children, while none remained significant among young *Pan* (Tab. 6). These results revealed (1) greater intra-individual consistency in task performance among children, in addition to the heightened inter-individual consistency demonstrated by the order of emergence analysis, and (2) greater inter-correlation of the social domain with other skills in children relative to *Pan* in line with past work showing a distinct social cognition "factor" in children but not chimpanzees (Herrmann, Call, et al., 2010).

Conclusions—Experiment 1

The results of our first experiment provide support for the possibility that humans exhibit accelerated ontogeny in our cognitive development relative to that of other species and that between humans and nonhuman apes there are variable patterns of cognitive development, particularly in the social cognitive domain. Taken together, these comparisons of the pace and pattern of development in children and same-age apes support the hypothesis that humans' accelerated ontogeny might stem from the relatively early emergence of specific social cognitive skills in human children, particularly those pertaining to goal understanding and cooperative

Table 6.   Correlations in Performance Across Cognitive Tasks in Children and Same-Age *Pan*, Experiment 1

Task Type	Genus	Tasks	Pearson Value	Significance
Social/Social	Children	Social inhibition and social obstacle	.548	.05
		Social inhibition and social learning	.673	.001
		GF barriers and intention emulation	.628	.001
	Same-age *Pan*	**No significant inter-task correlations**		
Social/Physical	Children	Social inhibition and transposition	.577	.01
		GF barriers and transposition	.503	.05
		Intention emulation and transposition	.522	.01
		Social learning and tool properties	.690	.001
	Same-age *Pan*	**No significant inter-task correlations**		
Physical/Physical	Children	Object permanence and tool properties	.616	.01
	Same-age *Pan*	**No significant inter-task correlations**		

Only correlations that were significant after Bonferroni correction for multiple comparisons are listed. Correlations between tasks are sorted according to domain—listing first the significant inter-task correlations between two social tasks, followed by significant correlations between a social and a physical task, and then followed by significant correlations between two physical tasks. Pearson correlation values and their relative significance are shown. All significant correlations in performance across tasks were positive.

motivations. Through several lines of analysis, our results prompt areas for future inquiry in suggesting that the pattern and pace of social cognitive development may differ significantly between children and younger apes.

EXPERIMENT 2

One possibility in interpreting our results from Experiment 1 was that the slower rate of cognitive development among 2- to 4-year-old *Pan* individuals was simply due to having matched human and *Pan* individuals based on absolute age rather than relative age. Critically, *Pan* individuals normally do not wean until 4 years of age, which is later than most estimates of weaning age in human populations (Kennedy, 2005; Sellen & Smay, 2001). After they are weaned, young *Pan* individuals are responsible for 100% of their foraging intake, with no active provisioning on behalf of their mothers—in stark contrast to typical patterns within our own species (Goodall, 1986; Kaplan et al., 2000; Kramer & Ellison, 2010). This suggests that *Pan* individuals may undergo a period of rapid cognitive development upon needing to forage for themselves and to independently navigate their social group at 4 years of age.

Thus in the present experiment, we examined a larger age range of *Pan* individuals spanning 2–6 years of age and followed them longitudinally for three subsequent years of testing (note that precise ages were unknown for the majority of individuals; individual ages were estimated to the closest year using the procedure discussed above for Experiment 1). This allowed us to track individuals through the period of

infancy and juvenility, with our oldest age group (8 years) mapping approximately onto the onset of the chimpanzee adolescent period (with menarche in females and spermatogenesis in males occurring around this time in captive chimpanzees (Coe, Connolly, Kraemer, & Levine, 1979; Marson, Meuris, Cooper, & Jouannet, 1991)). In this experiment we were able to discriminate between two alternatives: first, that *Pan* juveniles show a period of rapid cognitive maturation after weaning, similar to the rapid pace of development found among human children in Experiment 1, or instead, that *Pan* juveniles continue their modest rate of cognitive development throughout ontogeny. Further, we were able to validate the reliability of the patterns of development in *Pan* established from the cross-sectional sample in Experiment 1.

Methods

Subjects. Again, chimpanzees were tested at the Tchimpounga Chimpanzee Sanctuary in the Republic of Congo and bonobos were tested at Lola ya Bonobo in the Democratic Republic of Congo. Our sample consisted of 30 chimpanzees (16 males) and 14 bonobos (8 males) that ranged from 2 to 6 years of age in the initial data collection season (2 years: $n = 9$; 3 years: $n = 11$; 4 years: $n = 7$; 5 years: $n = 6$; 6 years: $n = 11$). We followed these individuals for three subsequent years of testing (2008, 2009, and 2010), enabling us to examine development occurring between 2 and 8 years of age (total sizes for each age group across 3 years of testing: 2 years: $n = 9$; 3 years: $n = 20$; 4 years: $n = 27$; 5 years: $n = 24$; 6 years: $n = 24$; 7 years: $n = 17$; 8 years: $n = 11$). To ensure that changes in performance between years were not a

result of increased familiarity with the tasks, we compared performance of these infants and juveniles to a sample of six adults (three chimpanzees, three bonobos, mean age = 13.2 years in 2008) tested in all 3 years. As in Experiment 1, owing to small sample size in particular age groups, we combined chimpanzees and bonobos for our analysis (differences between the two species are discussed elsewhere (Herrmann, Hare, Call, & Tomasello, 2010; Wobber et al., 2010)). The data from this experiment did not map precisely onto the cross-sectional data presented in Experiment 1 for the following reasons: (1) we utilized a larger age range here (testing individuals between 2 and 8 years of age), (2) the cross-sectional data set (Experiment 1) incorporated only individuals in the target age range participating in the test battery for the first time, while the longitudinal data set (Experiment 2) included only individuals who participated in all 3 years of data collection (2008–2010). Individuals who arrived too late to be included in the longitudinal data (e.g., in 2009) or who were not able to participate in 3 years of data collection (due to death or being reintroduced into the wild, see below) were not included in the data set for Experiment 2.

Design. Subjects participated in the same battery of cognitive tasks described in Experiment 1. Data were collected from chimpanzees in May/June 2008, June 2009, and June/July 2010. Data were collected from bonobos in July/August 2008, May/June 2009, and July/August 2010. Fifty-two subjects began the longitudinal testing but eight individuals did not complete it because they were reintroduced into the wild ($n = 5$) or died ($n = 3$).

Procedure. Procedures were identical to those described for Experiment 1, except that adult subjects did not participate two of the social cognition tasks (intention emulation and social learning) that involved breakable objects being passed into the test room. Their average social cognition performance thus represents the average of the remaining seven social cognition tasks. Task abbreviations are the same as those used in Experiment 1.

Analysis. Again, we began by quantifying the general rate of improvement across tasks to assess pace of development, and then investigated patterns of performance.

Rate of cognitive development. To examine improvements in performance across the multiple years of testing, we performed repeated measures ANOVAs with test year (2008, 2009, 2010) as a factor. We performed separate ANOVAs for the social domain, the physical domain, and the attentional/motivational controls. We performed these ANOVAs for our infant and juvenile subjects, as well as for the adult control group.

To examine improvement across tasks in more detail, we calculated difference scores for each task between each individual's performance in that task during the last year of testing (2010) and his or her performance in that task during the first year of testing (2008). This analysis tracked the degree to which apes' performance changed over the course of 2 years of development, and allowed us to determine the areas where individuals showed the greatest improvement.

Patterns of cognitive development. As in Experiment 1, we determined an AOE for each task, using the same individual emergence criteria as described previously (Tab. 3). The group-level AOE was defined as the age where 50% of individuals had met the emergence criterion either at or prior to that age (given that longitudinal data were available). AOEs calculated from the longitudinal data were likely to be older than those calculated from the cross-sectional data due to the smaller number of individuals in the youngest age categories (several 2-year-olds began the longitudinal battery but did not finish it due to the reasons described above, and so were included in the analyses for Experiment 1 but are excluded from the analyses for Experiment 2). In addition to looking at ages of emergence, we examined the order of task emergence to determine the degree to which this matched the patterns found cross-sectionally in Experiment 1. We determined the order of task emergence by ranking tasks according to the proportion of individuals that were ever successful in that task over all 3 years of testing. We also assessed levels of individual support for these patterns, doing so for the overall sequence and separately for the social and physical domains. Finally, similar to Experiment 1, we determined inter-task correlations, to validate the findings from Experiment 1 that young *Pan* individuals showed few inter-relationships in success across tasks relative to same-age children.

Results

Rate of Cognitive Development. A repeated measures ANOVA of *Pan* infant and juveniles' performance in the social domain revealed a significant effect of test year ($F(2,40) = 6.76$, $p < .01$). Post hoc tests demonstrated that *Pan* infants and juveniles performed better in 2009 than they did in 2008 (Bonferroni-corrected $p = .012$) and better in 2010 than they did in 2008

(Bonferroni-corrected $p = .006$). A similar effect of year was present in the repeated measures ANOVA for the physical domain ($F(2,41) = 6.71$, $p < .01$), with the only significant improvement in performance between 2008 and 2010 (Bonferroni-corrected $p = .003$). Finally, *Pan* infants and juveniles also shifted over the course of 3 years in their performance in the attentional/motivational controls (repeated measures ANOVA, $F(2,34) = 8.37$, $p = .001$), performing "better" (being more attentive and motivated) in 2010 than 2008 (Bonferroni-corrected $p = .006$) and in 2010 than 2009 (Bonferroni-corrected $p = .045$). Thus across the social, physical, and attentional domains *Pan* infants and juveniles showed significant improvements in their performance with age from the initial to the final year of testing (Fig. 7).

Importantly, we could rule out the possibility that these improvements were due to increased experience with the tasks by using our sample of six adults tested across all 3 years, concurrent with the infant/juvenile subjects. For these six adults, there was no significant effect of test year in repeated measures ANOVAs for the social domain ($p > .4$), the physical domain ($p > .09$), or the attentional/motivational controls ($p > .1$) (Fig. 7). These results thus indicate that the changes in performance measured among the younger subjects represented maturational change rather than familiarity-based improvements or variance in task administration across years.

We next analyzed the difference scores for each task, which tracked within-individual changes in performance from 2008 to 2010. We found that *Pan* juveniles
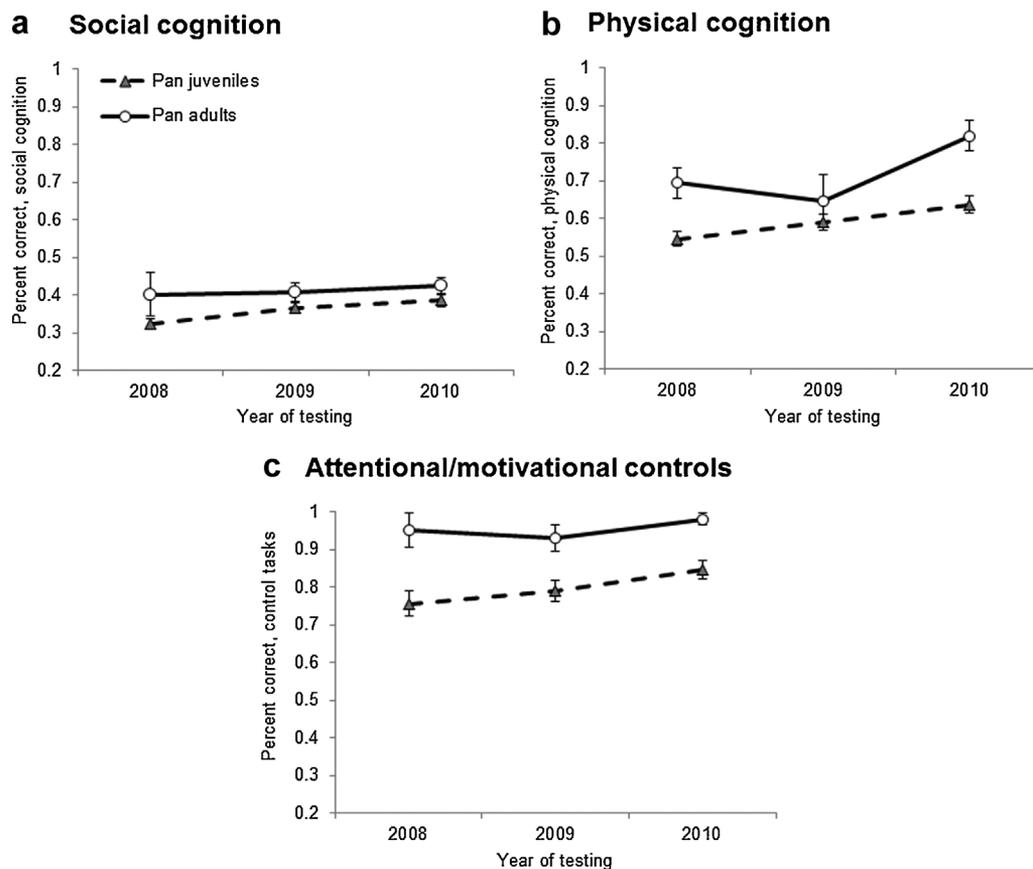

FIGURE 7 Average performance in *Pan* infants/juveniles and *Pan* adults across 3 years of longitudinal testing, Experiment 2. The *y*-axis denotes mean percentage correct in (a) nine social cognition, (b) five physical cognition, and (c) three attentional/motivational control tasks, and the *x*-axis denotes the three test years (2008, 2009, 2010). Average adult performance is shown with circles and solid lines, while average infant/juvenile performance is shown by triangles and dotted lines. Bars denote standard error. Performance in infants and juveniles improved in all three areas across the 3 years of testing, while performance in the adults did not (in physical cognition, there was a trend effect of year but this was not significant). Yet overall, the degree of improvement among *Pan* infants/juveniles was modest compared to that seen in children (Fig. 1).

improved in four of the five physical cognition tasks from the first to the last task administration, showing on average a 9.2% increase in performance. Meanwhile, they improved in seven of the nine social cognition tasks across this time period, showing a 6.1% improvement on average. Finally, subjects also became more attentive throughout the 3 years of testing, showing an average 8.9% "improvement" in their performance across the three attentional/motivational control tasks (Supplemental Fig. S3). Though these gains in performance led the effect of test year to be statistically significant in the repeated measures ANOVAs, these gains are modest compared to children's average improvement of over 30% in both the social and physical domains over the course of 2 years (see Fig. 1). Thus rather than *Pan* showing a rapid period of cognitive development in juvenility after an initial slow period in infancy, the results of Experiment 2 support the findings of Experiment 1 that *Pan* cognitive development progresses more slowly than that of humans throughout infancy and juvenility.

Patterns of Cognitive Development.

Age of emergence. In Experiment 1, there were several tasks for which *Pan* individuals did not meet the emergence criteria by the age of 4 years (see Tab. 4). With the longitudinal data set in this experiment, we were able to ascertain whether *Pan* juveniles eventually became successful at these tasks later on in development. Indeed, *Pan* individuals ultimately succeeded in four of the six tasks where they did not meet the emergence criterion in Experiment 1 (Tab. 4). However, there were two tasks where *Pan* juveniles never succeeded, even at the oldest age tested (8 years). Notably, these were tasks where children were successful even at 3 years of age: social learning and intention–emulation (Tab. 4). These results align with findings from with adult chimpanzees and bonobos showing that they are not as proficient as human children in imitative learning and cooperatively minded goal attribution (Horner & Whiten, 2005; Itakura & Tanaka, 1998; Myowa-Yamakoshi et al., 2012; Tomasello, Carpenter, Call, Behne, & Moll, 2005; Tomasello, Savage-Rumbaugh, & Kruger, 1993). However, what is notable is that the success of adult chimpanzees in competitively motivated goal attribution paradigms (Braeuer et al., 2006; Hare & Tomasello, 2004) was matched here only by *Pan* individuals at the older end of our age range, with success in the "goal understanding" task (adapted from the paradigm of Braeuer et al., 2006) only occurring at 7 years of age. This is in striking contrast to human children, where individuals in the first year of life begin to attribute goals to others while also starting to track others' attention and

behavior in rapid sequence (Behne, Carpenter, & Tomasello, 2005; Butterworth & Itakura, 2000; Carpenter et al., 1998; Woodward, 1998). Instead, we found that *Pan* individuals were able to track others' attention and behavior by 3 years of age but could only successfully comprehend others' goals much later on in development, at 7 years (Tab. 4). Goal understanding may thus be prioritized in human ontogeny relative to the socio-cognitive ontogeny of any other species, given its important role in cultural learning (Tomasello, 2009; Tomasello et al., 2005; Tomasello, Kruger, & Ratner, 1993). This finding highlights the importance of a comparative developmental perspective and prompts future targeted inquiry into the ontogeny of goal understanding in nonhuman animals.

Order of emergence. The order of task emergence for *Pan* juveniles determined from the longitudinal data (Experiment 2) mapped fairly closely onto that from the cross-sectional data (Experiment 1) (Fig. 8). As would be expected, a higher percentage of individuals met the task emergence criteria over 3 years of longitudinal testing than did so in 1 year of cross-sectional testing (though the older age of our Experiment 2 sample may also have accounted for this difference). However, the relative ordering of skills was still broadly similar, with three of the five physical cognition tasks among the best-ranking for *Pan* individuals while the most difficult tasks were the intention–emulation and social learning tasks.

Individual support for the longitudinal sequence of emergence was quite low, with no individuals matching the precise 14-task pattern determined by the group-level analyses. No individual in the longitudinal data matched the pattern of emergence determined by the cross-sectional analyses, nor did any individual in the longitudinal data match the emergence pattern found in children (Tab. 5). This supports the finding of Experiment 1 that patterns of development are highly variable in *Pan* individuals, at least for the present battery of tasks. *Pan* individuals showed greater consistency when examining emergence sequences separately by domain, with 4.5% of individuals matching the 9-task social emergence pattern and 31.8% of individuals matching the 5-task physical emergence pattern (though again both of these levels of support were less than found in Experiment 1). This both replicated our finding that the general patterns of success across tasks differed between young *Pan* and human children, and supported our claim that patterns of cognitive development are more consistent across individuals in children than in *Pan*. Future work is needed to determine whether certain abilities may in fact cluster together throughout development in *Pan* individuals that were not captured
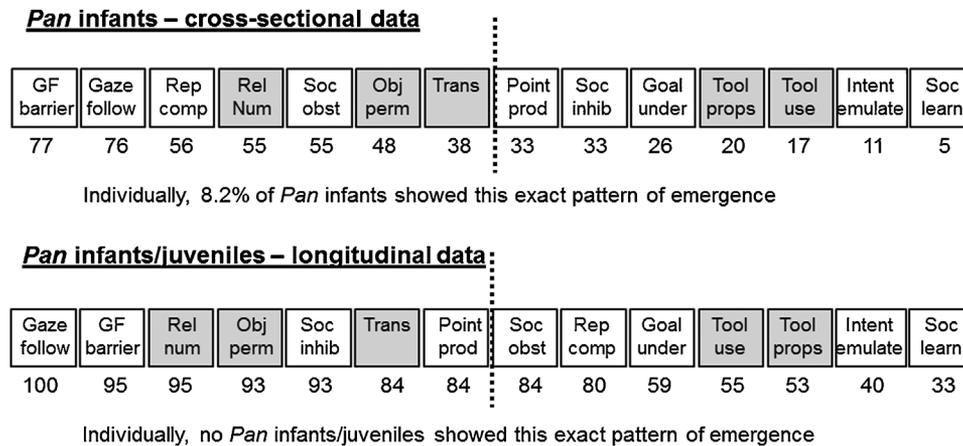
Pan infants – cross-sectional data

GF barrier	Gaze follow	Rep comp	Rel Num	Soc obst	Obj perm	Trans	Point prod	Soc inhib	Goal under	Tool props	Tool use	Intent emulate	Soc learn
77	76	56	55	55	48	38	33	33	26	20	17	11	5

Individually, 8.2% of *Pan* infants showed this exact pattern of emergence

Pan infants/juveniles – longitudinal data

Gaze follow	GF barrier	Rel num	Obj perm	Soc inhib	Trans	Point prod	Soc obst	Rep comp	Goal under	Tool use	Tool props	Intent emulate	Soc learn
100	95	95	93	93	84	84	84	80	59	55	53	40	33

Individually, no *Pan* infants/juveniles showed this exact pattern of emergence

FIGURE 8 Patterns of emergence across cognitive tasks in *Pan* individuals using the cross-sectional data set, Experiment 1, and longitudinal data set, Experiment 2. Each task is represented by its own box, with physical cognition tasks denoted by gray boxes. The percentage of individuals meeting the passing criterion for each task is shown under its respective box—for the longitudinal data, this represents the percentage of individuals who passed the task any time during the 3 years of testing. The dotted line denotes the halfway point among the 14 tasks, with skills to the left of this line those where individuals could be considered most successful. Individual support for patterns of emergence within each data set is also reported. There were few differences in pattern of emergence between the estimates of the cross-sectional and the longitudinal data, with the main changes in the social inhibition task (where individuals initially struggled but eventually succeeded) and the reputation comprehension task (where the reverse pattern was the case).

here, for example in capacities pertinent to foraging (Rosati & Hare, submitted).

Inter-task correlations. In Experiment 2 we found a greater number of significant correlations in performance across tasks among *Pan* individuals relative to Experiment 1. Yet similar to Experiment 1, *Pan* individuals showed more inter-relationships between tasks in the physical domain than tasks in the social domain. Across the 3 years of testing, there were in total 23 significant correlations between tasks within a given year (18 positive and 5 negative). Among the 18 positive relationships, 7 were between two social tasks, 5 were between two physical tasks, and 6 were cross-domain (thus 11 of these 18 relationships involved at least one physical cognition task). Critically, only one of these correlations (that between object permanence and transposition in 2009) was significant after correction for multiple comparisons (Tab. 7). This correlation aligns with previous findings demonstrating a distinct spatial cognition factor in adult chimpanzees encompassing performance on these two tasks (Herrmann, Call, et al., 2010).

Conclusions—Experiment 2

The results of Experiment 2 indicate that the rate of cognitive development in *Pan* remains slow throughout infancy and juvenility relative to the pace in human children. We found no evidence for a period in *Pan* development, either before or after weaning, when their rate of cognitive development matches that of 2- to 4-year-old children. We found further support for the patterns of skill emergence in *Pan* development determined by Experiment 1, with these patterns differing significantly from those of human children. We again found a large degree of inter-individual plasticity in patterns of development among *Pan* individuals, particularly within the social domain. To review the major findings for each type of analysis performed in Experiments 1 and 2, we provide a summary table (Tab. 8). These results indicate significant changes in both the rate and pattern of development between humans and young *Pan*, with notable shifts in the ontogeny of social cognition.

DISCUSSION

Our findings provide support for the hypothesis that there are significant differences in the pattern and pace of cognitive development between humans and our closest living relatives, chimpanzees and bonobos. First, our results demonstrated accelerated ontogeny in human cognitive development relative to other apes, with

Table 7. Correlations in Performance in Each Testing Year Within *Pan* Infants and Juveniles, Experiment 2

Task Type	Year	Tasks	Pearson Value	Significance
Social/social	2008	**No significant inter-task correlations**		
	2009	**No significant inter-task correlations**		
	2010	**No significant inter-task correlations**		
Social/physical	2008	**No significant inter-task correlations**		
	2009	**No significant inter-task correlations**		
	2010	**No significant inter-task correlations**		
Physical/physical	2008	**No significant inter-task correlations**		
	2009	Object permanence and transposition	.515	.05
	2010	**No significant inter-task correlations**		

Only correlations that were significant after Bonferroni correction for multiple comparisons are listed. Correlations between tasks are sorted according to domain—listing first the significant inter-task correlations between two social tasks, followed by significant correlations between a social and a physical task, and then followed by significant correlations between two physical tasks. Pearson correlation values and their relative significance are shown. The significant correlation in performance between the object permanence and transposition tasks was positive.

more rapid improvements among human children relative same-age chimpanzees and bonobos. Second, our findings revealed variable patterns of cognitive development between humans and *Pan*, with divergent patterns particularly apparent within the social cognitive domain, including greater inter-relationships of social cognitive skills in children relative to apes as well as evidence that in children, social cognitive skills underlay improvements in the physical domain. We did find a few patterns of development that were conserved

Table 8. Key Results From Each Analysis Type, Experiment 1 and Experiment 2

Analysis	Subtype	Result
Experiment 1: Cross-sectional data set		
Rate of development	GLM analyses	Children show accelerated rate of improvement, earlier success in social cognition
Patterns of development	Age of emergence	Cognitive development more rapid in children, elements of socio-cognitive development missing entirely in *Pan* infants
	Order of emergence	Children show earlier emergence of social tasks, more individual consistency in patterns of emergence, key genus differences in understanding others' goals
	Relative proficiency	Children show earlier proficiency in understanding others' intentions and goals, physical cognitive skills more comparable in within-individual rank across children and *Pan* infants
	Inter-correlations	Children show greater inter-task correlations, particularly in the social domain, suggests greater inter-relationship in skill development in children than in *Pan* infants
Experiment 2: Longitudinal data set		
Rate of development	Repeated measures ANOVA	Rate of improvement is slow among *Pan* infants and juveniles relative to children, but is more marked than improvement among *Pan* adults
Patterns of development	Age of emergence	Several tasks emerge much later on in *Pan* relative to human development such as goal understanding, tasks requiring cooperative motivations never emerge
	Order of emergence	Relative ordering of skills similar to cross-sectional result, physical cognition skills prioritized, skills pertaining to cooperative motivations least prioritized
	Inter-correlations	Greater inter-task correlations than cross-sectional sample, but still fewer than children, few inter-relationships solely within the social domain

Divisions are the same as those presented in the Results Sections. Using a variety of analytical techniques, these results provide support for the hypothesis that the rate and pattern of cognitive development vary significantly between humans and other apes. They also indicate specific skills that are fundamental to differences in cognitive development between human children and *Pan* juveniles.

between children and young *Pan*, such as the correlation between success in the object permanence and transposition tasks, which aligns with prior work suggesting that these tasks tap into similar underlying capacities (Barth & Call, 2006; Herrmann, Call, et al., 2010). These findings suggest that specific areas of cognitive development may be conserved across taxa, while others are more variable in depending on species-specific inputs. Our control analyses ruled out the possibility that the observed differences were due to differing levels of attention and motivation between species or age groups, or to aspects of rearing history in our nonhuman ape sample. These results thus suggest that human cognitive development is accelerated on the whole in comparison to our closest living relatives, with particularly marked changes in humans' development of socio-cognitive skills.

These results provide support for the Cultural Intelligence Hypothesis (Herrmann et al., 2007), with children showing earlier success than same-age apes in a suite of social cognitive capacities that are critical to learning from others—understanding others' attention and intention, as well as skills in imitative learning. Together with these distinctions between humans and *Pan* in socio-cognitive development, we found that children showed a more rapid pace of development across both the social and physical cognitive domains relative to same-age *Pan*. Though our results cannot definitively show that the social cognitive skills alone facilitated children's accelerated development (independent from say, the effects of language), the ordering-theoretic analyses from Experiment 1 support strong connections in children between success in specific early-emerging social capacities and success in a number of other areas. There are two main avenues by which future research can tease apart the relative contributions of social cognitive capacities relative to other capacities such as language in facilitating accelerations in development. The first is through the comparison of typically developing children with children who lack spoken language, to clarify the role that linguistic inputs play in facilitating cognitive development. The second is through studies of cognitive development in nonhuman animals that lack language entirely but possess greater cooperative motivations and capacities for social learning than the apes tested here, such as meerkats or domestic dogs (Hare, Brown, Williamson, & Tomasello, 2002; Thornton & McAuliffe, 2006; Topal, Gergely, Erdohegyi, Csibra, & Miklosi, 2009). Our findings highlight the role of comparative developmental studies in testing theories of cognitive development derived only from studies of typically developing infants and children.

A potential criticism of our approach is the use of conspecific experimenters for the human children but not *Pan* individuals. In favor of this technique, it enabled us to have a much greater degree of precision, performing methods identically between individuals and between tests, than if we had employed a confederate child demonstrator for our child subjects or a conspecific demonstrator for our ape subjects. Against it, having a conspecific demonstrator in certain social tasks could in theory augment the performance of nonhuman apes. Although one study of eye tracking did indeed suggest that chimpanzees follow the gaze of a human less readily than the gaze of a conspecific (Hattori, Kano, & Tomonaga, 2010), most social cognition tasks (including the ones utilized here) involve the perception of much less subtle cues. Indeed, numerous studies have demonstrated that nonhuman apes are able to interpret the actions, intentions, and dispositions of human experimenters, and even to follow their gaze direction reliably in geometric space and around barriers (Braeuer, Call, & Tomasello, 2005; Horner & Whiten, 2005; Russell, Call, & Dunbar, 2008; Warneken, Hare, Melis, Hanus, & Tomasello, 2007). In addition, studies employing both a human and a conspecific demonstrator have found little difference in chimpanzees' performance between the two situations (Hare & Tomasello, 2004; Itakura, Agnetta, Hare, & Tomasello, 1999; Myowa-Yamakoshi et al., 2012; Tomasello, Call, & Hare, 1998). Thus ample previous research indicates that nonhuman apes are able to successfully perceive human experimenters as social agents. Further, in the present study, any purported enhancement of children's performance by a conspecific demonstrator would not account for (1) the differing rate of improvement within each genus (since *Pan* 2-year-olds would have been similarly affected by this potential bias as *Pan* 4-year-olds) or (2) children's relatively more skilled performance in the physical cognition tasks (where the role of the experimenter is greatly reduced). Therefore we are confident that both child and *Pan* subjects were given equal opportunities to succeed in these experiments.

Though we discuss our findings as representative of species-typical development in children and nonhuman apes, an important caveat of our results is that we have only studied one population within each species. It is entirely possible that cross-cultural variation in human development might influence performance in the tasks employed here, as well as potential differences in the apes' rearing environments influencing their relative levels of success. Neither the humans nor the apes we studied were living in the environments that they evolved in, and so the effects of developed society (for humans) or a semi free-ranging environment (apes)

may have shaped their performance here. Despite these potential drawbacks, we would highlight that in none of our test populations were individuals living in deprived conditions. Chimpanzees in particular have been shown to exhibit deficits in cognitive development when reared in environmental or social isolation (Davenport, Rogers, & Rumbaugh, 1973; Turner, Davenport, & Rogers, 1969). The apes that we worked with live in African sanctuaries that provide rich social and physical environments unparalleled by most zoo and laboratory facilities housing nonhuman primates, with these sanctuaries meeting the "top 10" requirements for captive care established based on the needs of wild chimpanzees (Farmer, 2002; Pruetz & McGrew, 2001; Wobber & Hare, 2011). Nonetheless, variation in performance in cognitive tasks has been shown among apes even across highly enriched captive facilities (Bard et al., 2005; Vlammings et al., 2010), mirroring the cross-cultural variation in children's cognitive development that is now a growing topic of research (Callaghan et al., 2011). In some ways, populations at African ape sanctuaries may be better suited to study culturally variant phenomena given that apes at these sites come from varying backgrounds and even varying subspecies (Ongman, Colin, Raballand, & Humle, 2013). Extending these results to multiple populations, and documenting how developmental inputs shape performance across domains, will therefore be a fruitful direction for future study.

Finally, by employing a test battery approach here, we gained several strengths that were accompanied by a few drawbacks. First, through presenting our subjects with a diverse battery of tasks, we were able to investigate abilities that spanned a variety of domains, from capacities to reason about others to abilities to track objects in space. Importantly, as one of the first broad-scale investigations of cognitive development in chimpanzees using this large of a sample size, and the first such study of cognitive development in bonobos, we elected to take a more generalist approach in quantifying basic skills across multiple areas. To do so, we chose single task exemplars for a given ability, using paradigms that had been previously utilized in the literature. By choosing single task exemplars, we may have hindered our ability to determine the youngest possible AOE for a given capacity. For example, it might be that if we had targeted the ontogeny of object tracking capacities with sequentially more difficult tasks, we would have found signatures of object permanence earlier on in nonhuman ape development, as has been shown by detailed longitudinal studies performed previously (Spinozzi & Poti, 1993). However, the advantage of using a task battery approach is that because the tasks presented were near-identical in methodology across species and age groups, we were able to compare all of our subjects on equal ground, rather than losing inter-group comparability by tailoring tasks specifically to each subset of our sample. In addition, we were able to examine inter-relationships across multiple cognitive domains, which we would have been unable to do had we focused in more detail solely on one area of cognition. A stimulating direction for future research will be to investigate the capacities tested here in more detail, determining the degree to which specific task dynamics influence performance across nonhuman ape development. Moreover, beyond using paradigms well-established in developmental psychology, it will be exciting to develop paradigms that increasingly mirror the problems faced by chimpanzees and bonobos in the wild, and to measure children's success in these same areas.

Our results indicate that across species, shifts in the trajectories of cognitive ontogeny may underlie species differences in adult psychology. Further research is required to elucidate whether the changes in social cognitive development between *Pan* and humans are unique to our lineage, or whether patterns of social cognitive development are more variable across species in general. Additional study of nonhuman ape juveniles can target the specific aspects of cognitive development that differ from patterns found in humans, with our broad-scale analyses suggesting these differences will be most significant in the ontogeny of cooperative motivations and the understanding of others' goals. In addition, it is notable that apes improved in their performance on the attentional/motivational tasks with age while children did not, indicating that capacities for attention and executive function may emerge early on in human development but that apes "catch up" in these areas later on in ontogeny. Investigating patterns of psychological ontogeny across species will also provide insight into variations in developmental trajectory within our own species, such as in the case of cross-cultural variation in developmental inputs. On the whole then, greater investigation of the patterns of cognitive ontogeny across multiple domains both within and outside our species will provide important insight into the nature of human psychology.

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