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A Two-Year Longitudinal Study of Deferred Imitation of Object Manipulation in a Juvenile Chimpanzee (*Pan troglodytes*) and Orangutan (*Pongo pygmaeus*)

ABSTRACT: *Changes in deferred imitation of novel actions on objects were assessed over a 2-year period in two enculturated, juvenile great apes (one chimpanzee, Pan troglodytes, and one orangutan, Pongo pygmaeus). Both apes displayed deferred imitation, and both displayed improvements in deferred imitation over the 2-year period, although the magnitude of improvement was greater for the chimpanzee. This is, to our knowledge, the first experimental demonstration of longitudinal improvements of deferred imitation in great apes. The results were interpreted as reflecting maturationally paced cognitive differences consistent with other cognitive accomplishments in these species, and as demonstrating the influence that a species-atypical rearing environment can have on cognitive abilities in juvenile great apes. © 2000 John Wiley & Sons, Inc.*
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Deferred imitation is traditionally defined as the delayed reproduction of an observed action (or set of actions) performed originally by another individual. Considered to be more complex than immediate imitation, the development of deferred-imitative abilities has been studied extensively in human infants and young children (e.g., see Abravanel & Gingold, 1985; Bauer, 1997; Meltzoff, 1985, 1995; Piaget, 1962). Early research by Piaget and others (e.g., McCall, Parke, & Kavanaugh, 1977) indicated that deferred imitation was not observed in human children until the latter part of the second year of life. However, more recent research using innovative methodologies has reported deferred imitation in infants as young as 9 months of age (e.g., see Carver & Bauer, 1999; Meltzoff, 1995), although the complexity of behaviors imitated and the quality and quantity of deferred imitation increases between children's first and second birthdays (e.g., Abravanel & Gingold, 1985; Meltzoff, 1985).

According to both traditional Piagetian and neonativist (e.g., Meltzoff, 1995) perspectives, deferred imitation, which incorporates representation of actions into long-term memory stores, requires symbolic representation. Such representation occurs not only at the first-order level of expression, whereby actions are

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held in the mind but are not accessible to the infant for conscious reflection or extraction, but at a higher level, whereby the child can consciously retrieve the stored action from long-term memory and apply it to a new context. It is a complex mechanism that is not present at birth but rather unfolds in accordance with both maturational schedules and early environments favoring observational learning.

Imitation has also been extensively studied in the great apes. Most research has focused on immediate imitation, both in wild and captive apes (see Custance, Whiten, & Bard, 1995; Galef, 1988; Parker & McKinney, 1999; Whiten, 1996). Although there is some convincing evidence for immediate imitation of action in sign-language-trained and wild chimpanzees (e.g., of signs and facial expressions), there is less convincing evidence of immediate imitation of actions on objects (e.g., Tomasello, Davis-Dasilva, Camak, & Bard, 1987; Whiten, Custance, Gömez, Teixidor, & Bard, 1996). It seems clear that chimpanzees acquire some complex behaviors via mechanisms of social learning; however, it is less clear whether they learn via imitation or whether they use less sophisticated forms of mimetic learning, such as emulation (see Boesch & Tomasello, 1998, for review). Emulation, as a social-learning mechanism distinct from imitation, occurs when an animal observes another individual achieve some goal through the use of a particular behavior (getting ants from under a log by rolling the log), and then acts on the object to achieve the same goal, but using novel behaviors to do so (e.g., picking up the log). True imitation requires that an individual acquire a novel set of specific actions simply via the observation of a model (Tomasello, 2000).

There is little empirical evidence of deferred imitation in great apes. Russon and Galdikas (1993, 1995; Russon, 1996) reported incidences of deferred imitation (occurring at least 15 min after the demonstration) in rehabilitant orangutans. The subjects were orangutans who had been held captive by humans and were at a camp that provided support to ease their return to the wild. Naturalistic observations (395 hours) were made of 10 free-ranging orangutans over a 2-year period. Russon and Galdikas reported a total of 37 cases of deferred imitation in eight apes (adolescents and adults), many involving object manipulation (e.g., nailing two boards together and hammering with a third board; sweeping porch with household broom) (Russon, 1996). In research with the enculturated orangutan Chantek, Miles, Mitchell, and Harper (1996) reported that Chantek displayed his first delayed imitation of signs at 2 years 11 months of age. Subsequent research with Chantek emphasized immediate imitation, which Chantek demonstrated for most behaviors modeled. While these observations have greatly enriched our understanding of ape cognition and subsequently informed a new generation of ape imitation experiments, they occurred in largely uncontrolled conditions and the orangutans' behaviors must be interpreted cautiously.

There are at least two experimental studies demonstrating deferred imitation in great apes, each contrasting apes' actions on objects during a free-exploration baseline period with behaviors during a deferred phase, after viewing a human model demonstrate specific actions on objects (Bering, Bjorklund, & Ragan, 2000; Tomasello, Savage-Rumbaugh, & Kruger, 1993). In both studies, only apes that had extensive human contact (i.e., enculturated) displayed deferred imitation. In the Tomasello et al. (1993) study, two bonobos (*Pan paniscus*, ages 5 years, 0 months, and 10 years, 1 month) and one common chimpanzee (*Pan troglodytes*, age 4 years, 11 months) each demonstrated significant levels of deferred imitation. (Mother-reared bonobos and chimpanzees in this study did not display deferred imitation.) In the study by Bering et al., three common chimpanzees (age range: 2 years 1 month–5 years 5 months) and three orangutans (*Pongo pygmaeus*, age range: 4 years 3 months–5 years 5 months) each demonstrated at least one incident of deferred imitation, although there were substantial individual differences within each species.

Looking at the limited extant data on deferred imitation in great apes, we can begin to get a picture of when, in ontogeny, this ability develops. The youngest bonobo tested by Tomasello et al. (1993) who displayed deferred imitation was 5 years old. Bering et al. (2000) developed a measure to assess whether deferred imitation was greater than expected by chance, relative to behavior displayed at baseline, and reported above-chance deferred imitation for a chimpanzee at 3 years and 6 months, and for an orangutan at 4 years and 7 months. However, deferred imitation was observed on two of seven tasks in their study by a 2-year, 1-month-old chimpanzee, and observations of Chantek by Miles et al. (1996) indicate deferred imitation of signs at 2 years, 11 months. Similar to other cognitive accomplishments of infancy (e.g., object permanence and other contents of the sensorimotor period based on Piaget's observations), great apes seem to acquire deferred imitation somewhat later than human children (see Parker, 1996; Parker & McKinney, 1999).

The goal of the present study was to examine further the onset of deferred imitation in juvenile great apes by assessing changes in deferred imitation over a

2-year period in one chimpanzee and one orangutan. In the original study, the youngest orangutan and the youngest chimpanzee tested by Bering et al. (2000) showed relatively low levels of deferred imitation. Christopher, a 4-year, 3-month-old male orangutan, displayed deferred imitation on 40% of the tasks, and Noelle, a 2-year, 1-month-old female chimpanzee, displayed deferred imitation on 28% of the tasks. We hypothesized that these young apes may not have possessed the maturational readiness and/or sufficient experience in an enculturated environment for high levels of deferred imitation to be shown, and we thus selected them for further study. To assess developmental changes in deferred imitation, we conducted what is, to our knowledge, the first experimental longitudinal study of deferred imitation in a chimpanzee and orangutan.

Each ape was tested for deferred imitation on both several "old" tasks for which they had not previously demonstrated successful imitation, and on several "new" tasks. We hypothesized that levels of deferred imitation would be greater for these two animals than they had been earlier, reflecting developmental improvements in deferred imitation over a 2-year period.

METHOD

Participants

One chimpanzee (*Pan troglodytes*) and one orangutan (*Pongo pygmaeus*), that had participated in a deferred-imitation study 2-years earlier, served as subjects in this study. The apes were housed at the Center for Orangutan and Chimpanzee Conservation, a not-for-profit primate sanctuary located in Wauchula, Florida. The female chimpanzee, Noelle, was 4 years and 1 month old, and the male orangutan, Christopher, was 6 years and 3 months old at the beginning of the 2-year follow-up.

Both of the apes had been home-reared since early infancy, with both human and conspecific contact. The apes had been housed for 7 months prior to the beginning of the study at the Center for Orangutan and Chimpanzee Conservation in Wauchula, Florida. The apes spent most of their day housed with conspecifics (three older chimpanzees for Noelle and one older orangutan for Christopher) out-of-doors in a geodesic dome, 18 m in diameter and 15.5 m high. The domes included platforms, vegetation, and ropes for climbing and swinging, as well as human artifacts (e.g., toys, cardboard boxes, tires, children's pools, cups, bowls, blankets). At night, they were housed indoors in facilities connected to the domes. During the day, they also interacted with human caretakers. Prior to moving to the Wauchula facility, they had been housed, since early infancy, in facilities at Parrot Jungle in Miami, Florida. While at Parrot Jungle, the apes were housed with conspecifics in large cages containing a variety of human artifacts while one to three human caretakers supervised their activities, frequently interacting with them. Human contact included joint-attention strategies of learning each day; the apes were heavily exposed to human artifacts and encouraged to manipulate these objects. They traveled extensively throughout the park with human caretakers after the public had left, played in a large field behind the center, and stayed in a home environment each night.

Testing Environment and Apparatus

The tests were conducted in a bare, familiar enclosure. For most tasks (6 of 8 for Noelle and 4 of 7 for Christopher), the ape and the model were in a 4.1 m × 3.1 m enclosure, out-of-doors, connected to the dome. The remaining tasks (2 for Noelle and 3 for Christopher) were administered in the night house, an L-shaped room, approximately 24.5 m². Testing was done in the mornings or early afternoons, between January and May, 1999.

The model was a familiar caretaker.[1] During the baseline and deferred trials, the model was inside the cage, seated on a chair or stool, approximately 1 m away, facing the ape. An uninvolved observer stood outside of the enclosure, about 2 m away, and recorded behavior. Another uninvolved observer was outside of the enclosure and videotaped all sessions.

Materials

Three tasks for Noelle and four tasks for Christopher, for which they had failed to display the target or an approximation to the target behavior (defined below) 2 years earlier, were readministered. In addition, we developed four new tasks, consisting of materials and/or actions unfamiliar to the apes, which we administered to both subjects (see Table 1).

Procedure

The subjects were tested individually in the testing enclosure and were involved in only one session per

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[1] The third author, an adult female, had been the participants' primary caregiver since early infancy and had an extensive interactive history with all of the apes. She served as the model for 7 tasks for Noelle and 3 tasks for Christopher. An adult male caretaker served as the model for 1 task for Noelle and 4 tasks for Christopher.

Table 1.   Descriptions of Tasks and Actions Demonstrated used in Study and Definitions of Target (T) Behaviors and Approximations to the Target (AT) Behaviors

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Old Tasks

Form Board: Perforated plastic form board, plastic hammer, large plastic nail.

    Demonstrated Actions on Objects: Pick up the nail, place it in any hole in the wooden board, and then strike its head once with the striking surface.

    Target: Ape successfully manages to place the nail in one hole using its hands then proceeds to strike the nail with the head of the hammer at least once.

    Approximation: (a) Ape places the nail in one hole, then strikes the nail with the handle of the hammer; or (b) ape places the nail in one hole, turns the board over, then uses the hammer to strike the nail from the opposite side of the board.

Tongs and Cloth: Steel tongs (29.7 × 7.1 cm); piece of cloth (17 × 17 cm).

    Demonstrated Actions on Objects: Lift cloth from floor by using the tongs bimanually.

    Target: Ape picks up the cloth with the tongs, using both hands to squeeze the tongs.

    Approximation: (a) Ape seemingly attempts to pick up the cloth with the tongs but the cloth is not lifted off of the floor; or (b) The ape uses other means to squeeze the tongs and pick up the cloth (i.e., picks up the cloth using one hand to squeeze the tongs).

Hand Drill: Manual drill (21 cm in length).

    Demonstrated Actions on Objects: Pick up the drill with one hand, turn crank with other hand so that it revolves completely, 360°.

    Target: Ape holds drill with its hand then turns the crank so that it revolves completely, 360°.

    Approximation: (a) Ape holds the drill by the handle, and merely touches the crank, turning it slightly or not at all; or (b) ape does not hold the drill by the handle, but nonetheless manages to turn the crank so that it revolves completely. This may be accomplished by turning the crank while the drill is lying on the floor.

Bungee Cord (Noelle only): Bungee cord (non-expanded.57 m, expanded 1.1 m) with hook on one side only; the steel bar of the enclosure.

    Demonstrated Actions on Objects: Attach the hook of the bungee cord onto the steel bar of the cage, then stretch bungee cord so that it expands.

    Target: Ape attaches hooked end of the cord to a bar, then pulls the cord with its hands.

    Approximation: Without the ape's apparent intention, the hooked end of the bungee cord becomes attached to a bar. Ape then pulls the cord so that it stretches. A "no behavior" score was recorded if the ape seemed to pull the cord out of frustration.

New Tasks

Pipe and Ball: A PVC elbow-shaped pipe (diameter of opening = 4 inches), 14 inches across the long side of the elbow; hard plastic ball.

    Demonstrated Actions on Objects: Model holds pipe in one hand and ball in the other, over the pipe, and drops ball into pipe; ball exits other side of pipe and bounces on floor.

    Target: Ape holds pipe with one hand and drops ball with the other hand into one end of pipe, and the ball exits the other end and bounces on the floor.

    Approximation: (a) Ape holds ball in mouth or with its feet and drops it into pipe with ball bouncing on floor; or (b) pipe is on floor and ape drops ball into pipe, ball exits pipe, but "rolls" rather than falls out; or (c) ape holds pipe and drops ball in one end but catches it with hand/foot/lap on other end (i.e., ball does not bounce on floor).

Ball and Bag: Mesh laundry bag, with pull string; baseball.

    Demonstrated Actions on Objects: Model opens mesh bag, places ball in bag and shakes bag so that ball hits the floor.

    Target: Ape opens bag, drops ball into bag, and shakes bag.

    Approximation: (a) Ape opens bag and puts ball into bag, without letting go; or (b) ape holds both ball and bag in separate hands and shakes bag.

Plunger: A plastic plunger with 12 inch handle, screwed onto an 11-inch accordion-shaped bottom.

    Demonstrated Actions on Objects: Model holds plunger with one hand and unscrews handle with the other hand, removing handle from the bottom of plunger. (This required about 15 turns).

    Target: Ape holds plunger with hands and unscrews and removes handle, with either hand.

    Approximation to the target: (a) Ape holds plunger and unscrews handle at least three turns in succession, but fails to remove handle; or (b) apes makes a series of turns and the handle eventually is separated from the bottom of the plunger by pulling on the plunger end.

Post and Rings: A graduated plastic post (7.5 in.) attached to a curved platform; 3 plastic, doughnut-shaped rings of varying diameter.

    Demonstrated Actions on Objects: Model places three rings on the graduated post.

    Target: Ape places three rings on the post.

    Approximation: Ape places at least two rings on target. Placing and removing single ring repeatedly does not qualify.

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day, with each session lasting about 25 min. The tasks were presented in a predetermined order. The procedures were identical to those used 2 years earlier (Bering et al., 2000). Each session was divided into three parts. In Part 1, the baseline phase, the subject was given all of the objects involved in one task for a period of 4 min to determine whether the target behavior (that which would be demonstrated by the model) would be spontaneously displayed. The model encouraged the subject to interact with each object, without manipulating the objects him- or herself, so that by the end of the baseline the ape had interacted with each object for a significant portion of the 4-minute period. If the subject became distracted and had not touched the objects for a period of about 1 min, the model redirected the subject's attention to the objects. If the subject still did not manipulate the objects, they were handed directly to him or her. At the end of the baseline, the model placed the objects out of the ape's view, either under the seat of the model or outside of the enclosure.

Part 2 (demonstration) began 5 min after the conclusion of Part 1 and involved the model demonstrating the target behavior to the subject six times while the subject was attending to the displayed task (i.e., when ape's gaze was directed toward the model's actions). The model demonstrated the actions on the objects out of reach of the subject, and the subject was prevented from touching the objects during Part 2.

During Part 3 (deferred phase), the subject was re-presented the objects and encouraged to perform the task demonstrated in Part 2. The deferred phase began 10 min after the last demonstration. As in the baseline phase, the subject was given 4 min to interact with the objects. The model made no conscious gestures pertinent to the objects to cue the target behavior. The model also made no comment when the ape displayed the target behavior, minimizing the chance of social cueing. Occasionally, however, as in the baseline phase, the model encouraged the subject to manipulate and interact with the objects if he or she had not touched the objects for a period of about 1 min. No food or social rewards were given for successful imitation.

Coding Procedure

Video records of all sessions were used to code the data. Data from the baseline and deferred phases were analyzed in 30-second response intervals. We developed three categories of behavior for each task. A *target* (*T*) was coded when an ape displayed the behavior demonstrated by the model. (Note that apes could display these behaviors during the baseline

phase, before ever witnessing the model.) An *approximation to the target* (*AT*) was coded whenever an ape displayed a behavior with the objects that reproduced most, but not all, aspects of the modeled behavior. The criteria used to classify behaviors as targets or approximation to the targets for each task are provided in the Table 1. If the ape failed to display either the T or an AT behavior during the 4-minute interval, a *no imitative behavior* designation was recorded. In addition to coding for T and AT behaviors, we also coded whether the apes were in contact with the task materials with their hands, feet, or mouths for each 30-second interval.

Each session was scored by two independent coders, one naive to the purpose of the study and the other directly involved in the experimental procedure (the first author). Initial interrater reliability was 96.6% agreement (i.e., classifying the display of a target, approximation to the target, or no imitative behavior for each 30-second interval of each 4-minute session). All discrepancies were resolved by the two coders reviewing the videotape. In two cases, because of equipment failure, on-line records were used to code behavior.

RESULTS

Preliminary inspection of the frequency with which each ape was in contact with the objects during the baseline and deferred phases with either their hands, feet, or mouths, showed high and comparable levels of contact for both the chimpanzee and the orangutan.

Our primary concern was with changes in deferred imitation over the 2-year interval. At the initial (1997) test, which included seven tasks for both apes, Noelle had not displayed a T or AT behavior at baseline, and displayed one T and one AT behavior on the deferred phase, resulting in deferred imitation on 28% of the trials. Christopher, when considering only tasks on which he displayed neither a T nor AT behavior at baseline, displayed deferred imitation on one of four tasks (25%). He also displayed the more complete target behavior on the deferred phase for one task on which he displayed AT behavior at baseline. When this task is considered, his deferred imitation rate increased to 40% (2 of 5 possible tasks).

Table 2 presents the incidence of T and AT behaviors at both the baseline and the deferred phases for the 2-year follow-up (1999) for both apes. Noelle displayed no T and only one AT behavior on the eight tasks at baseline. During the deferred phase, she displayed two T (25%) and three AT behaviors (37.5%). When considering tasks on which an

Table 2. Incidence of Target (T) Behaviors, Approximation to the Target Behaviors (AT), or no Imitative Behavior (No) for Baseline and Deferred Phases to Display Behaviors for Each Ape by Task: 2-Year Follow-Up

	Noelle (*Pan troglodytes*)		Christopher (*Pongo pygmaeus*)	
	Baseline	Deferred	Baseline	Deferred
Old tasks				
Hand drill	AT	T	AT	AT
Tongs & cloth	No	No	No	No
Form board	No	T	No	AT
Bungee cord	No	No	–	–
New tasks				
Post & rings	No	No	AT	AT
Bag & ball	No	AT	No	No
Pipe & ball	No	AT	AT	T
Plunger	No	AT	T	T
% Target	0	25	14.3	28.6
% Approximation	12.5	37.5	42.9	42.9
% No imitation	87.5	37.5	42.9	28.6

improvement from baseline behavior was demonstrated on the deferred phase (i.e., including the task where she improved from an AT at baseline to a T at the deferred phase), Noelle displayed deferred imitation on 63% of the trials, more than doubling her rate of deferred imitation (from 28 to 63%) over the 2-year period.

Christopher displayed a T on one of seven tasks and an AT on three other tasks at baseline. During the deferred phase, he displayed a T for two tasks (28.6%) and an AT for three tasks (42.9%). When considering only tasks on which an improvement from baseline behavior was demonstrated on the deferred phase, Christopher displayed deferred imitation on 50% of the tasks (2 of 4). This represented only a small increase (40–50%) in the rate of deferred imitation over the 2-year period.

In order to obtain a statistical evaluation of these data, we assigned scores of 2, 1, and 0 each time an ape displayed the target, an approximation to the target, and no imitative behavior, respectively (cf. Bering et al., 2000). Then, for each ape, we computed the difference between scores on the deferred phase and scores on the baseline phase, and averaged them over the eight tasks for Noelle and the seven tasks for Christopher. We then conducted t-tests, based on the deferred-minus-baseline difference scores, separately for each ape, using tasks as the random variable and 0 as the expected value. Whereas deferred-minus-baseline difference scores for both apes were nonsignificant 2 years earlier, t's < 1.33, this difference was significant at the 2-year follow-up for Noelle, (mean

difference $= 0.88$, $t(7) = 2.77$, $p < .05$), but not for Christopher (mean difference $= 0.29$, $t(6) = 1.45$).

DISCUSSION

To our knowledge, this is the first experimental longitudinal study of deferred imitation abilities in great apes, and thus the first to demonstrate developmental improvements over time in deferred imitation for them. The improvement by the 4-year, 1-month-old chimpanzee over the 2-year period was substantial (from 28 to 63%, 2 years later). A smaller change in imitation was found for the 6-year, 3-month-old orangutan (from 40 to 50%).

The pattern for Noelle is consistent with the idea that the cognitive abilities underlying deferred imitation in chimpanzees were not well established at 2 years and 1 month of age, but were well established by the age of 4 years and 1 month. Parker (1996; Parker & McKinney, 1999) has summarized primate research indicating the average age at which various Piagetian sensorimotor substages are accomplished in different species. For a variety of contents, sensorimotor substage 6, which reflects the beginning of symbolic representation for Piaget (1962) and the advent of deferred imitation, is rarely achieved prior to 40 months of age in chimpanzees. Noelle's testings spanned this age; she was 25 months of age at the first testing and 49 months of age at the second. Noelle had displayed deferred imitation on two tasks (one T and one AT) during the initial testing, both for tasks

requiring only simple actions (clapping a pair of cymbals together, and hitting a ''drum'' with a drum stick). The tasks used in the 2-year follow-up were more complicated (both for the ''old'' and ''new'' tasks), requiring greater coordination of objects and actions. This finding is consistent with results with human children, who will show deferred imitation for simple behaviors months before they will show deferred imitation for more complicated tasks (e.g., Abravenal & Gingold, 1985; Meltzoff, 1985).

The 6-year, 3-month-old orangutan displayed deferred imitation on 50% of the tasks, up marginally from 40% 2 years earlier. Christopher displayed a T or AT behavior on four of the seven trials at baseline, reducing the number of trials on which deferred imitation could be observed. Developmental improvement may have been found, had the number of trials on which a T or AT behavior was not observed at baseline been greater. However, Christopher had displayed a T or AT behavior on a similar number of trials (3 of 7) 2 years earlier, suggesting to us that the pattern we observed for Christopher is stable over time and that increasing the number of observations would not change appreciably his pattern of performance. One possibility for the failure to display a greater increase in deferred imitation over the 2-year period is that Christopher, at 4 years and 3 months of age at the initial testing, already possessed the requisite cognitive abilities for deferred imitation, and that a deferred-imitation rate of about 50% represents ''mature'' performance for him. This is consistent with the interpretations of Parker and McKinney (1999) of the cognitive accomplishments of orangutans in terms of Piagetian substages of sensorimotor intelligence. Although the number of cognitive contents classified for orangutans was fewer than for chimpanzees, orangutans demonstrated most substage 6 abilities by 48 months of age, three months earlier than Christopher was at the initial testing. Although our statistical estimate of whether such imitation was greater than that during a baseline phase (and thus greater than expected by ''chance'') indicated that this was the case only for Noelle, Christopher's display of deferred imitation on 50% of the tasks is consistent with past research with orangutans (Bering et al., 2000; Miles et al., 1996; Russon & Galdikas, 1993, 1995). Such imitation presumably requires some level of mental representation (e.g., Meltzoff, 1995; Piaget, 1962).

Our inclusion of a baseline phase in this study makes it less likely that the behaviors we coded as imitation could be attributed to the particular affordances of the objects for the specific target behaviors. However, our use of the classification of ''approxima-tion to the target behavior'' could be seen as better reflecting emulation rather than true imitation. In emulation, one individual observes another interacting with an object to achieve a specific goal. That individual then interacts with the object attempting to attain the same goal, but does not duplicate the same behavior as the model to achieve that goal (Tomasello, 2000). Although we cannot state with certainty that some of the AT behaviors observed were not indeed examples of emulation as opposed to imitation, we think that that was not likely. To be classified as an AT, the ape still had to reproduce some aspects of the modeled behavior, making the classification based more upon the means (i.e., the specific behaviors) than the ends. Moreover, even if some of the AT behaviors are better classified as emulation, they were still demonstrated after a significant delay. This would require the ape to keep the goal in mind over the delay period and still seemingly involve a degree of mental representation that is not required for either immediate imitation or emulation. And, perhaps most importantly, the tasks used in the current study lacked the concrete goals (e.g., food rewards) implemented in other designs (e.g., Tomasello et al., 1987) and therefore seem less likely to induce emulation.

It is worth noting that the only great apes in which compelling evidence of deferred imitation of object manipulation has been observed are those that have had considerable contact with humans and human artifacts. The orangutan Chantek (Miles et al., 1996), the chimpanzee and bonobos in the Tomasello et al. (1993) study, and the chimpanzees and orangutans that served as subjects in the Bering et al. (2000) and the current study, were all enculturated apes. The rehabilitant orangutans studied by Russon and Galdikas (1993, 1995) had all been in captivity and many seemingly had been raised as pets. There has been some speculation that human-like cognitive abilities in great apes, particularly those associated with theory of mind, are found only in individuals that are raised much as human children (e.g., Call & Tomasello, 1996; Tomasello et al., 1993). With respect to imitation, demonstrating behaviors to a juvenile and requesting a response, social reinforcement for mimicked behavior, as well as shared-joint attention (e.g., pointing out objects and expecting the other to attend to those objects), are all behaviors in which human mothers engage their children and may contribute to children's development of imitative abilities. These are the same types of behaviors experienced by enculturated great apes and may foster an ontogeny of cognitive abilities that would otherwise not develop.

Animals, including humans and apes, inherit not only a species-typical genome but also a species-

typical environment that supports the expression of the genome to produce species-typical behavior (Bjorklund & Pellegrini, 2000; Gottlieb, 1998). It is the interaction of the animal's genotype over the course of development (including prenatal development) with standard environmental influences that produces the behavioral phenotype. When early environments are substantially modified, however, species-atypical developmental patterns are found (see Kuo, 1967; Gottlieb, 1992). What is compelling about the research with enculturated great apes, is that there is an intriguing possibility that rearing them much as human children are reared may produce some species-atypical cognitive abilities that are similar to those displayed by human children. Such findings may have implications for theories of human cognitive evolution.

NOTES

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