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A note on the development of deferred imitation in enculturated juvenile chimpanzees (*Pan troglodytes*)☆

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Abstract

In recent years, imitation has played a central role in conceptions of children's memory, representational, and social cognitive abilities; in nonhuman primate cognitive competencies; and the evolution of human culture. In this paper, we combine data from three studies that assessed deferred imitation in three juvenile, enculturated (human-reared) chimpanzees (*Pan troglodytes*), administered over a 4-year period, to assess the development of deferred imitation. The basic task used in each study involved a baseline, followed by a demonstration in which a model displayed some actions on objects to participants. After a 10-min delay, the participants were given the objects and evidence of imitation was noted. The number of trials on which chimpanzees displayed deferred imitation increased with age, both between and within participants. Developmental differences were most apparent on the more complex tasks that required coordination of actions on materials (e.g., putting a nail in form board and striking it with a hammer) than on simpler tasks (e.g., striking two cymbals together). Patterns of performance were similar when the complete set of actions

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(targets) were duplicated by the ape and when the ape duplicated only portions of the demonstrated behavior (approximation to the target). The results were interpreted as reflecting age-related changes in chimpanzees' abilities to engage in complex social learning after a delay, and arguably in the symbolic representational system supporting such abilities.

Keywords: Deferred imitation; Chimpanzees; Longitudinal assessment; Representation

1. Introduction

In recent years, imitation has been identified as having likely played a critical role in the evolution of culture (e.g., Heyes & Galef, 1996; Tomasello, 1999; Tomasello, Kruger, & Ratner, 1993a; Whiten, 2000). According to this view, reproduction of another individual's behavior, especially when that other is knowledgeable and engaged in solving a problem, facilitates the rapid emergence of adaptive behaviors in novel contexts. Such social learning not only circumvents the more sluggish processes associated with trial-and-error learning, but also, some have argued, serves as a foundation upon which social perspective taking is constructed. As such, social learning has become an important topic for investigation, both among researchers concerned with its ontogeny in children, and among comparative psychologists, particularly those concerned with nonhuman primate cognition.

2. Deferred imitation in humans

Investigations of imitation in infancy and early childhood have a long history (e.g., Abravanel & Sigafoos, 1984; Parton, 1976; Piaget, 1928), and imitation has been used as an indication both of representational abilities (e.g., Carpenter, Nagell, & Tomasello, 1998b; Meltzoff, 1995; Piaget, 1928) and long-term memory (e.g., Bauer, 2002; Bauer, Wiebe, Waters, & Bangston, 2001). Findings from research on children's capacity for *deferred imitation*—imitation that occurs following a significant period of time—suggest that the ability to recall and reproduce another's previous behavior is in place by about 9 months of age (e.g., Bauer et al., 2001; Meltzoff, 1989), and possibly younger (e.g., Collie & Hayne, 1999), although the complexity of behaviors imitated and the quality and quantity of deferred imitation increase over the second year of life (e.g., Abravanel & Gingold, 1985; McCall, Parke, & Kavanaugh, 1977; Meltzoff, 1985). For instance, research by Bauer and her colleagues (Bauer, 2002; Bauer, Wenner, Dropik, & Wewerka, 2000; Bauer et al., 2001) indicated age-related improvements in infants' abilities to imitate multi-step behavioral sequences after significant delays. For example, in one task, a model placed a bar across two posts, hung a plate from the bar, and then struck the plate with a mallet. One to 12 months later, infants were given the objects and the incidence of deferred imitation was noted. Although about half of the 9-month-olds tested displayed imitation of simpler two-sequence actions after a 1-month delay, they required at least three exposures to the events to achieve this level of performance, and few demonstrated successful imitation of the multiple-step sequences. Rates of deferred imitation increased substantially for 13-, 16-, and 20-month-old infants, with older infants demonstrating higher levels of deferred imitation over each delay interval than younger infants (Bauer et al., 2000).

Findings from Bauer's studies provide a similar developmental function as other studies using a conjugate reinforcement paradigm (see Rovee-Collier, 1999) and suggest an increasing ability to remember actions over infancy. Moreover, deferred imitation has been proposed to be a type of recall, which requires the retrieval of specific information in the presence of a cue. For example, McDonough, Mandler, McKee, and Squire (1995) presented deferred-imitation tasks, similar to those used with infants, to adult brain-damaged patients with anterograde amnesia, who are unable to acquire new explicit (i.e., declarative) information, but are able to acquire new information implicitly (i.e., without conscious awareness, as in procedural memory). The patients failed the deferred-imitation tasks, just as they failed the more conventional explicit memory tasks, suggesting that these tasks reflect a form of explicit (declarative) memory. This and other research have caused some to speculate that explicit memory, like its supposedly more primitive cousin implicit memory, is "online" from the earliest stages of life (Howe, 2000; Rovee-Collier, 1999).

Consistent with the evidence that deferred-imitation tasks reflect a form of explicit memory, many cognitive developmentalists view infants' ability for such imitation as suggesting the presence of a general symbolic representational system in which events are encoded and embedded in a conceptual framework devoted to different categories of situational schemas. More specifically, a number of researchers have interpreted the ability to display "true" imitation as reflecting perspective-taking abilities, with the imitator needing to understand the goals of the model, rather than reflecting a blind duplication of a model's actions (e.g., Carpenter, Akhtar, & Tomasello, 1998a; Charman et al., 2001; Meltzoff, 1995; Tomasello et al., 1993a). For example, Meltzoff (1995) had experimenters try, but ostensibly fail, to complete a target action on objects. When presented with these same objects after witnessing the experimenter's failure, 18-month-old toddlers completed the target behavior, thus demonstrating, according to the author, an understanding of the model's *intentions* toward the objects (see also Carpenter et al., 1998a; Carpenter, Call, & Tomasello, 2002).

3. Deferred imitation in nonhuman primates

In addition to the work with infants and young children, investigators have also examined the imitative competencies of other species (for a review, see Heyes & Galef, 1996; Zentall, 1996). From an evolutionary perspective, assessing the imitative skills of nonhuman primates, particularly humans' closest living relatives, chimpanzees, is important in establishing the phylogenetic foundations of basic representational functions and, ultimately, such things as pedagogy and culture (Tomasello et al., 1993a). It seems clear that the great apes are capable of complex social learning. Chimpanzees, in particular, live in complicated social environments with shifting dominance hierarchies, coordinated hunting parties, and coalitions among individuals, reminiscent of human social organization (e.g., Goodall, 1986; de Waal, 1982; Whiten et al., 1999). There is now good evidence of chimpanzee culture, with different troops having different traditions of grooming, greeting, and tool use (e.g., as in ant fishing) that are passed on from one generation to another (Whiten et al., 1999). Similar evidence has been reported recently for wild orangutans (van Schaik et al., 2003).

Although many primatologists and comparative psychologists have devoted a considerable portion of their research programs to studying imitation in great apes (and have also generated considerable discrepancies among the findings from these research programs), only a handful of studies have investigated the presence of deferred imitation in humans' closest living relatives (Bering, Bjorklund, & Ragan, 2000; Bjorklund, Bering, & Ragan, 2000; Bjorklund, Yunger, Bering, & Ragan, 2002; Tomasello, Savage-Rumbaugh, & Kruger, 1993b). Fewer still have reported on the *development* of deferred imitation in chimpanzees (Bjorklund et al., 2000). However, given its presumed symbolic representational demands, and also its empirically demonstrated association with declarative memory, the development of deferred imitation in chimpanzees would seem to be of prime importance for models of human cognitive evolution.

4. Forms of social learning

To this point, we have used the term "imitation" (and "deferred imitation") descriptively, meaning generally the duplication of important aspects of an observed behavior by a model. Comparative psychologists have pointed out, however, that not all forms of social learning, or learning by observation, are the same. Similar outcomes can be achieved via different underlying (i.e., cognitive) routes. For instance, Tomasello and his colleagues (e.g., Boesch & Tomasello, 1998; Tomasello, 1990, 2000; Tomasello & Call, 1997) have contrasted true imitation, in which an observer understands the goal of the model as well as copying important components of the model's behavior, with *emulation*, *mimicry*, *local enhancement*, and *stimulus enhancement* (see also Call, 1999; Call & Carpenter, in press). Emulation refers to social learning in which one individual observes another individual interacting with objects to achieve some outcome; the observer later interacts with those objects, and although not necessarily duplicating the actions of the model, through a trial-and-error process, achieves a similar outcome. In other words, the observer focuses on the *results* a model achieved and not on the specific behaviors the model used to achieve those results (see Call, 1999). Mimicry refers to an observer matching the actions of a model but with no notion of the model's goal. Local enhancement occurs when an individual is drawn to the location where another individual is interacting with objects; the observer then moves to that location, interacts with the same or similar objects and as a result acquires new behaviors via mechanisms of operant and classical conditioning. Stimulus enhancement is similar to local enhancement, except it is the stimulus rather than the location that attracts the observer's attention.

Somewhat surprisingly, few child-development researchers have differentiated among the various forms of social learning (see Want & Harris, 2002). Rather, most have assumed that any successful attempt by a child in reproducing the behavior of a model reflects "imitation," without specifying the cognitive operations that underlie performance. This approach is sensible for researchers who use deferred imitation as an indication of memory (e.g., Bauer, 2002); the successful reproduction of a model's action after a significant delay reflects memory, and the social-cognitive means by which that memory was achieved are not important. This shortcoming has been addressed by some researchers. For example, studies cited earlier about infants copying the *intended* behavior of a model (Carpenter et al., 1998a; Carpenter et al., 2002; Meltzoff, 1995) indicate that toddlers seem to appreciate a model's goal. Other research by Nagell, Olguin, and Tomasello (1993), discussed below, and that by Want and Harris (2001) suggest that 2-year-old children's observational learning is more likely to involve mimicry rather than true imitation or emulation. Thus, what research there is on the nature of young children's observational learning suggests that they may be aware of the goals of a model at an early age (18 months and perhaps earlier), although, in many situations, they may be prone to copy exactly the actions of a model, regardless of the outcomes of those actions. Such findings may reflect the social aspects of imitation, with children duplicating the actions of others as part of a social give-and-take, and may not indicate a failure to display either true imitation or emulation.

With respect to nonhuman primates, there is much debate whether the social learning displayed by great apes reflects true imitation, including the appreciation of the goals of the model, or some other forms of social learning, most likely emulation (see Call & Carpenter, in press; Custance, Whiten, & Bard, 1995; Galef, 1988; Tomasello, 2000; Whiten, 1996). For example, whereas chimpanzees have been shown to be able to copy arbitrary actions, such as facial expressions or hand signs (e.g., Custance et al., 1995; Hayes & Hayes, 1952), they are less successful when it comes to imitating actions on objects, as in tool use (e.g., Hirata & Morimura, 2000; Nagell et al., 1993; Tomasello, Davis-Dasilva, Camak, & Bard, 1987). For instance, in a study by Nagell et al. (1993), an experimenter modeled one of two behaviors to groups of 2-year-old children and chimpanzees, using a rake to retrieve an out-of-reach object. The children copied the actions of the adults, even when a more efficient way of solving the problem was possible. In contrast, the chimpanzees seemed to ignore the precise actions of the model, but rather used a single inflexible strategy for retrieving the object with the rake. In other research, chimpanzees watched a human model perform a series of actions on a box in order to open it to get a food reward (Whiten, 1998). Actions were performed in specified sequences (for example, open bolt 1, open bolt 2, rotate pin, and turn handle). Although two of four chimpanzees opened the box on their first attempt and three on their second attempt, there was no evidence to suggest that the apes matched the action sequence of the model on the first two trials. That is, they did not organize their behaviors in the same sequence as the model. However, the action sequences of the apes did match those of the model to a statistically significant degree for the third trial (with all four apes opening the box), although they did not copy with great fidelity the particular *behaviors* within those sequences. Apparently, the repeated demonstrations, along with their previous efforts to open the box, resulted in an increase in their matching the actions of the model, and resulted in greater success in retrieving the food.

5. Imitation in enculturated chimpanzees

The best evidence for imitation, rather than emulation or other forms of social learning, in chimpanzees has come from animals that have been reared much as human children. In several experiments, these *enculturated* chimpanzees showed evidence of imitation both for immediate (Tomasello et al., 1993b) and deferred (Bering et al., 2000; Bjorklund et al., 2000, 2002; Tomasello et al., 1993b) imitations. In contrast, mother-reared apes showed no evidence of imitation under controlled conditions (Tomasello et al., 1993b). Moreover, and perhaps somewhat unexpectantly, enculturated chimpanzees displayed significantly greater levels of deferred imitation (following 24- and 48-h delays) than 18- and 30-month-old children (Tomasello et al., 1993b). Although we are tempted to speculate that this indicates that an atypical rearing environment can yield significant changes in the quality of chimpanzees' cognitive development, in this case more in line with that of young children than conspecifics (Bjorklund & Bering, 2003; Bjorklund & Pellegrini, 2002), alternative explanations exist (e.g., enculturated apes may simply be more oriented to humans; emulation cannot absolutely be ruled out, see Call & Carpenter, in press). Nonetheless, these findings indicate that some advanced forms of social learning are within the ability of chimpanzees, affording the opportunity to investigate its development.

We have assessed deferred imitation in three juvenile, enculturated chimpanzees in three studies spanning approximately a 4-year period. Compiling results from these studies provides an opportunity to evaluate both within- and between-subject age-related changes in deferred imitation over a period of chimpanzee ontogeny when such skills apparently show rapid change. Data collection for the first study (Bering et al., 2000, hereafter referred to as the 1997 study) began in January, 1997, included all three animals, and established the basic procedures that were used in the subsequent studies. The ages of the chimpanzees at the beginning of this study were 25 months (Noelle), 42 months (Kenya), and 65 months (Grub). The second study (Bjorklund et al., 2000, hereafter referred to as the 1999 study) began in January 1999, and involved only Noelle; and the third study (Bjorklund et al., 2002, hereafter referred to as the 2000 study) began in August 2000, and included all three chimpanzees. This third study involved two experimental conditions, one the same deferred-imitation condition used in the earlier two studies, and a generalization of imitation condition, in which similar, but not identical, materials were given to the apes following the display of a target behavior. Only data from the deferred-imitation condition were included in the present assessment.

The basic procedure for each study was essentially the same (see Section 6.3 for greater detail). The chimpanzees were given a baseline period in which they explored one set of task materials (e.g., a plastic form board with hammer and nail). Following this, a familiar caretaker modeled a specific behavior with those materials (e.g., placing the nail into the form board and hitting it with the hammer), while the ape watched. Following a 10-min delay period, the ape was given the materials again and any evidence of reproducing the target behavior was recorded. Three classifications of behavior were derived: *target behavior* (T), in which an animal closely reproduced the behaviors of the model on the materials (e.g., placing the nail in the form board and hitting it with the head of the hammer); *approximation to the target behavior* (AT), in which the ape reproduced many but not all of the modeled actions (e.g., placing the nail in the form board and striking the nail with the handle, not the head, of the hammer), or *no imitative behavior*, in which there was no evidence of the animal reproducing the behavior of the model. Note that it was possible for an ape to display a target or approximation to the target behavior at baseline, before the behavior had been modeled. In such cases, displaying the same behavior during the deferred phase would not qualify as an incident of deferred imitation because the chimpanzee had spontaneously engaged in the behavior prior to observing the model.

In our previous reports, we classified a performance on the deferred trials as a "success" if the animal displayed improvement relative to baseline, making no distinction between trials on which such an improvement was achieved by displaying the target behavior or by an approximation to target behavior. Because our criteria for classifying a behavior as an AT included reproducing most aspects of the modeled behavior as well as a similar outcome, we believe that most AT responses are good candidates for true imitative behavior. However, it could be argued that T and AT behaviors reflect different underlying cognitive operations, with T behaviors, because of their closer correspondence to the modeled actions, being more likely to reflect true imitation than AT. In this report, we thus also examined the relative frequencies of T and AT behaviors on trials reflecting improvement in performance for each animal at each age tested.

In the present analysis, we also classified tasks in terms of their complexity. Some tasks required the ape only to perform simple actions on objects (e.g., a pair of cymbals, with the target behavior being holding a cymbal in each hand and striking together the faces of the cymbals), whereas others required more complex coordination of materials (e.g., the form board). Deferred imitation as a function of complexity was previously assessed only in the 1997 study (Bering et al., 2000). We classified tasks used in all three studies in terms of complexity to evaluate its effect on age-related changes in deferred imitation in our animals.

6. Study of deferred imitation in chimpanzees

6.1. Participants

The participants in the study were three chimpanzees (*Pan troglodytes*) housed at the Center for Orangutan and Chimpanzee Conservation, a not-for-profit primate sanctuary located in Wauchula, Florida. (In 1997, the Center was located on the grounds of Parrot Jungle in Miami, FL.) Names, gender, and ages of the participants at the start of the initial (1997) study were Grub (male, 65 months); Kenya (female, 42 months); and Noelle (female, 25 months). Each chimpanzee had been home-reared since early infancy, with both human and conspecific contacts. A more thorough description of their developmental history and living conditions of the apes can be found in Bering et al. (2000).

Noelle was tested in all three studies (1997, 1999, and 2000), at the ages of 25, 49, and 69 months, respectively. Kenya and Grub were tested only in the first (1997) and third (2000) studies, at ages 42 and 86 months for Kenya, and ages 65 and 109 months for Grub. All ages are computed from the date at which each of the three studies began (January 1997; January 1999; and August 2000). Data collection for each study continued for approximately four months.

6.2. Materials

In each study, 7 (1997, 2000) or 8 (1999) tasks were used to assess deferred imitation. These tasks are described in Appendix A. For purposes of analyses here, these tasks were classified further as involving simple actions on objects (simple tasks) or multiple actions on one or more different objects (complex tasks). Table 1 presents a list of the simple and complex tasks used in each of the three studies.

Notice also that some of the tasks were used in more than one experiment, meaning that an ape had been exposed to some tasks 2 or 3.5 years earlier. However, there was no difference in the tendency to display the target behavior at baseline as a function of whether an animal had been presented with a task earlier, even if it had displayed the target behavior at the earlier testing. Moreover, looking at tasks administered in the 1999 and 2000 studies, there was no appreciable difference in the likelihood of displaying deferred imitation for the tasks that the apes had been presented previously (7 of 11, 62%) and new tasks (13 of 18, 72%). (When data from the 1997 study were included, in which all the tasks were new, deferred imitation was displayed on 25 of 38 new tasks, 66%.) This suggests that behaviors on objects, acquired via observation but not practiced in the interim, are forgotten by chimpanzees over extended delays (see Bjorklund et al., 2002).

Table 1
Simple and complex tasks used in the three studies

Study 1 (1997)	Study 2 (1999)	Study 3 (2000)
Simple tasks		
Drum	Plunger	Plunger
Hand Drill	Hand Drill	Triangles
Cymbals		Cymbals
		Rake/Hoe
Complex tasks		
Form Board	Form Board	Music Box
Blocks	Post & Rings	Pipe Rattles
	Pipe & Ball	Pipe & Ball
	Bag & Ball	
Tongs & Cloth	Tongs & Cloth	
Bungee Cord	Bungee Cord	

6.3. Procedure

Testing for the 1997 study was performed at a different location than testing for the 1999 and 2000 studies. However, in all studies, tests were conducted in a bare, familiar enclosure.

All studies began with a baseline period in which the ape was given an opportunity to explore the materials for one task prior to any demonstration of the target behavior. The baseline period lasted 4 min in the 1997 and 1999 studies, but 6 min in the 2000 study. The reason for the longer baseline period in the 2000 study (Bjorklund et al., 2002) was because of the second experimental condition (generalization of imitation) of this study, described briefly in Section 1. Each animal was given both the materials to be used on the subsequent imitation task (e.g., cymbals) and the generalization of imitation task (e.g., trowels), necessitating a longer baseline period. Only data from the imitation tasks were included in the present analysis.

Immediately following the baseline period, a familiar caretaker sat about 1 m in front of the ape (usually on the opposite side of the bars of the enclosure) and demonstrated the target behavior six times to the participant. This was followed by a 10-min delay interval in which the materials were removed from the ape's sight. After the delay interval, the materials were given again to the animal for 4 min (deferred phase). In the 2000 study (Bjorklund et al., 2002), a deferred-imitation task sometimes followed the presentation of the generalization task, resulting in a longer delay and an interpolated activity. However, there was no difference in the overall percentage of deferred imitation displayed by the three apes when the imitation task was administered before (83%) versus after (78%) the generalization of imitation task. All sessions were scored online by an uninvolved observer and were also videotaped.

During both the baseline and deferred phases, the model or observer 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, the model encouraged the participant to manipulate and interact with the objects if he or she had not touched the objects for a period of about 30 s. No food rewards were given for successful imitations.

Video records were used to code the data. Data from the baseline and deferred phases were analyzed in 30-s intervals. As discussed previously, within each 30-s interval an ape was coded as displaying either a target (T), approximation to the target (AT), or no imitative behavior. The criteria used to classify behaviors as T or AT are provided for each task in Appendix A.

In each study, two independent coders, one naïve to the purposes of the study and the other directly involved in the experimental procedure, coded each session. Initial interrater agreement (i.e., classifying the display of a T, AT, or no imitative behavior for each trial) was 93, 92, and 85% for the

1997, 1999, and 2000 studies, respectively. All discrepancies were resolved by the two coders reviewing the videotape together. For several trials, because camera angles prevented the observers from seeing the ape's behavior, data were obtained from online records.

6.4. Results

An ape was credited with an incident of deferred imitation if it (1) displayed no imitative behavior at baseline but displayed either a target (T) or approximation to target (AT) behavior during the deferred phase, or (2) displayed an AT at baseline followed by a T at the deferred phase. Trials on which an AT was displayed at both the baseline and the deferred phases were classified as failures to display deferred imitation; trials on which a T was recorded at baseline were excluded from analyses (regardless of what behavior was displayed at the deferred phase) because participants' behavior at baseline precluded any possibility of displaying imitation during the deferred phase. Initial analyses examined overall improvements in performance on the deferred phase relative to baseline.

Fig. 1 presents the percentage of overall deferred imitation for each of the three apes at each age (in months). As can be seen, both Noelle and Grub

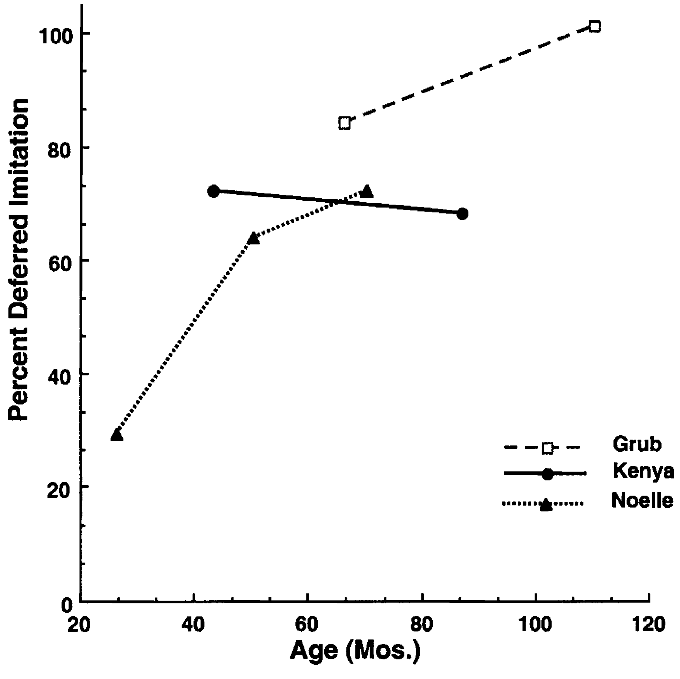

Fig. 1. Percentage of overall deferred imitation by age for each animal.

showed increases in overall deferred imitation with age, whereas Kenya showed a slight decline in imitation between 42 and 86 months (from 71 to 67%). Looking both within and between participants, levels of deferred imitation generally increased with age.[1]

The patterns varied somewhat between the simple and complex tasks (see Figs. 2 and 3). As seen in Fig. 2, levels of performance on the simple tasks were generally high for all animals at each age (ranging from 67 to 100%). In contrast, levels of deferred imitation on the complex tasks (see Fig. 3) increased with age for both Noelle and Grub, declined slightly with age for Kenya, and, looking across participants, were generally higher when assessed at older ages.[2,3]

In the data reported above, an animal was credited with displaying deferred imitation if it showed an improvement in performance relative to baseline. Thus, the data for T and AT behaviors are combined in Figs. 1–3. However, as noted in Section 1, T and AT behaviors may reflect different underlying processes, and for this reason we examined the results separately for successful imitative attempts that involved the ape performing a target behavior and those that involved performing an approximation to target behavior (see Table 2).

The first column in Table 2 presents the overall percentage of successful imitative attempts (i.e., improvements from baseline); the second and third columns present the percentage of such attempts that were classified as T or

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[1] The small sample size and number of observations per animal precluded either a within- or between-subject statistical assessment of the relationship between age and level of deferred imitation. Nevertheless, to obtain an idea of the degree to which age and imitative behavior were related to one another, we computed a correlation between age (in months) and percentage of overall deferred imitation for the seven pairs of observations collected for the three animals (ignoring the fact that the sample included both between- and within-subject data). This correlation was significant, $r = .82$, $p < .05$ ($n = 7$), supporting the impression provided by the data in Fig. 1 that deferred imitation increased with age over the juvenile period for the chimpanzees tested here.

[2] A correlation computed between age and percentage of deferred imitation for the simple tasks was nonsignificant, $r = .39$, $p > .38$, ($n = 7$), whereas this correlation was significant for the complex tasks, $r = .80$, $p < .05$, ($n = 7$).

[3] We also evaluated deferred imitation using a slightly more liberal criterion, in which trials on which an animal displayed an AT on *both* the baseline and deferred phases were eliminated from subsequent computations (as were trials on which an animal displayed a T at baseline), rather than counting them as failures (i.e., no imitation), as was done when using the more conservative criterion. [We had used this more liberal criterion in the reporting of results in two of our prior studies, Bering et al. (2000) and Bjorklund et al. (2000).] Using this more liberal criterion resulted in an increase in deferred imitation at 69 months for Noelle for the complex tasks (from 67 to 100%), and for Kenya at 42 months for the simple tasks (from 67 to 100%) and at 86 months for the complex tasks (from 67 to 100%), with corresponding increases for the overall measure. However, correlations using the more liberal criterion were almost identical to those using the conservative criterion: overall, $r = .80$, $p < .05$; simple tasks, $r = .14$, ns; and complex tasks, $r = .82$, $p < .05$ ($ns = 7$).

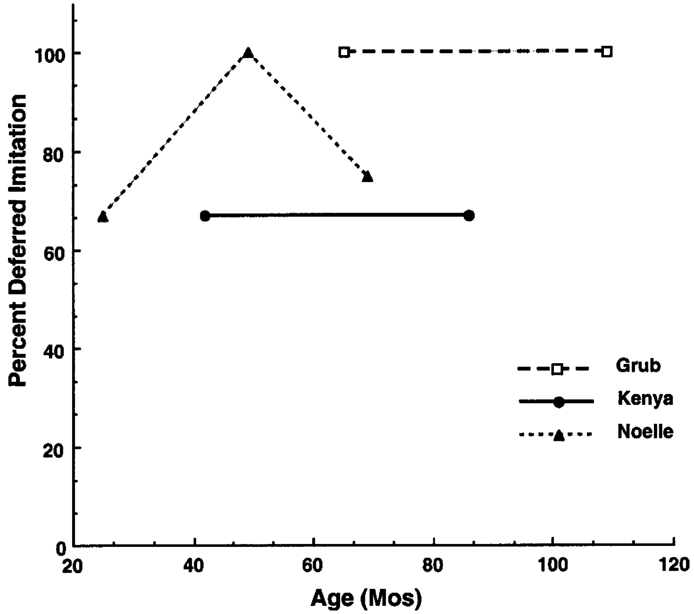

Fig. 2. Percentage of deferred imitation for simple tasks by age for each animal.

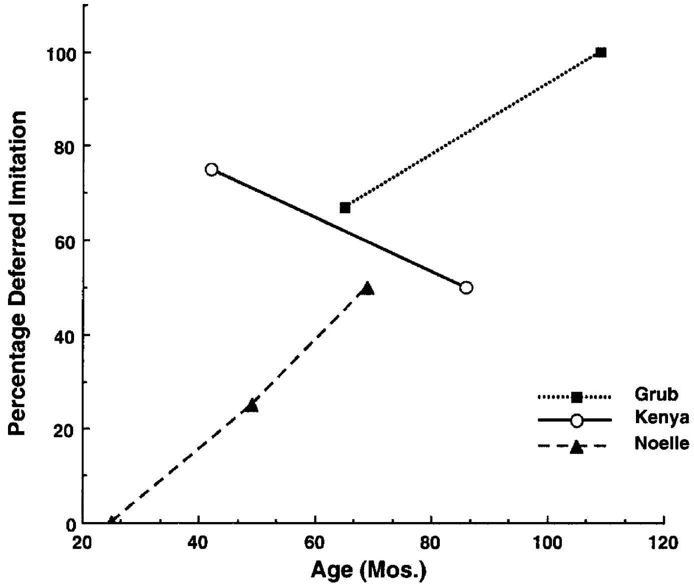

Fig. 3. Percentage of deferred imitation for complex tasks by age for each animal.

Table 2
Percentage of successful imitative attempts (i.e., improvements from baseline) and percentage of such attempts that were classified as target or approximation to target behaviors for each animal at each age

		Percentage of successful imitative trials (overall)	Percentage of successful imitative trials with targets	Percentage of successful imitative trials with approximation to targets
Grub	65 months	83	100	0
	109 months	100	50	50
Kenya	42 months	71	60	40
	86 months	67	50	50
Noelle	25 months	28	50	50
	49 months	63	40	60
	69 months	71	40	60

AT behaviors, respectively, for each animal at each age. As can be seen, all of Grub's successful imitative attempts at the age of 65 months (5 of 5, 100%) were classified as targets, whereas the percentage of targets at 109 months was 50% (3 of 6). For Kenya, 3 of her 5 (60%) successful imitative attempts at 42 months were classified as targets, with 2 of 4 (50%) of her successful attempts at 86 months being so classified. For Noelle, 1 of her 2 (50%) successful imitative attempts at 25 months was classified as a target; 2 of 5 (40%) of her successful attempts were similarly classified as targets at both 49 and 69 months. Overall, slightly greater than half of all successful attempts were classified as targets as opposed to approximations to target (18 of 33, 55%), although this value varied some what among the three chimpanzees (73, 56, and 42% for Grub, Kenya, and Noelle, respectively). We had also grouped the tasks in terms of complexity. Of the 17 simple tasks on which an ape showed improvement from baseline, 10 (59%) involved target behaviors; of the 16 complex tasks that showed improvement from baseline, 8 (50%) involved target behaviors. Thus, the apes were no more likely to display a target (as opposed to an AT) behavior during the deferred phase on the simple than on the complex tasks.

7. Discussion

The meta-analysis performed here reveals genuine changes in chimpanzees' abilities to engage in imitative learning after a delay, and arguably in the symbolic representational system supporting such abilities. In general, increases in age at testing predicted the likelihood of the chimpanzees' production of imitation on the delayed tasks, both within and between animals. These age-related improvements were especially apparent for the complex tasks, which involved reproducing a model's behavior on two or more objects (e.g., pipe and ball, post and rings). Age differences on the simple tasks (i.e., those involving a single action typically on one object) were, in fact, small, with even the youngest participant displaying relatively high levels of performance.

One aspect of these data that is striking is the degree to which this developmental pattern is similar to that found in children. For example, although deferred imitation of actions on objects has been reported for infants as young as 6 months old (e.g., Collie & Hayne, 1999), the number of actions infants and young children can copy successfully increases with age (e.g., Abravanel & Gingold, 1985; McCall et al., 1977; Meltzoff, 1985). For example, in research by Bauer et al., 2000, 13-, 16-, and 20-month-old infants were shown multiple-step sequences of actions and tested for their retention via elicited-imitation tasks 1, 3, 6, 9, or 12 months later. Although infants of all ages demonstrated above-chance levels of imitation at each delay interval, age differences were observed at each delay. There were many differences in the tasks used by Bauer and her colleagues with children and by us with chimpanzees, making any direct comparison inappropriate. However, the generally increasing ability with age to copy accurately a complex series of actions was evident for both children and chimpanzees. Interpretations about the comparability of underlying cognitive operations based on similar developmental patterns for different species must be made with great caution; yet, the similar developmental functions of deferred imitation of complex actions displayed by children and chimps are consistent with the idea that performance is governed by similar cognitive mechanisms. One interpretation is that these mechanisms involve explicit (i.e., declarative) memory representations, as well as the increasing ability to coordinate, retain, and retrieve these representations.

Another interpretation of this pattern of results is that the improvements may have more to do with maturational advances in representing sequential levels of object-oriented behaviors rather than deferred imitation in general (see Byrne & Russon, 1998; Whiten, 2002). In a series of experiments with an "artificial fruit processing" task, discussed briefly in Section 1, Whiten and his colleagues have shown that chimpanzees reproduce both the gist of modeled actions by reproducing the general sequence of a complex behavioral program, as well as more specific actions within a behavioral program (Whiten, 1998, 2002; Whiten, Custance, Gomez, Teixidor, & Bard, 1996). The general design of these experiments involves the ape being shown a Perspex box containing a desirable food reward, access to which is permitted by following a number of sets of alternative behavioral sequences and alternative actions on the outside of the box, such as removing or pushing a pin, poking or pulling a bolt, and so on. A human experimenter then demonstrates for the ape how to get inside of the box by following a certain (functionally variable) sequence of necessary behaviors on the box (bolt first, then pin *versus* pin first, then bolt), and also choosing one of two alternative behaviors at each sequential level (poke bolt, remove pin *versus* pull bolt, and push pin). It is therefore possible to see whether the apes are inclined to imitate both the sequence of general behaviors previously observed as well as the specific actions demonstrated at each sequential level.

Whiten has essentially found that chimpanzees are better imitators at the specific action level than they are at the sequential level, although with repeated exposure to a demonstration of a behavioral program they also begin to reproduce behavior in the general order performed by the model (see Whiten, 2002). In the current analysis, the improved performances of our animals on the complex tasks might reflect the development of this capacity for sequential level imitation, which might be especially apparent in human-reared apes. The recurrent exposure of these animals to goal-oriented human behavioral programs consisting of a series of actions on objects that are coordinated to achieve a goal (e.g., cleaning the cage, feeding the baby, and locking the gate) might promote human-reared apes' greater conceptualization of such behavioral programs rather than the myopic representation of discrete actions comprising these programs. Indeed, developing an understanding of behavioral scripts may be central to the human enculturation process.

One potential problem with our developmental interpretation involves the repeated testing of the animals on similar (in some cases identical) tasks. The age-related increase observed may thus be better attributed to practice effects rather than any underlying ability in imitative behavior. This seems unlikely for the present data. First, levels of successful imitation were no different between the "old" and "new" tasks. Second, the performance of different animals at similar ages was comparable. For example, Noelle was successful on 71% of the trials at 69 months, her third experience with the imitation task. This is similar to the 83% success rate that Grub showed at 65 months on his first exposure to the task. Likewise, Noelle was successful on 63% of the trials at 49 months on her second testing, comparable to Kenya's 71% success rate at 49 months on her first testing.

In our initial classification, we attributed deferred imitation to an animal if it displayed an improvement in performance on the deferred phase relative to baseline. This meant that an ape would often be credited with displaying deferred imitation by displaying an approximation to target (AT), rather than a target (T) behavior. In fact, 45% of all trials classified as showing deferred imitation involved ATs. Because an AT did not require as exact duplication of actions as did a T, it is possible that the ATs reflected emulation, which emphasize the same outcome as the model but not necessarily by the same means, rather than true imitation. Although this may be the case, we observed no systematic difference in performance as a function of whether a T or AT was displayed on trials classified as deferred imitation. In fact, about half the trials for both the simple and complex tasks involved ATs and the other half Ts. One interpretation of these results is that ATs are just as likely to reflect true imitation as Ts, which we think is reasonable, given how ATs were defined for each task (see Appendix A). However, it is also possible that the apes engaged in both true imitation (as reflected by Ts) and emulation (as reflected by ATs) and that both show improvement with age. This interpretation recognizes the complicated nature of emulation. Although true imitation, as defined by Tomasello (1990, 2000), may reflect more advanced cognition in that it requires both the representation of the model's goal and replication of many specific behaviors, emulation also involves complex cognition and may be well suited to attaining desired results in some settings.

What we can say with confidence is that deferred imitation increases over the juvenile period for enculturated chimpanzees. However, we are less confident in the universality of the mechanisms underlying this developmental change. The developmental differences reported here may be precipitated by mechanisms reflecting ontogenetic processes of chimpanzee cognition that are devoted to social learning and which govern the transmission of divergent behavioral forms in wild chimpanzees (Boesch, 1996; Whiten et al., 1999). Alternatively, given that deferred imitation of actions on objects is typically observed only in enculturated apes, the age-related changes we observed may reflect atypical developmental outcomes that are characteristic of human-reared animals only (e.g., Bjorklund, in press; Call & Tomasello, 1996). Representational changes are still envisioned to drive the sort of age-related improvements reported here, but species-atypical epigenetic processes (e.g., treatment as an intentional agent and social incentives for imitating) may have initiated these representational changes in the juvenile period we have addressed. It is also possible that raising chimpanzees much as human children may have made them more sensitive to social cues from humans and more motivated to duplicate the actions of humans, without actually altering, in any significant way, the underlying cognitive operations involved in social learning. In fact, the authors hold different opinions about which of the latter two interpretations of successful deferred imitation (and whether the behavior of our animals reflects true imitation or merely emulation) is preferred. Clearly, future research on the development of deferred imitation and other social–cognitive abilities should involve comparison groups of age-matched chimpanzees that differ in their early rearing experiences.

Appendix A. Description of tasks and criteria used for experiments (Dates in parentheses correspond to experiment/date in which tasks were used.)

A.1. Simple tasks

Drum (1997)

Materials. Plastic bowl (26.4 × 20.3 cm); wooden drumstick (26.1-cm length).

Demonstrated actions. Model turns the plastic bowl over upon the platform so that its face is down, then picks up the wooden drumstick, and uses it to strike the bottom of the bowl three times.

Target (T). The ape strikes the top of the drum at least twice with the drumstick. Note that strike refers to any seemingly deliberate and intentional motion, whether it be merely "tapping" or "beating." The drum must be placed in the correct position—open part of drum face-down.

Approximation (AT). The ape strikes the drum at least twice with the drumstick, but the drum is not in the correct position—the open part of the drum is face-up, or the ape strikes the drum only once.

Hand Drill (1997, 1999)

Materials. Manual drill (21-cm revolving diameter).

Demonstrated actions. Model picks up the drill with one hand, holding it either upright or downright, and turns the crank with the other hand so that it revolves completely (the drill was designed so that when the crank was turned the drill bit holder would rotate).

Target (T). The ape successfully manages to hold the drill using either its hands or its feet, either upright or downright, then proceeds to turn the crank so that it revolves completely—360°—at least once.

Approximation (AT). The ape successfully manages to hold the drill by the handle, again either upright or downright, and merely touches the crank with its hands or feet-turning it briefly or not at all; 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 a hard substrate in the test area (i.e., floor, cage shelf).

Plunger (1999, 2000)

Materials. Black, plastic plunger with handle (30.5-cm), screwed into accordion-shaped bottom (28-cm).

Demonstrated actions. (1) Model holds plunger bottom with one hand; (2) unscrews handle with other hand; and (3) removes handle from bottom plunger end.

Target. Participant holds plunger with hands, unscrews, and removes handle.

Approximation. Participant holds plunger and unscrews at least three turns in succession, failing to remove handle; or participant makes a series of turns and the handle is eventually separated from the bottom of the plunger by pulling on the plunger end.

Cymbals (1997, 2000)

Materials. Two metal instrumental cymbals (17.8-cm diameter) with small wooden knobs.

Demonstrated actions. (1) Model holds both cymbals by their knobs, one in each hand; (2) strikes objects together two times in close succession, producing a noise.

Target. Participant successfully holds both cymbals by their knobs, then strikes them together. Strike refers to a deliberate joining of the cymbals. As force of action might vary, noise is not necessarily invoked for T to be coded.

Approximation. Participant holds cymbals by the metal rather than by the knobs, then strikes them together—handle to handle; or participant correctly holds the cymbals by their knobs, but instead of striking the two together, slides one against the other.

Triangle (2000)

Materials. Musical triangle (15.25-cm/side), white rope attached to triangle, and 30-cm, silver solid metal rod approximately 1-cm diameter.

Demonstrated actions. (1) Model lifts triangle by rope; (2) strikes triangle with rod twice.

Target. Participant lifts triangle by rope and strikes triangle with rod twice.

Approximation. Participant holds triangle without holding rope/cord and strikes triangle with rod twice

Rake/Hoe (2000)

Materials. (A) Rake (26-cm), yellow, plastic; (B) Hoe (26-cm), blue, plastic.

Demonstrated actions. (1) Model holds rake/hoe by handle; (2) reaches over back with rake/hoe; and (3) scratches back repetitively with rake/hoe ends.

Target. Participant holds rake/hoe by handle and scratches back (either reaching over shoulder or behind its side) at least two consecutive times.

Approximation. Participant holds rake/hoe by handle and scratches its head or part of body other than back; or holds rake/hoe by end of object and scratches its back with the handle end. Also requires two consecutive motions to count as "scratching."

A.2. Complex tasks

Pipe and Ball (1999, 2000)

Materials. White PVC elbow-shaped pipe (12.1-cm length; 11.3-cm diameter), open at both ends, and green, hard plastic ball (7.6-cm diameter).

Demonstrated actions. (1) Model holds pipe in one hand and ball in other; (2) drops ball into pipe; and (3) ball exits other end of pipe and bounces on floor.

Target. Participant holds pipe and ball in opposite hands, drops ball into end of pipe, and ball exits the other end and bounces on floor.

Approximation. Participant holds ball in mouth and drops it into pipe with ball bouncing on floor; or participant drops ball into pipe while pipe is on floor, such that ball "rolls" through opposite end; or participant holds pipe and drops ball in one end but catches it with hand/foot/lap on other end.

Music Box (2000)

Materials. Yellow wooden box (50-cm length) open on one end (10- × 14-cm outside diameter opening; 6- × 7-cm inside diameter opening), with small music-producing disk attached to inside of bottom of box; and red, circular, hollow aluminum tube (61-cm length; 1-cm diameter).

Demonstrated actions. (1) Model inserts tube into box; (2) presses music disk on bottom, initiating brief computerized music. (This requires relatively precise movements.)

Target. Participant takes tube, inserts into box, and presses music disk, initiating brief computerized music.

Approximation. Participant takes tube and inserts into box such that it strikes the bottom but music is not initiated.

Pipe Rattles (2000)

Materials. PVC pipe (24-cm length; 8-cm diameter), red, closed on one end with removable blue cap on other; two small stones (approx. 3-cm).

Demonstrated actions. (1) Model removes cap from pipe; (2) inserts stone in pipe; (3) returns cap to open end of pipe; and (4) shakes pipe, producing noise.

Target. Participant removes cap, inserts stone into pipe, and returns cap and shakes, producing noise.

Approximation. Participant removes cap and inserts stone but does not place cover on pipe; participant removes cap, inserts stone, and shakes pipe without returning cover.

Form Board (1997, 1999)

Materials. Perforated wooden form board (24.1 × 17.8 cm), plastic hammer, and large plastic nail (5.3 × 1.0 cm).

Demonstrated actions. Model picks up the nail, places it in any hole in the wooden board, and then strikes its head once with the striking surface of the hammer.

Target (T). The ape successfully manages to place the nail in one hole using any means available (i.e., hands, feet, and mouth), and then proceeds to strike the nail with the head of the hammer at least once. Note, however, that the term *strike* refers to any contact made between the head of the hammer and the nail in the hole. The ape may use either a sideways striking motion (striking the nail on its side) or strike the nail as demonstrated (striking the head of the nail).

Approximation (AT). The ape successfully manages to place the nail in one hole, and then strikes the nail with the handle of the hammer (as opposed to the head of the hammer); successfully manages to place the nail in one hole, turns the entire board over, and then uses the hammer to strike the nail from the opposite side of the board.

Blocks (1997)

Materials. Three large plastic Lego blocks (6.1 × 6.1 cm) (blue, green, and white) with a face drawn on the white block.

Demonstrated actions. Stack the Lego blocks upon one another in interchangeable orders by color, so long as the white block is always placed on the top of the stack.

Target (T). The ape successfully stacks the three Lego blocks so that the white block (which has a face painted on it) is on top, using any means available.

Approximation (AT). The ape successfully manages to stack all three blocks, in any order.

Tongs and Cloth (1997, 1999)

Materials. Steel tongs (29.7 × 7.1 cm); piece of cloth (17 × 17 cm).

Demonstrated actions. Lift the cloth from a flat surface by using the tongs bimanually, raising it completely from the substrate.

Target (T). The ape successfully manages to pick up the cloth with the tongs, using both hands (or feet) to squeeze. The cloth must be lifted off the substrate at least briefly.

Approximation (AT). The ape seemingly attempts to pick up the cloth with the tongs but, for whatever reason, the cloth is not lifted off the substrate; uses other means to squeeze the tongs and pick up the cloth (i.e., the ape squeezes the tongs with mouth, or picks up the cloth using one hand to squeeze the tongs).

Bungee Cord (1997, 1999)

Materials. Bungee cord (non-expanded 11.8 m, the bungee cord expanded 19.1 m); the steel bar of the enclosure (61.1 m).

Demonstrated actions. Attach the hooked end of the bungee cord onto the steel bar of the cage and then stretch the bungee cord so that it expands.

Target (T). The ape successfully manages to attach the hooked end of the bungee cord to a bar and then proceeds to pull the cord so that the cord stretches. Note that intention is an important function of this task.

Approximation (AT). Without the ape's intention, the hooked end of the bungee cord somehow becomes attached to a bar. The ape proceeds to pull the cord so that it stretches. A "no imitative behavior" score was recorded if the ape seemed to pull the cord out of frustration from not being able to detach the hook from the bar.

Ball and Bag (1999)

Materials. Mesh laundry bag, with pull string; baseball.

Demonstrated actions. 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.

Post and Rings (1999)

Materials. A graduated plastic post (7.5 in.) attached to a curved platform; three plastic, doughnut-shaped rings of varying diameters.

Demonstrated actions. 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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