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The generalization of deferred imitation in enculturated chimpanzees (*Pan troglodytes*)

Abstract Deferred imitation of object-related actions and generalization of imitation to similar but not identical tasks was assessed in three human-reared (enculturated) chimpanzees, ranging in age from 5 to 9 years. Each ape displayed high levels of deferred imitation and only slightly lower levels of generalization of imitation. The youngest two chimpanzees were more apt to generalize the model's actions when they had displayed portions of the target behaviors at baseline, consistent with the idea that learning is more likely to occur when working within the "zone of proximal development." We argue that generalization of imitation is the best evidence to date of imitative learning in chimpanzees.

Keywords Deferred imitation · Chimpanzees · Enculturation · Generalization

Introduction

Chimpanzees are marvelous social learners. Evidence from free-living, captive, and laboratory animals has consistently shown that chimpanzees acquire complex behaviors, often involving the use of tools, in social contexts (e.g., Goodall 1986; Boesch 1991; McGrew 1992; Call and Tomasello 1994; Bard et al. 1995; Visalberghi et al. 1995). Recent claims have even been made for chimpanzee culture, with 39 distinct behaviors being identified as culturally transmitted, including fishing for ants and termites, nut cracking, and styles of grooming (Whiten

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et al. 1999). Yet, despite the consensus that chimpanzees, and likely other nonhuman great apes, possess impressive social-learning abilities, there has arisen an often acrimonious debate about the specific nature of these abilities, particularly surrounding the phenomenon of imitation (e.g., Nagell et al. 1993; Russon and Galdikas 1993, 1995; Byrne 1994; Call and Tomasello 1995; Custance et al. 1995; Tomasello 1996; Whiten et al. 1996; Heyes 1998; Whiten 1998).

Debate over what actually occurs in wild populations was sparked by studies of imitation in captive apes that showed chimpanzees and orangutans were not entirely proficient at imitation (e.g., Nagell et al. 1993; Call and Tomasello 1994, 1995; Tomasello et al. 1987). For example, Tomasello et al. (1987) trained an adult female chimpanzee to retrieve out-of-reach food treats by using a metal T-shaped bar. Some of the retrievals were difficult, as when the food was positioned behind the raised edges of the platform. In these difficult cases, the chimpanzee was trained to use the tool to employ a two-step method of retrieval. Naïve animals were then ushered into the cage and witnessed the trained chimpanzee's tool-use behavior. Later, these observers were more likely to use the tool to retrieve the food reward than were control animals, but, surprisingly, they did not imitate the demonstrator's two-step method of retrieval. Rather, they seemed to have learned something generally about the causal connection between the tool and the food, but nothing about the strategic use of the tool. In a follow-up study, an adult human experimenter modeled one of two behaviors for chimpanzees and 2-year-old children (Nagell et al. 1993). Both behaviors involved using a rake to retrieve an out-of-reach reward, but one was more efficient than the other. Whereas the human children tended to reproduce the exact actions they had seen performed by the experimenter, even when there was a more efficient way of going about the job, the chimpanzees essentially ignored the demonstrated method of retrieval and used a single inflexible strategy of getting the reward with the tool. The same experimental design was used for orangutans with nearly identical results – the apes paid little attention to the tool-

use strategies of experts, even when the demonstrators were conspecifics (Call and Tomasello 1994).

Such findings led Tomasello and his colleagues to propose that many complex chimpanzee behaviors may be transmitted via *emulation* (Tomasello 1990, 1996, 2000; Boesch and Tomasello 1998). In emulation, one individual observes another interacting with an object to achieve a specific outcome. The observer then interacts with the same or similar object in quest of the same or similar outcome, but does not necessarily reproduce the model's behavior, as in imitative learning. Rather, through a trial-and-error process, the outcome is achieved, which may or may not include the same actions used by the model. Thus, A may learn that B, while manipulating a rake, *somehow* obtained the food reward. Emulation does not involve, however, learning anything about strategic actions as a function of the intentions of the agent to bring about the final goal state.

> Imitative learning, as we have defined it, requires that the learner perceive and understand not just the bodily movements that another individual has performed (mimicking) and not just the changes in the environment in which the behavior has resulted (emulation learning), but the learner must also learn something of the "intentional" relations between these (i.e., how the behavior is designed to bring about the goal). (Tomasello and Call 1997, p. 310)

The important implication in all this is that, according to Tomasello, only organisms that are capable of perceiving others' behaviors as intentionally driven (i.e., caused by mental states such as knowledge) should be able to engage in "true" imitation. This definition assumes that the imitator understands what the demonstrator is *trying* to do (i.e., *why* he is acting), not simply *that* he is doing something. Alternatively, successful performance may reflect apes' histories of reinforcement for social learning, in that it may be indicative of a deliberate strategy in which they have learned that attending to and later reproducing the actions of others pays off (e.g., Carpenter et al. 1995). In other words, it would suggest that they had learned to learn. In either case, we argue, the criterion for true imitation would be met empirically, so long as apes successfully reproduce both the essential means and ends of a model's behavior in achieving a goal, something that had not been convincingly demonstrated in most controlled studies of social learning in chimpanzees.

The failure of apes to display imitation in problem-solving studies was in opposition to the many tales of spontaneous acquisition and reproduction of human behaviors by captive and pet animals. After observing such uncanny chimpanzee reenactments of their own household conduct, Hayes and Hayes (1952), for example, trained their home-reared chimpanzee Viki to reproduce a series of arbitrary actions (e.g., scratching the corner of her mouth, patting her head, spinning on one foot). After shaping her responses with food reinforcements for the first 11 demonstrations, Viki suddenly seemed to "get the idea" and began to generalize the rule to reproduce the actions she had just seen per-

formed. The authors reported that their participant subsequently mimicked 55 of 70 arbitrary actions. As a partial backlash against Tomasello and his colleagues' claims that apes were not, really, capable of imitation, Custance et al. (1995) replicated the Hayes and Hayes study with two juvenile nursery-reared chimpanzees under more controlled conditions and found similar results to those of Hayes and Hayes. Also, Miles et al. (1996) reported analogous findings with the language-trained orangutan Chantek.

Studies such as these are complemented by a suite of more classically anecdotal claims of imitation of nonfunctional bodily actions, such as de Waal's (1982) observation of a young male chimpanzee adopting the limping gate of an older member of his group, and Temerlin's (1975) observation of his home-reared chimpanzee Lucy making vomit attempts after watching her ill surrogate father over the commode moments earlier. In addition, apes that have been taught sign language have been said to learn some gestures by imitative means (Sanders 1985; Fouts et al. 1989). Indeed, evidence of early facial and bodily mimetic processes has been traced in chimpanzee ontogeny all the way to the immediate extrauterine environment, where just hours after birth chimpanzee neonates have been observed to mimic a variety of facial contortions (e.g., pursed lips, open mouth, tongue protrusion) demonstrated by a human experimenter (Bard and Russell 1999). Nearly identical neonatal imitation of facial displays has been found for human infants (e.g., Meltzoff and Moore 1977). Such mimetic processes might reflect a common social-cognitive adaptation that emerged before hominids split from the African apes.[1]

With respect to problem solving, differences in participant performance between studies of imitation of bodily actions and of object-related problem-solving tasks might lend credence to Tomasello and his colleagues' initial claims that chimpanzees are not capable of true imitation. Unlike imitation of arbitrary actions, the introduction of objects and/or goal-directed behaviors into the experimental paradigm generally has led to negative performance (e.g., Tomasello et al. 1987; Nagell et al. 1993; Call and Tomasello 1994, 1995; Myowa-Yamakoshi and Matsuzawa 2000, Experiment 1; but see Whiten et al. 1996; Whiten 1998).

The conclusion that chimpanzees are incapable of true object-related imitative learning is premature, however. There have been several controlled studies demonstrating imitative learning, over delay periods ranging from 10 min to 2 days, in human-reared (enculturated) chimpanzees (Tomasello et al. 1993; Bering et al. 2000; Bjorklund et al. 2000). The inclusion of a delay period in these studies is important; researchers assessing the development of imi-

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[1]Neonatal imitation may not involve the same underlying cognitive abilities as the type of imitation seen later in life, however, and may not serve a similar purpose. For example, it has been suggested that neonatal imitation, which drops off in frequency over the first 2 months of life, may serve to foster communication between the infant and its mother at a time when the infant has little intentional control over its social behavior (Bjorklund 1987; Legerstee 1991).

tation in human children consider delayed, or deferred, imitation to be more complex than immediate imitation and to involve the representation of actions held in long-term memory stores, which requires symbolic representation, even if the delays are as short as 5 or 10 min (e.g., Piaget 1962; Meltzoff 1995; Bauer 1997). In contrast to immediate imitation, deferred imitation might highlight the apes' ability to extract symbolically encoded information from long-term memory to apply to a problem-solving context at a later point in time.

In the initial study, Tomasello et al. (1993) reported greater deferred imitation of actions on objects for a group of enculturated versus mother-reared apes. In fact, the enculturated apes actually displayed higher levels of deferred imitation over a 48-h period than did groups of 18- and 30-month-old human children. Two of the three enculturated apes in the Tomasello et al. study were bonobos (*Pan paniscus*), however, calling into question the generality of this finding to common chimpanzees (*Pan troglodytes*).

Arguing that deferred imitation on objects is an important marker of symbolic representational abilities, Bering et al. (2000; see also Bjorklund et al. 2000) conducted a more detailed study of this cognitive-developmental milestone with their own population of young enculturated apes. With minimal changes to the core methodology used in the Tomasello et al. (1993) study, Bering et al. (2000) reduced, for pragmatic reasons, the period between exposure to the demonstrations and test trials to 10 min. While this delay is certainly less impressive than the 2-day delay in Tomasello et al.'s experiment, it still constituted a delay in which deferred imitation could be reliably assessed and was of a comparable duration to some studies on deferred imitation in human infants (e.g., Abravanel and Gingold 1985). Participants were three juvenile orangutans and three juvenile chimpanzees (with one, arguably, still in late infancy at 2 years of age). On seven tasks including four involving complex configurations of actions (e.g., placing a plastic nail in a form board and then striking it with a plastic hammer), Bering et al. found evidence of deferred imitation of object-related actions. This was the case for both *approximated imitation* (reproductions that included significant portions of the demonstrated actions) and *targeted imitation* (reproductions that more precisely mirrored the demonstrated actions). Although some approximations may have been examples of emulation, this was not likely, in that to be so classified required that the ape reproduce some aspects of the specific, modeled behaviors; *it required reproducing some part of the means as opposed to only the ends*. No species differences were found (although the oldest orangutan fared poorly in overall performance as a probable result of motivational constraints). A follow-up study conducted 2 years later showed improvements in deferred imitative performance for the youngest orangutan and chimpanzee participants, suggesting a developmental trend in imitative competence as a result of growing symbolic capacity (Bjorklund et al. 2000). Both Tomasello et al. (1993) and Bering et al. (2000; Bjorklund et al. 2000) argued that raising chimpanzees in a species-atypical environment, in these cases

an environment similar to that experienced by human children, produced a species-atypical pattern of cognitive development, one that was similar in some ways to that of human preschool children. We will not discuss further the enculturation hypothesis here (see Call and Tomasello 1996), other than to suggest that some rearing conditions may reveal latent cognitive abilities of animals that are not normally expressed. (We will return briefly to the evolutionary implications of enculturation research in the Discussion.)

As convincing as we believe these studies are that chimpanzees are indeed capable of deferred imitation (and thus imitative learning), they are not without alternative interpretation. For example, it is not impossible that the apes' performance could be attributed to mimicry, the reproduction of the models' actions without an understanding of the goal of those actions. One technique that we believe would be effective in further discriminating mimicry and emulation from purposeful learning is the *generalization of imitation*, in which target behaviors are modeled on one set of materials but imitation is assessed on a second, somewhat different set. The participant would not only have to identify and reproduce the target behaviors with the same set of objects used in the demonstration, but also would be required to understand that a similar goal, with a new set of objects, can be achieved by executing similar actions. It would not be sufficient for the ape only to identify a desired outcome and then attempt to achieve that outcome by trial and error, as in emulation, nor to reproduce exactly the observed actions with the same objects, as in mimicry. Rather, successful performance would suggest that the ape have some notion of the functionality of its own purposeful learning over a delay period, in that a failure to acquire means-related actions at initial demonstration would result in a failure to execute appropriate ends-related behaviors on a subsequent generalized task.

Our procedure is similar to those reported in recent studies with human infants by Hayne and her colleagues (Hayne et al. 2000; Herbert and Hayne 2000). For example, in the Herbert and Hayne (2000) study, 18- to 30-month-old infants were shown a series of actions on objects and then given either the same or different objects. Imitation of the actions on the objects was assessed either immediately or after 24 h and contrasted with a control group of infants who had not seen the demonstrations. Levels of deferred (but not immediate) imitation were greater when infants were given the same as opposed to the different items during the testing phase. Successful deferred imitation with the different items increased between 18 and 30 months of age, with performance being no different than that of the control group for the 18-month-old infants. Herbert and Hayne interpreted their findings as reflecting age-related changes in *representational flexibility*, with infants increasingly being able to store, organize, and retrieve multiple aspects of memory representations over time.

In the current study we assessed both the deferred imitation and generalization of imitation of actions on objects

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in three enculturated chimpanzees, each of which has displayed deferred imitation in previous research (Bering et al. 2000; Bjorklund et al. 2000). Participants received a baseline period in which they interacted with two sets of task objects to determine whether they would show the target behaviors spontaneously. A model then displayed a specific set of actions on one set of objects. After a 10-min delay, the apes were given two consecutive 4-min trials, one with the original materials (imitation condition) and another with a similar set of materials (generalization of imitation condition). Incidence of the target behaviors was recorded and contrasted with behaviors at baseline.

We anticipated that each of the apes would successfully imitate most of the target behaviors in the imitation condition, replicating our previous research. We also anticipated that the chimpanzees would model the target behaviors in the generalization of imitation condition, although we anticipated that, consistent with research with human children (Herbert and Hayne 2000), levels of performance would be lower than in the imitation condition. Successful modeling in the generalization of imitation condition would be the best evidence to date, we argue, for true imitation, in which animals reproduce the basic actions of a model to achieve a similar goal.

Methods

Participants

Participants were three juvenile chimpanzees (*Pan troglodytes*), each of which had participated in an imitation study 4 years earlier. The youngest chimpanzee also served as a participant in a longitudinal study of deferred imitation 2 years prior to the current study. The apes were housed at the Center for Orangutan and Chimpanzee Conservation, a not-for-profit primate sanctuary located in Wauchula, Florida. Names, gender, and ages of the participants at the start of study were: Grub (male, 9 years 1 month); Kenya (female, 7 years 2 months), and Noelle (female, 5 years 9 months).

All of the apes had been home reared since early infancy, with both human and conspecific contact. A more thorough description of their developmental history can be found in Bering et al. (2000). The chimpanzees spent most of their day housed with conspecifics out-of-doors in a large, geodesic dome, 18 m in diameter and 15.5 m high. During the day, the animals interacted frequently with human caretakers. At night, they were housed indoors in a smaller enclosure connected to the dome.

Materials

Table 1 presents the seven pairs of tasks that were used in this study. One set of materials for one of these tasks (Cymbals) had been used approximately 3.5 years earlier for each ape, and two other tasks (Pipe and Ball; Plunger) had been administered to the youngest chimpanzee approximately 1.5 years earlier. Each pair of tasks involved actions on similar, but not identical, objects.

Procedure

The tests were conducted in a bare, familiar enclosure. For most tasks, testing was conducted in the night house, an L-shaped room approximately 24.5 m². The remaining tasks were administered in a 4.1×3.1 m enclosure, out-of-doors, connected to the dome. Testing was done in the mornings or early afternoons, between

August and December 2000. Each ape participated in only one session per day, with each session lasting about 30 min.

Sessions were divided into four phases. In phase 1, baseline, the participant was given all of the objects from a single pair of tasks (i.e., objects for both the imitation and generalization versions of the same task) and allowed to interact with them for 6 min to determine whether the target behavior (that which would be demonstrated by the model) would be displayed spontaneously. We extended the baseline period to 6 min in the current experiment rather than using a 4-min interval as we have done in our previous studies (Bering et al. 2000; Bjorklund et al. 2000) and in the deferred phase of the current study. We increased the time so that the apes would have sufficient opportunity to interact with the objects from the two tasks (i.e., imitation and generalization). We limited the duration to 6 min (rather than 8 min or having two separate 4-min baseline intervals for the imitation and generalization tasks, for example) to avoid the diminution of the animals' attention to the objects during the baseline phase. Phase 2, demonstration, began immediately after the baseline phase and involved the model, a familiar caretaker, demonstrating the target behavior six times to the participant (see Table 1). The model was outside the cage, seated on a chair or stool, approximately 1 m away, facing the ape. For the four tasks that were novel to all animals, the two versions of each task (A and B) were used with comparable frequency for modeling the target behavior. For the three tasks that at least one of the apes had performed 2 or 4 years earlier, the "old" materials (e.g., cymbals) were used to model the target behavior.

Phase 3 began 10 min after the completion of the demonstration phase and involved either the deferred imitation or the generalization of imitation trials. Deferred-imitation trials involved the presentation of the same objects that had been used during the demonstration phase (e.g., cymbals), whereas generalization of imitation involved presentation of the similar, but not identical set of objects (e.g., trowels). For the four novel tasks, approximately half of the phase 3 trials involved deferred-imitation trials and the remainder generalization of imitation trials. For the three tasks that at least one of the apes had performed 2 or 4 years earlier, the generalization trials were always presented in phase 3 and the deferred-imitation trials in phase 4. Phase 4 immediately followed the completion of phase 3 and involved the presentation of materials not presented in phase 3 (i.e., materials for deferred-imitation trials if generalization of imitation had been presented in phase 3, or vice versa). In both phases 3 and 4, the ape was given 4 min to interact with the objects.

During phases 1, 3, and 4, 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, 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. For most trials, two uninvolved observers stood outside of the enclosure, about 2 m away, and recorded behavior. A third uninvolved observer was outside of the enclosure and videotaped all sessions.

Coding procedure

Video records were used to code the data. Data from the baseline and deferred phases were analyzed in 30-s intervals. Three categories of behavior were used to code the apes' responses in phases 1, 3, and 4. A *target* (T) was coded when the participant 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 the participant displayed a behavior with the objects that reproduced most, but not all, aspects of the modeled behavior. The criteria used to classify behaviors as T or AT for each task are provided in Table 1. If the participant failed to display either the T or an AT behavior during an interval, a *no imitative behavior* designation was recorded.

Table 1 Descriptions of tasks, materials, and demonstrated actions used in the study and definitions of target (*T*) behaviors and approximation to the target (*AT*) behaviors for each set of tasks

Pipe rattles

    Materials

        (A) 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)

        (B) PVC pipe (40 cm length; 5 cm diameter), blue, closed on one end with removable yellow cap on other; two pieces of wood chip (approx. 3 cm)

    Demonstrated actions

        (1) Model removes cap from pipe

        (2) Model inserts stones/wood chips in pipe

        (3) Model returns cap to open end of pipe

        (4) Model shakes pipe, producing noise

    Target

        Participant removes cap, inserts stones/wood chips into pipe, returns cap and shakes, producing noise

    Approximation

        Participant removes cap and inserts stones/wood chips but does not place cover on pipe; participant removes cap and inserts stones/wood chips and shakes pipe without returning cover

Rake/Hoe

    Materials

        (A) Rake (26 cm), yellow, plastic

        (B) Hoe (26 cm), blue, plastic

    Demonstrated actions

        (1) Model holds rake/hoe by handle

        (2) Model reaches over back with rake/hoe

        (3) Model 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"

Music box/pipe

    Materials

        (A) 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)

        (B) Green PVC pipe (24 cm length; 8 cm diameter) open on one end, small music-producing disk attached to inside of capped bottom of pipe; and blue, hollow, steel cubed tube (61 cm length; 1 cm diameter)

    Demonstrated actions

        (1) Model inserts tube into box/pipe

        (2) Model presses music disk on bottom, initiating brief computerized music. (This requires relatively precise movements)

    Target

        Participant takes tube, inserts into box/pipe, presses music disk, initiating brief computerized music

    Approximation

        Participant takes tube, inserts into box/pipe such that it strikes bottom but music is not initiated

Triangle/Chime

    Materials

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

        (B) Aluminum pipe (chime) (30.5 cm length; 3.2 cm diameter), yellow cord attached to pipe, and 40-cm, red, hollow, metal rod approximately 1.5 cm diameter

    Demonstrated actions

        (1) Model lifts triangle/chime by rope/cord

        (2) Model strikes triangle/chime with rod twice

    Target

        Participant lifts triangle/chime by rope/cord and strikes triangle/chime with rod twice

    Approximation

        Participant holds triangle/pipe without holding rope/cord and strikes triangle/chime with rod twice

Cymbals/Trowels

    Materials

        (A) Two metal instrumental cymbals[a] (17.8 cm diameter) with small wooden knobs

        (B) Two rubber-coated trowels (30.5×7.3 cm) with large wooden handles

    Demonstrated actions

        (1) Model holds both cymbals/trowels by their knobs/handles, one in each hand

        (2) Model strikes objects together two times in close succession, producing a noise

    Target

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

    Approximation

        Participant holds cymbals/trowels by the metal/rubber rather than by the knobs/handles, then strikes them together – handle to handle; or participant correctly holds the cymbals/trowels by their knobs/handles, but instead of striking the two together, slides one against the other

Pipe and ball

    Materials

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

        (B) White PVC straight pipe (19.7 cm length; 5 cm diameter), open at both ends, and white golf ball (5 cm diameter)

    Demonstrated actions

        (1) Model holds pipe in one hand and ball in other

        (2) Model drops ball into pipe

        (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

Plunger

    Materials

        (A) Black, plastic plunger[b] with handle (30.5 cm), screwed into accordion-shaped bottom (28 cm)

        (B) Red, rubber plunger with wooden handle (28 cm) screwed into circular bottom (13 cm diameter; 5 cm depth)

    Demonstrated actions

        (1) Model holds plunger bottom with one hand

        (2) Model unscrews handle with other hand

        (3) Model removes handle from bottom plunger end

Table 1 (continued)

Table 1 (continued)

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

[a]All participants had previously seen this demonstrated in Bering
et al. 2000
[b]The youngest participant, Noelle, had previously seen this demon-
strated in Bjorklund et al. 2000

Each session was scored by two independent coders, one naïve
to the purposes of the study and the other directly involved in the
experimental procedure (D.B.). The naïve coder was blind to the
identity of the trial phase for phases 3 and 4 (i.e., whether the ob-
jects the participants interacted with were the same as, or different
from, those used in the demonstration). Initial interrater agreement
was 85% (i.e., classifying the display of a T, AT, or no imitative
behavior for each trial), with a Cohen's kappa of 0.754. All dis-
crepancies were resolved by the two coders reviewing the video-
tape together. For several trials, because camera angles prevented
the observers from seeing the ape's behavior, data were obtained
from online records.

Results

Results are presented in two sections. The first examines
performance on the deferred-imitation tasks and the sec-
ond on the generalization of imitation tasks. For all tasks,
if an ape displayed an AT during one 30-s interval but dis-
played a T during a second interval, only the more ad-
vanced behavior (T) was coded for that task. Note that an
animal may have displayed several incidences of a T or
AT for a task, but each task was coded not in terms of the
frequency of displaying a particular set of behaviors (i.e.,
number of Ts or ATs), but in terms of whether a T or an
AT was displayed at least once during a phase. For the
four new tasks, there was no difference in performance as
a function of which task (imitation or generalization) was
assessed first.

Incidence of target and approximation
to the target behaviors during imitation trials

The incidence of T, AT, and no imitative behaviors at the
baseline and deferred phases for the imitation trials are
presented for each ape in Table 2. As can be seen, each
ape displayed at least one AT behavior during the baseline
phase. All three chimpanzees displayed an AT behavior
on the music box/pipe task; in addition, Noelle displayed
an AT behavior on the pipe rattles task and the rake/hoe
task. Both Grub and Kenya displayed a T behavior during
the baseline phase of the plunger task before the behavior
was demonstrated to them. Noelle displayed no T behav-
iors at baseline on the imitation tasks.

Looking at Table 2, it can be seen that each ape dis-
played either a T or an AT behavior during the deferred-
imitation phase for at least six of the seven tasks. Grub
displayed T behaviors on 57% of these trials and ATs on
43%; the comparable figures for both Kenya and Noelle
were 28% Ts and 57% ATs. Examining tasks on which an
ape could improve its performance from the baseline pe-
riod (i.e., omitting trials for which a target behavior was
displayed at baseline), Grub showed improvement on
100% of the trials (six of six) for the imitation tasks; com-
parable figures for Kenya were 67% (four of six) and for
Noelle 71% (five of seven) (see Fig. 1).

To obtain a statistical evaluation of these data, for each
task in phases 1, 3, and 4, we assigned scores of 2, 1, and
0 when an ape displayed a T, an AT, and no imitative be-
havior, 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 seven tasks. We then conducted
t-tests, based on the deferred-minus-baseline difference
scores, separately for each animal, using tasks as the ran-
dom variable and 0 as the expected value.

Mean difference scores for each animal and the corre-
sponding t-values (including data from all trials) are pre-
sented in the three left-hand columns of Table 3. First note
that, overall, the mean differences are of a moderate mag-
nitude (0.85; maximum possible difference=2.0). How-
ever, all three chimpanzees had mean difference scores
that yielded statistical contrasts that were significantly
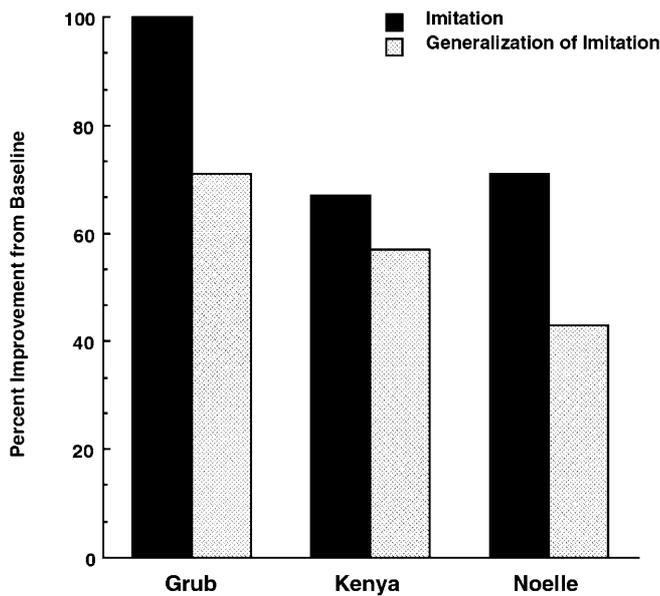greater than expected by chance (one-tailed tests).

Table 2 Incidence of target (*T*), approximation to the target (*AT*), and no imitative (*No*) behaviors for baseline and deferred phases for imitation task for each animal by task

Task	Grub		Kenya		Noelle	
	Baseline	Deferred	Baseline	Deferred	Baseline	Deferred
Pipe rattles	No	T	No	AT	AT	AT
Rake/hoe	No	AT	No	No	AT	T
Music box/pipe	AT	T	AT	AT	AT	T
Triangle/chime	No	AT	No	T	No	AT
Pipe and ball	No	AT	No	AT	No	AT
Cymbals/trowels	No	T	No	T	No	No
Plunger	T	T	T	T	No	AT
% Target	14%	57%	14%	28%	0%	28%
% Approximation	14%	43%	14%	57%	43%	57%
% No imitation	71%	0%	71%	14%	57%	14%

Fig. 1 Percentage of imitation and generalization tasks for each ape on which an improvement in performance at the deferred phase relative to baseline was observed (omitting tasks on which a target behavior was displayed at baseline)

Table 3 Mean difference in incidence of T, AT, and no imitative behaviors between deferred and baseline phases of the imitation and generalization of imitation trials and corresponding *t*-scores, separately for each animal (maximum score=2.0). Displays of T were assigned scores of 2; AT, scores of 1; and no imitative behavior, scores of 0

	Imitation			Generalization of imitation		
	Mean	SD	*t*-value	Mean	SD	*t*-value
Grub	1.14	0.69	$t(6)=4.05^{***}$	1.14	0.90	$t(6)=3.10^{**}$
Kenya	0.71	0.76	$t(6)=2.30^{**}$	0.57	0.53	$t(6)=2.62^{**}$
Noelle	0.71	0.49	$t(6)=3.56^{***}$	0.57	0.79	$t(6)=1.77^{*}$

$^*P<0.10$, $^{**}P<0.05$, $^{***}P<0.01$, one-tailed tests

We also computed difference scores and *t*-tests separately (1) omitting trials on which an animal displayed a T behavior at baseline, and (2) omitting trials on which an animal displayed a T or AT behavior at baseline. When omitting trials on which a T was displayed at baseline, difference scores and *t*-values were equal to (Noelle) or greater than [Grub, mean difference=1.33, $t(4)=5.75$; Kenya, mean difference=0.83, $t(5)=2.46$] those obtained when data from all trials were included. When omitting trials on which a T or AT was displayed at baseline, mean difference scores and *t*-values for the three animals increased slightly but overall did not change appreciably [Grub, mean difference=1.4, $t(4)=5.11$; Kenya, mean difference=1.0, $t(4)=2.83$; Noelle, mean difference=0.75, $t(3)=2.60$].

Incidence of target and approximation to the target behaviors during generalization of imitation trials

The incidence of T, AT, and no imitative behaviors at the baseline and deferred phases for the generalization of imitation trials are presented for each animal in Table 4. As can be seen, each ape displayed at least one AT behavior during the baseline phase. All three chimpanzees displayed an AT behavior on the music box/pipe task; in addition, Noelle and Kenya displayed an AT behavior on the pipe and ball task and Kenya displayed an AT behavior on the pipe rattles task. None of the animals displayed a T behavior at baseline on the generalization tasks. The overall frequency of T and AT behaviors displayed at baseline on the generalization tasks (29%) did not differ appreciably from the frequency of T and AT behaviors displayed on the imitation tasks (33%).

Looking at Table 4, it can be seen that each ape displayed either a T or an AT behavior during the generalization phase for at least three of the seven tasks (versus six out of seven for the imitation task). Grub displayed T behaviors on 57% of these trials and ATs on 14%; Kenya displayed T behaviors on 28% of the trials and ATs on 43%; and Noelle displayed T behaviors on 43% of the trials and demonstrated no AT behaviors. Examining tasks on which an ape could improve its performance from the baseline period (i.e., omitting trials for which a target behavior was displayed at baseline), Grub showed improvements on 71% of the trials (five of seven) for the generalization tasks; comparable figures for Kenya were 57% (four of seven) and for Noelle 43% (three of seven) (see Fig. 1). Overall, performance on the generalization of imitation tasks was somewhat lower relative to the imitation tasks for all animals.

Table 4 Incidence of target (*T*), approximation to the target (*AT*), and no imitative (*No*) behaviors for baseline and deferred phases for generalization of imitation task for each animal by task

Task	Grub		Kenya		Noelle	
	Baseline	Deferred	Baseline	Deferred	Baseline	Deferred
Pipe rattles	No	No	AT	AT	No	T
Rake/hoe	No	T	No	AT	No	No
Music box/pipe	AT	T	AT	T	AT	T
Triangle/chime	No	No	No	No	No	No
Pipe and ball	No	AT	AT	T	AT	T
Cymbals/trowels	No	T	No	No	No	No
Plunger	No	T	No	AT	No	No
% Target	0%	57%	0%	28%	0%	43%
% Approximation	14%	14%	43%	43%	28%	0%
% No imitation	86%	28%	57%	28%	71%	57%

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Statistical evaluation of these data was conducted in a manner analogous to the procedures described above for the imitation data. Mean difference scores for each animal and the corresponding *t*-values (including data from all trials) are presented in the right-hand column of Table 3. First note that, overall, the mean differences are of a moderate magnitude (0.76; maximum possible difference=2.0). Grub and Kenya had mean difference scores that were significantly greater than expected by chance; this value for Noelle was not significant (*P*<0.10, one-tailed tests).

We also computed difference scores and *t*-tests omitting trials on which an animal displayed an AT behavior at baseline. (None of the apes displayed a T behavior at baseline for the generalization of imitation trials.) Using this criterion, mean difference scores decreased slightly and *t*-values were no longer significant for Kenya [mean difference=0.5, *t*(3)=1.50] and Noelle [mean difference=0.4, *t*(4)=0.80], although the mean difference score increased slightly for Grub [mean difference=1.17, *t*(5)=2.65].

Discussion

All three enculturated chimpanzees, ranging in age from 5 to 9 years, displayed deferred imitation of actions on objects and generalization of imitation. Each ape tested in this experiment had demonstrated deferred imitation in previous studies (Bering et al. 2000; Bjorklund et al. 2000), but this is the first demonstration of the generalization of imitation in chimpanzees. Rather than merely imitating similar behaviors on identical objects, as in the deferred-imitation tasks we and others (e.g., Tomasello et al. 1993) have used, the apes in this study applied similar behaviors to different sets of objects to produce similar outcomes. The behaviors required for generalization of imitation were similar to those displayed by the model, thus reducing the likelihood that the tasks were solved by emulation, in which the animal has only the goal of the actions and not the specific behaviors in mind (e.g., Tomasello 1996, 2000); yet, because of changes in the materials[2] and, for some tasks, differences in the precise behaviors required for execution (e.g., holding the cymbals by their knobs, holding the trowels by their handles), it is unlikely that the generalization tasks reflect simpler mimicry. The present results, we argue, provide the best experimental evidence to date for deferred, imitative learning in chimpanzees.

Consistent with research with human infants (Herbert and Hayne 2000), each ape showed slightly higher levels of performance on the imitation than the generalization of imitation task, although this difference was substantial only for Noelle, the youngest chimpanzee. Noelle displayed an improvement from baseline on 71% of the imitation tasks, but on only 43% of the generalization tasks. It is worth noting that Noelle demonstrated three T behaviors on the deferred phase of the generalization task and no ATs. Of these three tasks, she had displayed an AT on two of the tasks at baseline. (For the third task, Noelle had shown an AT behavior on the imitation-task materials at baseline, although not on the generalization-task materials.) Similarly, although displaying twice as many ATs as Ts on the imitation tasks, the two tasks on which she showed the target behaviors were also preceded by ATs at baseline. Likewise for Kenya, of the two T behaviors she displayed on the deferred portion of the generalization task, both were preceded by ATs at baseline. This pattern was not observed for the oldest chimpanzee, Grub (only one of four of his T behaviors on the deferred phase of the generalization tasks was preceded by an AT at baseline), nor for the imitation tasks for either Kenya or Grub. This pattern suggests that generalization of imitation for the two youngest apes (and perhaps imitation for Noelle) was most likely to occur on tasks that they were "prepared" to acquire. That is, generalization of imitation was most apt to occur when the young chimpanzees had displayed some, but not all, of the target behavior previously, making the model's behavior particularly salient and effective (for related argument see Whiten 1998). This is reminiscent of "working in the zone of proximal development" (Vygotsky 1978), in which children are most likely to acquire new skills when adults or more skilled participants tailor their instruction to children's current abilities, often so that children perform tasks that are more difficult than they could perform alone.

To increase the number of tasks used in this experiment, we included three tasks on the imitation trials that we had used in previous research. The cymbals task had been given to each of the three apes approximately 3.5 years earlier (Bering et al. 2000), and Noelle (but not Grub or Kenya) had been given the pipe and ball and the plunger tasks approximately 1.5 years earlier (Bjorklund et al. 2000). It is worth noting that, despite displaying a T or AT behavior on each of these tasks when they were administered 1.5 or 3.5 years earlier, none of the apes displayed a T or AT behavior on these tasks at baseline in the current study. (Grub and Kenya did show Ts at baseline for the plunger, but they had not been given this task previously.) These results suggest that simple behaviors on objects, acquired via observation but not practiced in the interim, are forgotten by chimpanzees over extended delays.[3]

[2]Although different objects were used for the imitation and generalization tasks, the objects had similar affordances, and it is not clear from the present research how the degree of similarity between the objects used to display the target behaviors and the objects used in the generalization phase contributed to the apes' subsequent imitation of the target behaviors. Future research should investigate this question, examining the degree to which generalization of imitation is influenced by the perceptual similarity in the stimulus materials in addition to the actions of the model.

[3]Anecdotally, two months after displaying target behaviors on both the cymbals and trowels tasks, we readministered these tasks (including a baseline phase) to Grub for the purpose of demonstration to a filming crew. Grub did not display either T or AT behaviors at baseline for either task, but did so (vigorously) during the respective deferred phases for both tasks. Thus, it appears, and not surprisingly, that unpracticed behaviors acquired via imitation are not typically sustained in chimpanzees' cognitive repertoires.

The tasks used in the present study require relatively simple actions on objects that we believed each of the chimpanzees was capable of performing. Observations of social learning in the wild have typically focused on more complicated behaviors, such as those involved in termite fishing or nut cracking (see Whiten et al. 1999). It would be unlikely that these more complicated behaviors would be attained solely via imitative learning; rather, if imitation is involved, other types of learning mechanisms (e.g., emulation, trial and error, mimicry) would also occur, as chimpanzee juveniles gradually master the complexities of these tool-using tasks. There has been some research on social learning of more complex tool use by chimpanzees (e.g., Bard et al. 1995; Whiten et al. 1996; Whiten 1998; Myowa-Yamakoshi and Matsuzawa 2000), and one study, similar to the present one, investigated generalization of an acquired behavior to a more difficult task. Bard et al. (1995) gave juvenile chimpanzees a tube into which food was placed and dowels to retrieve the food. For one group of apes, a model demonstrated the target behavior before permitting the chimpanzees to attempt to retrieve the food themselves, whereas a second group was given the task without modeling. The 3- and 4-year-old chimpanzees (but not 2-year-olds) in the modeling condition subsequently were more successful in solving the food-retrieval problem and in generalizing their behavior to a more difficult task. One 4-year-old solved the problem on his first try after observing a conspecific, rather than a human, model the solution. The results are consistent with those of the present study. The absence of a baseline period, during which the apes in the modeling condition attempted to solve the problem prior to any demonstration, precludes a definitive statement about whether imitative learning, rather than other social-learning mechanisms, was involved. However, the findings of Bard et al. (1995) suggest that chimpanzees may use imitation, in part, to learn more complicated tool-using tasks, as well as the simpler tasks used in the present experiment.

As we noted previously, the best evidence of imitative learning (particularly after delays) is found in chimpanzees and other great apes with significant experience interacting with humans, similar to the animals tested in the present study (e.g., Tomasello et al. 1993; Miles et al. 1996; Russon 1996; Bering et al. 2000). The motivation for observing others' behaviors must be firmly in place before imitative learning can occur. Joint attention is pivotal in leading to imitation – otherwise observation of actions would not occur – but something must impel the ape to enter into the triadic interaction to begin with. For the enculturated ape, this *something* comes from an ontogeny in which it has explicitly benefited from reproducing actions on objects. During the course of development, humans treat enculturated apes as intentional agents. In contrast, wild chimpanzees do not treat their offspring in such a manner. For example, upon witnessing their offsprings' frustrated struggling with Coula nuts and anvils, chimpanzee mothers who are experts at solving this particular problem do not intercede on their behalves. A frequent occurrence in the home-rearing environment, in contrast, is that apes encounter problems with objects from cultural surroundings, and human caretakers advance on these scenes by solving such problems for them. The ape, of course, anxiously attends to these events, observing not only the final solution but also the way its caregiver went about resolving the difficulty. Over a succession of similar episodes during the animal's development, humans continually "tag" the enculturated ape's affective and cognitive experiences of problem states, interceding in the ape's behavioral strategies whenever they perceive that their charge is unsuccessfully going about working on a problem. The ape, in turn, comes to associate humans as problem-solving specialists and potentially learns that observation (and later reproduction) of human actions can reap big rewards.

Several researchers (Call and Tomasello 1996; Bjorklund and Pellegrini, 2002) have suggested that radical changes in rearing environment can result in changes in the ontogenetic pattern of cognition in a large-brained, slow-developing primate. Whether for human-reared chimpanzees such species-atypical environments produce only molar (i.e., behavioral) levels of change in sociality leading to enhanced imitative learning abilities (see Carpenter et al. 1995; Povinelli 1996), or changes in the epigenetic system leading to phenotypic expression of cognitive abilities that are otherwise suppressed under natural conditions (see Tomasello 1990; Bjorklund and Pellegrini, in press), cannot be discerned from the present results. Nevertheless, investigations into the cognitive development of enculturated great apes may provide a means for testing hypotheses about the role of rearing environments in human cognitive evolution (e.g., Gottlieb 1987, 1992).

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