Strategies Used to Combine Seriated Cups by Chimpanzees (*Pan troglodytes*), Bonobos (*Pan paniscus*), and Capuchins (*Cebus apella*)

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The authors investigated strategies used to combine seriated cups by apes (*Pan troglodytes* and *P. paniscus*) and monkeys (*Cebus apella*) using a protocol reported in P. M. Greenfield, K. Nelson, and E. Saltzman's (1972) study with children. It was hypothesized that apes would exhibit more hierarchical combinations of cups than monkeys, given apes' language capacity, and that apes would seriate the cups more efficiently than monkeys. As predicted, apes made many structures with the cups using a variety of strategies, and monkeys rarely combined the cups. After a training phase to orient monkeys to the task, the 2 genera did not differ in the strategies used to combine the cups or in efficiency in seriating the cups. Success in this task suggests that sensorimotor versions of hierarchically organized combinatorial activity are well within apes' and monkeys' abilities.

The organization of manual activity has been studied extensively in human children. Piaget (1954) pioneered the study of motor activity as an expression of cognitive function by identifying programs of action in the child's manipulation of objects. More recently, neo-Piagetian (Case, 1985, 1991) and information-processing theorists (e.g., Siegler, 1986, 1989) have examined the development of rule-guided behavior or strategies within this context. Others have explored the coordination of movement sequences, including the child's self-monitoring of the consequences of his or her actions in service of a goal (e.g., spoon use; Connolly & Dalgleish, 1989).

We were interested in analyzing the organization of movement sequences as an aspect of planning in nonhuman primates by comparing combinatorial manipulation of objects in two species of apes, bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*), and one species of monkey, the tufted capuchin (*Cebus apella*). The task of combining a set of seriated cups was chosen for this purpose.

Greenfield, Nelson, and Saltzman (1972) explored chil-

dren's development of rule-guided behavior in assembling seriated cups. They were specifically interested in the emergence of hierarchical organization of manual activity. Hierarchical organization occurs when lower level units are combined into higher level or more complex units. Greenfield et al. identified three strategies in children's manipulation of nesting cups (see Figure 1).

The strategies differ in the degree to which they necessitate hierarchical organization of sequential actions with the cups. The simplest way to combine the cups (the "pairing method") involves nesting or stacking two cups. In the "pot strategy," two or more cups are placed one at a time into or on top of a single cup (the pot). The "subassembly strategy" involves combining two or more cups, which are then placed as a unit (or subassembly) on top of or into one or more cups.

The subassembly strategy is considered the most complex because it requires a hierarchical combination of multiple cups. Two or more cups become a subunit, which functions as a single unit in the next movement sequence. Greenfield et al. (1972) noted that in subassembly, role reversal is evident in that the cup that is acted on becomes the actor in the subsequent movement sequence such that Cup B is first in a passive role (it receives Cup A) and then in an active role (the nested pair containing Cups A and B are put into Cup C as a unit). In the less complex form of combination, potting, there is no role reversal from passive to active role.

In children, these strategies appear in sequential order (Greenfield, 1991; Greenfield, Brazelton, & Childs, 1989; Greenfield et al., 1972). At 11 months of age, the majority of middle-class children in Cambridge, Massachusetts, like Zinacantec Maya children in Chiapus, Mexico, combined the cups by making pairs. By 21 months of age, the pot strategy becomes the dominant combinatorial method. By 36 months of age, the subassembly strategy was evident in both groups of children, although it was not the dominant
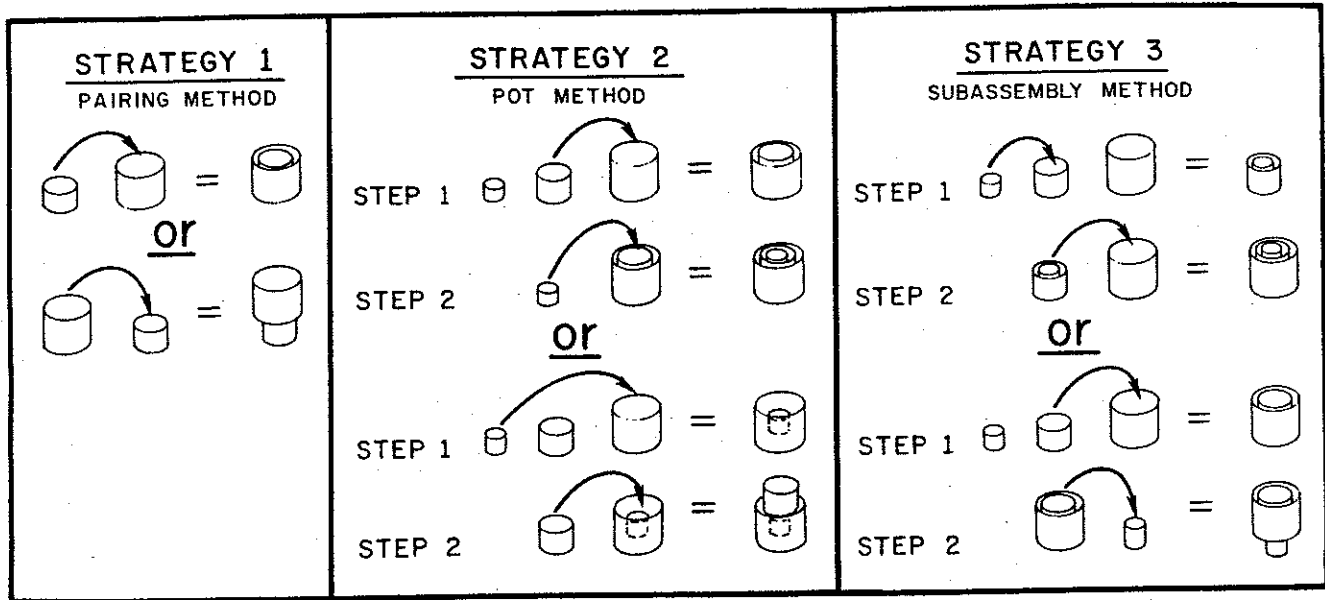
Figure 1. Strategies for combining nesting cups as identified by Greenfield, Nelson, and Saltzman (1972). Copyright 1972 by Academic Press. Reprinted with permission from the author and Academic Press.

strategy for most. There was a developmental progression from less complex to more complex hierarchically organized combinatorial activity. Thus, the developmental sequence has established cross-cultural validity.

Greenfield et al. (1972) argued that these three strategies contributed differentially to success at seriation. The majority of 11-month-olds consistently formed two-cup seriated structures by putting a small cup into a large cup using the pair strategy. However, at 16 months of age, the emergence of potting as the dominant strategy impeded seriation success to some extent because the sequential combination of multiple cups resulted in both nesting and stacking cups (e.g., when the children attempted to put a large cup into a previously constructed smaller nested pair). The 36-month-olds who engaged in the subassembly strategy were consistently able to seriate the cups and fit a sixth cup into the middle of a previously seriated five-cup set.

The theoretical explanation for this relationship between manipulative strategy and seriation is that in true seriation, each element in a series has a two-way or reversable relationship: A particular element must be conceived of as being smaller than the previous element but larger than the subsequent element (Inhelder & Piaget, 1969). The conception of a two-way relationship (Cup B is larger than Cup A and smaller than Cup C) becomes crucial in inserting a cup into the middle of a preexisting series. In contrast, a one-way relationship (e.g., always picking the largest remaining cup) suffices to seriate a set from scratch (i.e., "potting" one cup at a time). Thus, the pot strategy does not require awareness of a two-way relationship. To seriate using the subassembly strategy requires awareness of a two-way relationship. The recipient cup in Step 1 of the subassembly method is larger than the cup placed inside it, and the resulting pair is also smaller than the cup it is placed into in Step 2 (see Figure 1).

Hence, there is a theoretical and empirical relationship between the development of proficiency in seriation and manipulative strategy.

On a theoretical level, Greenfield (1991; Greenfield et al., 1972) posited parallels between the development of children's manipulative strategies and the development of grammatical and phonological constructions. The possibility of a neurally based developmental homology between language and action was explored (Greenfield, 1991). On the behavioral level, children combine two sounds into a meaningful syllable (e.g., "da") at about the same time as they combine two objects in a construction. They make "potlike" phonological constructions (e.g., two different consonants successively combined with a common vowel) at about the same time as they begin to use the pot strategy for combining objects. An example of a potlike phonological construction is "kye bye" (i.e., car bye-bye). Finally, paired sounds (e.g., "ba") are used as a unit or subassembly in more hierarchically complex constructions (e.g., "ball") at about the same time as the subassembly strategy commences in object combination.

The developmental trajectory of children's ability to combine nonverbal communicative elements follows a similar pattern. The child's use of a single element appears first (e.g., crying), followed by single elements that occur successively in a sequence (e.g., crying and pointing, crying and raising arms). Finally, the child begins to combine two or more elements simultaneously (Lock, 1978). These findings suggest a possible link between the cognitive capacities supporting human communication and instrumental action and point to the possibility that a single neural structure may be implicated in their organization.

Using the Greenfield et al. (1972) protocol in addition to a

similar one that we devised, we examined how apes and monkeys would combine nesting cups. Previous research with nonhuman primates in this area has documented the use of all three combinatorial strategies by both chimpanzees (Matsuzawa, 1991) and capuchins (Westergaard & Suomi, 1994). However, neither of the earlier studies closely followed the Greenfield et al. procedure. Westergaard and Suomi used more liberal definitions of combinatorial actions than did Greenfield et al., such as combinations of cups and other objects with projections in the cage as demonstrations of potting and subassembly. Furthermore, in neither study (Matsuzawa, 1991; Westergaard & Suomi, 1994) was the performance of two or more species in the nesting cup task directly compared.

Three hypotheses were central to our investigation. First, we predicted that apes would exhibit relatively more hierarchical combinations (subassemblies) of cups than monkeys, given that apes have demonstrated certain protogrammatical language capacities (Greenfield & Savage-Rumbaugh, 1990, 1991). Second, on the basis of the Greenfield et al. (1972) suggestion that success at seriating a sixth cup into the middle of a previously constructed five-cup set is related to use of the subassembly strategy, we hypothesized that (a) there would be a correlation between use of the subassembly strategy and success in inserting a sixth cup into a preexisting five cup series and (b) apes would seriate a middle sixth cup into a five-cup set more frequently and more efficiently than would monkeys. In other words, apes would be more likely than monkeys to use the subassembly strategy to remove the top cups in the set, insert a middle sixth cup, and replace the top cups as a nested unit into the set. A third hypothesis arising from Greenfield's developmental theory and data (Greenfield et al., 1989) was that subjects' microdevelopmental progression of combinatorial activity with the cups over the course of testing would reflect an increasing hierarchical complexity of actions (i.e., would advance from pairing to potting or from potting to subassembly).

Method

Subjects

The subjects in this experiment belonged to two species of apes (5 chimpanzees, *Pan troglodytes,* and 3 bonobos, *Pan paniscus*) and one species of monkey (4 capuchin monkeys, *Cebus apella*). At the time of the study, the youngest of the chimpanzees (3 males and 2 females) was 8 years and the oldest was 25 years. The age range of the bonobos (1 male and 2 females) was 8–14 years. Six of the 8 apes had language training before this study. Three of these (1 *P. troglodytes* and 2 *P. paniscus*) were conversationally reared (see Savage-Rumbaugh et al., 1993, for a review of the language training efforts with these subjects). All apes were living at Georgia State University's Language Research Center. The 4 capuchins were young adults, ages 5–10 years. All capuchins were living at the University of Georgia.

Test Materials

The materials used in this study were two sets of children's nesting cups that differed in height and color. The first set (Shelcore, Piscataway, NJ) contained six cups that were a mix of

yellow, red, and blue. The heights of the smallest and largest cups were 1.7 and 4.5 cm, respectively. The second set (Kiddie Products, Avon, MA) of six cups was shorter than the first set; the heights of the smallest and largest cups were 1.5 and 2.2 cm, respectively. Additionally, each cup was a different color and had a lipped rim. Capuchins were tested with the set of smaller multicolor lipped cups because it was assumed that the size of the large cups would hinder manipulation. The apes were first tested with the tricolor set of larger cups because of the presumed difficulty that the apes might have manipulating the smaller cups. However, the apes were tested on later trials with the smaller cups to rule out the possibility that the lip on the rim of the small cups facilitated manipulation for one group and not the other. As it happened, apes appeared to handle both sets with equal facility.

Procedure

The experiment consisted of trials with five and six cups. First, we presented subjects with five cups to manipulate. Subjects' participation in trials with six cups was contingent on whether they constructed a seriated set with the five cups. Subjects were immediately tested on their ability to fit a sixth cup into a fixed position of the previously seriated five-cup set. In one set of trials, subjects were given a sixth cup that fit into the middle of the seriated set (middle sixth-cup trials). In another set of trials, subjects were again given a sixth cup to fit into a previously nested set. However, the position of the sixth cup in the set varied from trial to trial (see variable sixth-cup trials). This set of trials was given only to subjects that reliably seriated five cups.

Subjects were tested individually either in an enclosed area with the experimenter (3 apes) or in a test cage with limited tactile access to the experimenter (5 apes and all capuchins). An array of cups on a flat surface (table or tray) was presented to subjects by the experimenter. The experimenter demonstrated nesting the cups, starting with the smallest cup first and using the subassembly strategy. After nesting the five cups, the experimenter took the nested set apart, placing each cup back in its original array position. Subjects were either handed all five cups simultaneously (i.e., the cups were either put into the test cage or pushed in front of the subject on the surface of a table) and were allowed to choose which cup to manipulate first, or they were simultaneously handed four cups followed by a fifth cup, designated as the "start" cup (following Greenfield et al., 1972). The size of the fifth cup (smallest, medium, or largest in the five-cup set) and opportunities to choose a cup were counterbalanced across test trials.

Subjects were given approximately 3 min per test trial to manipulate the cups. This trial length accommodated the subjects' interest in the task and allowed them plenty of time to attempt to seriate the cups. If a subject was working diligently at the conclusion of a trial, the trial was extended (usually about 1 min) until the subject was judged to have finished activity (e.g., by putting the cups down and moving away from the work area or handing the cups to the experimenter). A trial ended before 3 min if the subject made a five-cup seriated structure. If a subject seriated all five cups, it was handed a sixth cup that fit into the five-cup nested set. In this case, the trial ended when a six-cup seriated structure was made or after approximately 3 min elapsed after the subject received the sixth cup.

Capuchins completed one test trial per day, whereas the apes typically completed three to four test trials per day. Giving the apes multiple trials on the same day did not appear to affect performance in that their attentiveness to the task was consistent and their tempo of work similar from one trial to the next (personal observation). All test trials were videotaped. The experimenter gave verbal encouragement to apes and monkeys (e.g., "Keep working; you're

doing fine.") during trials and put cups back into the work area if they were knocked off the table or out of the test cage by subjects. At the conclusion of a trial, subjects handed the cups back to the experimenter. Subjects were given food treats between trials or at the end of the day's test period regardless of performance.

Table 1 shows the number of test trials for all subjects in trials with five and six cups. The variable number of apes' trials with five cups (see the 5 Large cups column in Table 1) is the result of videotaping difficulties. We aimed for a total of eight scorable trials.

Training series for capuchins. In the first round of testing (see the 5 Cups Pretraining column in Table 1), capuchins did not reliably combine the cups according to the strategies that were earmarked for analysis (pair, pot, and subassembly), and they did not make stable structures with the cups, whereas the apes did. Therefore, we supplemented scoring strategies for capuchins with two activity measures, including touching (the subject touches cup with hand) and combining cups (the subject combines cups in a manner that is not one of the three strategies, such as striking a cup with another cup). From these data and our behavioral observations, we concluded that the capuchins did not share our perception of the aim of the task (i.e., to combine the cups).

Given the vastly different rearing and test histories of the two genera, we determined that training the capuchins to combine cups would bring the capuchins to essentially the same starting point as the apes and would afford a more equitable comparison. Before the current study, the apes were routinely engaged in activities with objects, including anticipating the goals of the tasks and the intentions of the experimenters. These activities may have given them an advantage over the capuchins in this task. The apes had participated in a variety of tasks including picture completion, mazes, painting, Wisconsin General Test Apparatus tasks, construction activities, counting, and tool tasks. Two of the apes (Austin and Sherman) had previous experience with a video counting task that required seriation. To date, the capuchins' test history consisted of performing tasks such as two-dimensional mazes that were presented using a video-formatted testing paradigm in which manipulation of a joystick was congruent with movement of a cursor on a video screen (see Filion, Johnson, Fragaszy, & Johnson, 1994, for details on the capuchins' training and test activity with this system). The capuchins did have experience manipulating objects (e.g., browse and plastic toys) that were placed in their home cages on a routine basis.

The training series for capuchins consisted of four phases. In the first phase, capuchins were handed five cups and trained to give the cups back at the experimenter's request. The criterion for advancement to Phase 2 was that a subject give the cups to the experimenter for three of four consecutive requests. Capuchins took an average of 15 attempts to proceed to the second phase. In Phase 2 training trials, capuchins were given two cups and reinforced (with food treats) for manipulating, combining, and pairing cups. When a subject paired cups, by stacking or nesting, for six consecutive trials, it proceeded to Phase 3. The mean number of trials to reach criterion in Phase 2 was 19 trials. In the third phase, reinforcement was contingent on making freestanding structures of any form (nested or stacked cups) with three cups regardless of the strategies used. Thus, we were not explicitly training the capuchins to seriate the cups, although being able to make stable structures with more than two cups necessitates using some potting or subassembly actions. If creating a three-cup standing structure occurred for six consecutive trials, then the subject moved to Phase 4. The mean number of trials for capuchins to reach criterion in Phase 3 was 17. In the last phase, capuchins were reinforced for making at least one structure per trial containing four or five cups using any combination of strategies. In this phase, the reward was delivered at the end of the trial to avoid disrupting ongoing cup manipulations. If the subject made at least one structure of this type for six consecutive trials, it proceeded to a second round of testing with five cups. The mean number of trials to criterion in Phase 4 was 55. The duration of a trial ranged from 5 to 15 min in all training phases. Note that this type of systematic shaping was not required to bring either the apes or children (Greenfield et al., 1972) to the equivalent starting point.

Additional testing with five cups. Capuchins were tested a second time with five cups in the same manner as described in the *Procedure* section (see the 5 Cups Posttraining column in Table 1),

Table 1
Number of Test Trials for Each Subject

Subject	Test trials in chronological order							
	5 cups pretraining	5 cups posttraining	6th cup	Variable 6th cup	5 large cups	6th cup	5 small cups	Variable 6th cup
Capuchins								
Jobe	8	8	2	7				
Chris	8	8	6	3				
Xenon	8	8	8	9				
Xavier	8	8	0	0				
Chimpanzees								
Austin					8	7	9	9
Panzee					8	6	9	9
Sherman					8	8	9	9
Mercury					7	0	1	0
Lana					3	1	5	0
Bonobos								
Tamuli					8	1	0	0
Kanzi					7	7	9	9
Panbanisha					6	2	2	0

Note. Capuchins had no trials with a sixth cup before training because they failed to construct seriated sets. Analyses compared capuchins' posttraining trials with the apes' fifth- and sixth-cup trials with the large cups. All subjects used small cups in variable sixth-cup trials.

and 7 of the 8 apes were tested for at least one trial with five cups as a prelude to trials with a variable sixth cup (see the 5 Small cups column in Table 1). This five-cup test phase differed from the apes' first test phase in that the set of smaller multicolor lipped cups was used instead of the unlipped tricolor cups (see the 5 Large cups column in Table 1). We were interested in determining whether the lip on the rim of the set of smaller cups would facilitate manipulation (e.g., grasping and pulling one nested cup out of another cup) compared with the unlipped tricolor cups. Two repeated measures analyses of variance (ANOVAs) were used to determine whether the apes' performance would vary across test trials with large and small cups. In the first ANOVA we compared the number of seriated five-cup sets made with the large cups versus the small cups, $F(1, 5) = 1.50$, $p > .05$. In the second ANOVA we tested whether there would be a difference in the proportion of subassembly actions exhibited by the apes, $F(1, 6) = 0.85, p > .05$. Because no effect of the type of cup was found and more data were available for the apes in the first test phase, in the remainder of the analyses of the five-cup and sixth-cup test trials, we compared the apes' data with large cups with the capuchins' posttraining data.

Variable sixth-cup trials. To determine the generality of the subjects' ability to place a sixth cup into a seriated set, we gave 7 subjects (4 apes and 3 capuchins) that reliably seriated five cups an additional nine trials. In these nine trials, if a subject was successful in seriating five cups, then a sixth cup was given that was different from the one used previously (the cup that occupied the middle position in the set, fourth cup from the top). Subjects had the opportunity to nest each new sixth cup: second, third, or fifth from the top of the set, three times (see the Variable 6th-cup trials column in Table 1). The position of the cups was counterbalanced across nine trials. The set of small cups was used in these test trials with both genera.

Analyses

Scoring procedure for test trials with five and six cups. For each trial, three strategies used in combining the cups were successively noted: (a) pairing two cups (pair); (b) putting two or more cups successively into or onto one or more cups or putting a single cup into or onto two or more cups that had already been combined (pot); and (c) putting two or more cups as a unit into or on top of one or more cups (subassembly; Greenfield et al., 1972). Following Greenfield et al. (1972), we coded the sequence of moves that produced the final structure, defined as the largest stack constructed before being dismantled or terminated by the subject. In cases in which final structures were built using a combination of pot and subassembly strategies, the animal was credited with the less advanced pot strategy. As Figure 1 shows, the pairing strategy applied only to two-cup structures. Multiple final structures could be constructed within each trial. We also noted whether final structures were seriated.

We supplemented the Greenfield et al. (1972) scoring procedure with one in which each individual move with the cups, rather than sequences producing final structures, was coded. For example, if a subject paired two cups and then put the subunit into another cup, we scored both a pair and a subassembly, whereas Greenfield et al. scored this sequence as a subassembly. We made this change in the scoring because, unlike children, our subjects had a propensity to construct and dismantle structures during the course of a trial and because scoring successive moves, rather than complete sequences of cup combinations, seemed better suited to capture this activity. Both scoring procedures were applied to five-cup trials and to trials with a middle sixth cup. Trials in which the position of the sixth cup varied, a variation on the Greenfield et al. protocol, were coded according to only the individual-moves scoring scheme.

Additionally, for trials with six cups, subjects' successive moves with the cups, after being handed the sixth cup, were scored to analyze seriation in more detail. In particular, we assessed how subjects dealt with "blocking" cups that prevented seriation. In other words, how frequently did subjects place the cups out of order in the set such that seriation was impeded? Also, how often did they correct this type of error by removing cups that were out of order? For this purpose, we defined a move as grasping a cup and combining it with (regardless of the strategy used) or separating it from another cup (i.e., removing the cup from the set). We noted whether the move (a) created a block and thus prevented seriation or (b) facilitated seriation by removing a blocking cup. The detailed scoring scheme described here was applied only to trials with six cups because all subjects started with an equal number of cups blocking seriation of the sixth cup into the previously seriated set. For example, in trials in which the sixth cup occupied the third position from the top of the set, two cups (the first and second in the set) were "blocking" cups that had to be removed to fit the sixth cup into the set.

As mentioned previously, the capuchins rarely touched or combined the cups during their initial exposure to the task (pretraining trials). Descriptive data characterizing their manipulation of the cups (e.g., combinatorial activity, touching the cups) were calculated. Capuchins were retested after training; data from the posttraining test phase were used to compare monkeys with apes in the three sets of analyses that follow.

Strategies used in nesting cups. Two separate mixed-design ANOVAs (i.e., five-cup and middle sixth-cup trials) were used to examine subjects' use of strategies (the repeated factor was pair, pot, and subassembly) and to compare apes and monkeys (between-subjects factor) using proportional scores from data coded using the Greenfield et al. (1972) scoring scheme ($\alpha = .05$). Identical analyses were conducted using the data obtained by the individual-moves scoring scheme (three ANOVAs for five-, middle-, and variable sixth-cup trials; $\alpha = .05$). We also examined potential differences between genera in the use of the subassembly strategy in greater detail by using several t tests ($\alpha = .02$, Bonferroni correction) and correlations. We calculated whether apes and capuchins differed in their propensity to use the subassembly strategy by comparing the proportion of actions that were subassembly in trials with five cups, a middle sixth cup, and a variable sixth cup. Finally, we used a Spearman rank correlation coefficient ($\alpha = .05$) to determine whether there would be a relationship between use of subassembly (according to our scoring criteria) and the proportion of trials with the sixth cup and variable sixth cup that ended in a seriated set.

Seriation of nesting cups. We compared the proportion of trials in which apes and capuchins constructed a single seriated set in each of the three series of test trials (i.e., five cups; six cups, in which the sixth cup was the middle in the set; and variable sixth cup) using t tests ($\alpha = .02$, Bonferroni correction).

Efficiency in constructing seriated sets. Two measures of efficiency in nesting cups were examined. The first compared apes and capuchins on the number of moves performed in making a seriated set with five cups and when handed a middle or variable sixth cup to fit into a previously constructed five-cup set using t tests ($\alpha = .02$, Bonferroni correction). In this analysis, the number of moves included all three strategies as well as removing cups from a set. The second measure of efficiency dealt with placing the cups in a manner that prevented seriation (i.e., creating blocks) and correcting errors by removing cups, thereby facilitating seriation (i.e., removing blocks). Apes and monkeys were compared using t tests on the proportion of blocks removed to blocks created in middle- and variable sixth-cup trials.

Table 2
Distribution of Strategies in Monkeys and Apes Using a Sequential-Moves Analysis

	Strategy		
Test phase	Pair	Pot	Subassembly
Five cups			
Apes ($n = 8$)	53.9	39.6	6.5
Capuchins ($n = 4$)	57.2	38.1	4.7
Middle sixth cup			
Apes ($n = 7$)	63.6	35.0	1.4
Capuchins ($n = 3$)	0	93.6	6.4

Note. Pairing was the dominant strategy by both genera in trials with five cups (analysis of variance, $p < .05$). In sixth-cup trials, apes paired cups significantly more than did monkeys (t test, $p < .02$); monkeys used the pot strategy more than did the apes (t test, $p < .02$). These data were obtained using Greenfield, Nelson, and Saltzman's (1972) scoring scheme.

Results

In the first round of testing, only 2 of the 4 capuchins (i.e., Jobe and Xavier) made structures by combining the cups ($M = 0.15$ structures per trial across all capuchins). These 2 subjects used the pair strategy to make two-cup structures. On several occasions, one of the capuchins who did make structures (Jobe) and one of the capuchins who did not (Chris) grasped a cup and banged it against another cup and against the floor of the test cage ($M = 0.25$ cup combinations per trial other than pairing across all capuchins). In contrast, the apes attended to the experimenter's demonstration of constructing a seriated set and worked with the cups consistently for the duration of a test trial. All apes made multicup structures using a variety of strategies. Given that only 2 of the capuchins made stable structures and that on some trials they rarely made contact with the cups at all (the mean frequency of touching the cups was 6.22 per trial for all capuchins), in the remainder of the Results section we report the capuchins' posttraining data and compare them with the apes' data.

The style of manipulation of the cups varied within both genera from careful placement in nesting and stacking the cups to less controlled handling. Constructing and dismantling structures as well as working with multiple stacks characterized all of our subjects' combinatorial activity with the cups.

Strategies Used in Nesting Cups Using the Sequential-Moves Analysis of Greenfield et al. (1972)

After the capuchins' training, all three strategies to combine the cups (pair, pot, and subassembly) were shown by all species. In trials with five cups, pairing was the dominant combinatorial strategy for apes and monkeys, $F(2, 20) = 26.07, p < .05, R^2 = .64$ (see Table 2). Apes and monkeys did not differ in their proportional use of the three strategies in trials with five cups, $F(2, 20) = 0.08, p > .05$. However, the genera did differ in their proportional use of strategies in trials with a middle sixth cup, $F(2, 16) = 19.52,$

$p < .05, R^2 = .76$. In sixth-cup trials, apes used the pair strategy more often than did capuchins, $t(8) = 3.68, p < .02,$ $\omega^2 = .56$. The monkeys used the pot strategy significantly more than did the apes, $t(8) = 3.51, p < .02, \omega^2 = .58$. The proportional use of the subassembly strategy did not differ between the genera, $t(8) = 1.56, p > .02$.

Strategies Used in Nesting Cups Using the Individual-Moves Analysis

No strategy emerged as a dominant means to combine cups in trials with five cups, $F(2, 20) = 3.10, p > .05$ (see Table 3). In the test trials with the middle sixth cup, pot was the most frequently exhibited strategy by members of both genera, $F(2, 16) = 5.91, p < .05, R^2 = .35$. In trials in which the position of the sixth cup varied, subassembly was the dominant strategy used by subjects to combine the cups, $F(2, 10) = 11.25, p < .05, R^2 = .54$. There was no significant interaction between subject group (ape or monkey) and the percentage of use of strategy in trials with five cups or a middle sixth cup. However, there was a significant Genus $\times$ Strategy interaction in trials with a variable sixth cup, $F(2, 10) = 4.44, p < .05, R^2 = .21$. Further analyses revealed that the capuchins performed the pot strategy proportionally more often than did the apes, $t(5) = 3.30, p < .02, \omega^2 = .59$.

Subassembly Use in the Two Genera

Looking only at subassembly, which is the most advanced strategy, no difference was evident between apes and monkeys in any of the test trials: five cups, $t(10) = 1.10, p > .02$; middle sixth cup, $t(8) = 0.26, p > .02$; and variable sixth cup, $t(8) = 0.58, p > .02$ (see Table 3). Table 4 contains additional descriptive data for chimpanzees and bonobos. Using the individual-moves scoring scheme, we

Table 3
Distribution of Strategies in Monkeys and Apes Using an Individual-Moves Analysis

	Strategy		
Test phase	Pair	Pot	Subassembly
Five cups			
Apes ($n = 8$)	34.6	36.6	28.5
Capuchins ($n = 4$)	33.3	50.0	16.8
Middle sixth cup			
Apes ($n = 7$)	25.0	39.9	35.0
Capuchins ($n = 3$)	8.7	63.3	28.0
Variable sixth cup			
Apes ($n = 4$)	20.8	19.3	59.7
Capuchins ($n = 3$)	12.3	45.0	42.7

Note. Potting cups was the dominant strategy for both genera in trials with a middle sixth cup (analysis of variance [ANOVA], $p < .05$); subassembly was the dominant strategy used by monkeys and apes in variable sixth-cup trials (ANOVA, $p < .05$). Capuchins potted cups significantly more than did apes in trials with a variable sixth cup (t test, $p < .02$). Trials in which the position of the sixth cup varied were a variation on Greenfield, Nelson, and Saltzman's (1972) protocol.

found that subassembly constituted 25% of actions for conversationally reared apes and 31% of actions for other apes, $t(6) = 0.39$, $p > .02$. The 2 individuals with no language experience (1 *P. troglodytes* and 1 *P. paniscus*) had the lowest proportion of subassembly moves and seriated sets; these 2 also happened to be the youngest subjects. Chimpanzees used subassembly for 34% of moves, and bonobos used this strategy 20% of the time. Three of the 4 most proficient apes selected to participate in trials with a variable sixth cup were *P. troglodytes:* Austin, Panzee, and Sherman. These 3 apes were the only ones to seriate a variable sixth cup without error. One *P. paniscus* (Kanzi) met our selection criteria to participate in trials with a variable sixth cup.

Subassembly and Seriation

Subassembly combinations were significantly associated with efficiency in terms of the number of moves required to construct a seriated set after being handed a middle sixth cup, $r(10) = .76, p < .05$, two-tailed. For trials with the sixth cup in a variable position, there was insufficient variability to calculate a correlation in that 5 of the 7 subjects in this test series seriated the cups 100% of the time.

Figure 2 illustrates data from the subset of capuchins and apes that were selected to participate in variable sixth-cup trials. The data in this figure indicate that the proportion of trials ending in a seriated set increased from the middle sixth-cup test series to the variable sixth-cup test series in all but one subject (Chris). In addition, subassembly increased from middle sixth-cup trials to variable sixth-cup trials in all but one subject (Kanzi); this subject's proportional use of subassembly was consistent in the two test series (38% and 37%).

Microdevelopmental Trends in Strategies Using the Greenfield et al. (1972) Scoring Scheme

Individual subjects' predominant strategies by rank order are shown in Table 5. Consistent with our prediction, 5 of the

Table 4
Subassembly and Seriation in Trials With Five Cups Within the Genus Pan Based on an Individual-Moves Analysis

Species	Age (years)	Language	Subassembly (%)	Seriation (%)
P. troglodytes				
Austin	20	Y	53	88
Panzee	9	Y*	29	75
Sherman	21	Y	62	100
Mercury	8	N	9	0
Lana	25	Y	16	33
P. paniscus				
Tamuli	8	N	14	13
Kanzi	14	Y*	30	100
Panbanisha	9	Y*	16	33

Note. The column under the Language heading shows which individuals had prior language training (Y = yes; N = no); the asterisk denotes conversationally reared apes. The Seriation column shows the proportion of trials ending in a five-cup seriated set.
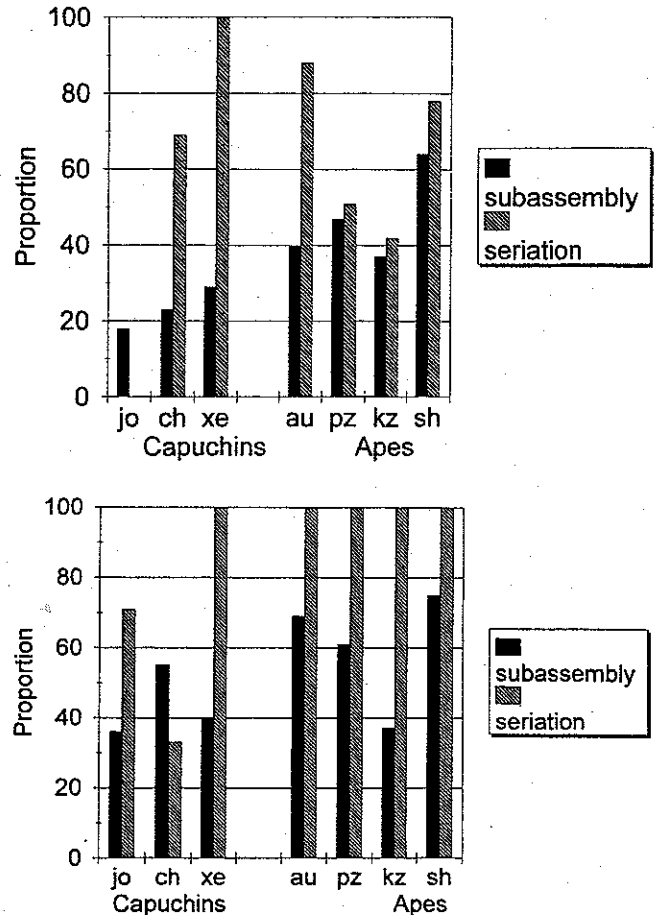

Figure 2. Subjects' use of the subassembly strategy was related to success at seriation in trials with the middle sixth cup (top). Both subassembly use and success at seriation increased from middle sixth-cup trials to variable sixth-cup trials (top and bottom) in a subset of capuchins and apes. Note that one subject (Jobe) did not seriate the cups in middle sixth-cup trials (top). jo = Jobe; ch = Chris; xe = Xenon; au = Austin; pz = Panzee; kz = Kanzi; sh = Sherman.

10 subjects who completed five- and middle sixth-cup trials shifted to a more complex strategy. Two subjects (Chris and Austin) did not shift to a more complex dominant strategy, but they did show evidence of a decreased use of the least complex strategy, pairing (Austin), or an increased use of the more complex strategy, potting (Chris), in sixth-cup trials. One ape (Lana) showed no change. Only 2 subjects (Tamuli and Panbanisha) showed, contrary to our hypotheses, movement toward a simpler strategy.

Seriation of Nesting Cups

Only one member of each genus (*Pan,* Mercury; *Cebus,* Xavier) never succeeded in making a five-cup seriated set. One capuchin (Xenon) seriated the cups successfully on every trial (25 trials from three test phases used for analysis), and 2 apes seriated the cups in all but 2 of their test trials (Sherman, 23 of 25 trials; Austin, 22 of 24 trials). These 2

Table 5
Subjects' Dominant Strategy Based on a
Sequential-Moves Analysis

| | Test trials | | | |
| | 5 cups | | 6th cup | |
Subject	Strategy	Proportion	Strategy	Proportion
Capuchins				
Jobe	Pair	56.3	Pot	100.0
Xavier	Pair	69.6	—	—
Chris	Pot	28.2	Pot	93.8
Xenon	Pair	75.0	Pot	87.5
Bonobos				
Tamuli	Pair	55.0	Pair	100.0
Kanzi	Pair	55.6	Pot	62.5
Panbanisha	Pot	72.7	Pair/pot	50/50
Chimpanzees				
Austin	Pair	45.5	Pair	43.8
Panzee	Pair	46.2	Pot	62.5
Sherman	Pair	45.5	Pot	60.0
Mercury	Pair	56.3	—	—
Lana	Pair	100.0	Pair	100.0

Note. Dashes denote that a subject did not meet criteria for testing in sixth-cup trials. Tamuli and Lana had a single trial with the sixth cup.

apes happened to be the two that had prior experience in a seriation task. Subjects in the two genera were equally likely to place five cups into a seriated set, $t(10) = 0.21, p > .02$. The proportion of trials in which a five-cup seriated set was constructed was 50% for capuchins and 55% for apes.

When presented with a novel sixth cup that fit into the middle of the five-cup nested set, members of both genera succeeded in placing the sixth cup in the correct position, and there was no significant difference in the proportion of trials that ended in completion of a seriated six-cup set, $t(8) = 0.46, p > .02$ ($Ms = 56\%$ for capuchins and 36% for apes). Similarly, when retested with small cups and a variable sixth cup (i.e., second, third, or fifth in the six-cup series), there was no significant difference between the 4 most proficient apes ($M = 100\%$) and the 3 most proficient capuchins ($M = 68\%$), $t(5) = 0.41, p > .02$.

Efficiency in Constructing Seriated Sets

Efficiency in the task (i.e., the number of moves performed to seriate the cups) was different between the apes and monkeys in test trials with five cups and a middle sixth cup. In the trials with five cups, the performance of the apes was more efficient than that of the monkeys, $t(8) = 3.08$, $p < .02$, $\omega^2 = .46$. The mean number of moves per trial required to construct a seriated set was 12.9 for the chimpanzees and bonobos and 30.1 for the capuchins. In trials with the middle sixth cup, capuchins made a seriated set in significantly fewer moves than did the apes, $t(4) = 3.36, p < .02$, $\omega^2 = .75$ ($Ms = 9.8$ for monkeys and 24.6 for apes). The large number of moves displayed by capuchins in the course of seriating five cups and by apes in inserting the sixth cup reflects both error corrections and a tendency to

dismantle structures, even those that were already seriated. In contrast, there was no difference between the genera in the number of actions performed to seriate a variable sixth cup, $t(5) = 1.08, p > .02$ ($Ms = 12.1$ for monkeys and 7.6 for apes). Recall that in trials with the variable sixth cup, the 4 most proficient apes and the 3 most proficient capuchins served as subjects.

Overall, the genera were similar in terms of placing the cups in a manner that prevented seriation (i.e., creating blocks) and in correcting errors by removing cups blocking seriation. In trials with the middle sixth cup, the apes created blocks to seriation an average of 13 times per trial and removed blocks to seriation 3.6 times on average. The mean number of blocks the capuchins created and removed per trial was 4.9 and 1.1, respectively. In trials with a variable sixth cup, there was an opposite pattern: Apes created blocks an average of 2.3 times per trial, whereas capuchins created blocks 7.5 times on average. The mean number of times apes and monkeys removed blocks during a trial was 0.64 and 1.4, respectively. When the proportion of blocks removed to blocks created was compared, we found no significant difference between genera, $t(5) = 0.08, p > .02$ (middle sixth cup), and $t(5) = 0.19, p > .02$ (variable sixth cup). There were 10 trials in which no blocks were created by 3 chimpanzees (Panzee, 1 trial; Austin, 7 trials; and Sherman, 2 trials) and 9 trials in which there were no blocks created by 2 capuchins (Jobe, 1 trial; Xenon, 8 trials).

Discussion

The most compelling finding in this study was our nonhuman subjects' proficiency in seriation, although this was not the primary focus of the study. Second, we were surprised at the degree of similarity between the monkeys' and apes' performance, although the monkeys required systematic training to perform the task as conceived by the experimenters. In the remainder of this section, we discuss the results with respect to the prediction that apes would display more complex combinatorial activity than capuchins given their demonstrated language capacities. Next, we relate our results to Greenfield's (1991; Greenfield et al., 1972) theory and findings with children. Finally, we comment on our nonhuman subjects' ability and efficiency in seriating cups as well as on the relation of seriation to strategy use.

Combinatorial Activity With the Cups in Initial Testing

As predicted, apes exhibited more hierarchically complex combinations with the cups than did monkeys in initial testing. The apes made stable structures with the cups using all three strategies to combine them (pair, pot, and subassembly). This finding is consistent with apes' demonstrated language capacities (Greenfield & Savage-Rumbaugh, 1990, 1991). It also concurs with other reports that have elucidated the complexity of apes' object manipulation in captivity. For example, Takeshita and Walraven (1996) reported that chimpanzees and bonobos frequently display compound

motor patterns with multiple objects, such as holding one object while rotating another. Chimpanzees in the wild have been observed to combine multiple objects in the context of tool use (e.g., Boesch-Achermann & Boesch, 1993; Matsuzawa, 1991, 1994). Placing a nut on an anvil, selecting the appropriate stone hammer, and pounding a nut with the hammer is a complex behavioral sequence that resembles the potting strategy exhibited by the apes in this study. Recall that in the potting strategy, two or more cups are placed in relation to a single base cup, the pot.

In the capuchins' initial trials, manipulation of the cups was rare. In fact, 2 subjects (Xenon and Xavier) failed to even touch the cups on several trials. Of the 4 subjects that were tested, 2 made several structures by forming nested pairs with the cups. However, several other forms of manipulation, such as banging cups together, were evident. The capuchins' pretraining data point to their spontaneous cup manipulation as being characterized by either a single action with a single cup (e.g., touching a cup) or a single action with a cup on a substrate (e.g., banging the cup on the floor of the test cage or against another cup). This is characteristic of their spontaneous interactions with small loose objects (Fragaszy & Adams-Curtis, 1991). Similarly, capuchins have been observed in foraging contexts to use tools by orienting objects to substrates or to a second object (e.g., Visalberghi, 1990; Westergaard & Fragaszy, 1987). Typically, tool use in capuchins involves a single action combining two objects, such as pounding a nut with a stone or sponging liquid with a paper towel.

The difference in the performance of apes and monkeys during the first round of testing may be representative of the types of object manipulation to which the two genera are predisposed. However, a caveat to this interpretation is that we are not in a position to state conclusively whether the forms of cup manipulation displayed by the apes were truly representative of their spontaneous rule-bound combinatorial strategies. This is because the apes had extensive past experience with objects in their living and test contexts, which may have given them a different starting point than the monkeys in performing this task. Nonetheless, note that this starting point was similar to that of the children in the Greenfield et al. (1972) study. Joint attention to objects between the apes and their caregivers is routine in their daily interactions. The absence of such experience in the capuchins prompted training sessions designed to orient the monkeys to the task of combining the cups. Once this was accomplished, the behavior of the monkeys differed little from that of the apes.

A Comparison of Strategies Used to Combine Cups in Pan and Cebus

After the training sessions with the capuchins, the apes and monkeys did not differ, according to either scoring scheme, in their propensity to use a particular strategy in trials with five cups. Pairing the cups was the dominant combinatorial strategy for both apes and monkeys using the Greenfield et al. (1972) scoring method. No dominant strategy emerged in five-cup trials using the individual-

moves method of analysis, and subjects showed a substantial proportional use of potting and subassembly. The different scoring methods should be considered when evaluating the disparity in these results. Recall that Greenfield et al. scored the overall strategies producing final structures in a trial, and, in the case of an intermediate use of more than one strategy, the least advanced strategy was coded. Scoring each individual move executed by subjects in a trial, rather than sequences of moves, results in an increase in the frequency of all strategies.

When handed a middle or variable sixth cup to seriate into the set, the monkeys tended to work with cups in the top portion of the set by removing cups and "potting" single cups into the intact bottom of the set. Some apes worked with all of the cups and often took the entire set apart. These individuals often constructed nested pairs and would dismantle and reconstruct the pairs until they contained the two cups that occupied the exact serial positions in the sets. This type of trial-and-error behavior preceded successful reseriation of the set using the subassembly strategy.

However, the proportional use of the subassembly strategy was not significantly different between genera or within the genus *Pan* regardless of the scoring method. Greenfield et al. argued that the subassembly combinatorial strategy is indicative of role reversal in that the cup that is acted on becomes a subunit and the actor in the next movement sequence. All three species demonstrated this hierarchical capacity, although it was not the dominant strategy for any subject.

If the results from trials with five cups are mapped onto the Greenfield et al. (1972) developmental analysis with middle-class U.S. children, the apes as a group performed identically to the 11-month-old children, in which 7 children used pairing as their dominant strategy and 1 used potting; the capuchins, as a group, were in between the 11- and 12-month level in the Greenfield et al. data. Three capuchins (after training), 2 bonobos, and all 5 chimpanzees used the pair strategy most often. Note that 3 of these 5 chimpanzees (Austin, Panzee, and Sherman) exhibited a dominant pair strategy that was just under 50%. Potting was the second most frequently used strategy in these subjects. Combinatorial activity in 1 capuchin (after training) and 1 bonobo was predominantly pot, the predominant strategy in 16- to 36-month-old children (see Figure 3). Unlike middle-class U.S. children between the ages of 20 and 36 months, no nonhuman subject showed use of a dominant subassembly strategy.

These data with capuchins are similar to Westergaard and Suomi's (1994) observations of capuchins, in which pairing was the most frequently used strategy and pot and subassembly were never the dominant strategy. Yet, the failure of both chimpanzees and bonobos to show subassembly as a dominant combinatorial strategy stands in contrast to previous results reported by Matsuzawa (1991). According to his observations and consistent with Greenfield's (1991) theory, chimpanzees exhibited a dominant subassembly strategy. These 2 chimpanzees happened to have had extensive language training in the form of a languagelike system that involved the use of lexigrams, or symbols that stand for
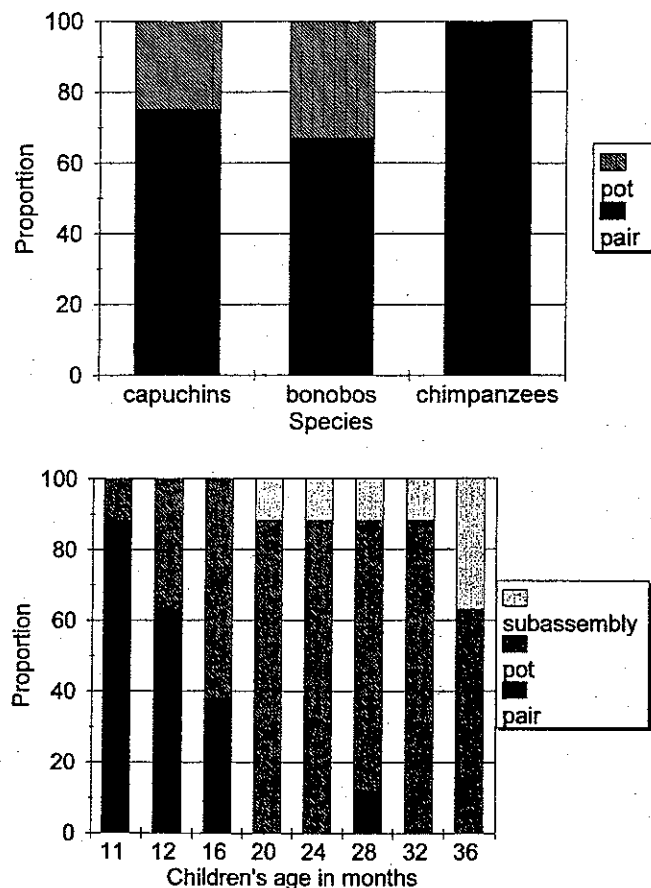
Figure 3. Proportional distribution of dominant cup combination strategies in apes, monkeys (top), and children (bottom). Data from children were taken from Greenfield, Nelson, and Saltzman (1972).

words (Matsuzawa, 1991). In the current study, no chimpanzee or bonobo, regardless of language training, used subassembly as the dominant means to combine the cups using Greenfield's criteria. Yet, by our analysis, subassembly did make up a small-to-moderate portion of cup combinations for both *P. troglodytes* and *P. paniscus* as well as for the 4 capuchins. Thus, hierarchical abilities in object manipulation were not specific to subjects that have demonstrated language skills.

Furthermore, conversationally reared apes did not demonstrate a greater proportional use of the subassembly strategy than other apes. This finding contradicts Tomasello's (e.g., Tomasello, Savage-Rumbaugh, & Kruger, 1993) assertion that enculturation (i.e., conversational rearing in apes) enhances the ability to imitate a model. We found no difference either within *Pan* or between *Pan* and *Cebus* in the use of subassembly to seriate the cups in response to the experimenter's demonstration of nesting the cups using this strategy.

The 2 youngest apes (Mercury, *P. troglodytes;* Tamuli, *P. paniscus*) exhibited the lowest proportional use of the subassembly method to combine the cups. Previous research has indicated that complex combinatorial activity is less

common in young chimpanzees (e.g., Matsuzawa, 1991; Mignault, 1985; Poti & Spinozzi, 1994) as well as in young children (Greenfield et al., 1972). Consistent with our prediction and with the theory of Greenfield et al. (1972), there appeared to be a developmental sequence in strategy use in most of our subjects. Seven of the 10 subjects that were tested in five- and sixth-cup trials either shifted to a more complex dominant strategy, showed decreased use of a less complex strategy, or demonstrated an increased use of a more complex strategy. Two of the 3 subjects that did not follow the expected microdevelopmental progression showed an increase in the least complex strategy: pairing. Note that these 2 subjects had only one trial with a sixth cup. Therefore, the extent to which the data for these 2 subjects reflects microdevelopment of their strategy use across testing is debatable.

A similar developmental sequence from single actions with single objects to multiple actions with multiple objects was reported by Matsuzawa (1994) in his observations of nut cracking in wild chimpanzees. Infant chimpanzees have been observed hitting stones (single action, single object). At about age 2, they progress to pushing nuts on stones (single action, two objects). Chimpanzees older than about age 3 are able to successfully crack open nuts with stones using a combination of multiple actions.

Seriation and Strategy Use

When we compared the apes' data with the monkeys' posttraining data, the two genera were equally likely to seriate five cups into a single nested set, and members of both genera were able to fit a sixth cup into the middle of a previously seriated set. In trials in which the middle cup had to be inserted into a seriated set, the use of the subassembly strategy was related to success in seriation, as was the case in the Greenfield et al. (1972) study. The majority of subjects in this test series did use the subassembly strategy, which happens to be the most efficient way (i.e., executing the fewest moves with the cups) to insert the sixth cup. In trials with a variable sixth cup, proficient monkeys and apes engaged in the subassembly strategy proportionally more often than pairing or potting. This clearly indicates that, as predicted, the most proficient subjects (4 apes and 3 monkeys) tended to form large constructions from the creation and manipulation of smaller subunits. Although the predicted relationship between subassembly strategy and the ability to insert a sixth cup into an existing series did materialize, the expected difference in favor of the apes was clearly absent.

Furthermore, when apes and monkeys created blocks to seriation, they performed actions to correct their errors with comparable efficiency. Similarly, young children have been observed to correct errors by restructuring cups in a nesting cups task (DeLoache, Sugarman, & Brown, 1985). In the current study, both monkeys and apes were equally likely to remove blocking cups. Our nonhuman subjects would often dismantle a structure and reassemble the cups, thereby producing multiple structures during a trial. In many cases, subjects would work on more than one stack of cups,

alternating between the stacks. This suggests that nonhuman primates and children differ in their style of constructing standing structures.

The substantial use of the least advanced combinatorial strategy—pairing—in nonhuman primates, coupled with the need for an additional scoring procedure to capture our nonhuman subjects' propensity to construct and dismantle structures, may reflect a potentially significant difference between children and nonhuman primates in hierarchical abilities. Recall that apes and monkeys frequently made nested pairs and dismantled structures during a trial before finally constructing a stable structure containing all or most of the cups. Children, on the other hand, dismantled structures infrequently and often built a single permanent structure using complex cup combinations (P. M. Greenfield, personal observation, 1972). Differences between children and our nonhuman subjects in the motivation to construct a stable seriated structure with multiple cups may speak to humans' unique ability to plan and to construct complex permanent structures. These differences may also reflect the distinctiveness of *Pan* and *Cebus* among nonhuman primates as extractive, destructive foragers whose lifestyles are characterized by opening and removing edible objects from substrates, such as termite fishing and nut cracking (Goodall, 1986; McGrew, 1974; Parker & Gibson, 1977).

In summary, we found our nonhuman subjects' competence in the nesting cup task particularly striking. Using a hierarchically organized manipulative strategy was within our nonhuman subjects' abilities and is consistent with evidence in both genera of a strong propensity to manipulate and combine objects (Fragaszy & Adams-Curtis, 1991; McGrew, 1992; Torigoe, 1985). Seriating a set of cups by size was not a difficult task for either *Pan* or *Cebus* (after training designed to orient monkeys to the task). Consistent with other reports, the capuchins and apes in our study could achieve serial ordering (e.g., in chimpanzees, Boysen, Bernson, Shreyer, & Quigley, 1993; in capuchins, D'Amato & Colombo, 1988, 1989).

Evolutionary Implications

If the development of strategies for object combination is related to the combinatorial capacities used in the evolution of language, one would expect the performance of humans to be superior to that of both apes and monkeys and that *Pan* (*P. troglodytes* and *P. paniscus*) would excel over *Cebus*. Comparing the performance of *Pan* in our study with the performance of young *Homo sapiens* in the study by Greenfield et al. (1972), and using the same coding system, this is what we found both before *Cebus'* training and in the most proficient group after *Cebus'* training (see Figure 3). Nonetheless, the performance of *Cebus* was stronger and that of *Pan* was weaker than anticipated on theoretical and empirical grounds (Greenfield, 1991; Matsuzawa, 1991). Do these cross-species commonalities in combinatorial capacities reflect an evolutionary potential in the common ancestor of all four species for the evolution of combinatorial activity

in domains such as language or other forms of intraspecies communication? Or are the domains of basic manual and linguistic combination less homologous than Greenfield (1991; Greenfield et al., 1972) has posited? Future comparative research involving both neural and behavioral assessment across domains is required to answer this important question. Unfortunately, researchers must await advances in functional neural assessment techniques before this question can be empirically addressed.

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