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ORIGINAL ARTICLE

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Do apes and monkeys rely upon conceptual reversibility?

A review of studies using seriated nesting cups in children and nonhuman primates

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Abstract The ability to seriate nesting cups as a sensorimotor task has posed interesting questions for cognitive scientists. Greenfield et al. [(1972) Cognit Psychol 3:291–310] found parallels between children's combinatorial activity with nesting cups and patterns of phonological and grammatical constructions. The parallels suggested the possibility of a neurally based developmental homology between language and instrumental action [Greenfield (1991) Behav Brain Sci 14:531–595]. Children who predominantly used subassembly, a hierarchical method of combining cups, succeeded at seriating nesting cups more often than those who did not. Greenfield and others [e.g., Piaget and Inhelder (1969) The psychology of the child. Basic Books, New York; DeLoache et al. (1985) Child Dev 56:928–939] argued that success in seriation reflects the child's growing recognition of a reversible relationship: a particular element in a series is conceived of as being smaller than the previous element and larger than the subsequent element. But is a concept of reversibility or a hierarchical form of object manipulation necessary to seriate cups? In this article, we review studies with very young children and nonhuman primates to determine how individuals that do not evidence conceptual reversibility manage the seriation task. We argue that the development of skill in seriation is experientially, rather than conceptually, driven and that it may be unnecessary to link seriation with cognitive conceptions of reversibility or linguistic capacities. Rather, in ordering a set of objects by size, perceptual-motor learning may enable contemplative refinement.

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Introduction

A sizeable body of literature documents both variety and complexity in children's manipulation of objects in free play and in goal-oriented tasks (e.g., Bruner 1973; McCall 1974; Fenson et al. 1976; Wood et al. 1976). In children, the ability to seriate, or order a set of objects by size from smallest to largest, has been interpreted as a form of logical cognition that stems from actions such as putting objects in piles, aligning objects, and arranging objects in an array (Inhelder and Piaget 1964; Woodward 1972; Langer 1980). Although there is ample evidence supporting children's facility in seriating objects in a set, the age at which they become proficient seriators is debatable and appears to be contingent on the nature of the objects and research methodology employed (Inhelder and Piaget 1964; Greenfield et al. 1972; Sugarman 1983; DeLoache et al. 1985; Ciancio et al. 1999). Given that manipulative propensities of many species of nonhuman primates rival that of children (e.g., Mignault 1985; Torigoe 1985; Takeshita and Walraven 1996), a matter of interest to comparative psychologists is whether seriation of objects is within apes' and monkeys' abilities, and if so, how their performance compares with that of children. To address this issue, we reviewed findings from comparative and developmental studies that have been conducted with children, chimpanzees, bonobos, and capuchin monkeys using tasks that require seriating objects. We pay particular attention to studies presenting nesting cups. In the course of this review, we discuss two issues of theoretical significance: (1) the interpretation of seriation as a skill that is conceptually mediated (Inhelder and Piaget 1964; Piaget 1969), and (2) the link between combinatorial activity with objects and language capacities (Greenfield et al. 1972; Greenfield 1991).

Is a concept of reversibility necessary for seriation ability?

Piaget (1969; see also Inhelder and Piaget 1964; Piaget and Inhelder 1969) proposed that seriating objects in a sensorimotor task was a basis of logicomathematical reasoning in that seriation involved understanding the additive relationship (and the reverse relationship, subtractive) among elements in a set. By conducting experiments requiring children to order sticks (using five to ten sticks) in an array from smallest to largest, Piaget was able to identify three developmental stages of seriation. In stage 1 (4 years old), the child has a binary concept of size when attempting to order the sticks. In other words, the child proceeds by selecting a stick, comparing it with another, and making a binary decision: one stick is smaller than the other. At best, the child at this stage is able to seriate two or three elements in a subseries but cannot incorporate all members in a single series. In stage 2 (6 years old), the child proceeds by trying many arrangements, incorporating all of the sticks into the array, and is often successful. Piaget (1969) termed seriation via trial and error at this stage non-operational seriation. He noted that if the child was given a stick to insert in the series, the child typically disassembled the array and started arranging the sticks in order from scratch. In operational seriation, or stage 3 (7–8 years old), the child systematically selects sticks and places them in a seriated array with minimal hesitation and while making very few errors. Additionally, the child is able to insert new items in the series correctly without starting from scratch. Piaget (1969) argued that successful seriation, and especially the ability to insert an element into a series, reflected the child's growing recognition of a reversible relationship, that one element in a series could be both larger than the previous element and smaller than the subsequent element. Thus, the role of a member reverses depending on whether the additive or subtractive relation is being considered. Piaget interpreted consistent seriation as a skill that is driven by the concept of reversibility, an abstract cognitive construct that reflects understanding of ordinal relations.

We perceive serious flaws in Piaget's treatment of the development of seriation. First, Piaget's reliance on the concept of reversibility to account for operational seriation in stage 3 fails to explain why seriation could be accomplished consistently, even if errors occurred. We are unwilling to accept Inhelder and Piaget's assertion that seriation in stage 2 is accomplished with a "primitive form of reversibility" as compared to "operational reversibility" in stage 3 (Inhelder and Piaget 1964, p. 287). Piaget left the differences between primitive reversibility and operational reversibility unclear. Additionally, we are left with the question of how and when the concept of reversibility develops in the child. Inhelder and Piaget (1964) state that reversibility originated in the child's sensorimotor activity, implying that perceptual-motor schema underlie the coordination of actions and development of relational understanding. Piaget's attempts to clarify the role of perception in developing seriation skill, however, are vague and wrought with ambiguities. On the one hand, perception of an ordered variability in size among elements contributes to the child's growing ability to arrange elements in a series. On the other hand, sensorimotor schema rather than perceptual schema are hypothesized to be the basis of seriation abilities (Inhelder and Piaget 1964). When examining presuppositions and methodology of the Genevan group, there is an untenable dualism between perception and action in the development of operational thinking (see Gibson 1987 for a related discussion). To illustrate, in one variation of the seriation task, tactile seriation, the child is asked to seriate ten sticks that differ in length by 0.8 cm. An opaque screen blocked their vision while they manipulated the sticks. Inhelder and Piaget (1964) report that 100% of 4-year-old children failed to seriate the sticks, 29% of 6-year-olds were able to seriate the sticks by trial and error, and 33% of 8- to 9-year-olds used the operational method (as outlined above in stage 3 seriation). It is not surprising that young children had such a difficult time with this task. Without the aid of vision, other perceptual, motor, and memory demands increased substantially. Many factors related to performance, such as attention, memory, motor skills, and comprehension of instructions must be considered in explaining children's performance on different variations of the seriation task.

Piaget and Inhelder must have recognized that reducing the number of perceptual modalities would impact performance on the seriation task. Their argument that operational seriation can be dissociated from seriation that arises from "graphic factors" or perceptual schema alone trivializes the importance of integrating components of a child's instrumental action system. Integration of vision, touch, memory, and movement planning and execution are essential for effective instrumental manual action in young children (see Bernstein 1967 and Case 1985, 1991 for related arguments). Although the premise of Piaget's structuralist theory is that developing capacities in perceptual and motor systems constrain and direct development, the contribution of these systems to developing cognitive constructs was inadequately articulated by Piaget and his colleagues (Bruner 1973; Gibson 1987, 1988).

The role of perception, action, and planning in children's manipulative play with objects was addressed in a subsequent study by DeLoache and her colleagues (1985; see also Sugarman 1983). These authors chose a much younger sample of children (age range of 18–42 months) compared with that of Piaget. Moreover, a set of seriated nesting cups was used instead of seriated sticks, thereby providing children with functional feedback during manipulation. DeLoache et al. (1985) chose to analyze children's errors and error corrections in pursuit of seriation to identify thought processes (e.g., monitoring one's actions with cups) and learning processes (e.g., generation and effective utilization of combinatorial methods of combining cups) in children working on a seriation problem. The authors argued that for young children to solve a seriation problem, errors must be detectable: that is, some feedback as to progression toward the solution must be available. This is the case in seriating nesting cups but is not apparent in the Piagetian stick task. By examining movement sequences in detail, De Loache et al. showed that procedural knowledge, in addition to structural knowledge, is relevant to the ability to seriate objects. Thus, the method and explanatory scope of DeLoache et al.'s investigation went above and beyond the supposition that abstract conceptual properties, such as reversibility, simply unfold from haphazard exploratory schemas as the child matures.

What DeLoache et al. (1985) found was that children as young as 24 months were able to seriate five nesting cups, and nearly all of the 42-month-old children were successful. These data indicate that the capacity to seriate objects is a skill that is developing at a much earlier age than Piaget predicted. Although seriation was within young children's abilities, more than half of children's actions with cups were errors (i.e., did not result in two or more cups being seriated). Interestingly, 61% of their mistakes were followed by correction attempts, suggesting attention to feedback from their combinatorial attempts. Additionally, differences were observed in how children of different ages attempted to correct their errors, with younger children being more likely to force seriation (i.e., by pushing a large cup onto a small cup) or decompose part of a stack without immediate subsequent reordering of cups. Older children were more likely to try an alternative base cup or top cup before decomposing the entire working stack, and they were more likely to reverse an unsuccessful attempt immediately by switching the position of a small base cup and large top cup. Children's perseverance at the task, coupled with varying combination orders after an error, contributed to their success.

Studies with children and nonhuman primates

A similar empirical approach to a seriation problem was adopted in subsequent studies comparing the performance of seriated nesting cups in children and adult apes and capuchin monkeys (Johnson-Pynn et al. 1999; Fragaszy et al. 2002). Obviously comparisons of the performance of subjects of different species and ages should be interpreted carefully. Adult apes and monkeys can solve some tasks where human children cannot, and vice versa. Variations in task performance or an understanding of task requirements may be attributed to different rates of ontogenetic development of mental, physical, or social attributes. However, given that heterochrony is common in phylogenetically related species, comparisons of nonhuman primates with humans of any age retain the possibility of enhancing our understanding of cognitive capacities and prompting alternate interpretations of commonly observed behaviors or developmental trends in certain species (Gould 1977). Indeed, this point is made in Greenfield's (1991) article in which she compares the performance of children nesting seriated cups to the performance of Kanzi, an adult bonobo.

Consistent with previous studies (Greenfield et al. 1972; DeLoache et al. 1985), we found that young children (11-, 16-, and 21-month-olds, n=12 in each age group) were rarely able to seriate five cups, although the ability to do this increased significantly with age. Only 2 of the 36 children tested were able to seriate a middle sixth cup into a previously seriated five-cup set. The performance of the children contrasts with the far better success of our nonhuman subjects (five chimpanzees, three bonobos, and four capuchin monkeys; see Figs. 1, 2). Apes and monkeys constructed seriated sets with five cups on at least half of their trials, and only one subject from each genus (*Pan* and *Cebus*) failed to seriate five cups or to insert a middle sixth cup into a previously seriated set. On some trials apes and monkeys were able to insert the sixth cup without disassembling the set, but on other trials, their first attempt to seriate the sixth cup failed, and they resorted to seriating the six cups from scratch. The three most proficient nonhuman seriators were Xenon (*C. apella*), Austin, and Sherman (*P. troglodytes*). The two chimpanzees happened to have had prior experience in a seriation task. Xenon, a novice at this task from the outset, was observed to seriate up to ten cups in

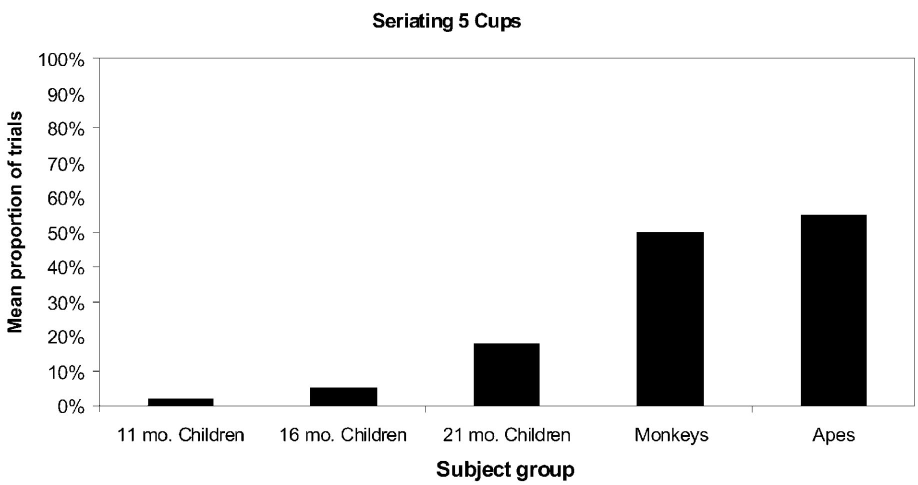

Fig. 1 *Cebus apella*, *Pan troglodytes* and *Pan paniscus* subjects seriate five cups more often compared with children

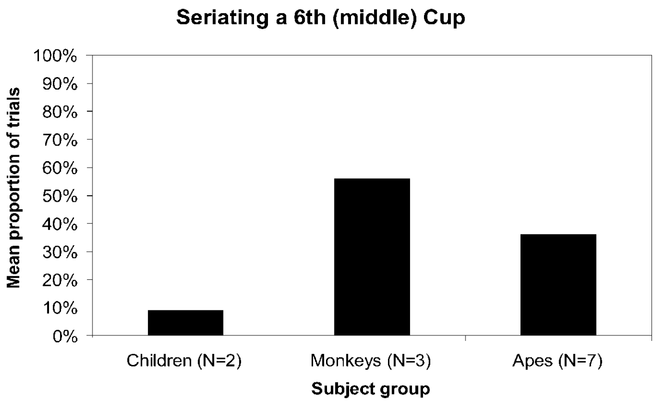

Fig. 2 *Cebus* and *Pan* subjects seriate a sixth cup into the middle of a previously seriated five-cup set more often compared with children

subsequent trials, putting his performance on par with that of Ai, the language-trained chimpanzee at Kyoto University (Matsuzawa 1991).

Some subjects were more efficient than others in constructing five-cup seriated sets. Apes and 21-month-old children were the most efficient, executing the fewest number of moves to construct five-cup seriated sets (see Fig. 3). Monkeys and 11-month-old children were the least efficient in seriating five cups, using nearly twice the number of moves as compared with the most adept subjects. This is a puzzling result, given that monkeys achieved a moderately high seriation success rate and 11-month-old children did not. Perhaps the youngest children did not evaluate the outcomes of their actions with respect to the overall goal of seriation or did not recognize seriation to be a goal. The monkeys comprehended seriation as a goal but were not reliably systematic in monitoring their actions toward reaching this goal, which contributed to a high frequency of actions with cups in pursuit of seriation. This explanation seems likely given that the 11-month-olds tended to bang cups together or against the floor, seemingly being as interested in hearing noises that the cups made as they were in combining them (A. Galloway, personal communication). In contrast, the monkeys' tempo of making multi-cup structures was steady during test trials, although the style of manipulation varied from careful placement to less-controlled handling of the cups.

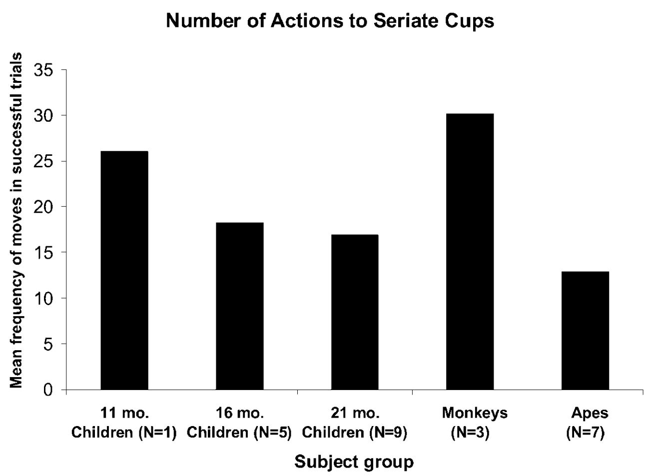

Fig. 3 *Cebus* subjects and 11-month-old children execute more actions to seriate five cups compared with *Pan* subjects and older children

Three chimpanzees and one capuchin were able to insert the middle sixth cup into the five-cup seriated set in the minimum number of three actions: removing the top two cups and nesting them into the middle third cup (subassembly), followed by moving this three-cup set as a unit into the bottom two cups (subassembly; see Table 1). Another less efficient strategy requiring four actions entailed removing the top cups and successively potting the middle sixth cup and the top cups in the set one at a time. Two capuchins and three chimpanzees utilized this strategy. Although bonobos were able to insert a middle sixth cup into the existing series, no bonobo was as efficient as the capuchins or chimpanzees. One of the children (16 months old) who managed to insert the middle sixth cup used the minimal number of three actions on a single trial, while the other successful child (21 months old) typically seriated the middle sixth cup using an average of 15 moves. This child's first action was to nest the middle cup in the top of the set. Following this unsuccessful attempt, the child disassembled the set and seriated the six cups from scratch. The direct manner in which capuchins and chimpanzees succeeded in inserting a cup into the middle of a series suggests planning and incorporating relational properties of the cups. The task of inserting a sixth cup was more challenging for the children.

To study further errors (e.g., attempting to place a large cup into a smaller nested pair of cups) and the nature of error corrections, we compared the performance of apes and monkeys with a sample of eight older children. These children, between 24 and 36 months of age, were able to seriate five cups and advance to trials where they had to insert a middle sixth cup. We scored the actions that each subject used to seriate a sixth cup. Each action was coded with regard to how it contributed to or worked against seriation of six cups. Analysis of these data revealed striking similarities in the incidence of children's and nonhumans' mistakes and in their correction attempts (see Tables 1, 2). Generally, subjects tended not to make errors. The percentage of moves that were mistakes was under 35% for all subjects. The fewest errors were made by one 30-month-old (20% of actions), one 32-month-old (20%), and one capuchin monkey (9%), while several ape subjects and one 30-month-old made the greatest number of mistakes (ranging from 34% to 56% of their actions). Additionally, the percentage of actions that involved repeating the previous incorrect action was low for apes and monkeys (8% and 5%, respectively), and only one child repeated mistakes, constituting 10% of her actions.

As shown in Table 2, the most typical response to making an error was placing the working cups aside and selecting other cups to combine (strategy 3). In other words, human and nonhuman subjects often left the problem

Table 1 Frequency of inserting a sixth cup into the middle of a previously seriated set using two methods

Subjects[a]	Using three moves (Remove top cups, two subassemblies)	Using four moves (Remove top cups, three pots)
Capuchins		
Chris	0	0
Jobe	0	2
Xavier[b]	–	–
Xenon	3	2
Bonobos		
Kanzi	0	0
Panbanisha	0	0
Tamuli	0	0
Chimpanzees		
Austin	4	1
Lana	0	0
Mercury[b]	–	–
Panzee	3	3
Sherman	1	1

[a] Data for children are not included in the table because of the low number of trials with insertion of the sixth cup. No child who was successful seriating the sixth cup used the subassembly method (column 1), and only one child used the pot method to insert the sixth cup (column 2)
[b] Xavier and Mercury did not have sixth-cup trials because they never seriated five cups

alone and turned their attention elsewhere. Alternatively, subjects would place the working cups aside and dismantle any cups they had previously combined, effectively starting over on the task (strategy 4). Another popular strategy was for a subject to take the working cup that he/she had attempted to seriate and shift to an alternate working stack (strategy 2). This entails consideration of one relation: working cup to base cup. Three children had a low percentage of moves in this category (ranging from 7% to 10% of actions). They opted to stick with their working stacks and remedy their errors in the most direct way, by removing the larger blocking cup(s) that prevented seriation of the smaller cup (strategy 1), as did one child and one capuchin monkey who never used strategy 2. Strategy 1 exemplifies a move toward the goal of the task, creating a seriated set, as it entails immediate reversal of an unsuccessful attempt to nest a cup (see also Woodward 1972 for a similar description of this strategy in a nesting cups task in children with cerebral palsy). This action may reflect the subject's consideration of multiple relations between at least three cups, the base cup, the blocking cup, and the working cup. Four children and one monkey employed this method of error correction on 10–22% of actions. They also had high rates of success in seriating both five and six cups. Two of the three bonobos, one of the five chimpanzees, and two of the eight children never attempted this strategy. The results with children in our sample are similar to De Loache et al.'s (1985) showing that children of all ages made mistakes with equal frequency, although the older children in our sample made absolutely fewer mistakes overall than children in De Loache et al.'s study.

Explaining seriation as a skill-in-action

The error correction data, and especially the efficient insertion of a middle sixth cup, point to seriation being achieved by activity in accord with relational properties of the cups rather than by random activity alone. If we accept the Piagetian interpretation of these results, then this is equivalent to stage 3 (operational) seriation and entails recognition of a two-way reversible relationship. A related structuralist interpretation is that our subjects were able to seriate cups because they possessed a binary concept of size, that one object is smaller than another (see Greenfield et al. 1972). But are we willing to attribute these forms of conceptual understanding to our nonhuman subjects whose facility in this task far surpassed that of the younger children and was comparable to that of older children? And what of those nonhumans who were not proficient seriators? Do some of our subjects exhibit these forms of logicomathematical reasoning and others do not? We do not think possession of a binary concept of size contributed to our subjects' success in the task. If they had this conceptual understanding, then we would not expect

Table 2 Making and correcting errors in pursuit of seriation of six cups

	Monkeys (n=3) (5–10 years old)	Apes (n=7) (9–20 years old)	Children (n=8) (24–36 months old)
Making an error – attempting to nest a larger cup (or cups) into a smaller cup (or cups) that is blocking seriation	23%	4%	25%
Correcting an error			
Strategy 1: removing a smaller cup in order to nest a larger cup into a stack	6%	6%	8%
Strategy 2: shifting to an alternate stack of cups with the larger cup(s) in hand	13%	20%	16%
Strategy 3: putting the larger cup(s) down and putting together different cups	39%	23%	34%
Strategy 4: putting the larger cup(s) down and dismantling the working stack	14%	9%	16%

Data are mean percentages of actions. Monkeys, apes, and children had similar error rates and made similar attempts to correct their mistakes (ANOVA, $P>0.05$). Immediately removing a smaller cup (or cups) from the stack that is blocking insertion of a larger cup is the most direct method of correcting an error (strategy 1) to see this common action: to pot a middle cup into the seriated set, then immediately attempt to put the set as a unit into the smaller middle cup (J. Johnson-Pynn, personal observation). However, we cannot rule out a binary decision about action: put cup on top of set, put cup underneath set. An action-based explanation is rooted in a salient action pattern, rather than a mental comparison guided by symbolic knowledge of a structural representation of smaller versus larger. This notion is consistent with Langer's (1980) assertion that the origins of logical operations arise from the relational coordination of physical and spatiotemporal movement patterns.

An explanation grounded in presence or absence, or in emerging use, of constructs such as reversibility or a binary concept of size as a basis for operational thought is an insufficient explanation for how individuals, human and nonhuman, master the skill of seriating objects. This is because a purely structuralist explanation (e.g., relying on the individual comprehending reversibility or not) describes rather than explains the course of the development of seriation.

The theoretical perspective on development of skill-in-action (e.g., Bernstein 1967; Manoel and Connolly 1997) offers an explanation for how seriation skill emerges and develops without reliance on purely abstract or symbolic thought (see also van Gelder 1998 for a related discussion on the primacy of perception in cognition). This approach emphasizes the individual's developing abilities to obtain and use relevant perceptual information to monitor ongoing action and plan upcoming action. Thus, the improvisational character of manual activity becomes the focus of analysis (Roberts and Ondrejko 1994). Different levels of action entail different levels of control and planning (Benson 1997). At the sensorimotor level, control of actions is continuous, such as by making postural adjustments or fine motor movements. On a more global level, control of actions is a step-like execution of individual movements or execution of a larger sequence of goal-oriented actions (Bidell and Fischer 1994; von Hofsten 1994).

Extending this framework to the nesting cup task, we can examine intentional and operational aspects of goal-oriented motoric skill (following Connolly and Dalgleish's 1989 discussion of intentional and operational aspects of skill). Intentional aspects of skill, or *knowing what*, concern the subject's intention to combine and/or seriate the cups (i.e., the task requirements) and knowledge about the properties of the cups (e.g., cups can be nested or stacked). Operational aspects, or *knowing how*, are concerned with grasping, holding, and carrying cups (e.g., grip patterns and hand use), controlling the orientation of cups relative to each other, and making stable structures with cups. Manual dexterity of the 11- and, to some extent, 16-month-old children may have been hampered by the struggle to maintain balance while sitting upright and reaching for cups to put into working stacks. Conversely, manual dexterity and postural control could have contributed to the success of our nonhuman subjects by constraining the degrees of freedom they had to manage in this task compared to the younger children. In other words, our nonhuman subjects were more practiced with their bodies than the children we worked with. To illustrate, several subjects used other parts of their bodies when assembling structures with the cups. Kanzi (*P. paniscus*) often used his feet to stabilize the cups (see Fig. 4), and Xenon (*C. apella*) was observed using several body parts simultaneously to hold and move cups, including his hands, feet, mouth, and tail. The variability and flexibility that characterized the motoric activity of our nonhuman subjects could have aided them in attending to action–outcome linkages and in coordinating actions to attain the unified goal of making a single seriated structure. Thus, prospective control of actions at these different levels contributes to seriation success, rather than, or in addition to, the inferred presence or absence of a logical representational structure such as reversibility. In any case, consideration of the physical as well as psychological status of the individual gives the skill-in-action model greater explanatory power over the traditional Piagetian approach. Others (e.g., Vauclair 1984; Poti and Spinozzi 1994) comparing the ontogeny of object manipulation skills in children and nonhuman primates echo this assertion.

Fig. 4 Kanzi (*P. paniscus*) uses his foot to hold a cup in the workspace while manipulating other cups with his hands

A theoretical explanation for a relationship between hierarchical methods of combining nesting cups, seriation ability, and linguistic capacities

Greenfield et al. (1972) identified three distinct combinatorial methods that children employed when assembling seriated cups. In the pair method, two cups are nested or stacked. In the pot method, two or more cups are placed consecutively into or on top of a single cup (the pot). The subassembly method entails combining two or more cups that are placed as a unit (or subassembly) into or on top of one or more cups. Greenfield et al. (1972) observed that these three combinatorial strategies contributed differen-

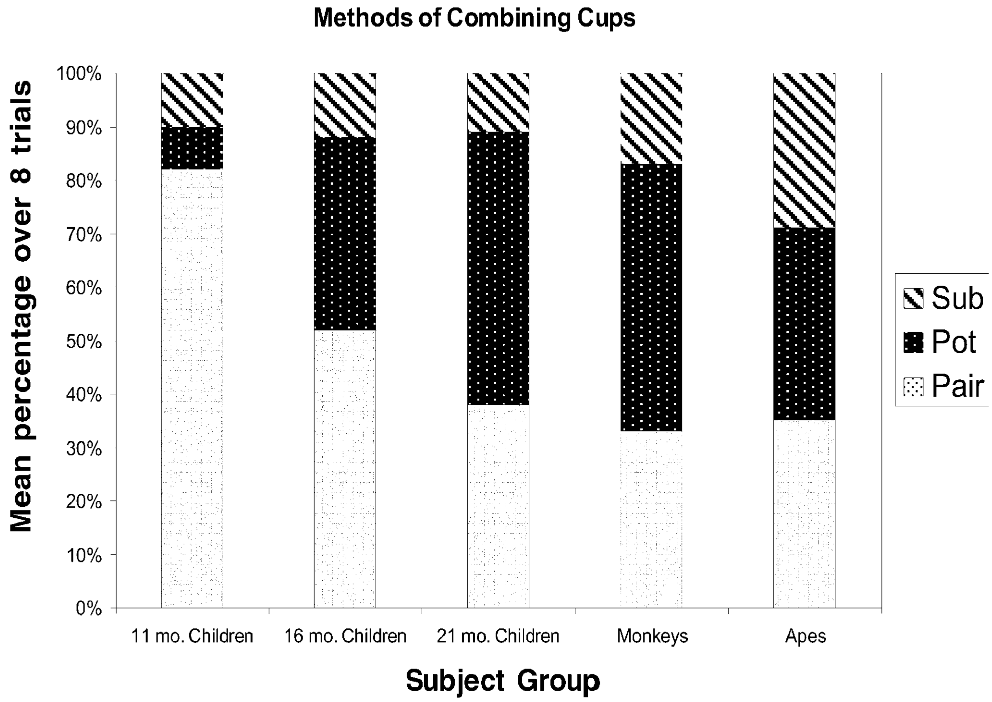

Fig. 5 *Cebus*, *Pan*, and 21-month-old children use subassembly (*Sub*) more often than 11- and 16-month-old children

tially to success in seriating a set of five nesting cups. Seriation success was related to use of the subassembly strategy, the only hierarchical combinatorial method. The authors argued that reliance on subassembly is evidence for two instantiations of reversibility. In subassembly, *role reversal* is evident when the cup that is acted on becomes the actor in the next movement sequence, such that cup 2 is first in a passive role (it receives cup 1) and then in an active role when the nested pair of cups 1 and 2 is put into a third cup (cup 3). To seriate using subassembly requires understanding a *two-way reversible relationship*. The recipient cup (cup 2) is both larger than the cup placed inside it (cup 1) and, as part of the resulting nested pair (cups 1 and 2), smaller than the cup it is placed into (cup 3).

The development of proficiency in seriation was linked to developmental differences in the hierarchical complexity of children's actions and in the development of reversibility (Greenfield et al. 1972). Greenfield (1991) also found parallels between children's combinatorial methods and patterns of phonological and grammatical constructions, suggesting the possibility of a neurally based developmental homology between language and instrumental action. The hypothesized relationship among hierarchical manipulation, seriation ability, and linguistic capacities generated from studies with human children leads to the prediction that children would demonstrate more hierarchically complex manipulative activity (i.e., subassembly), than apes or monkeys. Apes would be expected to use subassembly more than monkeys given that apes have demonstrated protogrammatical language and monkeys have not (Greenfield and Savage-Rumbaugh 1990, 1991). One might also expect that apes proficient at using lexigrams or symbols that stand for words would be more likely than non-language-trained apes to use subassembly, as the former are practiced at using hierarchical orderings of symbols in communication.

Research on apes' (*P. troglodytes* and *P. paniscus*, Matsuzawa 1991; Johnson-Pynn et al. 1999; Takeshita 1999) and monkeys' (*C. apella*, Westergaard and Suomi 1994; Johnson-Pynn et al. 1999) combinatorial activity with nesting cups has documented the use of pair, pot, and subassembly by all subjects. Hierarchical forms of manipulative activity with cups are well within nonhuman primates' abilities. The use of a hierarchically organized sequence of actions to combine cups is consistent with chimpanzees' and capuchins' strong propensity to manipulate and combine objects, especially in foraging contexts (Parker 1974; Parker and Gibson 1977; Fragaszy and Adams-Curtis 1991; Janson and Boinski 1992; McGrew 1992; Boesch and Boesch 1993). Examples of subassembly-type combinations include termite fishing in the Gombe community of chimpanzees, where a stick and termites are combined and moved as a unit into the chimpanzee's mouth (Goodall 1986). Using a towel to soak up liquid and bring it the mouth is a similar example in captive capuchins (Westergaard and Fragaszy 1987). A chimpanzee observed by Matsuzawa (1991) combined a supporting stone with an anvil stone to stabilize it before using a hammer stone to crack open an oil-palm nut, an example of hierarchical combination.

Apes and monkeys have been observed using subassembly to nest seriated cups more consistently than 11-, 16-, and 21-month-old children, although the dominant combinatorial method for monkeys, apes, and 21-month-old children was the pot method, where cups are added successively to a base cup (Fragaszy et al. 2002; see Fig. 5). Apes and monkeys did not differ in their use of these particular methods to combine cups, including subassembly (Johnson-Pynn et al. 1999). This finding coupled with the seriation data reported previously contradicts the prediction generated from Greenfield's (1991) theory, that children are more likely to use subassembly than nonhumans and that children should thus be more successful at seriation. The findings comparing language-trained apes to non-language-trained apes are inconclusive. Consistent with Greenfield's theory, Matsuzawa (1991) reported a dominant subassembly strategy in two language-trained chimpanzees. Conversely, Johnson-Pynn et al. (1999) reported that no ape, regardless of language training, used subassembly as a dominant means to combine cups. Hence, whether combinatorial strategies manifest from an underlying structural capacity that is central to language acquisition remains an open question.

Microdevelopment of combinatorial activity with objects: the importance of experience

Examination of empirical data from children, apes, and monkeys suggests to us that it may be unnecessary to link seriation with cognitive conceptions of reversibility or language capacities. Development of skill in seriation may be experientially driven, rather than conceptually driven. Microdevelopmental analysis of subjects' activity indicates that the complexity of combinatorial methods increases rapidly and is not dependent on an "all or nothing leap" from a stage where an individual lacks a concept of reversibility to a stage where an individual possesses a concept of reversibility. Adult apes and young adult monkeys shift to more complex combinatorial methods, including subassembly, over a series of as few as eight trials (Johnson-Pynn et al. 1999); a similar trend over the course of several trials occurs in children between the ages of 24 and 36 months. Young chimpanzees' (between 2 and 4 years of age) advancement from pairing cups to potting cups over the course of testing has been documented as well (Takeshita 1999). Corroborative evidence attesting to the importance of experience manipulating objects is also provided by Rosengart (2000), who observed a dramatic increase in subassembly use in capuchins in less than 2 days in an experiment designed to prompt the use of sophisticated action assemblages. These laboratory data concur with observations of wild infant chimpanzees (younger than 4 years of age) that show developmental increases in complex manipulation of stone tools in their attempts to crack open oil-palm nuts (Inoue-Nakamura and Matsuzawa 1997).

Along with experience, variety, flexibility, and perseverance in action appear to be key factors in nonhuman primates' and human children's success in seriating nesting cups (Fragaszy et al. 2002; H. Takeshita, personal communication). Seriating a set of nesting cups requires construction of a single standing structure from elements of differing sizes. This necessitates dynamic adaptation to task constraints involving the position of the cups in the workspace, the subject's bodily control, and the properties of the cups themselves. In nesting cups, reliance on a single combinatorial strategy is less likely to result in seriation in comparison with flexible execution of cup combinations to achieve the goal. If one cup is nested out of order, ensuing difficulties are better addressed by using a combination of actions, which may involve pairing, potting, and subassembly. Likewise, adaptation of planned movement sequences in line with changing task constraints contributed to the chimpanzee Ai's success in the serial task of ordering numbers (Biro and Matsuzawa 1999). Reliance on a fixed set of specific movement sequences is not the hallmark of skilled action (Connolly and Dalgleish 1989). Rather, skill is characterized by dynamic adjustments to changing constraints.

The ability to order a set of objects by size is inextricably tied to the individual's physical system for manipulating objects, and younger inexperienced subjects faced greater challenges in this respect. It is also affected by a species' propensity to manipulate objects (Fragaszy and Adams-Curtis 1991). This factor most likely contributed to the success of *Pan* and *Cebus* in this seriation task. It is feasible that behavioral tendencies enable perceptual-motor learning and precede a cognitive logicomathematical conception of reversibility. This assertion is congruent with Langer's (1980) argument that the roots of logical cognition are pragmatic rather than symbolic, and that symbolic relations have their origins in transformational actions with objects such as composing and decomposing sets of objects.

Evidence for symbolic reasoning and reflective abstraction in nonhuman primates continues to be vigorously investigated in a variety of domains (e.g., Poti 1997; Boysen et al. 1999; Kuhlmeier et al. 1999; Spinozzi et al. 1999). Nonetheless, this review underscores the need to discuss emerging and developing cognitive abilities without strict reliance on complex mental representations or symbol systems as has been the traditional approach in developmental (Piaget 1969) and comparative developmental (Antinucci 1990) psychology, and in cognitive science (e.g., Fodor and Pylyshyn 1988; Newell 1990). Rather, we should turn our attention to explicating how cognitive abilities like seriation arise and stabilize through the coordination and integration of an individual's physical and psychological systems. This approach has greater explanatory power than structuralist or representational theories because the focus is on the process of transformation in the development of skilled action. The skill-in-action theory (e.g., Bernstein 1967; Manoel and Connolly 1997), part of the family of dynamic systems theories (e.g., Thelen and Smith 1994; van Gelder 1998), represents a promising step in this direction.

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