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Primate Numerical Competence: Contributions Toward Understanding Nonhuman Cognition

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Nonhuman primates represent the most significant extant species for comparative studies of cognition, including such complex phenomena as numerical competence, among others. Studies of numerical skills in monkeys and apes have a long, though somewhat sparse history, although questions for current empirical studies remain of great interest to several fields, including comparative, developmental, and cognitive psychology; anthropology; ethology; and philosophy, to name a few. In addition to demonstrated similarities in complex information processing, empirical studies of a variety of potential cognitive limitations or constraints have provided insights into similarities and differences across the primate order, and continue to offer theoretical and pragmatic directions for future research. An historical overview of primate numerical studies is presented, as well as a summary of the 17-year research history, including recent findings, of the Comparative Cognition Project at The Ohio State University Chimpanzee Center. Overall, the archival literature on number-related skills and counting in nonhuman primates offers important implications for revising our thinking about comparative neuroanatomy, cross-species (human/ape) cognitive similarities and differences, and the evolution of cognition represented by the primate continuum.

I. INTRODUCTION

In recent years, studies of numerosity judgment, counting and other number-related skills have been investigated across a range of nonhuman species, although the more advanced demonstrations of complex cognitive processing with numbers have been reported for chimpanzees (e.g., Matsuzawa, 1985a; Boysen & Berntson, 1989; Boysen, 1993). And although the specter of Clever Hans still looms within the field of comparative psychol-

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ogy, more rigorous methods and creative paradigms are beginning to provide a clearer metric of primate counting capacities. These in turn have suggested additional ways that studies of numerical competence in monkeys and apes may shed new light on the evolution of cognition in general, and help clarify how specific adaptive pressures may have played a role in increasing intelligence, enhancing social cognition, and impacting upon cooperative living in the great apes and humans.

Because time, space, and number play critical roles in the day-to-day existence of many animals, birds, and even insects (Gallistel, 1989), it should not be surprising that a species such as the chimpanzee, with the demands of foraging for scarce resources within a finite spatial range, a complex social structure, including dynamic fission-fusion relationships, would be highly prepared to encode hierarchical relationships. Such cognitive flexibility permits this species to acquire, with human tutelage under captive conditions of enculturation, a number of complex cognitive skills, including facility with representational numerical symbol systems with which to overtly map quantities and, in some cases, arithmetic relationships (Boysen & Berntson, 1989; Boysen & Berntson, 1995). Further, chimpanzees have demonstrated the capacity to subsequently integrate such associated symbols into new, emergent relationships that can most easily be described as a "concept of number" (Boysen, 1993). Though some intriguing limitations have come to light (e.g., see Boysen, Berntson, Hannan, & Cacioppo, 1996), recent empirical studies of nonhuman primate numerical competence have provoked new thinking about animal models of counting, and parallel counting and computational skill development in children.

II. HISTORICAL PERSPECTIVES

Empirical investigations of sensitivity to quantity in primates were undertaken early in this century, beginning with Kinnaman's (1902) efforts to study the "mental life" of two captive rhesus monkeys. As part of a series of experiments, including what he referred to as "number tests." (p. 173), Kinnaman was interested in the possibility that monkeys had what might be called a number concept. To explore this, he presented the monkeys with a series of 21 bottles that were covered with paper, with only one bottle filled with food. The position of the filled bottle varied randomly through the series, and it was the monkey's task to select the correct bottle. Kinnaman maintained the food-filled bottle in the same position for 30 trials at a time, beginning with the bottle in the 4th position from the left. He was interested to see if the monkeys could find it reliably among the series of 21 bottles. The results suggested that the monkeys had difficulty selecting bottles that were placed in positions higher than six in the series, which was likely the result of interference from prior experiences with the correct bottle in positions 4, 2, 4, 1, 6, and 3, the order in which the problems were presented. Of the two monkeys, one was accurate in identifying the correct bottle after only a few trials as long as the filled bottle was in any of the positions between 1 through 6; the second animal was able to identify the correct bottle from among positions 1 through 3 only. Kinnaman also tested two children, including a 3-year-old and a 5-year-old, using marbles instead of food as the reward. He found that the older child could locate the marbles in the bottle when it was in position 1, 2, or 3, whereas the younger child could only identify the correct bottle in positions 1 or 2. Kinnaman concluded that the processes used by the monkeys and the children did not involve counting (or "numeration," as he referred to it), but rather, borrowing from Ribot (1899), a "perception of plurality" (Kinnaman, 1902, p. 179). He quoted Morgan (1894), noting that animals and prenumeric children were able to "sense" the difference between numbers of items, and this was not a process of counting or numeric relations (p. 180). Apparently it did occur to Kinnaman that feedback about specific spatial location, relative to the bottle's position in the series, might be sufficient for the animals to solve the problem, thus he did not specifically discuss the spatial learning explanation, per se. Instead, he appealed to a rather ephemeral sequentially based perceptual process by which the animals may have located the correct bottle.

Yerkes (1916) investigated a similar question using a method he referred to as the multiple-choice approach, to test the problem-solving abilities of several rhesus monkeys and one orangutan. His objective was to study the animals' ability to understand the ordinal positions of boxes (e.g., "secondness from one end of the group, middleness, simple alternation of ends, and progressive movement from one end of the group to another," (p. 10). Yerkes devised an apparatus that consisted of nine adjacent boxes, each with an entrance and an exit door, through which the subject had to pass in order to receive a food reward placed just beyond the exit of the correct door. Once the animals were familiar with the apparatus, testing was completed during which the monkeys and orangutan were required to choose the correct door from a series of doors available on a given trial. The correct door in the series was randomly determined, and not all doors were open (i.e., available as a choice) at the same time. Thus, only open entrance doors could potentially be correct. Yerkes' interest was whether primates were capable of using "ideation" of any sort to solve the problem. For example, if the correct response was to choose the middle door, the animals might find themselves confronted with five doors on one trial, or three possible doors on another. Thus, identifying a specific door or spatial location from a previous trial would not allow the animals to choose correctly on subsequent trials. Instead, they had to understand the concept of middle, or "choose the middle door," and respond accordingly. Yerkes concluded that the two monkeys used a trial-and-error strategy, while the orangutan solved the problem based on a greater conceptual or cognitive understanding of the task (and thus with greater "ideation," in Yerkes' term). He noted that the orangutan seemed to come upon the solution quite suddenly, representing what Yerkes believed was a different learning strategy. And, although the ape's solutions were conceptually based, he was nonetheless not highly successful, provoking Yerkes to report that the orangutan seemed to use his ideas ineffectively. He suggested that, although the orangutan had a technique, which was somewhat superior to the monkeys, perhaps the animal's young age, and thus lack of "mental maturity," contributed to his difficulties. A follow-up study by Yerkes several years later with chimpanzees in the same paradigm, in which the ordinal position of the door was again the correct solution to the task, revealed slow acquisition by the animals, with some strong right position biases evident in their choices (Yerkes, 1934). Four chimpanzees failed to acquire the middleness concept, although one chimp was able to learn to choose the alternate end doors on successive trials (e.g., choose door number 1 this trial, then choose last door next trial, and then repeat this sequence). One chimpanzee also learned to select the door in the second ordinal position from the end, regardless of the number of doors, although the task had also been solved by three monkeys (20 14), two pigs, a skunk, and a marten (10)! In a version of the task that required chimpanzees, monkeys, and orangutan to choose the last box in the series, all were successful. Thus, early efforts to investigate some features of primate understanding of ordinality were successful in providing evidence for accurate performance across several species of apes and rhesus monkeys.

Subsequent studies by Spence (1938), using a modified apparatus based upon Yerkes' multiple-choice task, which was very reminiscent, if not identical, to the Wisconsin General Test Apparatus (WGTA) identified later with the work of Harlow (1949), tested 17 chimpanzees on the same types of ordinality problems with which Yerkes' animals had struggled. These involved the middleness concept, the second-box, and end-box tasks, among others. In his version of the task, Spence presented the chimps with a series of small boxes positioned horizontally on a tray located behind a screen that could be raised and lowered, so that the correct box among the arrays could be baited with food, out of sight of the animals. The screen was then raised, and the tray of boxes pushed within the animals' reach. The entire apparatus was attached to the chimpanzees' cage, and was operated from behind by the experimenter. Spence found the chimpanzees were highly successful with the modified multiple-choice apparatus. For example, all but two animals learned the middle-box problem to a criterion of 12/12 trials, and the two remaining subjects achieved success with a less stringent criterion of 20/24. The animals learned the end-box problem the easiest, solved the second-box-from-the-end problem next, and had the most difficulty with the middleness concept. All chimpanzees also demonstrated generalization of solutions to novel presentations of the boxes in different spatial arrangements (Spence, 1938), supporting a cognitive/conceptual interpretation of their understanding of the task demands. Spence found no age differences among the animals, with infants, adolescents and adults equally proficient at acquiring the tasks. He also found that relearning tasks, for example the middleness problem, following acquisition of three subsequent problems, required one-sixth the number of trials to criterion, compared with initial learning. And, like Kinnaman, Spence did not specifically address the nature of the strategy that the animals may have been using for successful solution to the problems, but rather, characterized their trial-and-error patterns in considerable detail. There is little question, however, given the task parameters, that Spence's animals demonstrated an understanding of the ordinal positions of the boxes, at least for the middleness task. A simpler explanation could account for their solution of the end-box task that only depended upon perceptual/spatial information, and thus did not require an understanding of ordinality, enumeration or sensitivity to quantity of any kind. The animals' overall success with the Spence apparatus and multiple-choice problems, however, when compared to Yerkes' minimal demonstrations with similar conceptual problems, was likely attributable to the greater structure imposed by the apparatus, since the animals were no longer required to move through time and space, but rather, all attentional resources could be immediately focused upon simply choosing a box from among the simultaneously available series immediately within their reach.

A different approach was introduced by Woodrow (1929) to test monkeys for their ability to temporarily discriminate sequences of varying numbers of stimuli. In this task, the monkeys had to respond to auditory stimuli by reaching for food after three tones were sounded, but inhibit their response when they heard two tones. The monkeys were then tested for their ability to generalize to pairs of auditory sequences composed of 1–6 tones. Thus, the monkeys learned to discriminate the longer sequence of sounds from the shorter. Although Woodrow found that two of the monkeys were able to transfer their ability for discriminating 2 versus 3 tones to the novel presentation of 3 tones versus 4, when subsequent sessions were run during which he controlled for the length of each stimulus so that overall duration was equivalent, the monkeys experienced great difficulty. It appeared that the animals were using duration, rather than absolute number, to solve the task, although it is currently believed that the same cognitive mechanisms that subserve counting and timing can operate under test conditions which may require discrimination of either duration or number, depending upon task requirements (e.g., Meck & Church, 1983). For Woodrow's monkeys, discrimination of duration was adequate for solving the initial task, but when time of presentation was controlled, the animals were unable to immediately use number as the discriminative variable. Woodrow himself did not support the conclusion that the monkeys based their responses on an abstract concept of number, since they could not perform adequately when duration was controlled, and also because they required some relearning when the tones were once again evenly distributed in time following the control tests.

Additional studies with monkeys and numerical competence were completed by Kuroda (1931), who was interested in what he termed the "counting ability" of a single monkey (*Macacus cynomolgus*) in a multiple-choice task. The apparatus consisted of a wooden tray that was placed flat on a table top. Beneath the tray were seven chambers where the experimenter could place food without the monkey seeing its location. The top of the tray, visible to the monkey, had seven square holes lined up at the edge of the tray closest to the animal, through which he could reach to obtain the food from the chamber below. The holes were assigned the numbers 1 to 7, from the monkey's left to right, based upon their ordinal position. In addition, above each of the square holes was a small round light. The monkey was first trained to reach into the hole above which the light was lit. Once the monkey had perfected this task, a bell was introduced. Kuroda rang the bell one or two times, while illuminating the light over position 1 or position 2, respectively. The light was then turned off, and the monkey was tested on his ability to discriminate the correct location using the auditory signal (1 or 2 bells) alone. The subject demonstrated successful criterion performance after 768 trials. However, when the "3" stimulus was introduced, the monkey was unable to learn the correct association between the third position, and location of the food, and the study was terminated. Kuroda concluded by contrasting his results with Woodrow's (1929) temporal discrimination experiments, and claimed that Woodrow's monkeys' success could be attributed to the subjects' ability to distinguish more versus less, rather than their ability to discriminate number.

A decade later, Douglas & Whitty (1941) conducted a series of experiments to study what they termed "number appreciation" in several species of nonhuman primates. The experiments consisted of two types of paradigms, including simultaneously presented spatial arrays, or stimuli that were presented sequentially, and a series of studies were run using each approach. The first spatial task was conducted with a subadult male baboon (*Papio hamadryas*). The apparatus consisted of a small cage with bars on one side through which the subject could reach to choose between two small boxes, where food had been hidden under one. Cards with differing numbers of black dots painted on them in a series were placed on top of each box. The diameter of the dots and the total length of each line of dots were held constant, while the space between the dots varied. The cards represented the number pairs 1 & 2, 3 & 4, 5 & 6, and 7 & 8, and the subject was rewarded for choosing the predetermined correct number. The baboon was able to discriminate between 1 & 2, 3 & 4, and 5 & 6 after 300 trials. However, further training for discrimination between 7 dots versus 8 dots was not successful. The stimuli were modified so that the dots sequence on each card were equidistant from one another on the cards. With this change, the subject's performance fell below chance, and the authors concluded that his previously successful responses had likely been based upon density, rather than absolute number. The investigators conducted two more variations of the simultaneous, spatial paradigm with the same animal, changing the size, shape, and pattern of the dots, and the baboon's performance in both studies did not reach significance. Presumably, given the animal's failure with these tasks, Douglas & Whitty modified their procedures, and introduced a new type of spatial task, this time with a 12-year-old female chimpanzee as their subject. They used an apparatus that consisted of a board with rows of holes spaced 2" apart. White pegs were then inserted into the holes in patterns that matched the configuration of dots on cards which were similar to those used in their earlier experiments. Two cards representing different numbers were placed on each of two small food boxes located in front of the peg board. In order to solve the task, the subject had to match the perceptual shape of the peg pattern with the number of dots on the correct card. The chimpanzee was unable to discriminate beyond 1 versus 2 dots, and failed to discriminate the correct number if the pegs were located past the midline of the board, and thus appeared spatially near the incorrect food box. Thus, the investigators determined that the chimpanzee's performance was based upon a decision rule which mandated that the subject choose the box closest to the peg pattern.

A similar task using the same apparatus was completed with an immature sooty mangabey (*Cercocebus torquatus*). Douglas & Whitty (1941) hoped that the monkey would discriminate between 1 versus 2 when trained to relate the numbers with geometric symbols. Like the chimpanzee, however, the subject was only able to discriminate between the two numbers when the correct choice was located on the food box directly under the pegs. If the pegs were moved across the board, the animal's performance dropped below chance, leaving the experimenters to conclude, once again, that responses were based upon which box was closer to the discriminative stimuli (pegs), and were thus unrelated to absolute or relative number.

Following failures to demonstrate much success with number discriminations based upon simultaneously presented, spatial discriminations, the investigators conducted a series of studies based upon temporal discriminations, including tasks that used both auditory and visual modalities. The subject was a 3-year-old Guinea baboon (*Papio papio*) who was required to associate two rings of a bell with food presented in the left box, and one ring indicating that food had been hidden in the box on the right. After 900 trials, the animal failed to learn the discrimination, and the experiment ended. Next, this time using a different male Guinea baboon, an apparatus that consisted of a board containing rows of lights was introduced. Again, two small food boxes were located in front of the light panel, within reach of the subject. Two flashes of light were presented behind the baited box, and one flash behind the other, incorrect box. Both the onset and duration of the lights were varied randomly, and after 650 trials, the baboon learned to select the correct box following two light flashes behind it. The light sequences were then changed such that now four flashes signaled the correct box, and three flashes represented the incorrect one. Following completion of 1500 trials, with no generalization or transfer of the discrimination to the novel stimuli, the study was terminated. From the results of all experiments, the investigators concluded that visual/spatial stimuli were more difficult for nonhuman primates to discriminate than temporal stimuli.

Following their failures, Hicks (1956) took a similar approach but incorporated proper controls with the test stimuli. Eight rhesus monkeys were tested for their ability to discriminate three geometric shapes on a card from a series of cards with shapes numbering from 1 to 5. Hicks controlled for area of black versus white on the cards, so that the animals' responses could not be based on a perceptual schema, but rather were based on the number of elements. The monkeys' successful performance suggested that they had, in fact, learned a quantity-based concept of "three-ness," with moderate precision. However, Hicks noted that regardless of the definition one might use for a concept of number, it was virtually impossible for the experimental stimuli to not possess other characteristics besides number, some of which might contribute to the subjects' response strategies.

By 1964, Ferster felt comfortable referring to the results of his work with two young chimpanzees (aged 3 years) as "arithmetic behavior." He was inspired to conduct this research by Skinner's claims at that time that language could be studied using similar stimulus-response paradigms that behaviorists were using to study other aspects of behavior. Ferster thought it would be possible to teach chimpanzees symbols of the "language of mathematics" using the binary number system. His apparatus was housed in a small cage adjacent to the animals' living quarters, and was completely automated, consisting of a computerized panel that presented a sample stimulus and several response options. Initial training required the chimps to match a binary number represented by three lights, with two possible choices, one of which was the identical binary number. After the chimpanzees acquired this discrimination, Ferster suspected that they might simply be matching the sample and choice stimuli based on their perceptual similarity. To force the subjects to respond to the binary numbers as representations, Ferster next required them to select one of two possible binary number light stimuli that corresponded with a specific number of visual images (e.g., three triangles). Two additional variations of the binary number tasks included having the chimpanzees produce the correct binary number by turning the appropriate lights on or off. Each subject was also required to work for their daily ration, which was dispensed on a variable ratio schedule, rewarding the animal for every five, ten, or some specified number of successive correct responses. Under these test conditions and reward contingencies, both animals achieved remarkably accurate performance levels of better than 95% with the object-binary number matching task for numbers 1 to 7, frequently making fewer than 5 errors among 3000 trials. They performed with similar accuracy—one or two errors per 1000 trials—when required to produce the binary numbers for numbers 1 to 7 by controlling the light switches. Ferster concluded that the chimpanzees were not counting in an enumerative sense, and with additional training, they would be able to generalize their mathematical knowledge to count any quantities within their numerical repertoire (Ferster, 1964).

In their 1971 publication describing studies with a 3.5-year-old chimpanzee named Viki, Hayes and Nissen compared Viki's abilities on three number tasks with those of several nursery school children, ages 3.5 to 5 years old. In the first task, the subjects were presented with a tray containing two food wells. A card displaying a random pattern of dots (the stimulus card) was placed in a stand between the two food wells. A similar card (the response card) was placed over each food well. The subject's task was to match the stimulus card with the response card that displayed the same number of dots. The size and pattern of the dots were varied randomly, with 120 cards created to represent the numbers 1 through 6. The response cards were randomly presented in the pairs 1:4, 3:6, 2:4, 4:6, 3:5, 1:2, 2:3, 3:4, 4:5, 5:6. Viki's correct choice scores were not significantly different, and in some cases were better, than those of the 5 precounting nursery school children to which they were compared. Viki and the children had the most difficulty with pairs that contained more than three dots on each card and/or those which differed by only one dot. Two additional older children in the study (ages 4.5 and 5 years) attained consistently high scores, including the trials that had confused Viki and the younger human subjects.

A second task was designed to test Viki's ability to recall a specific number over a series of trials, thus requiring her to rely on memory of the initial discrimination. Using the same cards created for the number matching task, Viki was first asked to discriminate "two dots" from the pair of cards presented (1, 2; 2, 3; 2, 4) to a criterion of 45/50, or 90% CR. After a 10-day "vacation," Viki was asked to select "three" from the additional pairs (1,3; 2,3; 3,4; 3,5). Three weeks later, she was tested for her ability to select "4" from the pairs 2,4, 4,5, and 4,6. Viki had increasing difficulty with the three tasks, eventually failed the 4 versus 5 comparisons

In a final evaluation of her number-related capacities, Viki was taught to recognize and imitate a stimulus that was presented temporally. In this task, she was required to tap her finger the same number of times the experimenter tapped on the table top. The number of taps varied from 1 to 4, with the results compared to the performance of the same group of children who had participated in the number-matching task. Unlike the children, Viki was not able to imitate the correct number of taps on most trials. Hayes and Nissen (1971) reported, however, that the children commented that they had not understood the number aspect of the task without further verbal instructions, but initially thought they had to just tap on the table. This difficulty in understanding the task may have also been a source of confusion for Viki, because the experimenters did not have a means to further clarify the game to her verbally, as they did with the children. The authors further suggested the possibility that greater success might be achieved with a different research design, noting that counting dots on cards may be meaningless or unimportant to a chimpanzee.

A related study conducted by Rohles and Devine (1966) examined the acquisition of the concept of “middleness” by chimpanzees. They presented a 5.5-year-old experimentally naïve female chimpanzee with a series of pegs formed in a semicircle. The subject was to choose the middle item from a series composed of up to 17 pegs. The investigators suggested that discrimination of the middle peg could be considered a primary perceptual motor skill that may be automatic, and therefore independent of reasoning until the number of items in the series reached 11 objects, which was a number beyond they thought skills closely related to counting would have to be invoked for the chimpanzee to be able to correctly indicate the middle object. They reported she was successful with a 17-item series, and thus must have had some ability to use a counting-like strategy.

More recent studies of number-related skills, such as numerousnous judgments, have been investigated by Thomas and colleagues (e.g., 1980a, 1980b). Thomas, Fowlkes, and Vickery (1980b) presented two squirrel monkeys with two placards, each depicting a specific number of black circles. The purpose of the study was to determine whether squirrel monkeys were capable of conceptual numerousness judgment. The placards were presented in combinations that included 2 versus (3–7); 3 versus (4–7); 4 versus (5–7); 5 versus (6–7); 6 versus 7; 7 versus 8; and 8 versus 9. Using a modified WGTA, the monkeys were to select the card with the smaller number of dots. Both animals met criterion through 7:8, with one animal successfully completing discriminations of 8 versus 9 circles. It was difficult for the experimenters to determine if the monkeys used absolute or relative class concepts, and that conclusive evidence for conceptual numerousness judgments might be limited to the primate order (Thomas, Fowlkes, & Vickery, 1980b).

In a subsequent study, Thomas & Chase (1980a) explored the capacity of squirrel monkeys for relative numerousness judgments. Using a modified WGTA, 3 squirrel monkeys were presented with stimulus cards with black circles representing the quantities 2–7. Beneath the cards was a panel of three lights. When the center lamp was on, the monkeys were to select the card with the smallest number of circles, and when all lights were lit, the subjects were to choose the card with the largest number of circles. If the two end lamps were lit, the card with the intermediate number of circles was correct. Following testing, one monkey met joint criterion on all tasks. However, the experimenters also suggested that two monkeys’ ability to judge intermediate numerousness was evidence of their conceptual understanding of ordinality (Thomas & Chase, 1980a).

In a differing approach to examining sensitivity to quantity or conceptual understanding of number, Woodruff & Premack (1981) investigated proportionality and numerosity in chimpanzees. One adult and four juvenile subjects were tested for their understanding of proportion and number using conceptual match-to-sample tasks. In the first task, the chimpanzees were presented with a glass that was either ¼, ½, ¾, or completely full, and also given with a small wooden circle that had been dividend into quarters. The subjects were to place the same number of quarters (indicated on the circle) next to the glass, demonstrating that they recognized the relationship between the proportion of the glass that was filled, and the corresponding representation of proportion indicated by the symbols. A second experiment employed cylindrical blocks that were presented in pairs to the chimpanzees. The subject was presented with a sample stimulus of a specific number of cups, and the animals had to differentiate between number 1–6. It has not been established how proportionalities as those used by the experimenters are judged by humans (e.g., whether they depending upon labeling). However, because nonhuman primates, including the animals tested, do not have verbal skills, they are likely using a process of reasoning akin to analogy when comparing the two. The adult animal, Sarah, had responded at a level significantly above chance for both proportions and numbers, while the juveniles did not do as well. Nevertheless, the authors concluded that these studies reveal the presence of simple proportion and number concepts in nonhuman primates (Woodruff & Premack, 1981).

Departing from their artificial language studies, Rumbaugh, Savage-Rumbaugh & Hegel (1987) tested two adult chimpanzees on a discrimination task in which the subjects were presented with two trays, with each tray containing two food wells. During the initial task, only one food well was baited with varying amounts of candy (from 0 to 4 per well) on each trial. Thus, two separate quantities of candies were presented, and the animals were to choose one tray. Once the animals made a choice between the two trays, the other was withdrawn. When tested, both chimpanzees chose the trays that contained the larger quantity of candy 96.5% of the time. Next, both food wells in each tray were baited, and the animals permitted to chose between two trays, with each tray containing varying amounts of candy distributed between the two food wells. The experimenters used what they termed "nonmeaningful" as well as "meaningful" ratios in this phase of the experiment. A meaningful ratio was one in which a quantity was repeated in one tray, and where either of the quantities was still less than the larger single quantity in the other well, yet the first tray had the larger combined amounts. A nonmeaningful trial was one in which the pairs of quantities were identical, such as 3 candies and 2 candies versus 2 candies and 3 candies—that is, any comparison that did not really constitute a real choice. The results indicated that the animals chose larger amounts consistently on nonmeaningful trials, and improved their capacity to choose the larger combined array in meaningful trials. In a final phase when only meaningful trials were presented, the animals performed above chance with high accuracy. Novel trials in which larger arrays were presented (0–5) resulted in similarly accurate performance, with the chimpanzees also performing better with larger proportionate ratios (e.g., 2:3 better than 5:6). The investigators reported that the subjects seemed to be able to perform what Rumbaugh et al. termed summation operations, and that whatever process the animals were using to solve the task reflected a more complex form of number discrimination than previous studies. It was possible however, because all the candies were the same size, that the chimps were making judgments based on exposed surface area, for which the experimenters had not controlled. In conclusion, Rumbaugh et al. (1987) suggested that the chimpanzees subitized the amount in each pair of food wells, performed some type of elemental relational summation whereby they combined the subitized amounts, then compared these summations in order to make their final tray choice.

An addendum to the 1998 paper appeared in response to issued raised by Capaldi (personal communication to Rumbaugh, April, 1987), to address whether the animals were focusing on a single well, and perhaps selecting the tray with either the largest single amount, or avoiding the tray with the smallest single amount (Rumbaugh, Savage-Rumbaugh & Hegel, 1987). To address these issues, candies were arranged in a common quantity in one of each of the pairs of food wells, and paired with another quantity (OQ). In the first trial type, the other quantity was less than common quantity. In a second type of trial, the other quantity was greater than the common quantity, and finally, in the third type of trial, the other quantity was smaller in one tray, and larger than the common quantity in the other tray. Under these conditions, the chimps responded at greater than chance level to the tray containing the total larger quantity. The authors concluded that these findings further supported their original belief that the animals were using some kind of summation strategy in their selection. These data were questioned by Boysen & Berntson (1995; see discussion below) following their results with a quantity judgment task during which adult chimps were unable to learn to inhibit choosing the larger of two candy arrays, despite persistent training and negative reinforcement contingencies. Thus, it seems likely that Rumbaugh et al.'s chimpanzees would not have been able to correctly select, for example, the smaller combined quantity, if the task requirements had been different. Rather, the powerful perceptually-driven predisposition demonstrated by our chimpanzees (Boysen & Berntson, 1995; Boysen, Berntson, Hannan, & Cacioppo, 1996) was likely operating in the Rumbaugh et al. paradigm, and virtually automatically insured success by Sherman & Austin under the constraints of the task.

The first demonstration of numerical competence and/or protocounting utilizing abstract symbols was reported by Matsuzawa (1985a). His chimpanzee subject, a young female named Ai, was able to correctly assign cardinal values between 1 and 6 to arrays of 3-dimensional objects presented as a hand-held array (e.g., 5 yellow pencils). Ai had received previous cognitive training with a graphic symbol system (e.g., Asano, Kojima, Matsuzawa, Kubota, & Murofushi, 1982; Matsuzawa, 1985b; Matsuzawa, Asano, Kubota, & Murofushi, 1986). The visual symbols were affixed to a vertical keyboard that Ai could access on the wall of her testing room; individual keys bearing the symbols that represented specific food items and other familiar objects (e.g., key, pencil, etc.) were illuminated lightly, and then brightened when depressed. Simultaneously, as each symbol key was touched, a facsimile of the symbol appeared in a horizontal row projected above the keyboard. Thus, Ai's selections were indicated by the brightened keys on the keyboard, and the order in which she had selected a series of "words" was preserved in sequence on the projectors. Though she was not required to respond in any specific order, Ai imposed her own subjective syntax when responding to the presentations of differing quantities of colored objects, such as green key 4. Color symbols were sometimes selected first, followed by the object name (or object name/color), and finally the cardinal number representing the array size (Matsuzawa, 1985a).

More recent work with Ai and her number system has been reported by Murofushi (1997) to examine her ability to match semirandom patterns of 1 to 7 dots with their corresponding Arabic numerals. In a series of 4 experiments during which reaction time was assessed, and the nature of the sample stimuli were varied from among number, pattern and size of dots, and color/shape of sample stimuli, Ai demonstrated the ability to correctly label a set of dots or objects with the correct Arabic numeral. Initially, her previously acquired facility in labeling collections of real objects (Matsuzawa, 1985a) did not transfer to the computer-generated dot arrays, and additional training with the dot array stimuli was necessary for her to respond with accuracy. Analyses of Ai's reaction time performance for 1 to 6 dots indicated an increase in RT for the series containing 1 to 5 dots, which could suggest evidence for counting. However, reaction time for the second largest number (4) was shortest, even though her reaction time for 5 dots was shorter. This suggested that she was employing some different type of assessment process for the last number in the series, and that it was not likely based upon counting (Murofushi, 1997). The subsequent experiments in the series were designed in an attempt to further characterize Ai's concept(s) of numerosity, because her initial performance suggested that she might be utilizing an analogue estimation-type code, as suggested by Dehaene (1992). Overall, Ai's performance indicated that she was able to label a variety of stimulus sets that differed in color, size, form, or pattern with their correct corresponding Arabic numerals with great accuracy up to seven items. In general, her RT was essentially flat for the first three numbers, which is similar to observed RT functions for humans evaluating small arrays by a processing known as subitizing, an analogue magnitude-code process observed in adult humans with an established verbal number code (Dehaene, 1992; Gallistel & Gelman, 1992). Similarly, the increased latency shown by Ai as the number of dots increased is also comparable to the shift to a counting strategy by humans in comparable tasks (Kaufman, Lord, Reese & Volkmann, 1949; Mandler & Shebo, 1982). As the numbers presented to Ai increased to 5, 6 or 7, however, her reaction time decreased, suggesting that she was not counting the larger numbers, but rather, likely employing magnitude estimation, as suggested by Dehaene's triple-code model (Dehaene, 1992). More positively, however, Ai now readily generalized the Arabic labels to novel arrays of differing dot patterns, sizes of dots, or new heterogeneous arrays of objects, thus indicating that her labeling ability with numbers had become more independent of the perceptual attributes of the comparison stimuli (Murofushi, 1997), even though evidence for her understanding of the ordinal nature of the number sequence was minimal.

One area of study in our own laboratory for the past decade has been the exploration of counting and cognitive mechanisms which may subserve these capacities in the chimpanzee (e.g., Boysen & Berntson, 1989; Boysen, 1993, 1997). To date, topics we have investigated include transitivity and ordinality by chimpanzees (Boysen, Berntson, Shreyer, & Quigley, 1993); counting, including functional and symbolic representation of numbers, as well as simple addition (Boysen & Berntson, 1989); indicating acts associated with the counting process (Boysen, Berntson, Shreyer, & Hannan, 1995); and symbolically facilitated quantity judgments (Boysen & Berntson, 1995; Boysen, Berntson, Hannan, & Cacioppo, 1996). Different from most other animal cognition projects that have addressed number-related skills, such as work by Davis (1984) with raccoons, or studies with rats by Capaldi & Miller (1988), the chimpanzees in our numerical studies were not experimentally naive when we initiated our first counting task, nor have they been naive for any subsequent studies. For ethical reasons, we intend to maintain the chimpanzees as a group for their natural lifetime in captivity, and thus each new number-related skill was designed to contribute to the acquisition of subsequent skills as the animals matured. Because this more closely models the kind of scaffolded learning that occurs in human children, we believe it represents a reasonable comparison of the conceptual performance outcomes, in terms of similarities and differences, between populations of intentionally-tutored, enculturated captive chimpanzees, and typically reared children in the early stages of learning to count.

The procedures and tasks used to initially establish basic counting skills in the three chimpanzees in the first several years of our primate cognition project have been presented in detail in several formats, and were originally reported as a research report (Boysen & Berntson, 1989), several subsequent book chapters, and were also included in an edited volume (Boysen & Berntson, 1990; Boysen, 1993; Boysen & Capaldi, 1993; Boysen, 1997). A short overview here may be useful for clarifying the general approach for establishing number-related skills and teaching strategies used with our chimpanzee subjects, with additional details available in the papers and chapters noted.

Our original chimpanzee subjects first learned to associate or match placards that had 1 to 3 small, flat, round magnets affixed to them, which they matched with varying quantities of 1 to 3 candies. The matching training began when we presented a single-item array, represented by one candy, and then rewarded the subject with the candy if he/she selected the placard bearing one magnet. Next, test sessions during which 2 candies were presented (requiring the chimps to ignore the placard with only one magnet) were completed to criterion performance (85% CR for two successive sessions). Mixed trial sessions followed during which either 1 or 2 candies were presented on a given trial within the same session, and the chimpanzees were now required to make an explicit choice between the magnet arrays corresponding to either a 1-item or a 2-item candy array. Following stable performance with these choices, a third stimulus placard with three magnets was added to the response stimulus set, with the animals ultimately responding accurately when candy arrays composed of 1, 2, or 3 gumdrops were presented. Thus, the chimps were able to correctly choose from among placards bearing 1, 2, or 3 magnets when the corresponding arrays of candies were displayed. Arabic numerals representing the magnet arrays were then systematically substituted in ordinal sequence, until the subjects were correctly selecting the Arabic numerals 1, 2, or 3, in response to equivalent arrays of candies. All subsequent numbers (including 0, followed by 4, 5, 6, 7, and 8 (for some subjects) have been introduced directly in association with quantities of candy, without the placard-matching phase (Boysen & Berntson, 1989; Boysen, 1993).

In addition, a receptive comprehension task with numerals was initiated with the animals, in order to ensure that they could respond to the use of numbers by their teacher/experimenters, rather than only being able to indicate associated number labels for arrays of items (Figure 1). The comprehension task was introduced by presenting a single

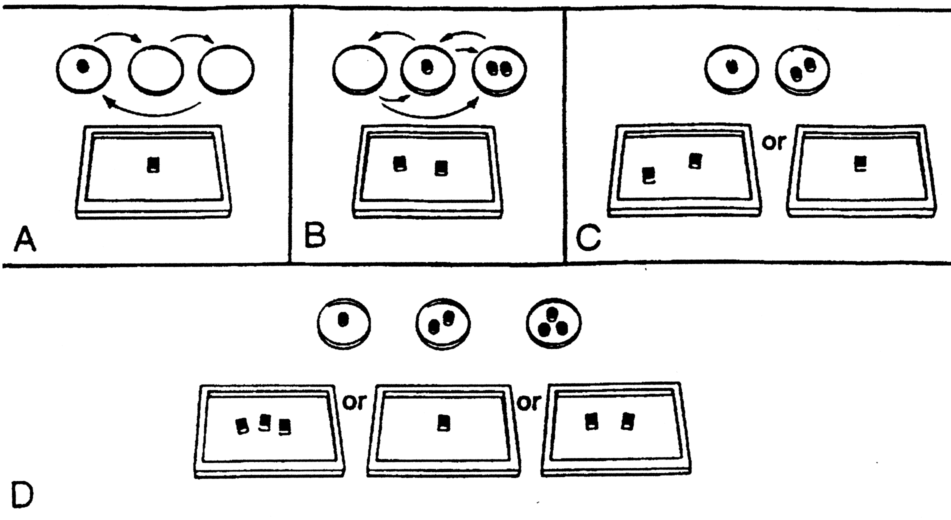

Figure 1. Stimuli used for all phases of the one-to-one correspondence task during which the animals were required to match the placard bearing magnet markers to the corresponding quantity of candy. Initial training entailed tracking one marker, mapped to one candy (A); phase 2 consisted of only trials in which two candies were presented, and the animals were required to choose the placard with two markers (B); in phase 3, trials consisting of either 1 or 2 candies were presented within the same session, thus required an explicit one-to-one match with the correct placard (C); and finally, all three trial types were presented within the same session such that the chimpanzees had to match arrays of 1, 2, or 3 candies with the correct placard.

numeral at a time (either 1, 2, or 3) on a video monitor, and requiring the chimps to select which of the magnet placards (used in the initial quantity matching task described above) represented the array corresponding to the depicted numeral. The receptive number comprehension task was readily acquired, and is viewed as one of several critical procedures necessary for providing the animals with the requisite skills necessary for grasping the representational nature of numbers (Boysen, 1993). These two tasks, productive labeling of candy arrays with Arabic numerals and receptive comprehension of numerals, represent the only two structured numerical tasks for which the chimpanzees were specifically trained. An appreciation of this fact—that the chimps received no additional intentional training with counting or other number-related skills—is important for recognizing the emergent number-related capabilities that were clearly evident as we continued to explore numerical competence with our ape subjects.

One of the most striking examples of such emergent capacities was revealed when a novel task was introduced to Sheba at age 6, when she had been working with numbers for approximately 2.5 years. In an attempt to move beyond the two structured counting tasks described above (productive labeling and number comprehension), a new numerical task was designed such that food items (oranges) in quantities of 0 to 4, and later, Arabic numeral placards, representing comparable quantities, were placed in two of three designated "hiding" places in the laboratory. A series of Arabic numerals that could serve as response placards were displayed on a low wooden platform adjacent to the three sites. The contents of the three sites could not, however, be seen once the chimpanzee had moved to the platform where the numbers were situated. We anticipated that, with enough training and patience, Sheba might come to understand what was being asked of her with this new numbers game. That is, she was to move from site to site, then return to the platform and select the Arabic numeral that represented the total number of items that were hidden among the three sites. From the first trial, during the very first session, and for two weeks of subsequent testing, Sheba demonstrated that she immediately understood the task demands, and moreover, achieved statistical significance with her performance from the beginning. As remarkable as this was, it was even more astonishing that, once we replaced the food arrays in the three sites with Arabic numerals representing 0 to 4, she was able to combine the numerals and report the correct total, represented by the number symbols alone, including zero (Boysen & Berntson, 1989). Young children also demonstrate such abilities, long before any formal training in arithmetic, through the use of spontaneously derived addition algorithms (e.g., Groen & Parkman, 1972; Groen & Resnick, 1977). That Sheba had also derived a new and emergent way of viewing quantities, reflecting an understanding of how to covertly manipulate increasing numerosity, was evident from her immediate capacity to sum both object arrays and representations of quantities in the form of number symbols on the first occasions that she had with each type of stimuli. Such capacities for creative, emergent skills, in this case representing a broader concept of number well beyond the specific number-related skills for which she had been tutored, may be unique among the great apes and humans, with respect to cognitive flexibility and information processing. Through cognitive processes and mechanisms not yet understood in either human children, adults, or apes, novel understanding and operationalization of new skills emerge following exposure and practice with precursor tasks. In this case, our chimpanzees were taught the associative link between number symbols and quantities, represented by arrays of candy or objects such as spools or junk objects. The animals also had experience decoding numerals, by matching a corresponding magnet array with the number, thereby demonstrating number comprehension. Apparently, in chimpanzees, as with very young children, these experiences were sufficient to encourage the elaboration of a sense of number that was conceptually well above and beyond the specific counting and training experiences to which the animals had been exposed.

Indeed, the facility with which Sheba approached these novel tasks suggested that she had a grasp of the enumeration process that was similar, if not analogous, to that of children. This suggestion was further supported by her spontaneous use of indicating acts during counting (e.g., touching the individual items in an array, rearranging and moving the items prior to selecting the Arabic numeral which represented the array), which correlated significantly with the number of indicating acts displayed, the number of items in the array on a given trial, and the cardinal number she selected for labeling the array (Boysen, Berntson, Shreyer & Hannan, 1995). These behaviors were remarkably similar to those described for young children in the early stages of learning to counting, during which such tagging behavior allows the child to organize those items in an array which have already been counted (and tagged), and those in a collection or array which remain to be counting. Such partitioning and tagging facilitates a more accurate count, and may be accomplished through a variety of methods, including touching each item, moving the individual items, or otherwise rearranging the array (Fuson, 1988; Gelman & Gallistel, 1978).

Although the chimpanzees' successes with number-related tasks, including demonstrations of emergent capabilities not specifically taught, have been considerable, more recently we have been more interested in the animals' failure to learn what we had expected would be a fairly easy number discrimination task. The animals' difficulties in demonstrating optimal competence has led to an intriguing set of studies focusing on quantity judgments (Boysen & Berntson, 1995; Boysen, Berntson, Hannan & Cacioppo, 1996). The first study was originally designed to explore strategic deception in the chimpanzee by using their knowledge of numbers and counting in a numerically based task that should have been readily learned. Two chimpanzees were to work as a team, with one chimpanzee given the opportunity to choose between two available candy arrays, one of which was a larger quantity than the other (e.g., 1 vs. 2 candies). Once an array was chosen (by pointing to one of two dishes of candy), the experimenter would intervene, and provide the second chimpanzee with the contents of the dish that had been indicated by the selecting chimpanzee. The selector chimp would then be given the contents of the remaining dish. Thus, it was to the selecting chimp's advantage to choose the dish containing the smaller number of candies, so that he or she could garner the larger remaining array.

During training, however, the selector chimpanzee was unable to inhibit choosing the larger candy array, given the two choices, on nearly every trial, and thus her partner always received the larger amount of reinforcement (the unselected, remaining candy array). Despite our efforts to increase the selector chimpanzee's motivation to respond optimally, by increasing the difference in quantities 1 or 2 candies, to 1 or 4, and finally 1 or 6 candies, our subject persisted in choosing the larger array each time. Her partner, who by now had had 24 sessions as the passive recipient of large quantities of candy, was then given the opportunity to serve as the selecting subject. She fared no better than the first animal, despite considerable opportunity for latent learning of the reward contingencies of the task while she had served as the passive recipient during the first part of training. This should have facilitated her acquisition of the reversed contingencies once the animals reversed their social roles. With the second chimpanzee's failure, it became extremely difficult to reconcile the inability of two highly test-sophisticated chimpanzees to demonstrate competence with the quantity judgment task. Therefore, instead of pursuing an alternative approach to studying strategic deception, we sought to understand the limitations of either our subjects, the task parameters, or perhaps both.

We initially addressed the issue of social competition as a potential factor—that is, did the presence and participation of another chimpanzee impact on the decision-making process, and were the initial results from the first two subjects replicable with other animals? We subsequently individually tested 3 additional adult chimpanzees who also had fairly comparable cognitive training with number symbols, and retested the two pilot

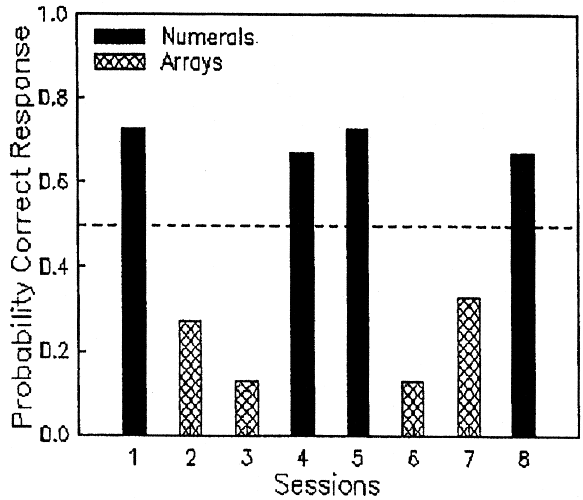

Figure 2. Quantity judgment performance following initial introduction of Arabic numerals as choice stimuli to Sheba & Sarah, followed by reintroduction of candy arrays stimuli, in an ABBA design (8 sessions).

animals, using two candy arrays per trial, with array sizes between 1 and 6. The resulting data indicated that all five of the animals' performances across 20 test sessions (16 trials per session) were remarkably similar, with overall correct responses (i.e., selecting the small quantity of candy, and thus garnering the larger, remaining candy array) ranging from 0.26 to 0.31. These data answered the two questions we sought to determine—namely, that social competition was clearly not a factor in determining an individual subject's choice in the task, and secondly, that rearing and/or experiential factors related to participation in previous cognitive studies did not have a significant impact on performance outcomes. These results pointed instead to possible intrinsic factors that were affecting the animals' choice behavior, regardless of their age, social rearing, or learning backgrounds.

To examine what other factors might be impacting on the quantity judgment task, we first contrasted the candy arrays with another set of choice stimuli, namely numerical symbols that were to represent the arrays in some test sessions. These stimuli were presented in an ABBA design, and compared with performance during sessions when candy arrays were used, for a total of eight test sessions. These results are presented in Figure 2, and clearly demonstrate the release from interference that occurred when number symbols were presented.

In this case, the animals readily selected the smaller Arabic numeral, after which the experimenter provided them with a corresponding quantity of candies, represented by the other unselected numeral, as a reward. A quantity of candies represented by the selected numeral was then provided to their partner, and was reliably the smaller quantity on most trials. Thus, the animals immediately, beginning with Trial 1 of the first session during which numerals were presented and throughout during all subsequent sessions when numerical stimuli were used, responded optimally in making quantity judgments, based upon the reversed-contingency parameters. That is, they reliably chose the smaller numeral, and consequently reaped the larger reinforcement, so long as numbers were available for choice. Each time that candy arrays were reinstated as choice stimuli, however, their performance plummeted below chance, suggesting a definitive response bias, or some type of interference mechanism operating that would not permit the animals to respond so as to benefit from the contingencies.

These new results generated additional questions related specifically to the nature of the choice stimuli. Was the hedonic value of the candy arrays so overwhelming that the animals were somehow compelled to choose the larger array, regardless of its impact on the actual reinforcement received? Were there other perceptual features that might be contributing to the animals' choice which pushed their overall performance below chance, given the two-choice task parameters? To address these questions, we selected collections of inedibles to serve as comparison stimuli, and chose collections of limestone gravel, which were larger by individual unit than the candy arrays (candy-coated, chocolate-covered peanuts), and also as a collection, represented a larger mass. Using the same ABBA design, the animals now chose between candy arrays on some sessions, and rock arrays during others, and their choices across sessions were compared. These data are presented below (Figure 3), and indicate that the perceptual features of the choice stimuli may have been the overriding factor in determining the animals' choices. That is, whereas there was more variability in the animals' performance when choosing between rock arrays (and receiving a corresponding number of candies as a reward), and two individual animals' performance was essentially at a midpoint between candy and number symbol arrays, the overall group effect was not significant. These results suggested that a powerful perceptual filtering mechanism was operating that interfered with the artificial contingencies imposed by the task parameters. In other words, there was a significant bias toward selecting the larger array, regardless of whether it was a candy or rock array, and this predisposition to respond to the larger perceptual mass could not be overridden by the reinforcement demands that consequently diminished the amount of reward that an individual animal obtained. This perceptual filter, given its pervasiveness across animals with dramatically different histories, suggests a mechanism reminiscent of Tinbergen's (1960) notion of a "search image." However, in this case, the template reflects numerosity, and not specificity of prey type. That is, a perceptual filtering mechanism is in place which predisposes the chimps to select the perceptually larger array, despite the suboptimal reward contingency following such choices. Similar rapid judgments have been demonstrated for human numerosity assessments in the subitizing literature (Mandler & Shebo, 1982), and also by empirical work, as described above, with a chimpanzee subject who was required to label arrays of dots that were presented for short durations (Murofushi, 1997). In the case of the quantity judgment task with our animals, however, smaller versus larger judgments would have been sufficient for maximizing reward, unlike most subitizing tasks with humans, which typically require a specific numerical judgment of array size. Selective advantages of such a perceptual filter or template could be of significant importance for a foraging omnivore like the chimpanzee (Boysen et al., 1996), and is

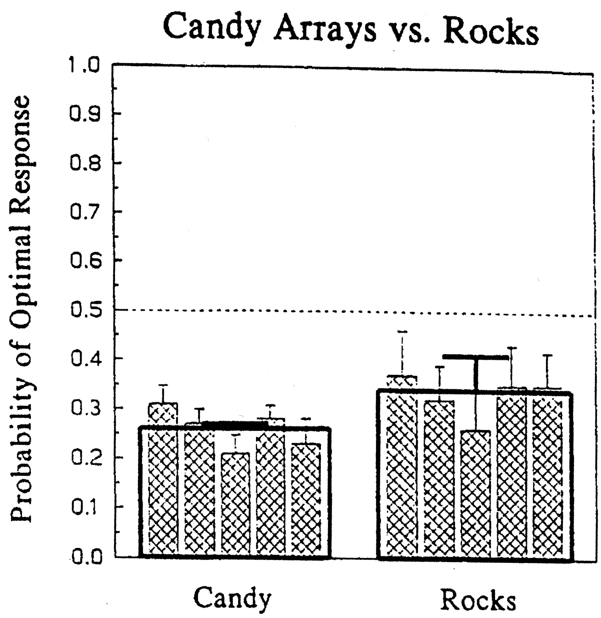

Figure 3. Mean probability of a "correct" response (optimal choice = select smaller quantity of stimuli, to receive larger remaining array as reward) when chimpanzees were presented with a choice between two arrays of differing quantities which were either composed of candies or rocks. Hatched bars represent overall performance for 5 session, collapsed for all five chimpanzees tested, for each type of stimuli. Large open bars represent overall mean performance (N = 5). Sessions were counterbalanced for stimulus type, but are presented in this format for illustrative purposes. Horizontal dotted line depicts chance performance.

likely reflected in both the pervasiveness of the interference effect across all the chimpanzees we have tested, as well as the persistence of the effect. We have now completed 5 studies with five subjects during which the interference has been consistent with the performance decrement demonstrated by the initial two chimpanzee subjects. Additional studies are currently underway to examine more explicitly the perceptual and cognitive variables that may be contributing to such response biases.

The experimental work on numerical competence in nonhuman primates presented here is not exhaustive, and clearly points to the potential for further exploration of these phenomena in nonverbal organisms. This has particular potential for studies with the great apes, whose demonstrated cognitive flexibility and capacity permits evaluation of number-based conceptual understanding and logico-mathematical inferential mechanisms to be assessed, without linguistic support.

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