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Chimpanzees as Natural Accountants

I define a natural accountant as an individual who can keep track of quantities coming into or leaving an account containing some type of commodity. I will argue that chimpanzees are very good at this type of accounting although in some instances their performance breaks down in ways that offer interesting insights into the emergence of arithmetic capacities. I will discuss how chimpanzees deal with operations that involve addition and subtraction of discrete quantities and other forms of quantity accounting. After outlining this evidence in favor of chimpanzee accounting in these kinds of tests, I offer some preliminary data from more naturalistic experimental methods that might further refine our understanding of how chimpanzees deal with quantitative and numerical information in foraging-like situations that better approximate real world situations. These accounting capacities reflect the emergence of arithmetic competence and the evolutionary foundations of mathematics.

KEY WORDS: *Numerosity, Chimpanzees, Accounting, Arithmetic, Mathematics, Quantity*

Introduction

Many nonhuman species are capable of dealing with quantitative information. The skills that have been demonstrated range from simple choices between food sets (e.g., Beran, 2001, 2004a; Call, 2000; Hauser *et al.*, 2000; Rumbaugh *et al.*, 1987) to comparisons among arbitrary stimuli on computer screens (Beran, 2007, 2008; Brannon, Terrace, 2000; Cantlon, Brannon, 2006, 2007; Judge *et al.*, 2005; Washburn, Rumbaugh, 1991) to mapping of quantity information onto symbols such as Arabic numerals (Beran, Rumbaugh, 2001; Boysen, Berntson, 1989; Matsuzawa, 1985; Pepperberg, 2006; Rumbaugh *et al.*, 1989). Despite a controversial history within comparative psychology (Rilling, 1993), this area of research is vibrant and it remains at the forefront of investigations into animal minds. New techniques have begun to probe the brain-behavior relations for such mathematical capacities (e.g., Diester, Nieder, 2007; Nieder, 2005; Nieder, Miller, 2004; Nieder, Merten, 2007; Roitman *et al.*, 2007), and this literature is at its historical apex in terms of the number of research papers produced (Figure 1).

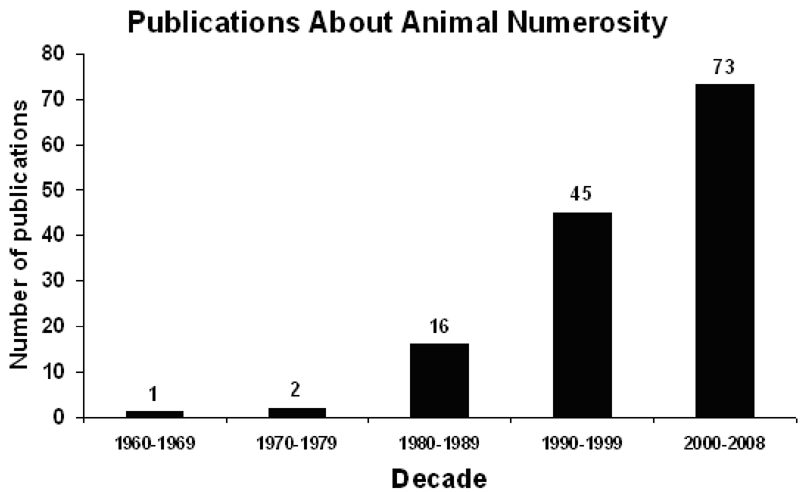

Figure 1. Historical trends for papers published on numerical cognition in nonhuman animals. Data come from a PsychInfo search conducted 09-21-2008 using the keywords animal and numerosity. Although other terms certainly also could be used (e.g., counting, numerousness, quantity), the trend shown here would be the same.

Initial research efforts were, in large part, designed to probe the question of whether animals can count (Kinnaman, 1902; see Boysen, Capaldi, 1993; Davis, Perusse, 1988). Counting is a special quantitative skill in that it provides a symbolic, absolute label for enumerated stimuli. Counting relies on multiple subroutines, including the tagging of individual items once and only once during the counting routine, the use of a stable order of numerical labels across enumerative instances, and the recognition that the last applied label represents the sum total of the set just enumerated (Gelman, Gallistel, 1978). Such counting skills take many years to emerge in human development, and counting is one of the critical processes underlying the subsequent arithmetical and mathematical development that occurs in humans (e.g., Carpenter *et al*., 1982; Gelman, 2006). As such, the search for precursors of counting skill in nonhumans has a long history (see Rilling, 1993). Romanes and Morgan, two of the principle researchers in the new field of comparative psychology at the turn of the 20th Century, took opposite views of animal counting. Romanes stated that animals could count, but Morgan disagreed and claimed that the issue of animal counting was really a matter of timing (Rilling, 1993). However, evidence from early studies suggested that numerosity was relevant to nonhuman animals in a variety of situations. Koehler (1951) trained birds to eat a specified number of food items and no more. Mechner (1958) reinforced rats for a response on lever B after a varying number of presses on lever A. Rats performed correctly on this task with some regularity for 4, 8, 12, and 16 responses. In one of the earliest research projects with chimpanzees, Ferster (1964) trained two chimpanzees to select one of two binary "numbers" to match a presented form with some number of shapes on it. The chimpanzees ultimately succeeded, although it took many trials for them to learn the correct responses. Later research, in the 1980s and 1990s, helped firmly establish the chimpanzee as an excellent subject for numerical cognition research. Three research teams deserve credit for these early studies.

Boysen and her colleagues provided some of the clearest evidence of skills that approximate the counting routines used by humans (Boysen, Berntson, 1989; see Boysen, Hallberg, 2000). Chimpanzees (and in particular one chimpanzee, Sheba) learned to label arrays of different kinds of items with the correct Arabic numeral label. After this training, labeling transferred to new kinds of items, and proper labeling occurred even when multiple sets in different locations had to be viewed and combined before Sheba could choose an Arabic numeral. These studies showed combinatorial, enumerative processes at work within a symbolic matching task, and other experiments even demonstrated some of the critical subroutines that support counting behavior (e.g., tagging items; Boysen *et al.*, 1995). Matsuzawa and his colleagues also used symbolic stimuli with chimpanzees. The chimpanzee, Ai, mastered naming one to six items with the correct Arabic numeral label (Matsuzawa, 1985). She could view any number of different things and then choose the numeral that matched that number of items (see also Biro, Matsuzawa, 2001; Tomonaga, Matsuzawa, 2002). Rumbaugh *et al.* (1989) took a different approach, although they also used Arabic numerals as symbolic stimuli. In their tests, the chimpanzee Lana learned to collect sets of items on a computer screen by moving a cursor. On each trial, Lana was presented with an Arabic numeral that indicated the number of items needed, and she had to collect that number from a random array shown on the screen and then end the trial. Lana was successful for numerals 1 through 4, indicating that she could track the number of collected items and relate that number to the number represented by the numeral. Subsequent studies with Lana and other chimpanzees (e.g., Beran, 2004b; Beran *et al.*, 1998; Beran, Rumbaugh, 2001) extended this performance to the numeral 7. All three of these research programs, therefore, outlined the capacities of chimpanzees for formal counting-like skills. However, these were studies designed more to investigate what chimpanzees might learn to do rather than what they naturally and spontaneously could do when confronted with problems of a quantitative nature. Other methods have been used for this purpose.

In one of the earliest experiments, Dooley and Gill (1977) showed that the chimpanzee, Lana, could select the larger of two quantities of cereal pieces. Rumbaugh *et al.* (1987) presented two chimpanzees, Sherman and Austin, with sets of food items, and they were allowed to choose one of the two sets and eat the items in that set. Both chimpanzees were very successful in this task right from the outset, and this was expected given that the test was ideally suited to match a necessary adaptive behavior (maximization of food intake) to an intuitive task demand (pointing to one set instead of the other). Rumbaugh *et al.* (1987) then increased the difficulty of the task by presenting the food items in two pairs of wells, each of which contained a separate set of items. Now, the chimpanzees had to sum the contents of two wells and choose which pair of wells was perceived to contain more items. The chimpanzees again succeeded, indicating that rudimentary summation, or combining of multiple sets across spatial locations, was within the behavioral repertoire of these animals. Subsequent experiments with other animals have shown the same effect in which animals maximize the food they obtain in these judgments (e.g., Anderson *et al.*, 2007; Hanus, Call, 2007; Hunt *et al.*, 2008).

Quantity Summation by Chimpanzees – Responses to Addition Operations

My interest in summation tasks came from the search for a test that would combine the need for responding to arithmetic operations and outline the perceptual threshold of chimpanzees in making these kinds of decisions. The intuitive nature of the task allowed for spontaneous responding, and I could present many different kinds of manipulations and determine how well the chimpanzees accommodated and represented the implications of such arithmetic operations on the quantitative nature of the stimulus sets. In one manipulation, I varied the presentation method so that items were seen only briefly, and only one at a time, before they were deposited into opaque containers. In this way, the chimpanzees had to attend to each item and tally its contribution to the overall amount of food in each nonvisible set. Then, the chimpanzees used those representations of amount as the basis for making a decision as to which set to choose. In the first study using this method (Beran, 2001), two chimpanzees, Lana and Sherman, were given choices between two sequentially presented sets of candies. The chimpanzees watched as items were dropped, one at a time, into two opaque containers. After all pieces were placed into the two containers, the chimpanzees then selected one container, and they received the contents of that container. Both chimpanzees performed at very high levels when comparing sets of up to eight items. Then, an addition operation was inserted. In that case, two separate sets were presented into each container. First, some items were dropped into the first container, and then another set was dropped into the second container. Then, a second set was added to each container, so that the chimpanzees had to update their representation of the quantities in each container before they would make a choice. Both chimpanzees again performed at high levels in comparing these combined sets of items and choosing the larger set (Figure 2). This performance extended even to addition operations that involved three separate sets going into each container at three separate times. These data showed that chimpanzees could sum multiple, sequentially presented sets in such a way that they could remember which of the two sets contained the larger number of items.

Despite these preliminary results, there was no way of knowing whether chimpanzees could enumerate these sets in ways that left them with representations of actual numerosity or quantity of food, or just the difference between the sets. In other words, I did not know whether the chimpanzees remembered which set was bigger or if they also remembered how many items were in each set. Consider the following situation: a person is seated at a table, on top of which are presented many coins of two different types. The person is asked to report which type of coin is more numerous. Although the person could separate and count each type of coin, and could compare those numerical labels and provide an answer, there is another method that would be equally successful. The person could repeatedly separate out one coin of each type, and continue to do this until the pile only had one type of coin remaining in it. That type of coin would be more numerous. However, despite accurately answering the original question, the participant would be unable to answer a follow-up question of the form “how many coins of type A (or B) were in the pile”. The person discerned only the relative quantity difference in the two types of coins without having any access to the absolute quantity of either coin type. The chimpanzees might similarly have responded in the previous experiments by keeping a running tally of the relative difference rather than the absolute amounts. To test exactly what information was being stored during these enumerative processes two sequentially presented sets again were placed into opaque containers (Beran, 2004). Then, a third set was revealed fully and remained visible during the chimpanzees’ selections. Thus, the chimpanzees had to choose among two different nonvisible, sequentially presented sets and a third, fully visible, alternative. Both chimpanzees reliably selected the largest of the three sets presented in this manner. This indicated that the chimpanzees were not assessing the sequential presentations solely on the basis of the difference in magnitude between the two sets. The chimpanzees instead were assessing the absolute magnitude of each set and remembering that magnitude for the decision phase of each trial. If the chimpanzees had not known how many items were in the nonvisible sets, then they would not have been able to determine that one of those sets was the better selection than the visible set (or that the visible set was the best option).

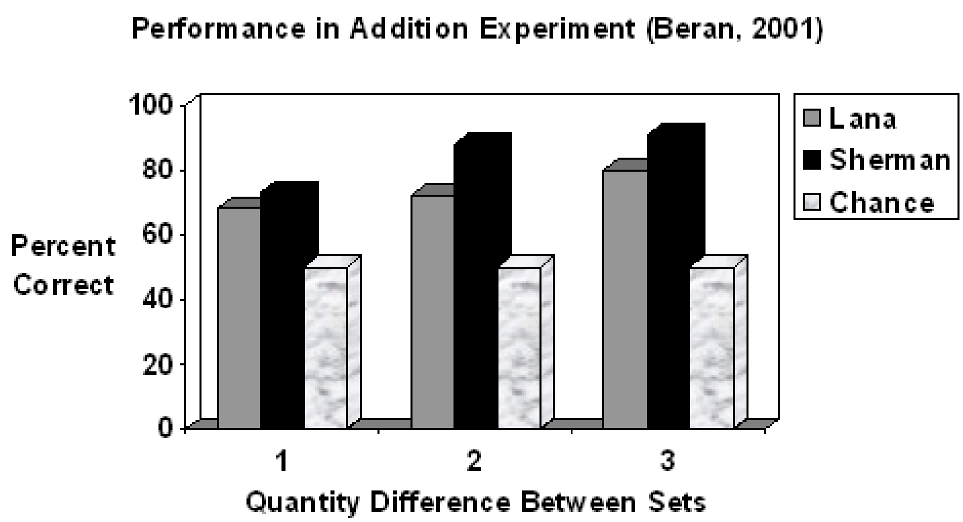

Figure 2. Performance of Sherman and Lana when comparing two sets of items created by adding sets of items at two different times to each container. The figure is based on data from Beran (2001).

What about temporally extended quantity judgment problems that involve additions of items? Chimpanzee accountants also make these kinds of accurate decisions after enumeration across longer time periods. Beran and Beran (2004) extended the time course for presentation of trials involving one-by-one accumulation of items in two hidden sets to 20 minutes. One experimenter repeatedly entered the test area over the course of 20 minutes and placed a single banana into one of two containers out of a chimpanzee's reach. Placement of bananas alternated between the two containers as well. The chimpanzee never saw more than one banana at a time, and once a banana was placed into a container it remained out of sight for the rest of the trial. After 20 minutes, a second experimenter, who did not know the total number of bananas in the containers, entered the test area and allowed the chimpanzee to make a selection. All four chimpanzees that were tested were highly proficient in choosing the larger quantities for a wide variety of comparisons including those with small numbers of items in each set and large numbers of items (Figure 3). This indicated that responding to addition operations over extended time periods was not a difficult task for chimpanzees, and their performance reflected accurate updating of their representations of the quantities in each container.

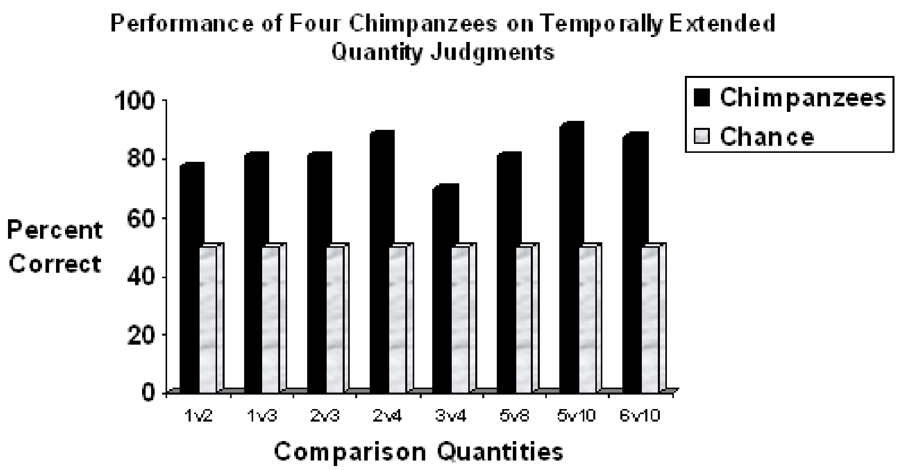

Figure 3. Group performance of four chimpanzees on temporally extended problems that involved comparing two sets of food items that were incremented by adding one item at a time randomly between the sets. In all cases, performance exceeded chance levels. The figure is based on data from Beran and Beran (2004).

Tracking Relative Reward Rates During Quantity Judgments

More recently, we have found that chimpanzees even appear to track the relative rates of return that they earn from multiple responses in quantity judgment tasks (Beran *et al.*, *2009*). This experiment emerged from anecdotal observations of the author during the studies outlined above. During these tests, chimpanzees would begin to exhibit interesting anticipatory responses toward the end of sessions. For example, near the ends of sessions in which they compared two sequentially presented sets, the chimpanzees might try to choose the first set even before seeing how many items were dropped into the second set. Or, they might begin to point to the second set after seeing only a small number of items be placed into the first set (but before they had seen any items being placed into the second set). This suggested that they had formed some sense of the average reward amount they had been receiving across earlier trials, and using that information to anticipate which set in the present trial would be the larger. When shown a first set that was small, they anticipated that the other set would be larger, and therefore should be chosen, or when shown a large first set they anticipated that the second set would be smaller and therefore the first set should be chosen.

Beran *et al.* (*in press*) formally investigated this possibility. Four chimpanzees completed sessions of 30 trials. The first 15 trials involved easy comparisons between two sets of food items that were uncovered one at a time and then recovered. After performing at very high levels in choosing the larger sets across these trials, the chimpanzees then completed 15 trials of a very different nature. In those trials, only one set was revealed, and the other contained an unknown quantity at choice time. This required the chimpanzees to assess the likelihood that the unknown quantity was larger than the known quantity, and we determined what factors influenced the choice of the unknown set. Rather than use a specific quantity as a threshold for choosing the known or the unknown set, the chimpanzees' choice of the unknown set varied in relation to the rate of return from responses in the first phase (when both sets were known). In other words, when the first 15 trials involved comparisons between relatively larger set sizes (e.g., from a range of 5 to 12 items), the chimpanzees were more likely to choose the unknown quantity when the known quantity had 5 or 6 items in it. However, when the first 15 trials involved comparisons between smaller set sizes (e.g., from a range of 1 to 6 items), the chimpanzees chose known sets of 5 or 6 items rather than choosing the unknown set. This flexibility in choosing unknown sets in relation to the average reward amounts obtained in the first 15 trials indicated that the chimpanzees' decisions in the face of uncertainty were guided by a sense of how well they were rewarded overall during the session. What is most impressive is that this information was calculated and retained by the chimpanzees despite its uselessness from the point of view of those first 15 trials, in which maximization of intake could occur through purely perceptual processing of visual stimuli and choice of the larger of two known sets. As such, this highlights the complex nature of quantitative representation and its application to decision-making situations that may involve uncertainty or incomplete information.

Failures of Chimpanzee Accounting – Subtraction Operations

Whereas chimpanzees ably deal with additions of items to sets, and the resulting effects of such additions on the absolute and relative quantities in those sets, subtraction operations seemingly are more difficult for them to deal with. In one experiment (Beran, 2001), only one of two chimpanzees successfully responded to trials in which items were first added to two containers but then a single item was removed from one of the containers. In a second experiment (Beran, 2004a), an initial quantity of food items was placed into one of the two containers in the same one-by-one manner already outlined. However, one set then was reduced in number prior to the chimpanzees' selections of a container. When multiple items were removed from that set in full view of the chimpanzees, they were as likely to select the originally larger set even when it had become the smaller set as they were to select the other (now larger) set. This failure showed that the chimpanzees incorrectly estimated the effect of the removal of more than one item on the relation between the sets. This suggests that performance may be qualitatively different in this subtraction situation than in the one-by-one additive manipulations from the earlier experiments. From an evolutionary perspective, this suggests that dealing with reductions in quantities that must be judged or remembered is a more recent capacity, a suggestion also supported by the developmental course of early arithmetic abilities in children (Carpenter *et al.*, 1982).

A Naturalistic Foraging-Like Study That Incorporates Numerical Information

Despite the overwhelming evidence in favor of numerical competencies in nonhuman animals, there remains little evidence that such capacities actually manifest in animal behavior in natural environments. This highlights a critical need for future research. When such behavior is seen, it usually involves situations that pertain to group size assessments by individuals (e.g., Agrillo *et al.*, 2007; Hunt *et al.*, 2008; Kitchen, 2004; McComb *et al.*, 1994; Wilson *et al.*, 2001). Another compelling example of the use of number in natural environments comes from research with meadow voles. These animals can compare the number of scent marks left by multiple individuals and may use that information for preferential mating with more dominant individuals (e.g., Ferkin *et al.*, 2005). Studies such as these, along with others in natural foraging environments, will afford an even better understanding of the natural accounting abilities of nonhuman animals.

I now offer data from a new paradigm designed to mimic on a small scale a foraging problem that involves memory for quantity and matching item retrieval to that memory for quantity. In this study, we attempted to move the issue of using quantity and numerical information into a more naturalistic task structure. We made use of the indoor-outdoor configuration of the chimpanzees' home area so that we might present a more realistic foraging-like problem to these chimpanzees. This problem would require the kind of mental accounting I have been discussing, but at a new and more advanced level in terms of the strategic implementation and use of numerical information encoded at one time and used at another.

We worked with two adult chimpanzees, Lana and Mercury. Both had shown repeated competence in many of the tasks already outlined, as well as a willingness to engage in this task with the sustained attention needed for good performance. The task itself was designed to require the chimpanzees to remember item identity in all cases, and simple quantity information in some cases. That information had to be retained and used as chimpanzees moved throughout a 750 square foot outdoor enclosure.

In that outdoor enclosure, we mounted 10 opaque boxes at a height of approximately 5.5 feet. These boxes were made of sturdy plastic and were each covered with a lid that was closed with a hinge. To open a box and investigate its contents, a chimpanzee had to raise itself by partially climbing the chain mesh and opening the hinged top. This was effortful and typically required at least 10 to 15 seconds for a full investigation. We initially left the newly mounted boxes outdoors at all times while being empty, so that the chimpanzees could search those boxes whenever they wanted. After a couple of weeks, chimpanzees entering the outdoor yard for the first time each day were no longer observed to approach or investigate the boxes. We then began the experiment.

In the experiment, a chimpanzee was shown indoors the contents of a small bucket. In that bucket was either a single piece of fruit (a banana or an orange, both of which are highly preferred fruits) or two pieces of fruit (two oranges, two bananas, or a banana and an orange). The experimenter then went outdoors where he was out of sight of the chimpanzee. He lifted the lid to every box and then dropped it loudly so that it was audible in the indoor area. In one or two of those boxes (depending on the number of fruits shown to the chimpanzee), he left a fruit. However, this produced no specific auditory feedback, and therefore the chimpanzee had no way of knowing where the fruit was located. He then left the outdoor yard, approached the chimpanzee in its indoor cage, and showed it the empty bucket. The chimpanzee then was released into the outdoor yard to investigate boxes at its own instigation.

Prior to the formal tests, the chimpanzees were each given trials in which they watched the experimenter hide one or two items in one or two boxes in the outdoor yard. In all trials, the chimpanzees immediately went to the correct boxes as soon as they were released into the yard. This confirmed both that their memory was sufficient for the time scale and also that when they had information about where an item was hidden they retained it perfectly. Therefore, the results we obtained in the test trials showed that the chimpanzees did not initially know the location of the food items because they always needed to search multiple boxes before finding a food item.

Returning to the test trials, the procedure allowed us to vary two things: the number of hidden items and also the identity of the items. This created three trial types of interest. In the first, only a single item was hidden. In the second, two different types of items were hidden, and in the third two items of the same type were hidden. We predicted that the chimpanzees would stop searching immediately when only a single item had been hidden and was found. However, when two items were hidden, performance might have differed as a result of whether the chimpanzees had to find two identical items or two different items. Here, we were able to present some trials with a numerical cue (e.g., two bananas) versus an identity cue (a banana and an orange). Our hypothesis was that number might not be as highly salient as identity, and the chimpanzees would be prone to make more mistakes when two identical items were hidden. First, they might not remember that two items were hidden if they only encoded item type into memory, and as a result they would stop without finding the two food items. Second, they might not accurately track the number of items retrieved and the number of items hidden when identity was the same, and as a result they would continue to search even after finding the two identical food items. These errors would be more prevalent than when two items were of different types or only a single item was hidden.

Each chimpanzee completed 20 trials. Of these, 8 trials involved a single item (four times with orange and four times with banana), 6 trials involved the mixed set (a banana and an apple), and 6 trials involved two of the same item (three times with two oranges and three times with two bananas). Once outdoors, a trial continued until 5 minutes had elapsed between searches of boxes. We recorded the order of searches, including re-searches of boxes previously opened on that trial.

The results partially confirmed the hypothesis. As shown in Figure 4a, both chimpanzees made far more additional searches after finding two identical food items than

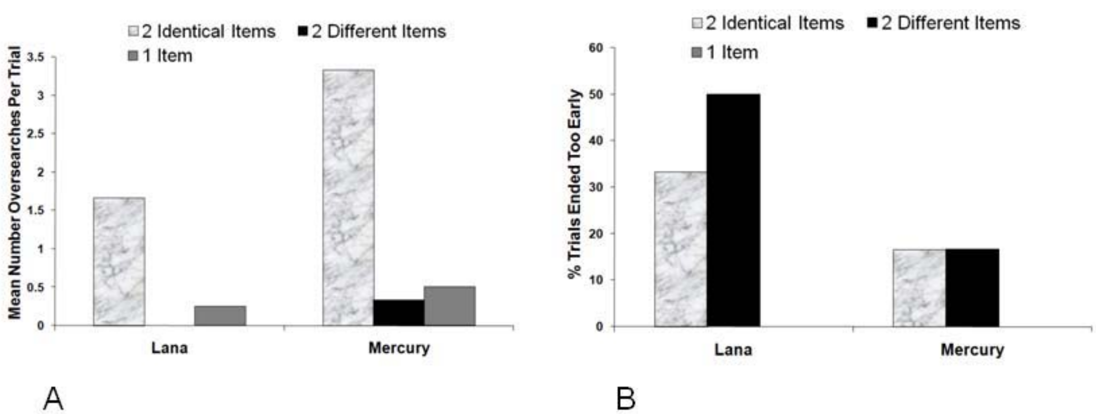

Figure 4. The performance of the chimpanzees in the foraging task. (A) – The mean number of oversearches for each condition. Lana and Mercury both oversearched most often for trials in which two identical food items were hidden; (B) – The percentage of trials in which searching ended prematurely, before all food had been found.

they did when finding two different items or only a single hidden item. Additional searches were those that occurred after all possible food items already had been found. However, the chimpanzees did not show a greater likelihood to stop searching too early in the condition with two identical food items compared to the other conditions (Figure 4b). Neither chimpanzee failed to find the hidden item when only one food item was presented. Mercury rarely stopped a trial without finding both hidden items in the other two conditions. Lana did so more frequently, but she did so on more trials when the items were different that when they were the same.

These results suggested that the chimpanzees reacted differently to the hiding of two identical items compared to one item or two different items. Because of the differences in performance in the conditions with two items, I offer that the chimpanzees had some difficulty encoding the abstract numerical property "two" in the identical two-item condition. When the food items were different, the chimpanzees could use item identity to help maintain accurate memory for what they were searching for in the outdoor yard. However, when the foods were identical, that identity was of only one item type. In that case, the chimpanzees might have failed to encode information about quantity in their memory for later use during the search. If they simply remembered "banana" or "orange," they would have ceased searching after finding the first item. However, they did not. At the same time, if they had remembered "banana" and "banana" (or "orange" and "orange"), without encoding a numerical property, performance should not have differed from the condition with two different items. But it did. Therefore, I propose that the chimpanzees encoded item type and item quantity, although the quantity information was tenuously available during the trials. Specifically, the chimpanzees seemed to treat two identical items as "some" bananas or oranges rather than exactly "two" bananas or oranges because of their tendency to oversearch on those trials. In fact, the chimpanzees searched more boxes after finding both identical food items on two thirds of the trials.

This semi-natural experiment offers some evidence that animals spontaneously encode a quantity property in a foraging-like task without any explicit training or rule learning. They seem to represent quantity at a non-specified level, akin to something like "some" fruits, or "a few" fruits, rather than with an exact numerical code. But, this offers a guide for future projects that better refine the nature of this representation, and also can examine how it might become refined with more practice and perhaps with some methodological interventions to emphasize the need for more exact numerical encoding. In this experiment, there was no real high cost to oversearching, and so one step would be to increase that cost to determine whether performance would improve as a result of refining the numerical information that was coded and stored for later use in the search process. Such manipulations would offer new insights into numerical processes as they are used in more natural foraging situations.

Summary - The Evolutionary Significance of Chimpanzee Accounting

Humans rely on mathematical routines such as counting, adding, subtracting, and estimating many times each day. Think back just through your day today, and you will discover a variety of ways that number has played a role in your behavior. Three eggs for breakfast, two sugars in your coffee, ten dollars to park the car, and remember to pick up nine shirts from the dry cleaner. This is but a small sampling of a typical day. However, it highlights the "bookkeeping" skills that are required for enumerating, tracking, and remembering quantity information that is critical to good decision-making. These capacities are not uniquely human, although more advanced mathematics that expand upon the capacities that we share with nonhuman animals may be uniquely human. Brains (both human and nonhuman) are designed to deal with numerosity and simple arithmetic operations upon sets of stimuli, and these shared capacities are perfectly suited to support survival in the natural environments in which humans evolved. Human ancestral species that could tell the difference between a tree with 20 pieces of fruit from another with only 6 pieces, or that could tell the difference between 2 predators or 4 predators on the horizon had a better chance to survive and reproduce. However, telling apart 15 and 16 fruits, or 5 and 6 predators, offers much less benefit in these situations. As such, approximate numerical representations are all that is needed. More recently, the humans learned to map symbols onto exact numerosities such that more complex mathematical feats (such as algebra and calculus) came within reach of the human mind and could be used to support uniquely human endeavors such as monetary systems, trade, and engineering. These kinds of higher-order mathematical operations are beyond the capacity of chimpanzee accountants, but they are based on the same foundational mechanisms for the representation of simple arithmetic operations. These kinds of studies, with chimpanzees and other animals, have outlined and will continue to outline the evolutionary and developmental foundations of mathematics.

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