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Chimpanzees (*Pan troglodytes*) Accurately Compare Poured Liquid Quantities

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Abstract

Although many studies have shown that nonhuman animals can choose the larger of two discrete quantities of items, less emphasis has been given to discrimination of continuous quantity. These studies are necessary to discern the similarities and differences in discrimination performance as a function of the type of quantities that are compared. Chimpanzees made judgments between continuous quantities (liquids) in a series of three experiments. In the first experiment, chimpanzees first chose between two clear containers holding differing amounts of juice. Next, they watched as two liquid quantities were dispensed from opaque syringes held above opaque containers. In the second experiment, one liquid amount was presented by pouring it into an opaque container from an opaque syringe, whereas the other quantity was visible the entire time in a clear container. In the third experiment, the heights at which the opaque syringes were held above opaque containers differed for each set, so that sometimes sets with smaller amounts of juice were dropped from a greater height, providing a possible visual illusion as to the total amount. Chimpanzees succeeded in all tasks and showed many similarities in their continuous quantity estimation to how they performed previously in similar tasks with discrete quantities (for example, performance was constrained by the ratio between sets). Chimpanzees could compare visible sets to nonvisible sets, and they were not distracted by perceptual illusions created through various presentation styles that were not relevant to the actual amount of juice dispensed. This performance demonstrated a similarity in the quantitative discrimination skills of chimpanzees for continuous quantities that matches that previously shown for discrete quantities.

Keywords

Chimpanzees; *Pan troglodytes*; Quantity Judgments; Continuous Quantity; Perceptual Illusion

Introduction

Great apes are excellent estimators of discrete quantities, particularly when food items constitute the sets to be compared (e.g., Anderson et al., 2005, 2007; Beran, 2001, 2004; Call, 2000; Hanus and Call, 2000; Rumbaugh et al., 1987; Shumaker et al. 2001). They succeed even when multiple sets of items are added together or when the presentations of sets take long periods of time (e.g., Beran, 2001; Beran and Beran, 2004; Call, 2000). They

compare visible sets to nonvisible sets (e.g., Beran, 2004). In addition, apes recognize the invariance of continuous quantities such as liquids when those liquids are transferred between containers of different sizes and shapes (e.g., Suda and Call, 2004, 2005). Thus, they show liquid conservation.

These types of skills suggest that apes also would be capable of quantifying continuous quantities even when choices cannot be made between two visible sets but must be made with limited visual information. However, we have little or no data to support this assertion, although a study with capuchin monkeys (vanMarle et al. 2006) indicated that representation of continuous quantity may be performed similarly to representation of discrete quantity. In addition, the skills that apes have shown in discriminating quantities suggest that apes may be able to overcome certain types of visual illusions that occur when continuous quantities are presented in certain ways. These illusions result because distance or length of presentation can affect representation of total amount in a way that leads to perceptual biases. For example, when liquids are poured into elongated containers as opposed to shorter, wider containers, the total amount is overestimated by children and adults (e.g., Piaget, 1969; Wansink and Van Ittersum, 2005).

In the present study, chimpanzees compared two amounts of poured liquids, using a variety of presentation methods, to determine how well they represented such quantities, and whether they were susceptible to perceptual illusions. In the first phase of Experiment 1, chimpanzees viewed two clear containers holding differing amounts of juice to establish a baseline performance level for discriminating between differing amounts of continuous substances. In the second phase of Experiment 1, two liquid quantities were presented by dispensing the juice from opaque syringes held 12 inches above opaque containers. This meant that neither quantity was visible at choice time. It also meant that the chimpanzees never saw both amounts at once. Instead, they had to remember the amount of liquid in each set.

In Experiment 2, one liquid amount was presented by pouring it into an opaque container from an opaque syringe, whereas the other quantity was visible the entire time in a clear container. This variation was necessary to discount the possibility that the chimpanzees were using the duration of pouring as the relevant cue rather than the amount of juice. Experiment 1 and Experiment 2 also required that chimpanzees conserve liquid quantities to successfully choose the larger amount. Conservation of quantity refers to the idea that physical quantities do not change just because their arrangement has been modified (e.g., Piaget, 1965). Like children (e.g., McGarrigle and Donaldson, 1974; Mehler and Bever, 1967), some animals have shown evidence of conservation of quantity. For example, they recognize that moving arrays of items into new configurations does not change the number of items in those arrays (e.g., Beran, 2007, 2008a; Czerny and Thomas, 1975, Muncer, 1983) and that changing the size and shape of containers holding continuous quantities does not change that amount of substance (Call and Rochat, 1997; Suda and Call, 2004, 2005; Woodruff, Premack, and Kennel, 1978). For organisms to succeed in understanding the invariance of quantity, they must understand that perceptual variations are not equivalent to quantitative variations, and this skill emerges rather late in development for children. In the present experiments, the poured liquids move from one type of container (a long cylindrical syringe) into another, and

sometimes must be compared without benefit of visual feedback, and these characteristics of the task seemingly require some degree of liquid conservation. These tasks also require that chimpanzees, to some degree, track the movement of quantities as they are poured. Although animals perform well in tracking discrete items through movements (e.g., Beran, 2008b; Santos, Barnes, and Mahajan, 2005), they have more difficulty tracking continuous quantities (e.g., Mahajan, Barnes, Blanco, and Santos, 2009), and so this may contribute to performance difficulties for the chimpanzees.

In Experiment 3, opaque containers again were used, and the heights at which the opaque syringes were held differed for each set, so that sets with smaller amounts of juice were sometimes dropped from a greater height, providing a possible visual illusion as to the total amount. This manipulation also served as a control because pouring liquids from a greater height provided more elongated visual feedback with regard to the liquid that was seen, and elongation has been established as promoting overestimation of amount in adult humans, even those trained specifically for pouring liquids (e.g., bartenders; Raghubir and Krishna, 1999; Wansink and Van Ittersum, 2003). If chimpanzees were susceptible to this illusion, they should have made more errors in this situation. All of these experiments provided data relevant to determining whether continuous quantity representation in chimpanzees is similar or dissimilar to representation of discrete quantity. Of particular importance is whether discriminative sensitivity of continuous quantities matches that established for discrete items by chimpanzees. These chimpanzees (e.g., Beran, 2004) have shown a high correlation between the ratio measure (small quantity divided by large quantity) and performance in choosing the larger discrete quantity, with higher ratios leading to poorer discrimination. This is also true of other nonhuman species including those tests with continuous quantities (e.g., Beran, 2007; Call, 2000; Cantlon and Brannon, 2007; Hanus and Call, 2007; Jordan and Brannon, 2006; vanMarle et al., 2006). It is also true that when discrete and continuous quantity discrimination is compared in human children larger ratios are needed for successful discrimination of continuous quantity than for discrete quantity (e.g., vanMarle, 2004, as cited by vanMarle et al. 2006). In contrast, capuchin monkeys performed equally well with continuous and discrete quantities (vanMarle et al. 2006). Thus, it was predicted that continuous and discrete quantity comparisons would correspond in terms of the ratio values required for successful performance by these chimpanzees.

Experiment 1 Methods

Participants

Three chimpanzees were tested. They were Lana (female, 37 years of age), Sherman (male, 34 years of age), and Panzee (female, 21 years of age). All were highly experienced in a variety of different cognitive tests, but none had ever been tested for their ability to judge continuous quantities.

Apparatus

The liquid quantities (fruit juice) were poured from opaque syringes with a capacity of 600 ml. The containers were clear cups (approximately 7.5 cm in diameter and 9 cm tall) or opaque cups (approximately 11 cm in diameter and 15 cm tall) made of plastic, and these

were positioned at opposite ends of a wooden bench (48 cm high, 67 cm wide, and 36 cm deep). The bench had a sliding top shelf that allowed both quantities to be moved toward the chimpanzee at the same time (see Figure 1).

Design and Procedure

In the first phase of the experiment, chimpanzees chose between two visible, continuous quantities. An experimenter was seated across from a chimpanzee, and he moved two clear containers out of view of the chimpanzees and used a syringe to fill each container with 100, 200, 300, 400, 500, or 600 ml of a fruit juice¹. These quantities were used in all experiments, and for ease of presentation, they will be referred to as 1 through 6 units in all subsequent places. Next, both containers were raised at the same time and placed on opposite sides of the bench. The experimenter then lowered his gaze and pushed the bench shelf forward, which moved both containers simultaneously within reach of the chimpanzee. After approximately 2 seconds the experimenter looked up to see which container was being touched by the chimpanzee. This constituted the response by the chimpanzee, and this is a well-established routine with these animals that minimizes the potential for inadvertent cuing because the experimenter cannot give any feedback about a response as it is in progress. Rather, he only can see the final selection. The chimpanzee then received the contents of the selected container to drink, and the contents of the other container then were removed. Given the size of the units of liquid used (a maximum of 2 oz on a trial), all trials allowed the experimenter to drop the full amount straight into the chimpanzee's mouth, so that it could swallow the full amount at one time. Thus, duration of drinking the selected container did not differ with the amount of liquid in that container to any substantial degree. Each chimpanzee completed 2 sessions of 15 trials. All possible combinations of 1 to 6 units were presented two times each and were counterbalanced for side placement.

Prior to the start of the second phase, all chimpanzees were given a single control session of 10 trials in which the two opaque containers were filled out of view with two amounts of liquid (100 ml and 400 ml). The containers then were placed on the bench and presented for a choice response. If the chimpanzees were able to look into the containers and see some cue to the larger amount, they would have performed above chance. This did not happen, confirming that there were no visible cues available when liquids already were in the opaque containers. At two other times during Phase 2, a similar short series of these trials was presented, and performance always remained at chance.

In the second test phase, the two opaque containers were placed on the ends of the bench. The experimenter filled two opaque syringes with the relevant amount of juice out of view of the chimpanzee by filling those syringes below the shelf of the apparatus from a large bowl of liquid. Syringes were filled in random order, not in sequence with their presentation into the opaque containers, and the experimenter used varying rates of filling them as well. In

¹These containers were filled out of view in such a way that the chimpanzees could not discern the time it took to fill either container. The apparatus had a concealed area beneath the shelf with an opaque front barrier that prevented chimpanzees from seeing preparation of out-of-sight containers. Liquids could be poured into containers here without visual or auditory feedback (because syringes were presented into the base of the containers). Liquids were dispensed also at different rates to dissociate time and amount. And, containers were filled in a spatial arrangement (left-right) that varied with their eventual presentation on the top on the shelf. Thus, chimpanzees could not associate out-of-view filling duration with amount, spatial location, or other forms of feedback.

addition, it often took some time to refine the amounts in each syringe so they were perfectly filled. Thus, time to fill syringes out of view was completely dissociated with the amount of liquid that went into each syringe. The experimenter held the first syringe with his left hand over the left container and dispensed the liquid at an even rate (approximately 100 ml/s) into the container from a height of approximately 22 cm. He then used his right hand to dispense the other quantity into the container on the right in the same manner. After both quantities had been presented, he pushed the shelf forward as in the first phase. Each chimpanzee completed 4 sessions of 15 trials. All possible combinations of 1 to 6 units were presented four times each and were counterbalanced for side placement.

Results

For this and all subsequent experiments, the alpha value was set at 0.05. The chimpanzees were nearly perfect in choosing the larger amount of juice in the first phase when both quantities were fully visible. Lana and Sherman both selected the larger amount on all 30 trials. Panzee made only one error in which she selected the container with 5 units over the container with 6 units. In all cases, these performance levels exceeded chance levels as assessed with a sign test, $p < 0.001$.

In the second phase, all three chimpanzees also exceeded chance levels of performance as assessed with a sign test, $p < 0.001$. Lana and Sherman selected the larger quantity on 78.3% of the trials, and Panzee selected the larger quantity on 76.7% of the trials. Performance as a function of the ratio between the two quantities is presented in Figure 2. This ratio measure is an excellent predictor of performance in discrete quantity comparison tasks (e.g., Beran, 2004, 2007; Call, 2000; Cantlon and Brannon, 2007; Hanus and Call, 2007; Jordan and Brannon, 2006; vanMarle et al., 2006). Combining the data from all chimpanzees showed a significant correlation between ratio and percent of trials in which the larger continuous quantity was selected, $r(9) = -0.90$, $p < 0.001$. In addition, all three chimpanzees showed this negative correlation individually: Lana $r(9) = -0.63$, $p = 0.04$, Panzee $r(9) = -0.77$, $p = 0.006$, and Sherman $r(9) = -0.92$, $p < 0.001$. The three chimpanzees were all correct on their very first trial in this phase. In addition, I examined performance on each of the individual comparisons the first time they were presented to each chimpanzee. There were 15 of these first-trial comparisons. Lana and Panzee both were correct on 13 of 15 trials ($p = 0.004$, binomial test), and Sherman was correct on 12 of 15 trials ($p = 0.018$, binomial test).

Finally, performance in choosing the larger continuous quantity was compared to previously collected data (Beran, 2004) with Lana and Sherman using a sequential presentation method with discrete items (marshmallows). The data from the current experiment were compared to the discrete item data from trials with the same numerical comparisons of 1 to 6 items in each set (Figure 2). An Analysis of Covariance with ratio as the covariate indicated that percentage correct in comparing discrete quantities was not significantly different from percentage correct in comparing continuous quantities, $F_{1,19} = 2.57$, $p = 0.13$.

Discussion

After establishing that chimpanzees were highly efficient in choosing the larger of two visible continuous quantities, it was demonstrated that chimpanzees successfully chose the

larger of two continuous quantities presented sequentially into opaque containers. The chimpanzees were very good at choosing the larger quantity even though neither quantity was visible at the time of responding. Performance in this comparison task was constrained by the ratio between the two quantities in the same way that comparisons of discrete quantities are constrained by the ratio. In addition, comparisons of two continuous quantities were not any higher or lower than comparisons of comparably related discrete quantities. In essence, the chimpanzees were as good at comparing continuous quantities as they were at comparing discrete quantities.

Despite this demonstration, a number of concerns remained regarding how the chimpanzees made their selections. In particular, it was important to establish that they were, in fact, making judgments of the actual liquid quantities as opposed to being responsive to some other potential cue. One likely possibility was temporal presentation duration. Because both liquids were dispensed at approximately the same rate, amount of liquid and duration of pouring were perfectly confounded. Thus, the chimpanzees may have been timing the pouring event rather than representing the amounts of liquids that were dispensed. Previously, this concern was addressed with these animals in a discrete item task. Food items were dropped one at a time into opaque containers, but then an additional choice option was presented in its entirety and while fully visible (Beran 2004). In that study, the idea was that chimpanzees could not time the dropping of items because one set had no such temporal quality. Instead, they had to estimate the number of items in the sequential set and compare that to a fully visible set.

To test whether the same kind of judgment can be made for continuous quantity, in the next experiment one set was dispensed from a syringe, while the second set was presented in its entirety at the outset of the trial and remained visible for the entire trial. In this way, the chimpanzees could not use any temporal cues to help guide their responses as they had to compare their representation of the poured quantity to a visible set. Instead, they had to represent the amount of liquid in one set and compare that to what they could see directly in another set.

Experiment 2 Methods

Participants and Apparatus

The same three chimpanzees were tested using the same apparatus.

Design and Procedure

In this experiment, the chimpanzees compared one fully visible quantity that was in a clear container to another quantity that was presented from an opaque syringe in the same manner as in the second phase of Experiment 1. The experimenter first placed the clear container with its quantity on the bench in full view of a chimpanzee. He then dispensed the second quantity into the opaque container using the syringe before allowing the chimpanzee to make a selection. Thus, chimpanzees were comparing a visible quantity with a nonvisible quantity at choice time. In other words, chimpanzees could see the visible quantity throughout the trial, but they had to watch as the liquid fell from the syringe so as to

estimate the amount in that set, because once it was in the container it was no longer visible. They had only the time during which it fell to see that liquid and estimate its amount. Each chimpanzee again completed 4 sessions of 15 trials, and all possible combinations of 1 to 6 units were presented four times each and were counterbalanced for side placement.

Results

All three chimpanzees exceeded chance levels of performance as assessed with a sign test, $p < 0.001$. Lana and Sherman selected the larger quantity on 81.7% of the trials, and Panzee selected the larger quantity on 86.7% of the trials. Performance as a function of the ratio between sets is presented in Figure 3. Combining the data from all chimpanzees showed a significant correlation between ratio and percent of trials in which the larger quantity was selected, $r(9) = -0.89$, $p < 0.001$. In addition, all three chimpanzees showed this negative correlation individually: Lana $r(9) = -0.74$, $p = 0.009$, Panzee $r(9) = -0.67$, $p = 0.025$, and Sherman $r(9) = -0.72$, $p = 0.012$. The three chimpanzees were all correct on their very first trial in this phase. I examined performance on each of the individual comparisons the first time they were presented to each chimpanzee. There were 15 of these first-trial comparisons. Lana was correct on 13 of 15 trials ($p = 0.004$, binomial test). Sherman and Panzee both were correct on 12 of 15 trials ($p = 0.018$, binomial test).

To compare performance in Experiment 1 to performance in Experiment 2, an Analysis of Covariance was conducted with ratio as the covariate and the percentage of trials correct as the dependent variable. This analysis indicated that performance in Experiment 1 and performance in Experiment 2 were not significantly different, $F_{1, 19} = 3.70$, $p = 0.07$.

Discussion

Chimpanzees performed at comparable levels to Experiment 1. This is important because it demonstrates that the chimpanzees' performance in Experiment 1 did not rely on the temporal cue of liquid pouring duration. If the chimpanzees were only attending to the presentation time of each quantity, in this experiment they would have failed because one set was presented in its entirety in such a way that it offered no temporal cues that could be correlated with the total amount of juice. In addition, the data from this experiment indicated that chimpanzees could compare visible continuous quantities to nonvisible continuous quantities at the point where a response was made, and they did so at high levels. Seeing the liquid earlier in the trial (as it fell into the containers) was sufficient for them to generate a representation of that amount.

The likely explanation for what occurred during the experiment is that the chimpanzees watched the dispensed liquid as it fell into the container and then used a representation of that amount for comparison to the visible set. They likely benefitted from experience in the first experiment, where they had a chance to refine that representation of amount on the basis of seeing liquid fall into opaque containers. Certainly that experience helped them in the same circumstance (watching liquids fall) to generate an estimate of the amount in the container and then compare that to the other, fully visible liquid quantity. Thus, as with discrete sets (Beran, 2004), information obtained and remembered from when the liquids

were visible and falling was stored in a quantitative form conducive for comparison with another, fully visible quantity at the point of a choice response.

The final experiment was designed to assess whether chimpanzees were susceptible to a visual illusion of overestimating continuous quantity on the basis of the height from which that quantity was presented. As noted, this illusion occurs because the greater height creates the impression that more liquid has been seen than actually is the case. If chimpanzees are susceptible to this illusion, performance should decrease compared to Experiment 1. The working hypothesis was that the chimpanzees would be susceptible to the illusion, based in part on previous research that showed that nonhuman primates show similar perceptual errors to humans by overestimating the quantity of discrete items in regularly arranged configurations compared to random arrangements (Beran, 2006). Thus, chimpanzees may also show such perceptual biases on the basis of non-quantitative information during presentation of continuous quantities.

The final experiment also controlled one additional aspect of the previous two experiments that might have acted as a cue to the chimpanzees. When liquids were dispensed from syringes into containers, they provided auditory feedback as they splashed into the bottom of the container. As more liquid was poured, this sound changed, and this might have offered a cue as to the total amount. Although this seems unlikely, especially in Experiment 2 where only one quantity gave any such auditory feedback (because the other was presented already in a container), it was important to confirm this was not a cue used by the chimpanzees. By raising the height of the syringe for one of the two presented quantities in Experiment 3, this ensured that all trials would produce much more auditory feedback from the quantity presented from a greater height, independent of the actual amount in that set. In other words, this manipulation meant that the amount that fell further always was louder as it splashed into the opaque container even if it was the smaller amount.

Experiment 3 Methods

Participants and Apparatus

The same three chimpanzees were tested using the same apparatus.

Design and Procedure

In this experiment, both sets again were presented from opaque syringes into opaque containers as in the second phase of Experiment 1. However, the difference in this experiment is that the second quantity was always presented from a much greater height (45 cm) so the liquid was visible for a longer period of time. In addition, this manipulation had the consequence that this second quantity always produced much more auditory feedback in the form of filling liquid in the bottom of the container. Thus, on every trial this auditory feedback was stronger for this set than for the other set, and for all trials in which the ratio was .50 or larger there was more visual feedback from the second quantity as well because the set was released from twice as high. All other procedural details were the same as in the previous experiments. Each chimpanzee again completed 4 sessions of 15 trials, and all

possible combinations of 1 to 6 units were presented four times each and were counterbalanced for side placement.

Results

All three chimpanzees exceeded chance levels of performance as assessed with a sign test, $p < 0.001$. Lana selected the larger quantity on 80.0% of the trials, Panzee selected the larger quantity on 83.3% of the trials, and Sherman selected the larger quantity on 78.3% of the trials. The three chimpanzees were all correct on their very first trial in this phase. I examined performance on each of the individual comparisons the first time they were presented to each chimpanzee. There were 15 of these first-trial comparisons. Panzee was correct on 13 of 15 trials ($p = 0.004$, binomial test). Sherman and Lana both were correct on 12 of 15 trials ($p = 0.018$, binomial test). This confirmed that the chimpanzees were not responding to the auditory feedback or the greater pouring height, or else they always would have selected the set falling from the syringe that was held higher.

Performance as a function of the ratio between sets is presented in Figure 4. Combining the data from all chimpanzees showed no significant correlation between ratio and percent of trials in which the larger quantity was selected, $r(9) = -0.45$, $p = 0.16$. Only one chimpanzee, Panzee, showed a significant negative correlation on an individual basis, $r(9) = -0.67$, $p = 0.024$. Lana, $r(9) = -0.32$, $p = 0.33$, and Sherman, $r(9) = -0.05$, $p = 0.89$, showed no significant correlation. In large part, this lack of a correlation was because of the more constant level of performance for the chimpanzees across all ratios except the two largest ratios. This difference from the previous experiments required a closer evaluation of the possible effect of which set was released from the greater height.

Combining all trials with ratios of .50 or larger in which the larger amount was presented from a shorter height (and, thus, gave a smaller amount of visual feedback and auditory feedback), the chimpanzees performed at levels significantly above chance in choosing the larger amount: Lana – 83.3%, Panzee – 83.3%, Sherman – 66.7%. In addition, their overall performance was equally high on those trials (78% correct) as it was on the trials in which the larger amount of juice was poured from the greater height (85%), $X^2(1, N = 108) = 0.98$, $p = 0.32$. However, for the two largest ratios, .80 and .83, the chimpanzees performed lower when the larger set was poured from the shorter height (41.6%) than when it was poured from the greater height (91.6%), $X^2(1, N = 24) = 6.75$, $p = 0.009$. Thus, the chimpanzees overall were not susceptible to the illusion created by raising the height at which the quantity was dispensed, but they did show a bias based on height for the most difficult comparisons. It is important to note that, in this experiment, pouring duration was confounded with amount, so that cue still remained for the chimpanzees. But, what chimpanzees could not use was height of the syringe or the more novel sound of liquid hitting the container from a greater height as a cue in this experiment. It is also important to note that the chimpanzees may have benefitted from performing this experiment after gaining experience in the previous experiments, and thus their performance may reflect a refined ability to discriminate poured liquids that occurs only with such experience.

General Discussion

It is well established that apes and other animals are very good at comparing discrete sets of items and choosing larger or smaller quantities of such items. It is well known also that such performances are constrained by the effects of Weber's law, whereby the accuracy of discrimination of two sets is consistent only if relative differences are increased along with increases in the magnitude of the sets. The present study offers two new findings to our understanding of the quantitative skills of nonhuman animals.

The first is the chimpanzees perform nearly identically in comparing continuous quantities as they do in comparing discrete quantities. Although it was not surprising that they could select the larger of two visible continuous quantities given past demonstrations of their excellent discrimination of very small differences between items (e.g., Menzel, 1961; Menzel and Draper, 1965), it was impressive that they could do so when neither quantity was ever visible in its entirety and when the point of responding occurred in the complete absence of any visual information. Chimpanzees still successfully selected the larger of two continuous quantities, and subsequent experiments indicated that visual quantity guided responding as opposed to temporal cues or possible auditory feedback. Thus, chimpanzees selected the larger of two liquid quantities through a variety of presentation forms, and they did so in ways that were seemingly identical to how they represent discrete quantities.

For both discrete and continuous quantity comparisons, Weber's law was obeyed in the chimpanzees' performances. These data, suggestive of analog representation of continuous and discrete quantity, are well predicted by the *accumulator model* for the nonverbal representation of quantity (Meck and Church, 1983; for reviews see Brannon; 2007; Brannon and Roitman, 2003; Cantlon, Brannon, and Platt, 2009; Gallistel & Gelman, 2000). This model involves a pacemaker that puts out pulses, and a mode switch that can be opened and closed to pass these pulses to the accumulator. The pacemaker can operate in either a clock mode in which the switch operates in a run or stop mode, or it can operate as a counter for individual events. The value of the accumulator is passed to working memory, and the current value of the accumulator can be compared to previously stored accumulator values from other events. A mechanism like the accumulator may be used by chimpanzees in an event mode for discrete items, and they may use the same mechanism in a start/stop mode not only for temporal information but also to encode quantitative information presented in a continuous manner. Thus, the timer mode could operate for estimation and representation of continuous quantity through the same gating principles of 'turning on' as long as the animal sees this continuous stream of liquid and then 'turning off' after presentation is complete. Importantly, the data from Experiment 2 indicate that chimpanzees can encode information using an accumulator-like mechanism in a start/stop mode and compare that representation to another quantity that was not subject to a start/stop switch but instead offered a singular perceptual event regarding total amount of liquid present. This demonstrates the flexibility of an accumulator mechanism for quantity representation.

The second new finding pertains to the relatively benign effect of varying the height of presentation on continuous amount estimation in chimpanzees. Even when the height of one quantity was such that it provided much more visual feedback and produced more auditory

feedback, the chimpanzees were not distracted from the relevant dimension of total amount of liquid in the two sets. Thus, this illusion was not detrimental to performance of the chimpanzees except at the most difficult discrimination levels where they did show some susceptibility to erroneous decision making.

The successful performance on all experiments indicates that the chimpanzees were able to conserve the quantities through various manipulations and forms of presentation, adding new evidence to that provided by previous studies (e.g., Beran, 2007; Call and Rochat, 1997; Suda and Call, 2004, 2005). They also showed some degree of object tracking for these continuous quantities, a manipulation that has presented difficulties for other nonhuman species (e.g., Mahajan, Barnes, Blanco, and Santos, 2009) and a skill that arises later in development for human children than tracking of discrete, rigid objects (e.g., Cheries, Mitroff, Wynn and Scholl, 2008; Chiang and Wynn, 2000). Future studies could vary other presentation aspects such as the width of the liquid stream and the rate of presentation by varying the syringe opening and the pressure at which the liquids were dispensed. It would be intriguing if chimpanzees also could account for how those aspects of presentation affected the total amount of liquid in the two containers. Such studies might provide additional data on the extent to which chimpanzees act as folk physicists, a question of ongoing debate in the comparative literature (e.g., Hunt et al. 2006; Povinelli, 2000; Silva et al. 2005). They also would help further outline our understanding of the breadth of animal quantitative skills.

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References

- Anderson US, Stoinski TS, Blooms Smith MA, Marr MJ, Smith AD, Maple TS. Relative numerosness judgment and summation in young and old Western Lowland gorillas. *J Comp Psychol.* 2005; 119:285–295. [PubMed: 16131257]
- Anderson US, Stoinski TS, Blooms Smith MA, Maple TS. Relative numerosness judgment and summation in young, middle-aged, and old adult orangutans (*Pongo pygmaeus abelii* and *Pongo pygmaeus pygmaeus*). *J Comp Psychol.* 2007; 121:1–11. [PubMed: 17324070]
- Beran MJ. Summation and numerosness judgments of sequentially presented sets of items by chimpanzees (*Pan troglodytes*). *J Comp Psychol.* 2001; 115:181–191. [PubMed: 11459165]
- Beran MJ. Chimpanzees (*Pan troglodytes*) respond to nonvisible sets after one-by-one addition and removal of items. *J Comp Psychol.* 2004; 118:25–36. [PubMed: 15008670]
- Beran MJ. Quantity perception by adult humans (*Homo sapiens*), chimpanzees (*Pan troglodytes*), and rhesus macaques (*Macaca mulatta*) as a function of stimulus organization. *Int J Comp Psychol.* 2006; 19:386–397.
- Beran MJ. Rhesus monkeys (*Macaca mulatta*) enumerate sequentially presented sets of items using analog numerical representations. *J Exp Psychol Anim Behav Proc.* 2007; 33:42–54.
- Beran MJ. Rhesus monkeys (*Macaca mulatta*) succeed on a computerized test designed to assess conservation of discrete quantity. *Anim Cogn.* 2007; 10:37–45. [PubMed: 16868737]
- Beran MJ. Capuchin monkeys (*Cebus apella*) succeed in a test of quantity conservation. *Anim Cogn.* 2008; 11:109–116. [PubMed: 17549530]

- Beran MJ. Monkeys (*Macaca mulatta* and *Cebus apella*) track, enumerate, and compare multiple sets of moving items. *J Exp Psychol Anim Behav Proc.* 2008; 34:63–74.
- Beran MJ, Beran MM. Chimpanzees remember the results of one-by-one addition of food items to sets over extended time periods. *Psychol Sci.* 2004; 15:94–99. [PubMed: 14738515]
- Brannon EM. The representation of numerical magnitude. *Curr Opin Neurol.* 2006; 16:222–229.
- Brannon, EM.; Roitman, J. Nonverbal representations of time and number in animals and human infants. In: Meck, W., editor. *Functional and neural mechanisms of interval timing.* New York: CRC Press; 2003. p. 143–182.
- Brannon EM, Terrace HS. Representation of the numerosities 1–9 by rhesus macaques (*Macaca mulatta*). *J Exp Psychol Anim Behav Proc.* 2000; 26:31–49.
- Call J. Estimating and operating on discrete quantities in orangutans (*Pongo pygmaeus*). *J Comp Psychol.* 2000; 114:136–147. [PubMed: 10890585]
- Call J, Rochat P. Perceptual strategies in the estimation of physical quantities by orangutans (*Pongo pygmaeus*). *J Comp Psychol.* 1997; 111:315–329. [PubMed: 9419878]
- Cantlon JF, Brannon EM. How much does number matter to a monkey (*Macaca mulatta*)? *J Exp Psychol Anim Behav Proc.* 2007; 33:32–41.
- Cantlon JF, Platt ML, Brannon EM. Beyond the number domain. *Trends Cogn Sci.* 2009; 13:83–91. [PubMed: 19131268]
- Cherries EW, Mitroff SR, Wynn K, Scholl BJ. Cohesion as a constraint on object persistence in infancy. *Dev Sci.* 2008; 11:427–432. [PubMed: 18466376]
- Chiang WC, Wynn K. Infants' representation and tracking of multiple objects. *Cogn.* 2000; 77:169–195.
- Czerny P, Thomas RK. Sameness-difference judgments in *Saimiri sciureus* based on volumetric cues. *Anim Learn Behav.* 1975; 3:375–379.
- Gallistel CR, Gelman R. Non-verbal numerical cognition: From reals to integers. *Trends Cogn Sci.* 2000; 4:59–65. [PubMed: 10652523]
- Hanus D, Call J. Discrete quantity judgments in the great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus*): The effect of presenting whole sets versus item-by-item. *J Exp Psychol Anim Behav Proc.* 2007; 121:241–249.
- Hunt GR, Rutledge RB, Gray RD. The right tool for the job: What strategies do wild New Caledonian crows use? *Anim Cogn.* 2006; 9:307–316. [PubMed: 16941156]
- Jordan KE, Brannon EM. A common representational system governed by Weber's law: Nonverbal numerical similarity judgments in 6-year-olds and rhesus macaques. *J Exp Child Psychol.* 2006; 95:215–229. [PubMed: 16808924]
- Mahajan N, Barnes JL, Blanco M, Santos LR. Enumeration of objects and substances in non-human primates: Experiments with brown lemurs (*Eulemur fulvus*). *Dev Sci.* 2009; 12:920–928. [PubMed: 19840047]
- McGarrigle J, Donaldson M. Conservation accidents. *Cogn.* 1974; 3:341–350.
- Meck WH, Church RM. A mode control model of counting and timing processes. *J Exp Psychol Anim Behav Proc.* 1983; 9:320–324.
- Mehler J, Bever TG. Cognitive capacity of very young children. *Science.* 1967 Oct 6.158:141–142. [PubMed: 6054816]
- Menzel EW. Perception of food size in the chimpanzee. *J Comp Physiol Psychol.* 1961; 54:588–591.
- Menzel EW, Draper WA. Primate selection of food by size: Visible versus invisible rewards. *J Comp Physiol Psychol.* 1965; 59:231–239. [PubMed: 14288348]
- Muncer SJ. "Conservations" with a chimpanzee. *Dev Psychol.* 1983; 16:1–11.
- Piaget, J. *The child's conception of number.* New York: Norton; 1965.
- Piaget, J. *The mechanisms of perception.* London, UK: Rutledge Kegan Paul; 1969.
- Povinelli, DJ. *Folk physics for apes: The chimpanzee's theory of how the world works.* Oxford, UK: Oxford University Press; 2000.
- Pylyshyn ZW, Storm RW. Tracking multiple independent targets: Evidence for a parallel tracking mechanism. *Spatial Vision.* 1988; 3:179–197. [PubMed: 3153671]

- Raghubir P, Krishna A. Vital dimensions in volume perception: Can the eye fool the stomach? *J Marketing Res.* 1999; 36:313–326.
- Rumbaugh DM, Savage-Rumbaugh ES, Hegel MT. Summation in the chimpanzee (*Pan troglodytes*). *J Exp Psychol Anim Behav Proc.* 1987; 13:107–115.
- Santos LR, Barnes JL, Mahajan N. Expectations about numerical events in four lemur species *Eulemur fulvus*, *Eulemur mongoz*, *Lemur catta* and *Varecia rubra*. *Anim Cogn.* 2005; 8:253–262. [PubMed: 15729569]
- Shumaker RW, Palkovich AM, Beck BB, Guagnano GA, Morowitz H. Spontaneous use of magnitude discrimination and ordination by the orangutan (*Pongo pygmaeus*). *J Comp Psychol.* 2001; 115:385–391. [PubMed: 11824901]
- Silva FJ, Page DM, Silva KM. Methodological-conceptual problems in the study of chimpanzees' folk physics: How studies with adult humans can help. *Learn Behav.* 2005; 33:47–58. [PubMed: 15971492]
- Suda C, Call J. Piagetian liquid conservation in the great apes (*Pan paniscus*, *Pan troglodytes* and *Pongo pygmaeus*). *J Comp Psychol.* 2004; 118:265–279. [PubMed: 15482054]
- Suda C, Call J. Piagetian conservation of discrete quantities in bonobos (*Pan paniscus*), chimpanzees (*Pan troglodytes*), and orangutans (*Pongo pygmaeus*). *Anim Cogn.* 2005; 8:220–235. [PubMed: 15692813]
- vanMarle K, Aw J, McCrink K, Santos LA. How capuchin monkeys (*Cebus apella*) quantify objects and substances. *J Comp Psychol.* 2006; 120:416–426. [PubMed: 17115863]
- Wansink B, Van Ittersum K. Bottoms up! The influence of elongation on pouring and consumption volume. *J Consume Res.* 2003; 33:1512–1514.
- Wansink B, Van Ittersum K. Shape of glass and amount of alcohol poured: Comparative study of effect of practice and concentration. *Br Med J.* 2005; 331:1512–1514. [PubMed: 16373735]
- Woodruff G, Premack D, Kennel K. Conservation of liquid and solid quantity by the chimpanzee. *Science.* 1978 Dec.1 202:991–994. [PubMed: 17798798]

Figure 1.

The test apparatus. The bench allowed for baiting of containers out of view of the chimpanzees. Containers were presented on the top of the bench and were either opaque (left in figure) or clear (right in figure). Syringes were opaque so that liquids could only be seen once they were dispensed.

Figure 2.

Total performance of the chimpanzees in selecting the larger quantity as a function of the ratio between the two quantities. The dark line shows performance with the continuous quantities of Experiment 1 (the bars indicate the range of performance for the three chimpanzees). The light line shows performance of Lana and Sherman when previously tested on the same quantitative comparisons but with discrete items (Beran, 2004).

Figure 3.

Total performance of the chimpanzees in selecting the larger quantity as a function of the ratio between the two quantities in Experiment 2. The bars indicate the range of performance for the three chimpanzees.

Figure 4.

Total performance of the chimpanzees in selecting the larger quantity as a function of the ratio between the two quantities in Experiment 3. The bars indicate the range of performance for the three chimpanzees.