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What counts for ‘counting’? Chimpanzees, *Pan troglodytes*, respond appropriately to relevant and irrelevant information in a quantity judgment task

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Abstract

Nonhuman animals quantify all manner of things, and the way in which this is done is fairly well understood. However, little research has been conducted to determine how they know what is or is not relevant in the instances in which they quantify stimuli. We assessed how four chimpanzees chose between two sets of food items when the items were distributed across separate spatial arrays. Each item was covered by a container, and then was revealed in sequence so that neither whole set was visible at one time. After all containers were revealed, some were revealed again. The chimpanzees should have ignored items that were seen a second time and instead enumerated each item only once. In another test, some of the items were transposed in location and then uncovered again. Here, the chimpanzees needed to recognize that the newly shown food items were ones they already had seen. Overall, the chimpanzees were successful in selecting the truly larger array of items despite these potential distracting re-presentations of items. Discrimination performance also reflected analogue magnitude estimation because comparisons of sets that differed by larger amounts were easier than comparisons that differed by smaller amounts. Thus, chimpanzee quantity judgments for nonvisible sets of items are inexact, but they include an aspect of control for determining when items are uniquely presented versus re-presented.

Keywords

approximate number system; chimpanzee; enumeration; *Pan troglodytes*; quantity judgment; transposition

One of the most widespread cognitive abilities found in the animal kingdom is the ability to make relative quantity judgments (RQJs) for sets of items (Brannon & Roitman 2003). When shown two or more sets of items that vary in their quantity (e.g. number and amount), nearly all species tested to date have passed this test by selecting the relevant quantity. These species include many genera, including fish (Agrillo et al. 2008, 2012; Piffer et al. 2012), amphibians (Uller et al. 2003; Krusche et al. 2010), birds (Emmerton 1998; Rugani et al. 2009; Garland et al. 2012), and a large variety of mammals (e.g. Ferkin et al. 2005;

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Jaakkola et al. 2005; Ward & Smuts 2007; Irie-Sugimoto et al. 2009; Abramson et al. 2011; Perdue et al. 2012; Vonk & Beran 2012; Yaman et al. 2012). The most widely studied species are the nonhuman primates (e.g. Call 2000; Beran 2001, 2004; Anderson et al. 2005, 2007; Hanus & Call 2007; Tomonaga 2007; Addessi et al. 2008; Evans et al. 2009; Mahajan et al. 2009), all of whom show competencies in a variety of tasks that involve judging quantities, including auditory quantity judgments (e.g. Beran 2012) and even judgments between sequentially presented sets of items that can take a long time to complete (e.g. Beran & Beran 2004).

Most researchers now have converged on the consensus that animals represent quantities through an approximate form of representation, such as that proposed in the accumulator model (Meck & Church 1983; Gallistel & Gelman 2000; Brannon & Roitman 2003), in other descriptions of the approximate number system (ANS; Cantlon et al. 2009), and in models describing the neuronal bases of numerical and quantity representation (e.g. Nieder & Merten 2007; Nieder & Miller 2003). In all of these models, quantities and numbers are represented with an inherent inexactness, and that inexactness increases as a function of the true value of the set (i.e. perception and representation of quantities follows Weber's law). For this reason, it is more difficult to make a comparison between eight items and 10 items than it is between three items and five items, even though both comparisons differ by only two items. At the same time, a comparison between three items and six items is as difficult as a comparison between six items and 12 items, because the ratio of the small set to the large set remains the same in both cases. Thus, we now know a lot about how animals represent quantities, and what constrains their ability to tell the difference between two or more choices, and to order the magnitude of sets on the basis of their numerical properties or other quantitative properties (such as size or amount; see Gallistel & Gelman 2000; Brannon & Roitman 2003; Cantlon 2009; see also Nieder 2005).

The accumulator model describes how an organism could increase the stored representation of inexact quantity and use the resulting addend to make relative or absolute judgments (Meck & Church 1983). The stored representation within the accumulator for the total quantity of a set is increased by one tally or pulse for each item that is enumerated. At the end of the enumeration, the accumulation is stored in memory as an approximate magnitude (due to the inherent variability that occurs with each analogue pulse that accumulates). These stored quantities then can be compared to guide choice behaviour (Gallistel & Gelman 2000). The accumulator may even operate in such a way that subtraction operations could be represented, presumably by having the stored representation diminish when a subtractive event is experienced. There is some evidence that nonhuman animals can respond appropriately to subtractions, although this sometimes appears to be a more difficult manipulation for them to accommodate (e.g. Brannon et al. 2001; Beran 2004; Rugani et al. 2009). For example, Sulkowski & Hauser (2001) presented rhesus monkeys, *Macaca mulatta*, with a variety of comparisons of sets of edible and inedible food items where items were removed from sets after initially being seen. They found that the monkeys attended to the type of objects seen, presumably dismissing irrelevant items when judging the arrays, and responded appropriately to the consequence of the arithmetic manipulations that were performed on those relevant items. However, what remains unknown is whether the mechanism that operates to generate representations of quantity is under the voluntary control of the organism, or whether it simply activates whenever a sensory input occurs that is of the relevant stimulus type (i.e. food item rather than nonfood item) for the task being performed. In other words, although it seems clear that a mechanism such as the accumulator will update its representation of the quantity of food items it perceives in an array, we do not know whether the accumulator does this automatically whenever an item is perceived, or only when a uniquely relevant item is perceived. For example, a chimpanzee might be faced with the choice of two small piles of nuts to approach and carry to a site with

a hammer stone. One pile is larger than the other, but as the chimpanzee approaches, a single new nut falls near the smaller pile and causes the other nuts in that pile to move around. Does the resulting new location of items already accommodated in the representation of this smaller set cause the chimpanzee to erroneously overrepresent the quantity in that set, or does the chimpanzee ignore that visuospatial change because it is not a relevant quantitative change? One assumes the latter outcome is likely, especially given that chimpanzees (and other animals) seem to understand number conservation and other aspects of basic physical changes that do or do not impact the items around them (e.g. Woodruff et al. 1978; Call & Rochat 1996; Suda & Call 2004, 2005; Beran 2007, 2008). However, this assumption should not be taken lightly, and it may factor more broadly into the nature of chimpanzee numerical cognition, especially with regard to capacities related to formal counting procedures. Gelman & Gallistel (1978) outlined five counting principles that all children must meet to be proficient counters. Of particular importance here is 'one-to-one correspondence', which means that each item in a to-be-enumerated array is to be tallied exactly once, with no skipping and no double counting (the other four principles are 'stable order', 'cardinality', 'abstraction' and 'order irrelevance'). Misrepresentation of quantity occurs if items are missed or are counted or tallied more than once, and so mechanisms must be in place to monitor and control the guided process of one-to-one correspondence during counting. This one-to-one correspondence often takes time to develop in children, along with each of the other counting principles. In the present study, we directly assessed whether such spatial changes cause misrepresentations of quantity by animals, or whether such one-to-one correspondences can occur without true counting routines.

The present experiment combined a spatial memory component with the main quantity judgment requirement. There is a large amount of research addressing spatial memory in nonhuman animals (e.g. Gibeault & MacDonald 2000; Menzel et al. 2002; Sanford & Clayton 2008; Scheid & Bugnyar 2008; Albiach-Serrano et al. 2010; Perdue et al. 2011), but little research has addressed the interaction of quantity discrimination and the spatial distribution of items in multiple arrays (e.g. MacDonald 1994). However, in one case (A. Garland, M. J. Beran, J. M. McIntyre & J. Low, unpublished data), chimpanzees and New Zealand robins, *Petroica longipes*, were presented with two sets of items, each distributed across an array of seven locations that consisted of occluders that could (or could not) have food items hidden beneath them. Subjects chose between the two 7-location arrays, presumably in an attempt to choose the array with the most food items distributed under the occluders. Both species performed at above-chance levels on this quantity judgment, although the ratio of items between sets was a significant predictor of performance in chimpanzees but not in robins.

In the present experiment, chimpanzees were presented with two arrays of food items to choose from, in which all items were hidden under individual containers. This allowed us to present each item in a distinct spatial location within an array. We also could selectively re-reveal certain items, either by lifting the container at that location more than one time (Phase 1), or by transposing containers to each other's locations and then re-revealing them (Phase 2). Chimpanzees have successfully tracked objects through transpositions in past experiments (e.g. Beran & Minahan 2000; Call 2003; Barth & Call 2006), thereby showing that they understand the object permanence of items that move with their respective occluders. These different manipulations meant that items could be revealed more than once, and when that occurred, the chimpanzees would have to recognize that those items were not new items within the array and did not increase the overall quantity of that array. This would require some degree of control over the tallying mechanism that generated the two representations of the otherwise nonvisible sets that constituted the two choice options. If the chimpanzees performed at high levels, this would indicate that they tallied items once and only once even when the items were presented multiple times within the same trial. This

may also provide evidence that the mechanism that represents quantities does not automatically increment the quantity representation simply on the presentation of a food item, if the chimpanzee recognizes that a particular item has already been seen on that trial. Success would indicate that the mechanism for quantification of sets of items is responsive to controlled decisional processes about what items do (or do not) change the value of the represented quantity of a given array.

METHODS

Subjects

Four adult chimpanzees, two males (Sherman, 37 years old, and Mercury, 23 years old) and two females (Lana, 40 years old, and Panzee, 24 years old) were tested. These chimpanzees are housed in a facility that affords them daily access to indoor and outdoor living areas that consist of natural substrate and climbing structures as well as other forms of enrichment, and they spend time in various social arrangements in which they are housed with each other throughout each day. They voluntarily separate from each other for experimental testing such as was used in this project. These chimpanzees had a long history of making quantity judgments of visual and auditory sets (e.g. Beran 2001, 2004, 2012; Beran & Beran 2004), although they had only limited experience in judging quantities that were spread among multiple locations within an array. In another experiment (A. Garland, M. J. Beran, J. M. McIntyre & J. Low, unpublished data), food items were spatially distributed under different containers within two arrays. Items were shown one at a time by removing the containers covering them, and this was done once, and only once, for each container. The aim of the project was to compare the ability of chimpanzees and robins to sum quantities across spatial arrays. The results indicated that the chimpanzees performed at a high level and showed the signature ratio effects seen in other experiments that require relative quantity judgments by these apes (e.g. Beran 2001, 2004; Beran & Beran 2004).

Testing of the animals was approved by the Georgia State University Institutional Animal Care and Use Committee (IACUC approval number A10021) and the institution was compliant with U.S. Department of Agriculture regulations. These experiments provided a form of enrichment for the chimpanzees and did not present any risks or adverse effects.

Materials

The apparatus consisted of a mobile cart with an attached tray secured to a track. This mechanism allowed the experimenter to slide the tray back and forth to allow the chimpanzee to make a selection. A divider separated the tray creating two distinct halves where the stimulus sets were presented. A window blind was affixed to the mobile cart, allowing the researcher to bait each trial without being observed by the animal. Opaque white cups (diameter = 5.5 cm, height = 5.8 cm) were used to conceal individual candies on either side of the tray during each trial. The same apparatus was used for both phases of the study.

Procedure

Each chimpanzee was tested individually and completed a single 10-trial session per day. Sessions were completed in the late morning to early afternoon (1100–1230 hours) prior to the early afternoon feeding to ensure that there was a constant motivational state. Before each trial the experimenter placed five cups upside down on each side of the surface to form a distinct array. Each array contained three cups in the front row and two cups in the back row, spaced so that the chimpanzees could easily see all five cups from their seated position. The blind was lowered to allow the experimenter to bait the cups without the chimpanzee observing. The number of cups that concealed candies in each array varied from one to five

items across trials, and the side with the larger quantity was counterbalanced throughout sessions. During baiting, the experimenter lifted and replaced all cups and repeated some lifts so that there was no correlation between baiting duration or baiting movements and the actual number of candies left under cups in an array.

To control for unintentional cuing, the experimenter avoided eye contact while pushing the tray forward and looked down so that he could not see the chimpanzee or any movements that the chimpanzee might make. A second experimenter, out of direct view of the chimpanzees, announced and recorded the selection. This ensured that neither experimenter could inadvertently cue the chimpanzee to point to a particular array. After the chimpanzee selected an array, the first experimenter removed all cups from that array, scooped all the candies from that array into his hand, and then dropped them into the chimpanzee's hand for consumption. Figure 1 presents a schematic outline of the two test phases.

Phase 1

In this phase, the specific comparisons (i.e. the number of baited cups in the two arrays) were 1:2, 1:3, 1:4, 2:3, 2:4 and 3:5. Upon completion of baiting the cups, the experimenter raised the blind and proceeded to lift each cup to reveal its contents. Cups were revealed one at a time starting with the array on the left side (chimpanzee's right) followed by the array on the right side (chimpanzee's left). Each cup was raised for 1 s before being lowered again. In 20% of trials, after all cups were lifted once, the experimenter pushed the tray forward to allow the chimpanzee to point to one of the two sides of the apparatus. In the other 80% of trials, the experimenter relifted some of the cups. Within this 80% of the trials, half of the trials had a repeat component only on the left side and half had a repeat component only on the right side (i.e. there were never trials in which both sides underwent the relifting of cups). Three types of trials with relifted cups were completed. One type consisted of a re-reveal of a cup with a candy under it as well as a re-reveal of a cup without a candy. The second type consisted of a re-reveal of two cups with a candy under each as well as one cup without a candy. The third type re-revealed all cups in one of the arrays. After all manipulations of the arrays were completed, the experimenter pushed the tray forward and allowed the chimpanzee to make a selection by pointing to one of the two sides of the tray.

This phase included six sessions over a 2-week period. Each chimpanzee completed 60 trials in this phase. All trials could be classified into one of three types: control trials, low distraction trials and high distraction trials. Control trials were those in which each cup was lifted once and only once before a chimpanzee made a choice. Low distraction trials were trials in which the partially re-revealed set was either truly larger or truly smaller (even if the chimpanzee erroneously overestimated the number of items seen because of the re-reveals; e.g. seeing four items on the left and one item on the right, with the item on the right shown a second time; e.g. $4 > 1 + 1$). High distraction trials involved a truly smaller set that was re-revealed in such a way that it could be misperceived to be equal to or larger than the truly larger set (e.g. three items versus two items, with both items in the two-item set shown again so that four items were viewed on that side; e.g. $3 < 2 + 2$). These trial types were analysed individually.

Phase 2

In this phase, the specific comparisons presented were 1:3, 2:3, 2:4, 3:4 and 3:5. Phase 2 included five sessions over a 2-week period, and each chimpanzee completed 50 trials. Phase 2 followed the same general procedure as Phase 1, with the only difference being that cups on the right side always received a transposition component. After all cups on the left side and then the right side were revealed, two pairs of cups (in which one cup contained a

candy and one did not, in each pair) were transposed within the array, then re-revealed. The transposition occurred by simultaneously sliding one pair of cups, and then the other, across the board so that each cup within a pair took the place of the other cup. This meant that in both instances, after being transposed, the empty cup and the cup containing candy had exchanged locations within the array. At the end of these manipulations, four of the five cups within the right array were in new locations compared to the first reveal. For trials where the total amount of candy on the right side was only one item, one pair of empty cups was transposed within the array. While being transposed, the cups were not lifted, so the contents were not revealed at that time. After the cups were transposed and the re-reveal was completed, the chimpanzee was allowed to make a selection.

These transpositions should not have led to increased estimates of the quantity in the second array if the chimpanzees could accommodate the nature of the transpositions (e.g. Beran & Minahan 2000; Call 2003; Barth & Call 2006). For this phase, trials in which the larger set was on the right side were considered to be the easier trials, because the transpositions and re-reveals only could have made those sets appear even bigger to the chimpanzees. Trials with the larger set on the left were considered the more difficult trials, because the transpositions and re-reveals on the right side meant that the chimpanzees could have misperceived the quantity of candies on the right to be equal to or larger than the left array, even though some of those candies were the same ones the chimpanzees had already seen.

RESULTS

The chimpanzees successfully selected the truly larger array of candies in all trial types of Phase 1 (Fig. 2). Binomial tests confirmed that for every trial type for each chimpanzee, performance was significantly better than chance ($P < 0.05$). For each chimpanzee, there was no significant difference in performance across the three conditions (chi-square test: Lana: $\chi^2_2 = 1.04$, $P = 0.59$; Sherman: $\chi^2_2 = 1.49$, $P = 0.47$; Panzee: $\chi^2_2 = 1.43$, $P = 0.49$; Mercury: $\chi^2_2 = 1.07$, $P = 0.58$), indicating that they performed similarly in all cases. Table 1 presents each chimpanzee's performance on each individual comparison used in this phase. A comparison of performance on the first and last session indicated no differences in chimpanzees' performance over time (% correct first and last session, Fisher's exact test: Lana: 100% and 100%, $P = 1.0$; Mercury: 90% and 80%, $P = 1.0$; Panzee: 90% and 90%, $P = 1.0$; Sherman: 100% and 80%, $P = 0.47$).

Figure 3 shows performance in Phase 2 by each chimpanzee for trials where the larger set was on the left (more difficult trials) or on the right (easier trials). Sherman and Lana performed significantly better than chance on both trial types (binomial test: $P < 0.01$). Panzee and Mercury performed significantly better than chance on trials where the larger set was on the right (binomial test: $P < 0.05$), but neither differed significantly from chance levels on trials where the larger set was on the left (binomial test: Panzee: $P = 0.11$; Mercury: $P = 0.23$). There was no difference in performance between trial types for Sherman (Fisher's exact test: $P = 0.23$), Lana ($P = 1.0$) or Panzee ($P = 0.76$). Mercury, however, performed significantly better on trials where the larger set was on the right than he did on trials where the larger set was on the left (Fisher's exact test: $P < 0.001$).

As in Phase 1, a comparison of performance on the first and last session indicated no significant differences in chimpanzees' performance over time (% correct first and last session, Fisher's exact test: Lana: 80% and 100%, $P = 0.47$; Mercury: 70% and 80%, $P = 1.0$; Panzee: 80% and 80%, $P = 1.0$; Sherman: 100% and 90%, $P = 1.0$; Table 1).

DISCUSSION

Four chimpanzees were presented with sets of food items that were spatially distributed under individual containers. After observing the one-by-one uncovering of these sets, the chimpanzees also saw additional manipulations of these sets, all of which functioned to re-present items that already had been seen. These manipulations potentially could have led the chimpanzees to overestimate the number of items in those sets, but in most cases, the chimpanzees still selected the set with the overall larger amount of food. Thus, despite manipulations that involved re-showing, or moving the items to new locations and then showing them again, the chimpanzees recognized which presentations of food items were relevant and which were not, and responded at very high levels in most cases. In essence, these results suggest that chimpanzees do know what 'counts for counting', although the actual mechanism that provides the representations of set size is most likely not a formal counting routine, but instead, involves the use of a relative quantity judgment process (RQJ).

These chimpanzees have a long history of successfully performing RQJs in which they are presented multiple sets of items, and in some cases this included observing additions or subtractions to sets (e.g. Beran 2001, 2004, 2012; Beran & Beran 2004). In those tests, all items that were seen were relevant to the representations that the chimpanzees formed and used to choose between sets. They had never seen trials in which some items were presented more than once, but did not increase the quantity in sets. In these experiments, the chimpanzees saw individual food items, each under a unique container, along with empty containers that held no food items. Previous research showed that the chimpanzees could tally across these containers and choose the spatial set that held the larger number of total food items (A. Garland, M. J. Beran, J. M. McIntyre & J. Low, unpublished data). Here, we manipulated the sets after all containers were revealed to see whether this would create a distraction and disrupt the accurate representation of true set sizes. For the most part, these manipulations were not detrimental to the chimpanzees' performances. However, there were some individual differences, especially in Phase 2. Most of the chimpanzees performed well, but one chimpanzee (Mercury) in particular showed a bias to choose the array on the right, which was always the last array revealed (and manipulated via transposition). Thus, performance was not always high and may have been influenced by local enhancement for the last array revealed. Given Mercury's success in Phase 1, however, it seems unlikely that he chose the last array simply because it was the last one revealed; instead, it seems more likely that his estimation of array quantity was affected by the transposition of the array.

The present results suggest that chimpanzees do understand that not all food items they see should be tallied, because some items are not relevant. This was true when sets were shown and then re-shown, and also when containers were transposed first, and then re-shown. In the latter case, the re-revealed items were actually in new spatial locations. This did seem to make the task more difficult for some of the chimpanzees, but some were still very successful in choosing the overall larger amount of food. Therefore, these chimpanzees seemed to know which items needed to be attended to and uniquely tallied, and which items could be ignored.

At a theoretical level, these results are important because they indicate that the mechanism used to represent quantities in an approximate manner can operate, at least in chimpanzees, in a controlled mode. This control involves selectively determining which of the viewed items should be tallied, which suggests some degree of voluntary monitoring of items as well as selective processing of the perceived stimuli, with regard to their effect on the analogue representation of quantity. This would be a critically necessary feature of a model (e.g. the accumulator) if it were to support different kinds of quantification processes, particularly for complicated quantity judgments such as those pertaining to moving items

that change in location but not numerosness (e.g. Beran 2008; Beran et al. 2011), or to those that occur after arithmetic operations (e.g. Boysen & Berntson 1989). For example, the accumulator does not represent numerosity or other quantities exactly (Meck & Church 1983; Cantlon et al. 2009), but it would need to accurately distinguish and represent events that were relevant tallies (e.g. uniquely seen food items) without automatically tallying any event or item that was perceived (e.g. any food item of that set, whether previously seen or not). The present results suggest that, at least in chimpanzees, this process does occur. The question for future research is how flexibly chimpanzees and other animals can accommodate more complicated events that offer distractions to true representations of quantity. Such studies will illuminate new aspects of the nonverbal approximate number system that is shared across many species and that likely underlies much of the mathematical cognition that emerges in human development.

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- Animals discriminate between quantities, but do they know what 'counts' in such discriminations?
- Four chimpanzees chose between two arrays of food items.
- Sometimes, individual items were seen more than once.
- These re-presentations of items needed to be ignored for accurate judgments of array quantities to occur.
- Chimpanzees selected the correct arrays with more food despite these attempts to bias their judgments.

Phase 1

Phase 2

Figure 1.

A schematic of the two test phases. In Phase 1, food items were hidden under each array (a). Each cup was then lifted, in succession, as shown in (b) and (c) for the first two cups, and this continued for all cups. Then, some cups were lifted a second time, and sometimes those again had a food item underneath (d), but sometimes did not (e). In Phase 2, cups again were baited (f), and all cups were lifted in succession (g, h). Then, two pairs of cups in one of the arrays were transposed in position (i). After these transpositions, food items that already had been seen were now in new positions (j). All cups in that array were then lifted again in succession.

Figure 2.

Mean percentage of trials in which chimpanzees selected the truly larger array of candies in Phase 1, where each cup was lifted once (control), the partially re-revealed set was either truly larger or truly smaller and should not be misperceived (low distraction), or a truly smaller set was re-revealed in such a way that it could be misperceived to be equal to or larger than the truly larger set (high distraction). Chimpanzees' performance was significantly better than chance (shown by the horizontal line) in all conditions and was equivalent across all three conditions.

Figure 3.

Mean percentage of trials in which chimpanzees selected the truly larger array of candies in Phase 2, where the larger set was on the left or on the right. Asterisks indicate conditions in which the selection of the truly larger array of candies was significantly better than chance (shown by the horizontal line).

Table 1

Performance (number of trials) in which the correct array was chosen by each chimpanzee for each comparison in Phase 1 and Phase 2

	Lana	Sherman	Panzee	Mercury
Phase 1				
1:2	9/10	10/10	6/10	8/10
1:3	10/10	10/10	10/10	9/10
1:4	8/8	8/8	8/8	8/8
2:3	10/10	8/10	9/10	7/10
2:4	10/10	9/10	9/10	7/10
3:5	10/12	10/12	11/12	11/12
Phase 2				
1:3	10/10	10/10	7/10	9/10
2:3	10/10	9/10	7/10	7/10
2:4	9/10	10/10	8/10	7/10
2:5	10/10	10/10	7/10	5/10
3:4	8/10	8/10	7/10	6/10

Two arrays of five cups were presented that differed in the number of cups baited with candy; the correct array had the larger number of baited cups.