Published in final edited form as:

J Exp Psychol Anim Behav Process. 2012 January ; 38(1): 23–29. doi:10.1037/a0024965.

Quantity Judgments of Auditory and Visual Stimuli by Chimpanzees (*Pan troglodytes*)

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Abstract

Many species can choose between two visual sets of stimuli on the basis of quantity. This is true when sets are both visible, or are presented one set at a time or even one item at a time. However, we know comparatively little about how well nonhuman animals can compare auditory quantities. Here, three chimpanzees chose between two sets of food items when they only heard each item fall into different containers rather than seeing those items. This method prevented the chimpanzees from summing the amount of visible food they saw because there were no visual cues. Chimpanzees performed well, and their performance matched that of previous experiments with regard to obeying Weber's law. They also performed well with comparisons between a sequentially presented auditory set and a fully visible set, demonstrating that duration of presentation was not being used as a cue. In addition, they accommodated empty sets into these judgments, although not perfectly. Thus, chimpanzees can judge auditory quantities in flexible ways that show many similarities to how they compare visual quantities.

Keywords

Chimpanzees; Numerical Cognition; Quantity Judgments; Auditory Stimuli; Empty Sets

It is well-established that nonhuman animals can be very good at quantifying all kinds of things in their environment. They can show counting-like abilities as they label or create sets to match a cardinal value (e.g., Beran & Rumbaugh, 2001; Boysen & Berntson, 1989; Capaldi & Miller, 1988; Matsuzawa, 1985; Pepperberg, 1994; 2006; Roberts, Roberts, & Kit, 2002; Tomonaga & Matsuzawa, 2002; Xia, Emmerton, Siemann, & Delius, 2001). They can respond accurately to arithmetic manipulations in which sets of items are increased or decreased in number through addition and subtraction of items (e.g., Beran, 2001, 2004; Beran & Beran, 2004; Call, 2000; Sulkowski & Hauser, 2001). And, they can make relative numerosness judgments in which two sets are compared on the basis of the quantities within them. In fact, in the visual domain, this is such a widespread ability that it has been demonstrated in nearly all species tested to date, including great apes, monkeys, pigeons, dolphins, parrots, horses, dogs, voles, fish, salamanders, and others (e.g., Addessi, Crescimbeni, & Visalberghi, 2008; Aïn, Giret, Grand, Kreutzer, & Bovet, 2009; Anderson et al., 2005; Beran, 2007; Boysen & Berntson, 1995; Brannon, Cantlon, & Terrace, 2006; Brannon & Terrace, 2000; Cantlon & Brannon, 2006; Dadda, Piffer, Agrillo, & Bisazza,

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2009; Emmerton, 1998; Evans, Beran, Harris, & Rice, 2009; Ferkin, Pierce, Sealand, & delBarco-Trillo, 2005; Hanus & Call, 2007; Jaakkola et al., 2005; Kilian, Yaman, von Fersen, and Gunturkun, 2003; Pepperberg, 2006; Santos, Barnes, & Mahajan, 2005; Uller, Jaeger, Guidry, & Martin, 2003; Uller & Lewis, 2009).

There is also some evidence that nonhuman animals can process auditory numerical information. Meck and Church (1983) demonstrated that rats could discriminate auditory signals on the basis of the number of cycles in each signal. Davis and Albert (1986) trained rats to discriminate three sequentially presented sounds from two or four. Jordan, Brannon, Logothetis, and Ghazanfar (2005) reported that monkeys could perform a cross modal matching task where they heard a combination of monkey calls and matched that to images containing the same number of monkeys. Jordan, MacLean, and Brannon (2008) then demonstrated that monkeys could match a presented number of sounds to an array of shapes equal in number, suggesting that cross-modal representation of number was robust. Such demonstrations of cross-modal matching indicate that for animals, like for humans, number operates across modalities. Number also operates for animals in more natural settings. For example, lions may use auditory numerical information in assessing group strength (McComb, Packey, & Pusey, 1994) and chimpanzees may also use the number of calls from nearby animals to estimate relative strength before approaching (Wilson, Hauser, & Wrangham, 2001).

Tests with sequentially presented items are well suited for assessing the estimation of auditory numerical stimuli, but they have rarely been used. More typical are studies that use visual stimuli. For example, Beran (2001, 2004; Beran & Beran, 2004) reported that chimpanzees performed at high levels when they were shown two sets of food items that were placed, one item at a time, into opaque containers and then were allowed to select one of the containers. Performance is usually constrained by the ratio between sets, not solely on the basis of the magnitude of the sets, and this reflects analog magnitude estimation (see Brannon, 2006; Brannon & Roitman, 2003; Gallistel & Gelman, 2000). Subsequent use of the one-by-one sequential presentation method with rhesus monkeys (Beran, 2007), capuchin monkeys (Beran, Evans, Leighty, Harris, & Rice, 2008; Evans et al., 2009), gorillas, bonobos, and orangutans (Hanus & Call, 2007), and even adult humans who were prevented from counting the arrays (e.g., Beran, Taglialatela, Flemming, James, & Washburn, 2006) indicated this same relation between performance and ratio between sets. This suggests that a similar mechanism may be operating across species to facilitate performance on this task. However, this kind of test has rarely been given in the auditory domain, where animals would have to attend to, and presumably sum, the number of items heard rather than seen.

In this study, chimpanzees were presented with two sets of food items to choose between. In the first experiment, the chimpanzees listened as an experimenter dropped food items into two opaque containers. Each item was dropped one at a time, and the only feedback the chimpanzee could use to determine which set had more food in it was the number of sounds the chimpanzee heard. Another experiment presented only one set in this way, whereas the other set was fully visible throughout the trial. Thus, chimpanzees had to make a cross-modal comparison, in an effort to provide additional data relevant to determining whether quantity representations by animals are amodal much like those of humans (see Jordan et al., 2008). A number of different quantity combinations were used that have not been tested systematically with sequential auditory and cross-modal stimuli in previous research. Performance in each of these conditions was evaluated on the basis of the ratio between sets to assess whether quantity judgments of auditory sets followed the same general constraints seen when only visual sets were used (i.e., analog magnitude estimation). It was expected that chimpanzees could make discriminations between auditory-auditory comparisons and

between auditory-visual comparisons, and that, as with studies using visual-visual comparisons, performance would be constrained by the ratio between sets. These tests offer new insights into the spontaneous quantity judgments of primates.

Experiment 1

Methods

Participants—Three chimpanzees were tested: Lana (female, 38 years of age), Sherman (male, 36 years of age), and Mercury (male, 22 years of age). All were experienced in a variety of different cognitive tests, including judgments of food quantities (e.g., Beran & Beran 2004).

Apparatus—The apparatus consisted of a bench that was 48 cm high, 67 cm wide, and 36 cm deep. The bench had a sliding drawer on top that could be pushed forward so that items on it moved simultaneously within reach of the chimpanzee in its home cage. Mounted to the front was an occluding blind that could be lowered between trials to prepare trials. Two opaque containers were placed at opposite ends of the bench, and a white opaque tube (32 cm high, 9 cm wide, 6 cm deep) was used to drop food items into the containers.

Procedure—Each chimpanzee was tested individually. The blind on the apparatus was lowered to a point where the experimenter could hold his hand behind the blind and drop food items (M&Ms candies) into an opaque tube that had been lowered into the container on the chimpanzee's right side. The chimpanzee could see the tube, and that it was in the container, but it could not see the experimenter's hand or any food items. After dropping all of the items into that set, the tube was pulled out of the first container and moved to the second container, where the second set was presented in the same way. Food items were dropped at a pseudo-random rate to try to control any confound between the duration of presenting the items and the number of items (i.e., sometimes the smaller set took longer to present than the larger set whereas the reverse was true on other trials). In addition, the tube remained in each container after the last item was dropped into that container for approximately two extra seconds to also help avoid this confound.

After both sets had been presented, the tube was removed and the shelf was moved forward so that the chimpanzee could make a selection by touching a container. The experimenter could see which container was selected by looking down and through the slats of the blind, but the chimpanzee could not view the experimenter's face. The selected container was emptied and the contents were given to the chimpanzee, and then the next trial was prepared. Each chimpanzee completed 40 trials across three sessions, with each session consisting of 12 to 15 trials. All possible comparisons of 1 to 5 candies were presented four times each, in random order, and with the larger set occurring on each side of the apparatus equally often.

Before testing began, the chimpanzees were trained that they needed to attend to the sound of falling food items. For these training trials, the chimpanzees were presented with only one food item, dropped into one of the two opaque containers. Thus, all trials were a comparison between one food item and nothing in the other set (counterbalanced for side across trials). Chimpanzees received 10 trials in a session, and they were considered to understand the task when they were correct on 8 of 10 trials within a session.

Results

During training, Sherman and Mercury met criterion in the very first session. Lana required two sessions to meet the training criterion. For the test trials, each chimpanzee performed significantly better than chance in choosing the container with the larger number of food

items (all $p < .05$, binomial test). Lana was 72.5% correct, Mercury was 67.5% correct, and Sherman was 85% correct. Performance was fairly consistent across the experiment although slightly lower at the beginning. Overall, the chimpanzees were correct on 63.3%, 80%, 80%, and 80% of the trials in the 4 blocks of 10 trials. A comparison of overall performance on the first 30 trials (10 from each chimpanzees) to the last 30 trials (10 from each chimpanzee) showed no significant change in performance, $\chi^2 (1, N = 60) = 2.05, p = .15$.

The data were combined across all three chimpanzees so that performance could be analyzed as a function of the ratio of the smaller set size to the larger set size. These results are presented in Figure 1. There was a significant correlation of ratio and percentage of trials correct, $r(7) = -.75, p < .01$.

Discussion

When both sets of food items were presented in such a way that the chimpanzees could only hear items fall into containers without seeing them, all were successful in choosing the larger amount. The chimpanzees also showed the characteristic ratio effect previously shown in these animals and others when tested with sequentially presented and visible food sets (e.g., Beran, 2001, 2004; Hanus & Call, 2007). Two methodological issues were important to address, however. The first was that the control measures used to prevent the timing of set presentation duration were not perfect. Larger sets necessarily took longer to present in some trials because of the pseudo-random presentation pace that was used, and the chimpanzees may have used this information to some degree in making their judgments. The second issue was that dropping items sequentially into the sets produced not only clear auditory signals that each item had, in fact, hit the bottom of the container, but there was also the possibility that larger sets gave more feedback of candies hitting each other. The chimpanzees may have used that information to guide choices, and this would be different from enumerating and estimating the quantity of individual items they heard fall into the containers. To discount these two concerns, Experiment 2 introduced a cross-modal component through three phases of testing. Now, chimpanzees heard one set of items being dropped sequentially, but the other option was fully visible throughout the trial. This set had no presentation duration (it was already present), and it produced no auditory feedback. The chimpanzees had to estimate the quantity that they heard fall into the container and compare that to a set they could see so that they could attempt to choose the larger total amount of food.

In the final phase of Experiment 2, the chimpanzees sometimes saw the tube go into the container, but no items were dropped. The question was whether they recognized and could deal appropriately with an empty set. Empty sets have infrequently been tested as a quantity with nonhuman animals, although there is some evidence that they can and do accommodate the impact of an empty set on their judgments of quantity. For example, rhesus monkeys that were trained to match quantities to each other had no difficulty accommodating empty sets when matching them to other empty sets or including empty sets as part of a numerical ordering task (Merriitt, Rugani, and Brannon, 2008). A grey parrot previously trained to label sets of items with a vocally produced label showed some ability to label sets with nothing it them using the response “none” (Pepperberg, 2006; Pepperberg & Gordon, 2005). An adult female chimpanzee with previous training in the use of Arabic numerals 1 to 9 also incorporated the numeral 0 into three different numerical tasks: one where the chimpanzee had to select numerals corresponding to the number of items presented on a computer screen, one where she had to match sets of the appropriate size to numerals presented as samples, and one where she was required to respond to numerals sequentially, arranging them into an ascending series (Biro & Matsuzawa, 2005).

Experiment 2

Methods

Participants and Apparatus—These were the same as in Experiment 1. However, the opaque container on the chimpanzee's left was replaced with a clear plastic bowl.

Procedure—While the blind was lowered, the experimenter placed a complete set of candies into the container on the chimpanzee's left. He then partially raised the blind and presented the sequential auditory set into the container on the chimpanzee's right in the same manner as described in Experiment 1. All other details of the trial presentation were the same.

In Phase 1, each chimpanzee completed 40 trials across three sessions using the same comparisons as in Experiment 1. In Phase 2, a total of 12 comparisons were presented, some of which were new. In this phase, the following comparisons were presented for four trials each to each chimpanzee: 1:2, 1:3, 1:4, 3:6, 4:6, 4:8, 5:7, and 5:8. The following comparisons were presented for eight trials each to each chimpanzee: 2:3, 2:4, 2:5, and 3:5. All comparisons were presented in a random order. Each chimpanzee completed four sessions in this phase.

In Phase 3, a total of 12 comparisons were presented. The following comparison was presented for four trials each to each chimpanzee: 6:8. The following comparisons were presented for eight trials each to each chimpanzee: 0:1, 0:2, 0:4, 1:4, 2:4, 6:10. The following comparisons were presented for 12 trials each to each chimpanzee: 2:1, 4:6, 4:8. All comparisons again were presented in a random order. When an empty set was included, it was always the sequential set because these chimpanzees rarely ever would point to an empty visible set that had nothing in it, so trials of that type had little or no value. Each chimpanzee completed the 88 total trials of this phase across four sessions.

Thus, by the end of testing, a variety of new comparisons were presented including those from Experiment 1 and other comparisons that exceeded the values used in Experiment 1. This ensured that the chimpanzees could not use any remembered cues from Experiment 1, such as duration time for the larger sets, to help them determine whether the auditory set contained more items than the visible set without actually looking at the visual set.

Results

Each chimpanzee performed significantly better than chance in choosing the container with the larger number of food items (all $p < .01$, binomial test). Lana was 81.25% correct, Mercury was 78.13% correct, and Sherman was 78.65% correct. Figure 2 presents the data combined across all chimpanzees as a function of the ratio of the smaller set size to the larger set size. There was not a significant correlation of ratio and percentage of trials correct, $r(10) = .18$, $p = .56$. Performance remained high across all ratios.

For all chimpanzees, there were varying degrees of bias on erroneous selections to choose the sequentially presented auditory set. Mercury selected that set on 26 of 42 error trials ($p = .16$, binomial test), Sherman selected that set on 30 of 41 error trials ($p < .01$), and Lana selected that set on 35 of 36 error trials ($p < .01$). These errors, however, were tightly focused on only certain comparisons. Across all three chimpanzees, 85% of the errors that occurred in which the auditory set was selected over the visual set involved auditory sets of 0, 1, or 2 items. When zero items were in the sequential set, the chimpanzees often chose that set over one visible item (79.2% of trials were incorrect), but not over two or four visible items (25% and 8.33% of those trials were incorrect, respectively). When one item was in the sequential set, the chimpanzees often selected that set over two visible items

(62.5% of trials were incorrect) but did so less often for visible sets of three, four, or five items (41.7%, 20.8%, and 33.3% of trials were incorrect, respectively). When two items were in the sequential set, the chimpanzees often selected that set over three visible items (61.1% of trials were incorrect) but did so less often for visible sets four or five items (23.3% and 27.8% of trials were incorrect, respectively). So, it was not that specific visible sets always (or never) were selected, or that specific auditory sets always (or never) were selected, but it depended on the number of items in both sets.

Discussion

In this experiment, duration and any auditory cues given by candies falling and piling into the bottom on the containers were eliminated as possible cues that varied across the choice options for the chimpanzees. Despite this, performance remained high. The chimpanzees successfully selected the larger set whether it was presented in a sequential, auditory manner or whether the full set was visible throughout the trial. Although the expectation might have been that the chimpanzees would more likely select the visible set when making an error, because of the certainty of the contents of that set, this was not true. Two of three chimpanzees showed a strong opposite bias, preferring to select the sequential set. Why this occurred remains unclear. Perhaps auditory stimuli are more salient and thus the chimpanzees overestimated the quantities in that set. Perhaps the visible set, when it consisted of relatively small numbers of items, was simply not perceived as large enough to be selected. This seems unlikely, as previous studies have shown that small sets will be selected so long as they are the biggest quantity possible at that time for the chimpanzees to obtain (e.g., Beran, 2001, 2004). In addition, at least a few times the chimpanzees chose the sequential set over a visible set of five items, which was the largest set size used in Experiment 1.

Previous experiments with these same chimpanzees used the sequential versus simultaneous method with visual sets and consistent locations for both stimulus sets (e.g., Beran, 2004), and ratio effects were evident as were high levels of performance. This suggests that it is more likely the use of auditory sets that produced results that varied from those typically found for quantity judgment tasks. However, it was possible that the ratio effect found in Experiment 1 might not remain after the cross modal task was given, and that the chimpanzees might now respond differently to auditory-auditory comparisons. Thus, the chimpanzees were returned to the auditory-auditory condition to see whether the correlation of performance and ratio would be reinstated. This would allow an assessment of whether the correlations differ significantly as a function of procedure.

Experiment 3

Methods

Participants and Apparatus—These were the same as in the previous experiments.

Procedure—The procedure was nearly identical to that of Experiment 1. The only difference was that another temporal control was included, whereby the experimenter always took longer to drop the food items into the first set compared to the second set. Thus, time was again partially controlled as a cue to the greater quantity. All chimpanzees again completed 40 trials across two sessions.

Results and Discussion

Lana was 70.0% correct, Mercury was 75.0% correct, and Sherman was 65% correct. The data were combined across all three chimpanzees so that performance could be analyzed as a function of the ratio of the smaller set size to the larger set size. These results are presented

in Figure 1. There was a significant correlation of ratio and percentage of trials correct, $r(7) = -.70, p < .01$. Performance was compared for Experiment 1 and Experiment 3 controlling for the effect of ratio by using ANCOVA. There was not a significant difference in performance across these two experiments, $F(1, 15) = 0.70, p = .42$. Thus, performance in Experiment 3 closely matched that of Experiment 1.

General Discussion

This study offers three new insights into the relative quantity judgment skills of chimpanzees. First, chimpanzees can compare two sequentially presented sets of auditory stimuli, and they will select the larger quantity even when they have no visual information to guide responding. In Experiment 1 and Experiment 3, the chimpanzees showed the ratio effect common in many other kinds of quantity judgment tasks, indicating that the chimpanzees were using analog magnitude estimation to guide responding. As the auditory sets became increasingly closer in quantity, it became more difficult for the chimpanzees to choose the correct set.

Second, the chimpanzees showed that they could make cross-modal quantity comparisons by choosing between a sequentially presented auditory set and a fully visible, simultaneously presented set. These tests were important for confirming that the chimpanzees were not using presentation duration or some aspect of auditory feedback from candies hitting each other as a cue to the correct response. Rather, they were listening to the sequential set, forming an approximate representation of the quantity in that set, and comparing that representation to what they could see in the visible set. This result matches that from previous studies with both discrete (e.g., Beran, 2004) and continuous quantities (Beran, 2010) in which chimpanzees compared sequential presentation to simultaneous presentation of visual sets. Chimpanzees made correct choices in the present test much as they had in those previous studies.

One interesting aspect of these present tests is that the ratio effect was not found in the cross modal task, primarily because performance remained high across the range of ratios presented. This indicates that perhaps this type of cross modal comparison is in some way easier for the chimpanzees. Perhaps storing quantitative representations through different perceptual experiences places a lower demand on working memory in chimpanzees, or perhaps the chimpanzees had an easier time making the comparisons because they did not need to watch the sequential set because there was nothing to see. Rather, they may have been able to look at the visible set throughout the trial to estimate whether the sequential set was larger or smaller than that set. These possibilities remain for further testing.

The third new insight pertains to empty sets and biases in choosing small sequential auditory sets. When nothing was dropped, and they heard no candies, the chimpanzees sometimes did well in choosing the visible set. This was not true for all cases, though, as small number of candies in the visible set often led to a result where the chimpanzees received nothing for selecting the empty set. Although this perhaps indicates some limit on the flexible accommodation of empty sets into cross-modal quantity judgments, it is important to note that the chimpanzees showed the same difficulty when the sequential set had one item compared to only two items in the visible set. And, errors were made less frequently for small auditory sets and empty auditory sets when the visible sets were relatively larger. This suggests it is less about the absolute size of either the sequential set or the visible set and more about the absolute size of both sets within a trial. Small auditory sets are only incorrectly selected in relation to relatively small visible sets. Additional tests with empty sets and small sequentially presented sets of auditory stimuli will be required to confirm what causes this difficulty for the chimpanzees.

In summary, these experiments demonstrate another capacity of chimpanzees for dealing with quantitative information. They can use auditory information to estimate quantity and compare auditory quantities to other auditory sets and to visual sets. Certainly, the task sophistication and previous experiences of these chimpanzees contributed to this high performance because they were so well trained to pay attention to quantity. However, it seems plausible and even likely that other species should show the same capacities given how widespread other quantity judgment skills and numerical processing abilities extend across the many species that have been tested. Increasing the use of cross modal tests like this one and other tests that assess numerical processing of non-visual stimuli is important, as it will provide additional evidence of the extent to which quantity estimation and numerical cognition in nonhuman animals is domain-independent and flexibly applied across modalities.

Acknowledgments

This research was supported by Grant HD-38051 and Grant HD-060563 from the National Institute of Child Health and Human Development and by Grant BCS-0924811 from the National Science Foundation. The author thanks Ted Evans and David Washburn for their comments on an earlier version of this paper.

All applicable institutional rules and regulations regarding animal care and use were followed in the care and testing of the chimpanzees, and the experiment complied with all laws of the United States of America.

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Figure 1. Performance of the chimpanzees (combined) in Experiment 1 and Experiment 3 as a function of the ratio between sets. The horizontal line shows the chance level of performance.

Figure 2. Performance of the chimpanzees (combined) in Experiment 2 as a function of the ratio between sets. The horizontal line shows the chance level of performance.