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The Origins of Counting Algorithms

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Abstract

Humans' ability to count by verbally labeling discrete quantities is unique in animal cognition. The evolutionary origins of counting algorithms are not understood. We report that nonhuman primates exhibit a cognitive ability that is algorithmically and logically similar to human counting. Monkeys were given the task of choosing between two food caches. First, they saw one cache baited with some number of food items, one item at a time. Then, a second cache was baited with food items, one at a time. At the point when the second set was approximately equal to the first set, the monkeys spontaneously moved to choose the second set even before that cache was completely baited. Using a novel Bayesian analysis, we show that the monkeys used an approximate counting algorithm for comparing quantities in sequence that is incremental, iterative, and condition controlled. This proto-counting algorithm is structurally similar to formal counting in humans and thus may have been an important evolutionary precursor to human counting.

Keywords

counting, mathematical cognition, animal cognition, cognitive development, nonhuman primate

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Human counting affords a kind of condition-controlled logic wherein counters can increment a set by labeling items "one, two, three, four, . . ." until some condition is met. For example, items can be incremented until all items are counted, until the number of items counted reaches a target number, or until the items counted outnumber the value of another set. In the study reported here, we asked whether this condition-controlled logic, inherent in human counting, is a feature of nonhuman quantitative reasoning. Evidence that nonhuman animals' quantification includes logic that is inherent in human counting would provide a new theoretical basis for connecting the principles of human counting with the principles of evolutionarily primitive quantity systems.

Nonhuman animals do not use words like *one, two,* and *three*, or numerals like *1, 2*, and *3*, to "count" in the way that humans do. Nonetheless, it is well established that monkeys and other animals can approximate quantities without these symbolic labels (Gallistel, 1989; Gallistel & Gelman, 1992). For example, research studies using computerized tasks have shown that monkeys can roughly determine which of two sets of dots has the larger number (Beran, 2007; Brannon & Terrace, 1998; Cantlon & Brannon, 2006a, 2006b). Other studies have shown that apes and monkeys compute simple addition outcomes (Beran, 2001; Cantlon & Brannon, 2007). For example, monkeys can discriminate that when three objects are combined with five more, the total number is eight, not two or four. Monkeys also have been shown to discriminate quantities spontaneously, in naturalistic foraging tasks. Semiwild and experiment-naive primates can choose the larger of two sets of food items without any prior exposure to quantity decision tasks (Barnard et al., 2013; Flombaum, Junge, & Hauser, 2005; Hauser, Carey, & Hauser, 2000). Many animal species, including even birds and fish, estimate quantity (Agrillo, Dadda, & Bisazza, 2007; Emmerton, 2001; Pepperberg, 2006). A nonsymbolic sense of approximate quantity is likely a fundamental component of animal cognition (Gallistel, 1989).

The basic quantity skills of nonhuman animals are comparable to some of the numerical skills that human infants and young children exhibit in experiments on prelinguistic mathematical concepts (Brannon, 2002;

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Lipton & Spelke, 2003; Wynn, 1992; Xu & Spelke, 2000). For example, when a set of 5 objects is combined with a set of 5 objects behind a screen, 6-month-old human infants are surprised if the screen is lifted to reveal only 5 objects (i.e., they look longer than they do if the screen is lifted to reveal 10 objects; McCrink & Wynn, 2004; Wynn, 1992). Thus infants, children, and nonhuman animals possess cognitive mechanisms for representing and operating on numerical values. However, unlike nonhumans, human children go on to learn a verbal counting routine. An area that has not been well explored is the extent to which nonhumans possess the logical operations that form the basis of verbal counting. Although some studies have shown that, with training, monkeys can compare sequentially presented sets (Beran, McIntyre, Garland, & Evans, 2014; Jordan, MacLean, & Brannon, 2008), and other studies have shown that, with training, animals can associate quantitative meanings with numerals or words (Boysen & Bernston, 1989; Pepperberg, 2006; Tomonaga & Matsuzawa, 2002), none have defined the logical algorithms of sequential quantification in nonhuman animals that could serve as precursors to human counting.

All current formalizations of nonsymbolic quantification assume that mental comparison happens at the end of incrementing, not item by item (Dehaene, 2009; Meck & Church, 1983). However, this assumption is based on an absence of data rather than a positive argument that comparison occurs only after all items are incremented. Other theories from the animal-learning literature posit that nonhuman animals represent a conditioned gradient of reinforcement across sets of items to discriminate quantity (e.g., Mechner, 1958; Ferster & Skinner, 1957). No studies have tested whether nonhuman animals spontaneously compare the relative values of two sets as they are in the process of quantifying. This question is important because the answer to it will indicate the extent to which the primitive quantity routines of nonhuman animals contain logical elements of human counting—an issue central to discovering the evolutionary origins of human counting.

Here, we show that monkeys spontaneously compare a remembered quantity against item-by-item changes in the value of a new quantity, and thus keep constant tabs on the relative values of sets by comparing them incrementally. Furthermore, using a novel Bayesian data analysis, we show that the monkeys' spontaneous behavior is explained by a cognitive algorithm that is algorithmically and logically similar to human counting.

Method

Monkeys (N = 2; *Papio anubis*) were presented with a choice task in which pieces of food (shelled peanuts) were sequentially placed into two food caches that were spatially separated by at least an arm's length. Each food cache was baited with a different quantity of food items, from 1 to 8. The food caches were baited consecutively, such that all food items were placed one by one into the first food cache before the second food cache was baited one by one. After the two caches were baited, the animal was permitted to choose between them and indicated her choice by touching it. Upon making a choice, the animal was given the contents of her chosen food cache. We included two control conditions to exclude the possibility that the animals' quantity choices were determined by experimenter cuing or by the temporal duration of stimulus presentation.

Subjects

Two olive baboons (*Papio anubis*), housed and tested at the Seneca Park Zoo in Rochester, New York, participated in these experiments. The zoo provided primate chow and fresh fruits and vegetables to the subjects every morning, and water was available ad libitum. Research with these subjects was approved by the Seneca Park Zoo Conservation & Research Committee.

The subjects did not have prior laboratory training in quantity discrimination. At the time when these data were collected, both subjects were experiment naive: Neither animal had participated in an experimental task other than the current decision task, in which they were reinforced with food on every trial and thus not conditioned to discriminate quantity.

As in many primate studies, a sample size of 2 was sufficient for our goals. In contrast to most human research, our study was not aimed at making inferences about a population. Rather, our primary interest was in exploring whether counting-like behavior is possible in nonhuman animals. Logically, a demonstration of possibility requires only a single example.[1] Thus, a small sample size is sufficient for determining whether a cognitive capacity is possible in a population. A small sample also is ideal for collecting hundreds or thousands of measurements from the same individuals over long periods of time, which can provide rich insights into cognitive processes. The limitation of a small sample size is that it licenses population-level inferences only if the population is mostly homogeneous. Indeed, there are reasons to expect that nonhuman primates are homogeneous in their cognitive capacity for quantitative reasoning because the ability to make quantitative judgments is phylogenetically widespread among animals (Gallistel, 1989), and thus is likely to appear in most individuals. However, the issue of whether or not our observations can be extrapolated to the population level is independent of our conclusion that counting-like behavior is possible in a nonhuman animal.

Fig. 1. Illustration of the task apparatus. After placing food items in two of the cylinders, the experimenter slid the panel toward the monkey so that she could make her choice by poking her finger through the port in front of the desired cylinder.

Apparatus

The main apparatus was a small, short rectangular sliding tabletop (75 cm long × 35 cm deep × 17 cm high; see Fig. 1). Three sides of this sliding panel were shielded by plexiglass, to prevent the baboons from interacting with the apparatus until the appropriate time. The remaining side (a long side) was open so that an experimenter could work the apparatus. There were three equally spaced ports (2.5-cm diameter, 30 cm apart) in the plexiglass that the subject could use to indicate her choices. In front of each port was an opaque cylinder. The cylinders were open on both ends so that the experimenter could drop items into them and also lift them up, leaving their contents on the panel. Once items were dropped into the cylinders, the items were hidden from the subject. After two cylinders were baited with items, the panel was slid forward toward the subject so that she could make her choice. The items to be enumerated were shelled half peanuts.

Procedure

Main experiment. Each session was conducted by two experimenters. One experimenter worked the apparatus while the second recorded the subject's choices, monitored the first experimenter for trial accuracy, and also operated a video camera, which was used to record each session. A session was conducted when a subject could be temporarily isolated from the troop in an enclosure, which happened one to three times a week per monkey. Each session lasted approximately 30 min.

On each trial, two cylinders were baited sequentially, one item at a time. For example, if the experimenter was testing the numerical pair 3 versus 6, three peanuts (Set 1) were placed into one cylinder one at a time, and then six peanuts (Set 2) were placed into a second cylinder one at a time. The experimenter touched the cylinders in the same way and for the same amount of time for each peanut. To initiate a trial, an experimenter showed the subject one peanut, holding it about 30 cm from the subject and above the experimental panel. Each peanut was presented to the subject in the same way for 2 s and then placed into a cylinder; there was a 2-s delay between items. To ensure that subjects did not base their choices on the spatial location of the sets of food items, we designed the trials so that across a session, the larger and smaller numerical values were equally likely to appear in any one of the three cylinders. Note that although there were always three cylinders on the sliding panel, only two of these cylinders were baited with food on a given trial. The presence of the third cylinder allowed us to monitor subjects' understanding of the general task requirement that only baited caches should be chosen. Subjects almost never selected the empty cylinder (1% of trials), which indicates that they understood the task.

After the cylinders had been baited with peanuts, the panel was pushed forward, and the subject was allowed to make a choice from among the three cylinders. In order to prevent gaze cuing, once the panel was pushed forward, the experimenters looked down at their laps until the subject indicated her choice by poking her finger through the port in front of the desired cylinder. Then, the experimenter removed the cylinder covering the desired food, and the food reward was fed, one peanut at a time, to the subject through the same port. If there was no food under the chosen cylinder, the subject received no reward. When the subject had received the entirety of the reward, the experimenter removed the other two cylinders from the panel, revealing their contents, and removed all remaining food items. The experimenter then pulled the panel back, away from the subject, and reset the board. The next trial was initiated. This procedure was used throughout the experiment.

Interspersed with the sequential trials just described were trials in which food items were presented simultaneously. In these trials (50% of all trials), the two sets of food items to be compared were presented all at once, one set in each hand, and then placed into their cylinders. The numerical values of the sets were the same as in the sequential trials (i.e., values of 1 to 8 items). These simultaneous trials were randomly intermixed with sequential trials across the experiment. The simultaneous trials are not the focus of this report, and data from these trials were not included in any of the analyses reported. However, both animals made highly accurate choices on the simultaneous trials (mean accuracy = 80%; Monkey 1: 130 out of 170 trials, $p < .001$; Monkey 2: 160 out of 194 trials, $p < .001$), and they showed a numerical ratio effect in their performance (Monkey 1: $R^2 = .49$, Monkey 2: $R^2 = .90$). We included simultaneous trials in each session so that subjects would not be biased to use the duration of presentation to make their discrimination, given that on simultaneous trials, the two sets were presented for the same total duration.

Subjects were tested on a total of approximately 175 sequential trials over 10 to 12 sessions. The number pairs tested were all possible pairs of the numbers from 1 through 8 (27 different numerical comparisons). Subjects completed approximately 6 trials for each number pair. The order of the test trials was randomized within and between subjects. Note that the subjects were reinforced on every trial in that they received the food items in the cylinder they chose. The only way that this reinforcement could be construed as differential reinforcement is if the animals actively discriminated the quantity of the reward they received from the quantity of the reward they did not receive. Thus, the animals were not trained to discriminate quantities at any point in this experiment, and the animals' discrimination abilities derived from their spontaneous quantitative cognition.

Experimenter-cuing control. Immediately following the main experiment, a control condition was conducted to rule out the possibility that experimenter cuing led the animals to their quantity choices during the main experiment. If the subjects had relied on experimenter cues to make their choices, then they would fail to select the greater set once those cues were removed. In this condition, one experimenter fully baited the first cylinder, and then the second experimenter baited the second cylinder. Each experimenter read the numerical value of the food items to be placed in the cylinder from a trial list that showed the quantity of only one set. The two experimenters sat back to back so that they could not see each other. Thus, each experimenter knew only the value for the cylinder he or she baited and did not see the baiting of the other cylinder. This procedure eliminated the possibility of subconsciously cuing the animals.

The subjects were first familiarized with this new procedure with values of 1 versus 2 and 2 versus 9. Both subjects performed above chance in the first session with this new procedure (binomial tests; mean accuracy = 75%, $p < .05$; Monkey 1: 19 out of 24 trials, $p < .01$; Monkey 2: 17 out of 24 trials, $p < .05$). The subjects were tested with these two numerical comparisons until they reached 70% accuracy for two sessions (24 trials/session). Monkey 1 required the minimum of two sessions to reach criterion, and Monkey 2 required four sessions. The subjects then were tested on approximately 100 additional trials of this control condition. The number pairs tested were 1 versus 5, 1 versus 6, 1 versus 7, 1 versus 8, 2 versus 5, 2 versus 6, 2 versus 7, 2 versus 8, 3 versus 5, 3 versus 6, 3 versus 7, 3 versus 8, 4 versus 5, 4 versus 6, 4 versus 7, and 4 versus 8. The subjects completed approximately 6 trials for each number pair. The order of the test trials was randomized within and between subjects.

Timing control. Following the cuing control condition, we tested performance in a second control condition, to rule out the possibility that the relative presentation duration for the two sets determined the animals' choices during the main experiment. If the subjects had relied on timing cues to make their choices, then they would fail to select the greater set once those cues were removed. As mentioned, the two sets were presented for the same total duration in the simultaneous trials of the main experiment, and the animals successfully discriminated the number of items in the sets on those trials. Thus, it is unlikely that the subjects used the relative duration of the baiting of the two caches as a cue to the larger amount on the sequential trials. Nonetheless, we presented control trials to rule out the possibility that the animals had used total duration as a cue during the sequential trials of the main experiment. In these control trials, the duration of the baiting time for one of the cylinders was 30 s. On half of the trials, the set with the larger numerical value had the 30-s baiting time, and on the remaining half of the trials, the smaller quantity had the 30-s baiting time. Note that for all the quantities tested in these control trials, 30 s was longer than the maximum baiting time in the protocol of the main experiment.

The subjects were tested on a total of 48 trials over two sessions: 24 control trials randomly intermixed with 24 trials with the standard baiting-time protocol from the main experiment (i.e., 4 s per item for both sets). The number pairs tested were 2 versus 4, 2 versus 6, and 4 versus 6. The subjects completed 8 control trials and 8 standard trials per number pair. The order of the test trials was randomized within and between subjects.

Data coding

The animals' choices were coded off-line by two independent coders (interrater reliability: $\kappa = .875$, $p < .001$). Also coded were the animals' movements between the caches (*switches*) prior to making a choice. A trial was not coded for switches if the monkey did not sit at the cylinder with Set 1 prior to sitting at the cylinder with Set 2 (15%), if the videotape was dark or no video was available (7%), if the switch point was ambiguous because the

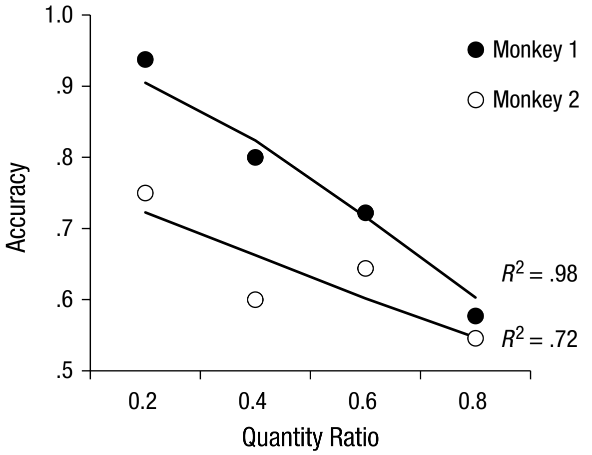

Fig. 2. Ratio effects in the main experiment. Each monkey's accuracy in choosing the larger quantity is graphed as a function of the ratio of the two quantities. Solid lines represent the predictions from the model used to obtain the Weber fractions.

subject engaged in some other activity before moving from Set 1 to Set 2 (5%), or if the monkey switched back to the first cache after moving to the second (2%). Switching behavior was coded in 111 sequential trials for Monkey 1 and 137 sequential trials for Monkey 2 in the main experiment, 108 trials for Monkey 1 and 99 trials for Monkey 2 in the cuing control condition, and 44 trials for Monkey 1 and 41 trials for Monkey 2 in the timing control condition.

Results

Both monkeys chose the larger quantity on the majority of trials coded for switching in the main experiment (mean accuracy = 68%; Monkey 1: 81 out of 111 trials, $p < .001$; Monkey 2: 86 out of 137 trials, $p < .001$). Mean accuracy was comparable when we included all trials in the main experiment (mean accuracy = 67%; Monkey 1: 108 out of 161 trials, $p < 0.001$; Monkey 2: 127 out of 190 trials, $p < 0.001$). As expected, the monkeys' discrimination abilities were modulated by the numerical ratio between the choices (Fig. 2): As the ratio between the quantities increased, the monkeys' accuracy at choosing the larger quantity decreased. This ratio effect is a common characteristic of nonsymbolic numerical discrimination and is known as Weber's law (Gallistel & Gelman, 2000). The monkeys' actual accuracy fit the predicted accuracy under a model of Weber's law (following Cantlon & Brannon, 2006b; Pica, Lemer, Izard, & Dehaene, 2004; Monkey 1: $R^2 = .98$, Monkey 2: $R^2 = .72$;). Their average sensitivity to differences between numerical values was 0.86 (their Weber fraction). This means that the monkeys required nearly a 2:1 ratio between the two quantities to reliably identify the larger one. Prior research has found finer quantity discrimination in nonhuman primates (e.g., Cantlon & Brannon, 2006b; Nieder & Miller, 2003). However, in contrast to the subjects in that prior research, the subjects in the current study had no prior training with quantity discrimination and were rewarded with food on every trial. Differences in experience and motivation could explain the differences in quantity discrimination across the studies.

A more surprising characteristic of the monkeys' behavior occurred in the moments leading up to their final quantity choice. On 37.5% of trials in the main experiment, they physically moved from the first set to the second set *before* the experimenter had finished baiting the second cache. There was no requirement in this task for the animals to make a speeded decision, and thus their switching from one set to the other was based on spontaneous on-line decision making (see Video S1 in the Supplemental Material available online for a video of this midbaiting switching behavior in a monkey). These spontaneous switches were generally logical in that they largely occurred when the second set was larger than the first (M = 70%, SD = 4%, 64 out of 93 trials, $p < .001$; Monkey 1: 24 out of 33 trials, $p < .01$; Monkey 2: 40 out of 60 trials, $p < .01$). This result suggests that the animals were spontaneously switching to Set 2 on the basis of the relative values of Sets 1 and 2.

We analyzed, trial by trial, when during the baiting sequence the subjects physically moved from Set 1 to Set 2. To do this, for each Set 2 item, we coded whether or not the animal had switched by the time that item was added to Set 2. We then plotted the proportion of switches as a function of the relative value of Set 2 compared with Set 1 (Fig. 3). The data showed that as Set 2 approached and exceeded the value of Set 1, the monkeys were increasingly likely to switch from Set 1 to Set 2 (cumulative Gaussian goodness-of-fit tests: average $R^2 = .90$, $R^2 = .91$ for Monkey 1, $R^2 = .82$ for Monkey 2). Note that we examined the relative value of Set 2, not its absolute value; it was the difference in quantity between the two sets, not the absolute value of one set, that drove the subjects' switching behavior. Figure 3 also shows that extreme differences in cardinality (high and low values on the x-axis) led to extreme differences in behavioral patterns: There were virtually no switches when Set 1 was much larger than Set 2, and most switches occurred when Set 2 was much larger than Set 1. This pattern is what would be expected if the subjects had made repeated mental comparisons of the quantities throughout the baiting.

The animals' probability of switching to Set 2 was constrained by their Weber fraction (0.86). To visualize the match between their behavior and psychophysical predictions based on their Weber fraction, we calculated the predicted probability that an animal with a 0.86 Weber

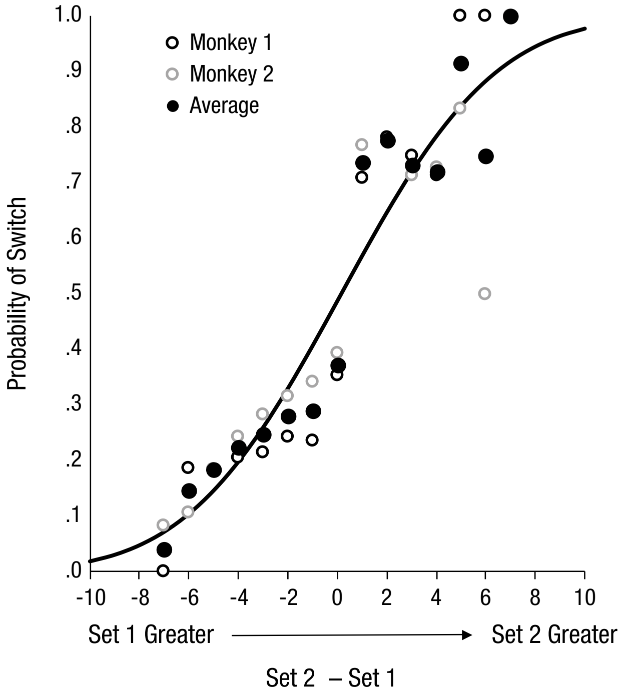

Fig. 3. Probability of switching behavior as a function of the value of Set 2 relative to the value of Set 1. The graph shows separate probabilities for Monkeys 1 and 2 as well as average probabilities, along with the best-fitting cumulative Gaussian curve.

fraction would switch to Set 2 for each combination of Set 1 and Set 2 values that was presented in the experiment. We then overlaid these predictions on the graph in Figure 3 (see Fig. S2 in the Supplemental Material), in order to compare the predicted probabilities with the actual time course of switching in the monkeys. The predictions based on the monkeys' Weber fraction accounted for the observed probabilities of switching ($R = .97$, $p < .001$; Fig. S2). In addition, the relation between the predictions based on the Weber fraction and the probability of switching remained strong after we controlled for the experiment-wide probability that Set 2 would be larger than Set 1 for each value of Set 1 (partial $R = .84$, $p < .001$). These results support the conclusion that the animals continuously compared the quantities of the sets using approximate representations of quantity.

We also analyzed the value of Set 2 at the point when the animals switched and found that this value was proportional to the total number of items in Set 1 (Fig. 4); the number of items in Set 2 at the switch point was greater for larger values of Set 1. This finding reinforces the claim that the monkeys' switching behavior was based on a running comparison of quantity. This finding is also important because it shows that the influence of the relative values of the two sets on the animals' switching behavior was observed not only in the probability of a switch but also in the value chosen as the switch point. The relation between the value of Set 1 and the switch point was observed both when the animals chose the greater quantity (correct trials) and when they chose the smaller quantity (incorrect trials), but the average switch point was considerably lower on the incorrect trials. On average across both correct and incorrect trials, the monkeys switched from Set 1 to Set 2 in the middle of the baiting sequence when the value of Set 2 was 1.4 items less than the value of Set 1 (switch point minus value of Set 1 = −1.5 for Monkey 1 and −1.3 for Monkey 2). Thus, the monkeys switched to Set 2 when it was approximately equal to Set 1.

As explained earlier, to rule out the possibility that subconscious cuing by the experimenter influenced the animals' behavior, we conducted a cuing control condition. In this condition, the human experimenters could not give subconscious cues to the correct choice because they did not know which cache was correct. As in the main experiment, we found that both animals frequently switched to Set 2 before all the food items were placed in the cylinder (38% of trials) and were more likely to switch to Set 2 as its value increased relative to Set 1 (cumulative Gaussian goodness-of-fit tests: $R^2 = .92$ for Monkey 1 and $R^2 = .94$ for Monkey 2). Thus, the animals exhibited quantity-dependent switching behavior even when the experimenters were naive to the quantities presented and unable to provide cues to the larger value.

We conducted a timing control condition to test the possibility that the animals discriminated the two sets on the basis of total duration of set presentation, instead of the number of items in each set. In this condition, one set on each trial was presented for a total duration of 30 s, which always was longer than the baiting duration of the second set. The monkeys performed above chance on the duration control trials (mean accuracy = 71%, $p < .05$; Monkey 1: 16 out of 24 trials, $p = .07$; Monkey 2: 18 out of 24 trials, $p < .05$), and there was no significant difference in performance between these control trials and the standard trials (standard trials: 79% correct; control trials: 71% correct), $\chi^2(1, N = 96) = 0.89$, $p = .35$. The animals did not have a bias toward picking the cache with the longer baiting time (that cache was chosen on 44% of the control trials). This suggests that the monkeys quantified the items in each cache, not the duration of presentation. Also, the animals exhibited spontaneous switching during the timing control trials (55% of trials), and they were more likely to switch to Set 2 as its value increased relative to Set 1 (cumulative Gaussian goodness-of-fit tests: $R^2 = .95$ for Monkey 1 and $R^2 = .94$ for Monkey 2).

The results from the main experiment and control conditions indicate that the monkeys' switching behavior is best described as due to the monkeys' iteratively comparing quantities rather than to experimenter cuing or the monkeys' sensitivity to baiting duration. The data are

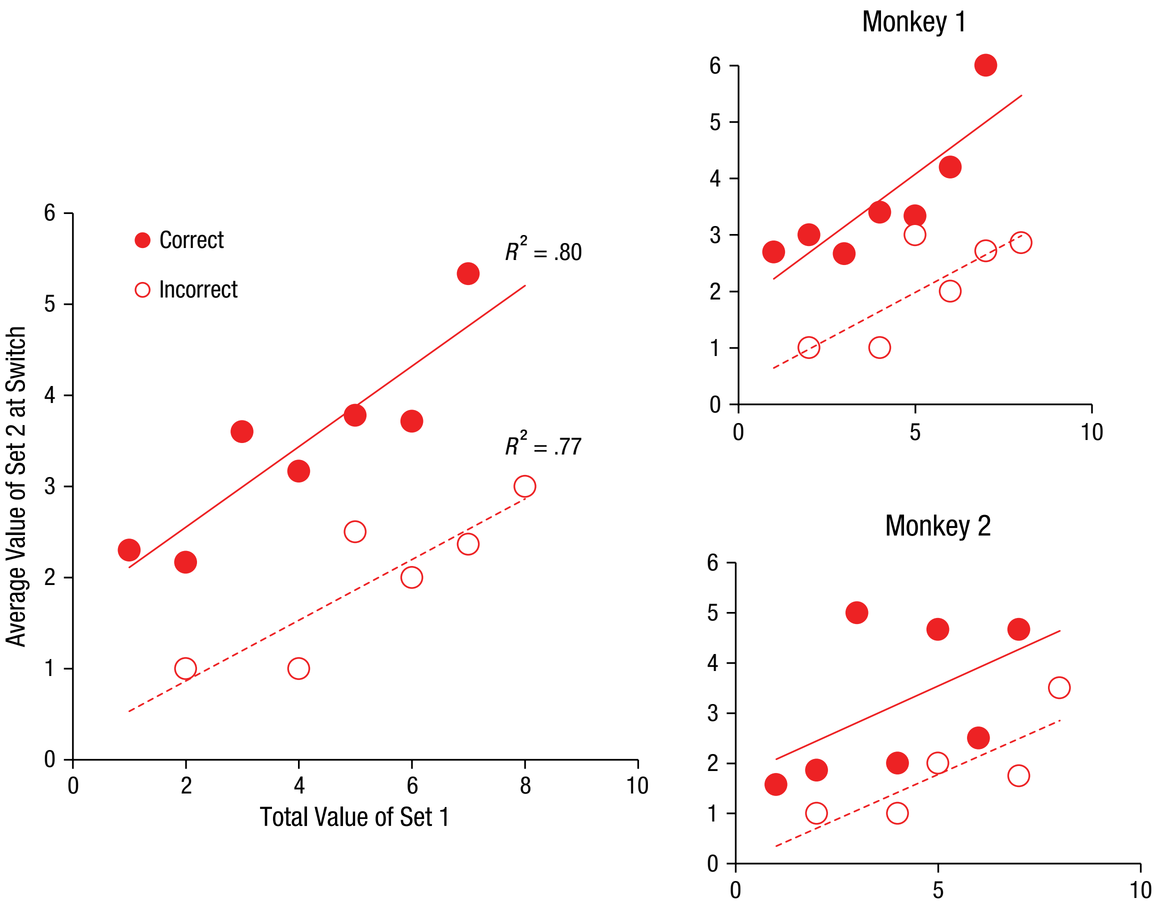

Fig. 4. Average switch point. The average value of Set 2 at the time of midbaiting switches is graphed as a function of the total value of Set 1. Results are shown separately for correct and incorrect trials, averaged across both monkeys (left) and for each monkey individually (right). Solid lines and *R* values represent the linear relation between the value of Set 1 and the switch point.

consistent with the conclusion that the monkeys sequentially compared the value of the first set with the item-by-item changes in the value of the second set. This type of increment-and-compare algorithm is an instance of a condition-controlled loop. Every time an item was added to Set 2, the monkeys (a) incremented their mental representation of the value of Set 2 and (b) mentally compared Set 1 and Set 2. They looped through iterations of this routine until Set 2 was approximately equal to or greater than Set 1, at which point they terminated the routine and committed to choosing Set 2. If this condition for the relative values of the two sets was not met, they defaulted to choosing Set 1. Because the quantitative representations that the monkeys used as the basis of this algorithm were approximate, as indicated by the numerical ratio effects shown in Figure 2, their representations of the relative values of the two sets were noisy, and thus their switch points were only approximately related to the relative values of the sets.

We used a Bayesian data analysis to formalize a noisy increment-and-compare algorithm and test how well it explained the monkeys' switching behavior in the main experiment. This data-analysis technique allowed us to specify a space of algorithms the monkeys could have used, but leave the particular algorithm to be determined from the behavioral data itself: Some settings of the model parameters corresponded to alternative accounts of the animals' cognitive processes (e.g., processes that did not involve counting). By inferring the most likely combination of parameters from the behavioral data, we were able to obtain statistical evidence for or against each of these alternatives. Our approach builds on recent applications of Bayesian data analysis to children's performance on numerical cognition tasks (Lee & Sarnecka, 2011; Sarnecka & Lee, 2009).

For the model, we assumed that the animals represent the value of Set 1 as an approximate quantity with scalar variability. For each item added to Set 2, they (noisily) increment an approximate mental counter and compare the value of this counter with that for Set 1; they tend to switch if Set 2 contains more items. Each of these key steps was parameterized with a variable whose value was inferred from the data. These parameters included (a) the variability of accumulators for Sets 1 and 2, (b) a baseline rate of switching, (c) a rate of switching when Set 2 has more elements than Set 1, (d) the probability of incrementing Set 2 when each element is added, and (e) a baseline attentional probability specifying how often an entire trial is ignored. Some settings of these parameters lead to viable alternative algorithms that do not count and compare, contrary to what we hypothesized. For instance, if the probability of incrementing Set 2 when each item is added is close to zero, this would mean that the representations of quantity are not updated with each item. If the baseline probability of switching is high, behavior is not dependent on the relative quantities of the two sets, and depends perhaps only on time. If Sets 1 and 2 are given very different noise (Weber ratio) values, it may be that the two sets are represented by qualitatively different systems. If quantities are precisely enumerated, the analysis will recover Weber ratios that approach zero. Exact counting therefore corresponds to a particular setting of the model parameters that could be supported by the data. Thus, by determining the parameter values that were most consistent with the behavioral responses, we effectively tested these alternative accounts against the parameter values implied by the increment-and-compare algorithm.

We used a standard sampling approach to find the likely range of the parameters given the observed behavioral data from the main experiment. The model traded off between parameter values that occurred in a likely a priori range and those that fit the data well. We chose simple and standard forms for the priors and likelihood. The accumulator-variability parameters were given Gamma(2,1) priors on the variance. For the baseline switching rate, we chose a Beta(1,9) prior, corresponding to a low baseline expectation for switches. The remaining three parameters were each given uniform (Beta(1,1)) priors, corresponding to no initial biases for particular values. This made their inferred values closely track the behavioral data. A Bernoulli likelihood was used to determine the probability of having switched at the time each food item was added. For simplicity, the outcome—whether or not an animal switched—was treated as independent for each food item, conditioned on the parameters and observed set items. Where possible, intermediate variables were integrated out (collapsed).

The model was run using PyMC (Patil, Huard, & Fonnesbeck, 2010) to sample values from the posterior distribution on these parameters, given the behavioral data. A Markov-chain Monte Carlo procedure was run for 500,000 steps, drawing a sample every 200 steps. The model was tuned for 50,000 steps using PyMC's defaults and run for 150,000 steps of burn-in. The quality of the model's inference was assessed using the standard method of running multiple chains from different starting positions. This revealed quantitatively similar results between chains. Our code is available under the GNU public license from author S. T. Piantadosi. Introductions to these Bayesian analysis methods can be found in Kruschke (2010) and A. Gelman et al. (2013).

The Bayesian analysis yielded a posterior distribution on each variable, quantifying how strongly one should believe each possible parameter value is the true one given how the animals behaved in the experiment. Figure 5 shows these posterior distributions and reveals that the most likely parameter values are consistent with the increment-and-compare algorithm: The monkeys were found to have very high probabilities of incrementing with each additional element of Set 2 (Fig. 5d). They also had low baseline probabilities of switching (Fig. 5b) and high probabilities of switching when they believed that Set 2 contained more elements than Set 1 (Fig. 5c). Thus, their behavior was statistically consistent with sequential updating of Set 2, combined with decisions to switch based on comparisons of approximate cardinality. The model recovered Weber fractions from the monkeys' switch trials (Monkey 1: 0.89 for Set 1 and 0.64 for Set 2; Monkey 2: 0.81 for Set 1 and 0.82 for Set 2) that were similar to the 0.86 Weber fraction calculated with simple fits of the monkeys' performance across all trials, which helped to validate the general approach (Figs. 5a and 5b). This was true even though the ratios for Set 1 and Set 2 were treated independently by the analysis. Indeed, all estimates of the monkeys' Weber fractions indicate considerable variability in their underlying representations of quantity, which is consistent with nonexact representations. The analysis also revealed a moderate degree of inattention on each trial (Fig. 5e), which means that some behavioral noise may plausibly represent failures to attend.

We also tested whether this model of quantitative processing accounted for the monkeys' behavior in each control condition. The posterior distributions of all variables derived from the control data replicated qualitatively and quantitatively those derived from the main experiment's data (see Fig. S1 in the Supplemental Material). For all key variables, the ranges and modes of the posterior distributions were similar to those obtained in the main experiment, though some small numerical differences were observed in the probability of inattention on each trial. Most critically, both control conditions showed a probability of incrementing close to 1.0 and Weber ratios consistent with approximate representations of both sets. In general, these analyses confirmed that the monkeys' quantitative switching behavior in the control conditions also was consistent with an increment-and-compare algorithm.

In general, these results show that the monkeys' behavior was consistent with an increment-and-compare

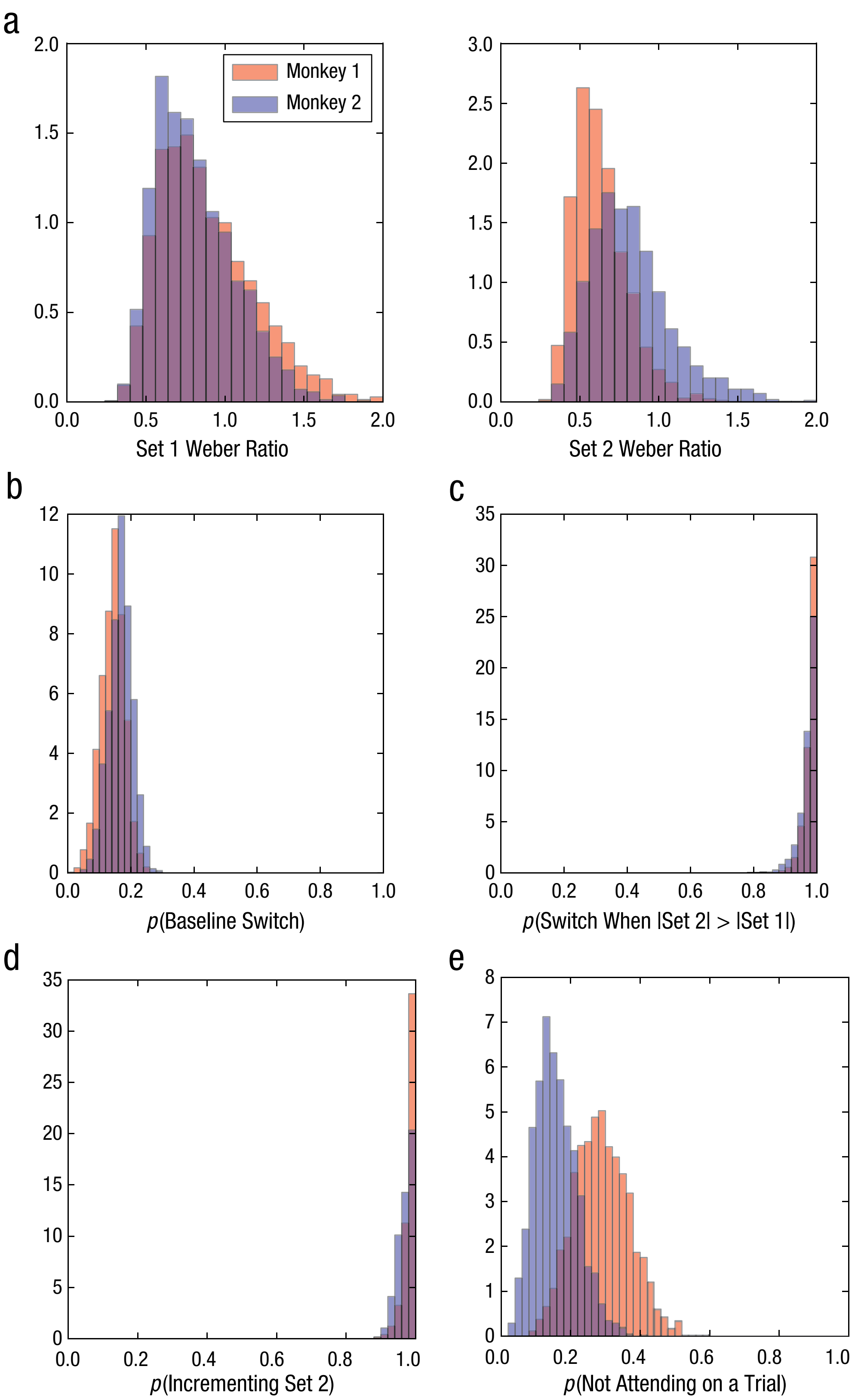

Fig. 5. Results of the Bayesian analysis: posterior distributions on model parameters for (a) the sensitivity of the accumulators for Set 1 (left) and Set 2 (right), measured by the Weber fraction; (b) baseline probability of a switch; (c) the probability of a switch when Set 2 was greater than Set 1; (d) the probability of incrementing Set 2 when each food item is added; and (e) the probability of not attending to a trial.

algorithm, across both the experimental and the control conditions. Alternative accounts—corresponding to particular alternative settings of the model's parameters—were not supported.

Discussion

This article offers (a) a novel observation of *spontaneous* incremental quantity processing in nonhuman primates, (b) a novel theoretical contribution in the formalization of a cognitive algorithm underlying nonhuman quantification that parallel principles inherent in human counting, and (c) a novel methodological contribution in the implementation of a Bayesian analysis technique to test this algorithm against the experimental data.

Although many studies have examined the capacity of nonhuman animals for quantitative representation, there has been no formal proposal of the cognitive algorithm that animals use to compare quantitative representations. The dominant nonverbal quantity model proposed by Gibbon, Meck, and Church (Gibbon, Church, & Meck, 1984; Meck & Church, 1983) has been implemented mostly as a conceptual model. In that model, animals compare quantities only after representations are entered into memory—there is no pathway for updating or comparing representations item by item. We found that monkeys spontaneously compared a given quantitative value against item-by-items changes in a second value. The data show that nonhuman primates inherently increment and compare quantitative values using a type of sequential logic observed in human counting (Carey, 2001; Dehaene, 1997; Gallistel & Gelman, 1992). In human counting, an internal counter is sequentially incremented for each item in a set until some condition is met (e.g., a target number is reached, all items are counted, or one set is greater than another). Our data indicate that nonhuman primates have the ability to use this type of condition-controlled quantitative logic to make sequential nonsymbolic judgments of quantitative values. Moreover, our data show that animals can use this quantitative comparison process spontaneously, in that switching behavior was not required by the task. The data from the control conditions show that the animals did not rely on experimenter cuing or the temporal duration of the sequences to make quantity choices. The animals' spontaneous switching behavior during quantitative decision making provides insight into the cognitive algorithm underlying their choices.

By capitalizing on the monkeys' spontaneous switching behavior, we formalized a proposal for the cognitive algorithm that the animals used to compare quantitative representations. We tested an increment-and-compare mechanism in a Bayesian model analysis. This novel approach is powerful because it provides a theory-driven statistical test of the whole parameter space associated with the model. The algorithm that we tested predicted that the animals noisily increment an internal counter for each item presented in a set and then compare each updated value against their internal representation of a comparison value. The results showed that these parameters accounted for the animals' spontaneous switching behavior and quantitative choices. Alternative explanations of the animals' behavior, including an inability to approximate quantity accurately, an absence of Weber's law, an inability to compare item-by-item changes in quantity, or random switching, would have corresponded with parameter values that were not supported by the behavioral data. Instead, parameter values implementing an increment-and-compare algorithm were supported by the data. The increment-and-compare algorithm accounted for the animals' quantity choices across all conditions of the experiment, including the timing and cuing control conditions. The model results provide strong statistical evidence that an increment-and-compare algorithm underlies the observed behavioral data.

Our results provide novel evidence of a sequential comparison algorithm available to nonhuman animals, but we did not explore which perceptual dimensions this capacity relies on. In particular, the inputs that monkeys use to incrementally compare quantities could be numerical, spatial, or a combination of the two. Animals likely use a combination of numerical and volumetric properties of objects in order to quantify sets of food items (Stevens, Wood, & Hauser, 2007). In humans, evidence of simultaneous numerical and spatial impairments in patients with parietal cortex damage indicates that numerical representations and spatial representations are interdependent (Zorzi, Priftis, & Umiltà, 2002). Thus, the computations underlying judgments of spatial extent bear a close cognitive and neural relationship with those underlying numerical judgments in humans. Current theories suggest that human mathematical concepts are evolutionarily and developmentally derived from the cognitive and neural mechanisms of spatial processing (Dehaene & Cohen, 2007). We hypothesize that the sequential comparison algorithm supported by our data is an important computational precursor to the emergence of human counting, regardless of whether it is specific to numerical judgments or operates more generally over spatial quantities such as surface area or volume. This algorithm and counting are connected by the way in which representations of quantity are processed and updated sequentially, rather than by the inputs that the algorithm takes.

Our data provide evidence that to compare quantities in sequence, nonhuman primates use a type of sequential logic that is algorithmically and logically similar to human counting. Human counting requires incrementation, iteration, and condition-controlled logic. The counting-like algorithm that the monkeys used spontaneously in this task contains those logical elements. It is incremental in the sense that with each item added to a set, the algorithm increments a mental counter. It is iterative because it performs an iteration of mental comparison for each item added to the comparison set. Finally, it is condition controlled because with each iteration of comparison, the algorithm checks whether the second set is approximately equal to or greater than the first set, and if it is, the algorithm commits to choosing the second set. These logical rules underlying monkeys' quantitative judgments are inherent in human counting.

Previous research in developmental psychology has been aimed at identifying relations between nonverbal quantity estimation and human counting. R. Gelman and Gallistel (e.g., 1978; see also Gallistel & Gelman, 1992, 2000) related specific principles of verbal counting to specific principles of nonverbal counting mechanisms. For example, they argued that a "stable order principle" (R. Gelman & Gallistel, 1978, p. 79) in which the tags used to enumerate a set are ordered consistently, is observed both in children's verbal counting behavior and in the accumulator mechanism of Meck and Church's (1983) nonverbal counting model for nonhuman animals. Gelman and Gallistel proposed that skeletal principles provide the scaffolding upon which verbal counting routines emerge, and there is support for elements of this "first principles" theory (e.g., Cantlon & Brannon, 2006a; Cantlon, Fink, Safford, & Brannon, 2007; Gallistel & Gelman, 1992, 2000; Geary, 1995; R. Gelman, 1990; R. Gelman & Brenneman, 1994; Izard, Pica, Spelke, & Dehaene, 2008; Mix, 2002; Spelke, 1994; Starkey, Spelke, & Gelman, 1990). The types of principles that relate nonverbal quantification and human counting differ between our proposal and first-principles proposals. However, our conclusions are consistent with the general claim that a set of core algorithmic operations rooted in nonverbal quantity representation forms the basis of verbal counting.

Although there are structural similarities in the algorithms underlying nonhuman "counting" and those underlying human counting, human counting extends beyond the capacity of counting by nonhuman primates because it includes a symbolic component wherein each item in a set is put into correspondence not just with an internal counter, but also with a term in the ordered list of number symbols (Dantzig, 1954) or, in the case of earlier humans, a slash on a stick or bone. Human counting also gives rise to conceptual inferences about the structure of numerical sequences, such as the successor function (Carey, 2001). Nonhuman primates do not have a formal symbolic system for labeling item-by-item changes in set size or making symbolic inferences about number sequences. The absence of a symbol system prevents nonhuman primates from composing a precise representation of quantity. Yet our results indicate that nonhuman primates possess the cognitive operations that are logically necessary for sequentially tracking and comparing quantities item by item. Animals can use this counting-like logic in the absence of a symbolic system of number to make approximate comparisons of quantitative values in sequence. The fact that this proto-counting logic is present in nonhuman primates indicates that it predated counting and tallying in human evolutionary history, and perhaps was a critical piece of cognition for the human invention of formal counting.

Author Contributions

J. F. Cantlon and A. M. Barnard developed the study concept. All authors contributed to the study design. Testing and data collection were performed by A. M. Barnard, K. D. Hughes, and S. Ferrigno. All authors performed the data analysis and interpretation under the supervision of J. F. Cantlon. J. F. Cantlon, S. T. Piantadosi, K. D. Hughes, and S. Ferrigno wrote the manuscript. All authors approved the final version of the manuscript for submission.

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The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Supplemental Material

Additional supporting information can be found at http://pss.sagepub.com/content/by/supplemental-data

Note

1. For example, if we want to know whether it is possible for a woman to achieve grand-master performance in chess, we need only look at the performance of Judit Polgar to see that it is.

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