



Evidence for a non-linguistic distinction between singular and plural sets in rhesus monkeys

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Received 9 October 2006; revised 5 November 2007; accepted 16 November 2007

Abstract

Set representations are explicitly expressed in natural language. For example, many languages distinguish between sets and subsets (*all* vs. *some*), as well as between singular and plural sets (*a cat* vs. *some cats*). Three experiments explored the hypothesis that these representations are language specific, and thus absent from the conceptual resources of non-linguistic animals. We found that rhesus monkeys spontaneously discriminate sets based on a conceptual singular–plural distinction. Under conditions that do not elicit comparisons based on approximate magnitudes or one-to-one correspondence, rhesus monkeys distinguished between singular and plural sets (1 vs. 2 and 1 vs. 5), but not between two plural sets (2 vs. 3, 2 vs. 4, and 2 vs. 5). These results suggest that set-relational distinctions are not a privileged part of natural language, and may have evolved in non-linguistic species to support domain general quantitative computations.

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Keywords: Sets; Singular/plural; Language; Evolution of language; Number; Parallel individuation

1. Introduction

Many fundamental components of human cognition, including knowledge of language, mathematics, and logic, implicate an underlying system for representing sets and relations between them. Much is known about set representations in humans, in large part because these representations are made explicit in natural language. For example, we know that human adults distinguish between sets and subsets (e.g., *all* vs. *some*), and between singular and plural sets (e.g., *a cat* vs. *some cats*). Far less is known about the pre-linguistic origins of these linguistic representations, and whether the conceptual distinctions they encode are available to infants prior to language acquisition. No previous study has investigated set-relational representations in non-human animals. Evidence that non-human animals *can* represent set-relational distinctions in the absence of language would suggest that linguistic set representations may emerge from species-general conceptual resources. Here, we begin this investigation by testing whether non-human primates make a privileged distinction between singular and plural sets, independent of the absolute magnitude of plural sets.

Previous studies have found that human adults, infants, non-human primates, and other species derive non-linguistic quantificational information from two distinct mechanisms: (1) a system of parallel individuation (PI) for representing small sets of individuals in working memory and (2) an analog magnitude system (AM) for representing the approximate cardinal value of sets (Dehaene, 1997; Feigenson, Dehaene, & Spelke, 2004; Gallistel, 1990; Hauser & Spelke, 2004; Pylyshyn, 2003). The PI system has a limited capacity, and permits the parallel representation of 3 (human infants) or 4 (adult humans and adult rhesus) individuals per set (Barner, Thalwitz, Wood, Yang, & Carey, 2007; Cheries, Wynn, & Scholl, 2006; Feigenson & Carey, 2003; Feigenson & Carey, 2005; Feigenson et al., 2004; Hauser & Carey, 2003; Hauser, Carey, & Hauser, 2000; Jiang, Olson, & Chun, 2000; Luck & Vogel, 1997; Pylyshyn, 2003; Vogel, Woodman, & Luck, 2001; Wood, Hauser, Glynn, & Barner, 2008; see also Uller, Jaeger, & Guidry, 2003, for evidence of a set-size limit in salamanders). The limits of PI are likely subject to individual differences (e.g., possibly due to different training histories; see Vogel et al., 2001) and may also be affected by contextual factors that interfere with PI representations (see Cheries et al., 2006). PI represents each individual in a set with a distinct mental symbol (sometimes called an “object-file” when the individuals in question are objects). For sets of 1 individual, one mental symbol is instantiated. For sets of 2 individuals, two separate symbols are deployed, and so on (see Fig. 1).

These representations permit the comparison of two sets on the basis of one-to-one correspondence, so long as *both* sets are within the limit of PI (i.e., PI cannot support the comparison of sets within its limits with sets beyond its limits). For example, human infants prefer to crawl to a bucket into which 3 crackers have been placed, one at a time, over a bucket with only 1 or 2 crackers. However, most babies fail to show a preference for comparisons of 2 vs. 4 or even 1 vs. 4, even though these

Stimulus array	PI	AM
		
		
		

Fig. 1. Arrays of one, two and four apples, with cartoons of corresponding parallel individuation (PI) and analog magnitude (AM) representations.

comparisons stand in equal or greater ratios, and despite the fact that one of the two sets being compared is within the limit of the system.¹ This evidence has been taken to mean that, when using PI, most infants cannot keep track of more than 3 objects per set and that sets of more than 3 disrupt PI representations altogether (though individual differences may exist between infants, and even across different testing conditions). For free-ranging rhesus monkeys, studies using similar non-training methods have found evidence for a set limit of 4 objects (Hauser et al., 2000). For example, when apple slices are placed one at a time into two containers, most rhesus monkeys approach the side with more slices for comparisons of 0 vs. 1, 1 vs. 2, 2 vs. 3 and 3 vs. 4. However, the animals appear to choose randomly for comparisons of 4 vs. 6 and even 3 vs. 8. In almost all reported conditions subjects succeed when both sets contain 4 or fewer objects, but fail whenever one of the sets is greater than 4.² Finally, studies of visual working memory in human adults provide evidence for a capacity limit of 3 or 4 for tracking and retaining representations of visual objects (e.g., Jiang et al., 2000; Luck & Vogel, 1997; Vogel et al., 2001). Together, the results from studies of human infants, non-human animals, and human adults provide evidence that a common working memory system supports the maintenance of object representations across human ontogeny and primate phylogeny.

Studies of AM indicate that many species have the capacity to represent the approximate magnitudes of various stimuli, including sets (see Fig. 1). The primary

¹ In fact, infants' choices are based on overall amount of cracker stuff, such that they should prefer 1 large cracker that amounts to more overall stuff than 2 small ones (Feigenson, Carey, & Hauser, 2002). However, this summing over continuous amount is limited to sets within PI: infants cannot sum over sets of 4 or more crackers. Feigenson et al. conclude that features of individual crackers can only be retrieved and subjected to comparison if the crackers themselves can first be represented as objects by PI.

² There was one exception to this. Subjects succeeded at comparisons of 3 vs. 5. However, they also failed at 4 vs. 8 and even 3 vs. 8, suggesting that the 3 vs. 5 result may be an anomaly obtained by chance. We address this question in Experiment 2.

signature of AM representations is scalar variability: error in the representation of numerosity grows linearly with the size of the set being represented. As a result, the discriminability of two sets is a function of the ratio between them (see Cordes, Gelman, Gallistel, & Whalen, 2001; Dehaene, 1997; Gallistel, 1990). Further, unlike PI, AM places no upper limit on the size of sets that can be represented, and represents each set with a single magnitude. The ratio-limit signature of AM representations has been found in human adults, infants, rats, and various other species (Barth, Kanwisher, & Spelke, 2003; Brannon, Abbott, & Lutz, 2004; Brannon & Terrace, 1998; Brannon & Terrace, 2000; Cantlon & Brannon, 2006; Cordes, Gelman, & Gallistel, 2002; Gallistel, 1990; McCrink & Wynn, 2004; Platt & Johnson, 1971; Shettleworth, 1998; Whalen, Gallistel, & Gelman, 1999; Xu, 2003; Xu & Spelke, 2000; Xu, Spelke, & Goddard, 2005). Several studies document AM representations in rhesus monkeys (Brannon & Terrace, 1998, 2000; Cantlon & Brannon, 2006; Flombaum, Junge, & Hauser, 2005). For example, looking-time studies reveal a capacity to discriminate 4 objects from 8, but a failure to discriminate comparisons where the ratio between sets is smaller, such as 4 vs. 6 (Flombaum et al., 2005).

Before continuing, we would like to dispel a possible misunderstanding of the claim that there are two distinct systems of representation with numerical content. We do not claim that AM is a “large number” system and PI a “small number” system. Experiments from various species make it clear that AM is defined for small sets as well as large sets (e.g., Beran, 2007; Beran & Beran, 2004; Brannon & Terrace, 1998, 2000; Call, 2000; Cantlon & Brannon, 2006; Cantlon & Brannon, 2007; Dehaene, 1997; Lewis, Jaffe, & Brannon, 2005; vanMarle, Aw, McCrink, & Santos, 2006; vanMarle & Wynn, 2003).³ Our interpretation of the literature, instead, is that there are two different ways of representing numerical information, distinguishable by their distinctive processing signatures (see Feigenson et al., 2004, for review). Though it may not be possible to provide a complete account of when one system or another is activated, experimental manipulations that demonstrate the isolation of a system can provide strong evidence for its independence from other systems, and permit a detailed characterization of its representations and the computations it supports.⁴ Both PI and AM presuppose a prior assignment of individuals into sets, such that these sets can be compared either by one-to-one correspondence or according to their

³ PI representations do not always track each individual in a small set, but may also be deployed for tracking larger sets as a whole (vanMarle & Scholl, 2003; Wynn, Bloom, & Chiang, 2002), thus increasing the total number of individuals tracked beyond the limit of 3 or 4.

⁴ For example, the study of AM representations in human adults is made possible, in part, by methods which prevent adult subjects from using other available systems of quantification, such as counting. In studies of AM, human adults are presented sets rapidly, and asked to estimate the size of each set. Their failure to generate exact responses is not taken as evidence that human adults are unable to count, but rather that under these circumstances counting cannot be deployed (since it requires more time than is made available during the experiment). Below, reasoning here is similar. By finding conditions under which AM is not triggered, we may be able to characterize how sets are represented in absence of AM. Factors like time, method of presentation, and training history may all factor into when AM is triggered, perhaps in interaction with absolute size of the sets being presented (i.e., such that representations of small sets are less robust than those of larger sets).

approximate magnitudes. However, little is known about whether such set representations supply their own conceptual distinctions independent of PI and AM. In order to support PI and AM, set representations would need, minimally, to distinguish between individuals and sets: while AM representations assign a single magnitude value to an array, treating it as a unitary whole, PI representations require that each individual in each set be indexed distinctly and represented by its own symbol. Thus, pre-linguistic humans and non-human animals *should* have the capacity to distinguish individuals and the sets that they comprise. The question is whether non-verbal creatures actually ever do so, and if they do, whether these representations support the kinds of distinctions required for interpreting natural language – i.e., whether set-relational distinctions, like that between singular and plural sets, can be made in the absence of language. If language is necessary for representing such distinctions, then neither non-human animals nor pre-linguistic infants should represent them.

Recent experiments with preverbal human infants (aged 10- to 20-months) show a dramatic failure to draw upon a singular–plural distinction under conditions where PI representations are triggered. In experiments designed to explore the set-size signature of PI, Feigenson and colleagues (Feigenson & Carey, 2005) documented that infants fail to distinguish singleton sets from sets of 4. Shown 4 crackers placed sequentially into one bucket and 1 cracker placed into another bucket, infants failed to choose the bucket with the larger set, even though they robustly succeeded at 1 vs. 2, 1 vs. 3, and 2 vs. 3 comparisons. Also, using a manual search task, Feigenson and Carey (2005) found that when infants were shown a set of 4 balls hidden inside a box, they failed to continue searching after retrieving just 1 ball, despite searching longer under conditions where 3 balls were originally hidden and one was retrieved. Besides confirming that PI representations underlie performance on these tasks (i.e., by revealing a set limit of around 3), these studies document a striking failure to deploy set-relational representations under these circumstances. To distinguish 1 vs. 4, the baby would only need to represent the set of 4 as “more than one” or as a plural set. In fact, the earliest age at which English-speaking children successfully distinguish 1 vs. 4 in the manual search task is 22-months, and their success is predicted by their production of plural nouns in speech (Barner et al., 2007). This correlation between children’s acquisition of the singular–plural morphology and their capacity to distinguish singular and plural sets raises the question of whether set-relational representations depend on language for their deployment.

Determining the role of language in the deployment of set representations is crucial to understanding the essential cognitive differences between humans and non-human animals. Beyond supporting computations of object tracking and numerical systems, linguists, psychologists, philosophers and mathematicians routinely explain human language, logic, and mathematical knowledge via appeal to set and/or lattice theoretic structures (e.g., Barner & Snedeker, 2005; Chierchia, 1998; Link, 1998; Quine, 1963; Russell & Whitehead, 1927). To determine why only humans exhibit these capacities, it is essential to explore not only linguistic contributions to their emergence, but also to document possible non-linguistic conceptual precursors.

In humans, there is some evidence that elementary set representations are deployed by early visual processes, providing reason to expect similar capacities in

non-human animals. Specifically, recent studies indicate that human adults can represent sets without necessarily tracking each individual set member. When groups of objects move together as united sets (i.e., undergo common motion), adult subjects can track up to 4 sets at a time with the same ease that they track 4 single objects (vanMarle & Scholl, 2003), suggesting that these plural sets can be indexed *qua sets* in visual attention (see also Wynn et al., 2002). In this case, sets are apparently individuated by way of Gestalt principles like spatio-temporal contiguity and the common motion of the individuals that comprise them. This raises the question as to whether similar manipulations would trigger set representations in non-human animals, and further, whether such representations would support set-relational distinctions like that between singular and plural sets. To our knowledge, there is no psychological research that has investigated this type of set representation in non-human animals, and thus no previous empirical research on the evolutionary origins of set-relational distinctions in semantics and mathematics. Instead, previous studies have focused on the non-linguistic representation of objects and approximate magnitudes. To establish that rhesus monkeys are capable of set-relational quantification beyond that implicated by AM and PI representations, we would need evidence of set representations that are indifferent to magnitude or to set size, and that are subject to logical operators that encode relations between sets (e.g., akin to linguistic expressions such as *a, some, most, many, all*).

The empirical question that we address here is whether set-relational representations can be isolated in animals that lack language, and, if so, whether non-linguistic set representations supply the same kinds of distinctions that are made explicit in natural language. Previous studies have investigated this question by examining distinctions like that between singular and plural sets in pre-linguistic human infants and, as noted above, have found correlations between their deployment and the emergence of singular-plural morphology in language. Here we expand this investigation by examining whether rhesus monkeys distinguish between singular and plural sets (i.e., between one and many). Specifically, we asked whether there are conditions under which sets of more than one are treated as equivalent (independent of their magnitude), but as distinct from sets of one.

To isolate set-relational representations, we attempted to create experimental conditions that would not trigger PI or AM. As noted above, previous research suggests that this is theoretically possible given two conditions: (1) the sets are small, such that AM representations are less likely to be activated, and (2) individuals in each set do not move independently, but are presented as united sets in either static arrays or moving as a collection. We again acknowledge that AM *can* be elicited for representing small sets under many different conditions, but that it is demonstrably not triggered under all conditions in which rhesus macaques attend to small sets of individuals. We reasoned that if rhesus monkeys track whole sets but not the individuals that comprise them, then PI should not allow comparison of set magnitudes using one-to-one correspondence. Also, in cases where the number of objects is greater than 4, PI should not be activated as this exceeds the limits previously found in rhesus monkeys. Finally, if sets are presented only once (i.e., without training or extensive familiarization), and contain a small number of individuals, AM may not be

spontaneously activated either. If neither PI nor AM are activated, and if the monkeys spontaneously represent the distinction between singular and plural sets, subjects should distinguish between single individuals and sets of individuals (e.g., 1 vs. 2 and 1 vs. 5), but should fail to distinguish between two sets of more than one (e.g., 2 vs. 3, 2 vs. 4, and 2 vs. 5). In sum, we seek to determine whether there are contexts in which neither PI nor AM representations are spontaneously activated, and if so, whether set-relational distinctions, like that between singular and plural sets, can be made in their absence.

2. Experiment 1

We adapted a forced-choice foraging paradigm that has provided evidence of PI representations in previous studies (Hauser et al., 2000; Wood et al., 2008). Subjects were allowed to choose one of two sets of apples that were hidden in two boxes. In previous studies, food objects were introduced into the boxes one at a time. In Experiment 1, objects were presented as united sets, arranged in rows that underwent common motion. We hypothesized that this method of presentation would decrease the likelihood that PI would be elicited for individual objects (though it might still be deployed for tracking sets as a whole). If so, and if subjects distinguish between singular and plural sets, then they should succeed at singular–plural comparisons (1 vs. 2 and 1 vs. 5) but not plural–plural comparisons (2 vs. 3, 2 vs. 4, and 2 vs. 5).

2.1. Methods

2.1.1. Participants

We tested 80 male and female adult rhesus monkeys (16 in each of 5 conditions) living on the island of Cayo Santiago, Puerto Rico (Hauser & Carey, 1998; Rawlins & Kessler, 1987). Here, and in all subsequent experiments, we did not test individual animals more than once in any particular condition, and all comparisons were performed between-subjects. Animals were differentiated based on alpha-numeric tattoos, ear notches, gender, age, and distinctive facial features.

2.1.2. Materials and procedure

For each trial, two researchers first found a lone monkey (i.e., not engaged in social behavior, and not flanked by competing monkeys). The experimenters approached the monkey and placed two opaque boxes (35 cm × 35 cm × 35 cm) 2 m apart and 2–5 m from the test subject (see Fig. 2a). One researcher then crouched between the boxes and attracted the attention of the subject. He then rapidly placed food objects into the boxes as the subject watched (with only a few seconds elapsing between placements into the first and second box). Apples were attached with Velcro in rows to two rectangular pieces of white foam-core, to permit their presentation as united sets. For each comparison, one set of apples was revealed and then hidden before revealing and hiding the second set. The second researcher filmed from approximately 8 m behind the first researcher. After presenting the food

a) United Sets

Researcher kneels between boxes.



Adds one set of apples to a box, as a united set.



Reveals and adds a second set to the remaining box, as a united set.



Walks away from the boxes toward camera person.



Waits with camera person, maintaining back to subject.

(b) Independently moving individuals

Researcher kneels between boxes.



Adds one set of apples to a box, one apple at a time.



Adds a second set to the remaining box, one apple at a time.



Walks away from the boxes toward camera person.



Waits with camera person, maintaining back to subject.

Fig. 2. Forced-choice procedures of Experiments 1 and 2.

items, the first researcher turned 180 degrees and walked away from the boxes at an even pace, providing the test subject an opportunity to approach one of the boxes. When the subject had approached one of the two boxes, the camera person stopped the trial and the subject was prevented from obtaining the apples. In a small number of cases, the animal retrieved one or more apples.⁵

⁵ We devised two techniques to prevent animals from retrieving the apples. For Experiment 1 (and all trials in which apples were presented as united sets), the presentation board was placed apples-down in the box so that the animals could not easily grab individual apples; when they did reach for apples, they were more likely to take only the board, since the Velcro only barely held the apples in place. For Experiment 2 (and all trials in which the apples were presented sequentially), a piece of foam-core was placed midway down the box (and out of sight from subjects) with an apple-sized hole cut in it. Apples were dropped through this hole, such that animals would need to reach through the it to retrieve them.

Trials were aborted when the test subject (1) failed to watch any part of the presentation (2) was distracted by another individual during the presentation or choice period, or (3) failed to choose one of the boxes. The decision to abort was made by the experimenter who was filming the procedure. There was an average of 9.6 aborts per condition in all of the experiments presented in this paper. The mean number of aborts per condition for Experiment 1 was 9.8, for Experiment 2, 12.2, for Experiment 3, “U–I”: conditions 7.7, and for Experiment 3, “I–U” conditions, 7. Here, and across all of the experiments presented in this paper, there was no difference in the rate of aborts for conditions in which animals succeeded and chose a greater number ($M = 9$ across all conditions) vs. those in which they failed and chose randomly ($M = 10.5$ across all conditions; $U = 57.5$, $p > .86$, using a Mann–Whitney U test).

To verify these judgments, a subset of the subject videos ($N = 218$) were coded in the lab by two undergraduate research assistants. One research assistant (RA-1) queued subject videos to the point immediately after both sets had been hidden. The second research assistant (RA-2) was blind to which sets were presented, and the condition. When RA-2 was ready, RA-1 started the video and asked RA-2 to judge whether the animal had made a choice, and if so on what side. This was done for both the aborted trials and the non-aborted trials. Trials were called aborts only if both sets had been presented. In all cases that were codable, the blind coder agreed with the original abort judgments, resulting in 64 aborts, 138 non-aborted trials, and 16 videos that were classified as neither (e.g., animals who were approached but were uninterested, and were not presented the stimuli). For the non-aborted trials, the blind coder’s judgment of the monkeys’ choices (i.e., large or small set) agreed 100% of the time with the original online coding by the camera person (in three cases the videos provided insufficient information for the research assistant to make a judgment).

Of the 64 aborts, RA-2 judged in 61 cases that the animal failed to advance towards the boxes. In the three remaining cases, the animals approached the boxes but were aborted due to interference from other animals who approached simultaneously.

Subjects were given a comparison of either 1 vs. 2, 1 vs. 5, 2 vs. 3, 2 vs. 4 or 2 vs. 5. Order of presentation (larger set first vs. smaller set first) and box into which the larger set was placed (left vs. right) were counterbalanced across subjects.

2.2. Results and discussion

Subjects demonstrated a significant preference for the box with the greater number of apples for 1 vs. 2 (13 of 16 subjects; $p < .02$, binomial test) and 1 vs. 5 (12 of 16; $p < .04$) but not for 2 vs. 3 (8 of 16; $p > .5$), 2 vs. 4 (9 of 16; $p > .4$) or 2 vs. 5 (6 of 16; $p > .8$; Fig. 3). A 2×2 log-linear analysis for cross-categorized frequency data examined effects of set size (smaller quantity vs. larger quantity; e.g., 1 vs. 5), and comparison type (singular–plural vs. plural–plural), and found a significant difference between the singular–plural conditions (25 successes, 7 failures in total) and the plural–plural conditions (23 successes, 25 failures in total), $G^2(1) = 7.6$,

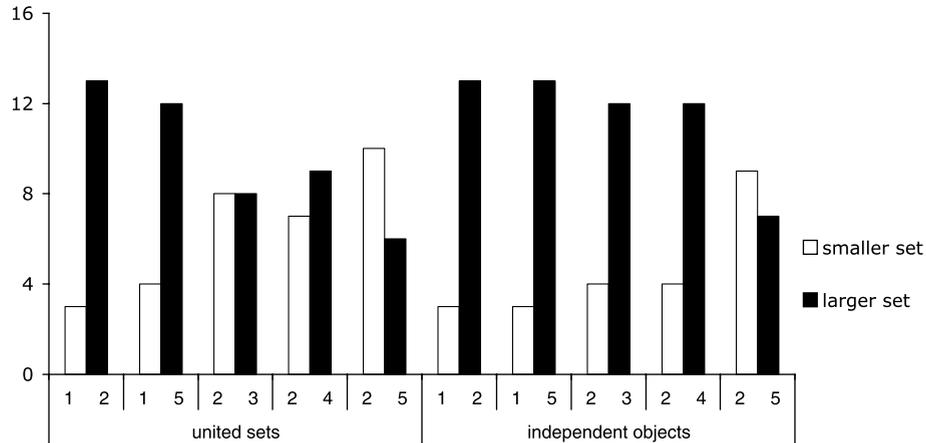


Fig. 3. Choice of larger or smaller set of forced-choice procedure of Experiments 1 and 2, for united sets and independently moving objects.

$p < .01$. Thus, rhesus monkeys distinguished between singular and plural sets but not between plural sets when objects were presented as united sets.

Under the conditions of this experiment, rhesus monkeys spontaneously distinguished between singular and plural sets, but not between two plural sets. Also, the pattern of data obtained in this experiment cannot be explained by PI representations (because the distinctions between 2 vs. 3 and 2 vs. 4 are within the capacity of PI, yet animals fail at 2 vs. 4, and because 5 is beyond the capacity of PI, yet animals succeed at 1 vs. 5). They also cannot be explained by AM representations (because sensitivity is not predicted by the ratios between the sets). The 1 vs. 5 comparison did exhibit a larger ratio than any other comparison, but the 1 vs. 2 comparison, on which they also succeeded, had a ratio equal to or smaller than two conditions in which the subjects failed (i.e., 2 vs. 4 and 2 vs. 5). Thus, ratio effects cannot explain the total pattern of results. Further, the pattern of findings cannot be explained by differences in the total number of objects presented in each trial (i.e., in both boxes combined). The subjects distinguished between singular and plural sets when the total number of objects was 3 or 6 (i.e., for the 1 vs. 2 and 1 vs. 5 comparisons, respectively), but failed to distinguish two plural sets when the total number of objects was 5, 6, or 7 (i.e., 2 vs. 3, 2 vs. 4 and 2 vs. 5, respectively). In sum, these results indicate that rhesus monkeys represented these sets as “an apple” or as “some apples,” making no further distinctions among the plural sets (2, 3, 4, and 5). They displayed a form of set-relational quantification distinct from PI and AM.

What factors influence the activation of one representation over another when multiple possibilities exist (e.g., PI, AM or set-relational quantification alone)? We believe that it may be impossible to specify exactly when one system or another will be activated. For example, it is probably impossible to predict the circumstances under which a human adult will encode an array of apples as “some apples” (using set-relational quantification), or “about 20 apples” (using AM), or “that one, that

one and that one” (using PI). While this may be impossible to determine, we can nonetheless predict the different patterns of numerical discrimination that should be observed when each is deployed. PI should show a characteristic set limit, AM should allow discrimination of any size set with a ratio limit, and set-relational quantification should support distinctions between sets, subsets and individuals, without encoding magnitude. By manipulating those factors that are known to affect the activation of systems, we can obtain information relevant to the nature and function of each, and potentially provide evidence that the different patterns of data – the signatures of different systems of representation – are stable and replicable.

In Experiment 1, we hypothesized that PI would not be activated for individual objects under conditions where objects do not move independently. Under these conditions, arrays can be tracked using a single index assigned to the set, rather than via a series of distinct indexes for each set member. In support of this hypothesis, previous studies that have found evidence for PI have presented monkeys with small sets of objects that move independently, using single trials and no prior training (Hauser et al., 2000). In all of the experiments implicating PI, except one, rhesus monkeys failed to distinguish sets of 5 or more objects from sets within the limits of PI. The exception to this was a 3 vs. 5 comparison, at which subjects succeeded (Hauser et al., 2000). However, they also failed at 3 vs. 8, raising the possibility that the 3 vs. 5 result was an outlier obtained by chance. Below we explored this possibility. Also, since Hauser et al. (2000) tested subjects with apple slices, it is possible that their results do not generalize to whole apples (e.g., because of some unanticipated interaction between numerical contrast and the absolute amount of food presented). Experiment 2 explores the hypothesis that the critical difference between Experiment 1 and previous studies that elicited PI was indeed the mode of stimulus presentation.

3. Experiment 2

Experiment 2 tests the hypothesis that PI is engaged when single objects are presented as independently moving individuals. If it is, then the signatures of PI should be found when small sets are presented one individual at a time, as in previous studies that document limits of PI in rhesus monkeys (Hauser & Carey, 2003; Hauser et al., 2000; Wood et al., 2008) and in human infants (Barner et al., 2007; Cheries et al., 2006; Feigenson & Carey, 2005; Feigenson et al., 2002). To explore this, we tested rhesus monkeys on the numerical comparisons of Experiment 1, but presented apples as independently moving objects that were hidden individually. In addition, we included a 3 vs. 5 comparison, since in Hauser et al.’s (2000) study this was the only comparison with sets greater than 4 at which rhesus monkeys succeeded (including a comparison of 3 vs. 8), raising the possibility that the result was an anomaly obtained by chance. If PI is engaged, subjects should succeed at 1 vs. 2, 2 vs. 3, and 2 vs. 4, since these are within the limits of PI for rhesus monkeys. Also, subjects should fail at 2 vs. 5 and 3 vs. 5, since 5 is outside the limits of PI (recall that for PI to compare two sets, both must be within its limits).

Based on prior studies with this population and method, we had no specific prediction for the 1 vs. 5 comparison. Although 5 is outside the set size limit of rhesus monkeys, the results of Experiment 1 indicate that they can perform a 1 vs. 5 comparison independent of PI, based on an independent distinction between one and many. Thus, an additional question of Experiment 2 was whether the set-relational distinction between singular and plural would persist when PI representations are *also* activated. This question is important, since previous studies have found that at least until 24-months of age, human infants can deploy either PI *or* the singular/plural distinction (i.e., not both in parallel), and that until 22-months of age, they fail to deploy the singular–plural distinction under circumstances where objects are presented as independently moving individuals (Barner et al., 2007).

3.1. Methods

3.1.1. Participants

We tested 80 male and female adult rhesus monkeys (16 in each of 5 conditions).

3.1.2. Materials and procedure

We again used the forced-choice foraging method (Fig. 2b). Subjects were given a comparison of either 1 vs. 2, 1 vs. 5, 2 vs. 3, 2 vs. 4, 2 vs. 5 or 3 vs. 5. The procedure was identical to that in Experiment 1, except that apples were revealed individually and hidden one at a time in rapid succession. As before, all apples destined for one box were hidden before apples were hidden in the second box (see Hauser et al., 2000). The experimenter then walked away, allowing the monkey to choose between the boxes.

3.2. Results and discussion

Subjects demonstrated a significant preference for the box with the greater number of apples for comparisons of 1 vs. 2 (13 of 16 subjects; $p < .02$), 1 vs. 5 (13 of 16; $p < .02$), 2 vs. 3 (12 of 16; $p < .04$), and 2 vs. 4 (12 of 16; $p < .04$) but not for 2 vs. 5 (7 of 16; $p > .8$) or 3 vs. 5 (10 of 16; $p > .4$; Fig. 3).

When objects moved independently as individuals, subjects in Experiment 2 succeeded at 1 vs. 2, 2 vs. 3, and 2 vs. 4, as is predicted when PI is activated. Also, subjects showed the predicted failure at 2 vs. 5 and 3 vs. 5 (since their PI limit is known to be 4). This pattern of data implicates PI, replicating previous studies with apple slices (Hauser et al., 2000). Under these conditions, involving single trials with small sets where each object is seen only once, monkeys fail if both sets are pluralities and at least one exceeds the limits of PI (e.g., 2 vs. 5, 3 vs. 5, 4 vs. 5 and 3 vs. 8). The one numerical comparison that did not replicate was 3 vs. 5, suggesting that the previously reported success in Hauser et al. (2000) may have been due to chance. Finally, the monkeys' success at 1 vs. 5 suggests that set-relational representations are maintained when other systems, in this case PI, are also engaged. Given the large ratio between 1 and 5, this success is also consistent with AM representations. However, the failures at 2 vs. 5 and 3 vs. 5 are not, since these ratios are well within the dis-

crimination capacity of rhesus AM number representations. Also, AM would not predict failure for these conditions coupled with success for 1 vs. 2. In sum, adult rhesus monkeys, unlike human infants, appear able to compute set-relational distinctions such as “singular vs. plural” in the absence of linguistic representations, while also creating and maintaining working memory models of the distinct individuals in small sets.

4. Experiment 3

In the third experiment we further explored the conditions under which set-relational representations are activated in isolation, and when PI representations are also available. Specifically, we asked whether spatio-temporal cues that support indexing a collection of objects as a set are overridden by previous experience with objects as independently moving individuals. We contrasted two conditions. In the first, we initially revealed the objects in each array as a united set on a single presentation board, and then moved the objects one at a time into a box. Since apples were experienced last as independently moving objects, we expected that PI would be activated and that the results of Experiment 2 would be replicated. The second condition reversed this order of events. For each set, we revealed objects one at a time to subjects, placed them onto a single presentation board, and then moved the united set into a box. Thus, monkeys first saw the objects move independently, but their last experience was like that in Experiment 1, where the sets moved as wholes. Of greatest interest was the second condition. Once PI is activated, is it maintained throughout the experiment (leading to the pattern reported for Experiment 2) or does the experience of collections moving as rigid wholes inhibit PI and lead to set-relational quantification alone (leading to the pattern reported for Experiment 1)?

4.1. Methods

4.1.1. Participants

We tested 128 male and female adult rhesus monkeys (16 in each of 8 conditions).

4.1.2. Materials and procedure

We again used the forced-choice foraging method. Subjects were given a comparison of either 1 vs. 2, 1 vs. 5, 2 vs. 4 or 2 vs. 5, and were tested under one of two conditions: (1) presentation of objects first as united sets, then as independently moving individuals (U–I), or (2) presentation of objects first as independently moving individuals, then as united sets (I–U).

4.1.2.1. United, then independent (U–I). The experimenter revealed a united set of apples on a single board, and then moved individual apples one at a time into a box. He then revealed a second united set of apples and moved those apples one at a time into a second box. He then walked away, allowing the subject to choose between the boxes.

4.1.2.2. *Independent, then united (I–U)*. The experimenter moved apples one at a time onto a board, and then moved the entire united set into a box. He then placed apples one at a time onto a second board and moved that united set into a second box. He then walked away, allowing the subject to choose between the boxes.

4.2. Results and discussion

In the U–I condition, subjects selected the box with the greater number of apples for comparisons of 1 vs. 2 (12 of 16 subjects; $p < .04$), 1 vs. 5 (12 of 16; $p < .04$), and 2 vs. 4 (12 of 16; $p < .04$), but not for 2 vs. 5 (7 of 16 subjects; $p > .8$; Fig. 4). These results were thus identical to the results for independently moving individuals in Experiment 2. Placing the apples one at a time into the buckets engaged PI, in spite of the fact that the apples were initially introduced as parts of united sets.

In the I–U condition, subjects selected the box with the greater number of apples for 1 vs. 2 (13 of 16 subjects; $p < .02$) and 1 vs. 5 (12 of 16; $p < .04$), but not for 2 vs. 4 (9 of 16; $p > .4$) or 2 vs. 5 (6 of 16; $p > .8$; Fig. 4). Overall, there was a significant difference between the singular–plural conditions (25 successes vs. 7 failures in total) and the plural–plural conditions (15 vs. 17; $G^2(1) = 6.82$, $p < .01$), which persisted when the difference between the small and large ratio comparisons was subtracted ($G^2(2) = 7.07$, $p < .05$). The difference between the small and large ratio comparisons was non-significant, $G^2(3) = 1.32$, $p > .05$. These results were thus identical to those for united sets in Experiment 1.

Across the conditions described above, the 2 vs. 3 and 2 vs. 4 conditions are crucial to determining when PI is activated (though these are not the only trials relevant to assessing whether animals can distinguish singular and plural sets). PI can resolve both 2 vs. 3 and 2 vs. 4 when objects are presented as independently moving individuals, whereas set-relational representations, in isolation, do not distinguish between

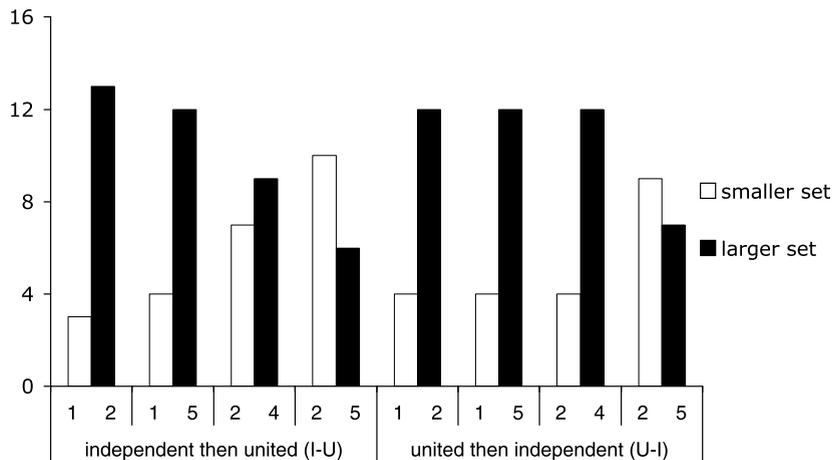


Fig. 4. Choice of larger or smaller set for Experiment 3, for objects last seen as independently moving (U–I) or in united sets (I–U).

sets of 2, 3, 4, and 5. Overall, including the two experiments in this paper that present independently moving objects placed one at a time into buckets, we have carried out a total of 6 conditions testing the 2 vs. 4 comparison with between 10 and 16 monkeys in each condition (Hauser et al., 2000, plus unpublished data). When objects are hidden one at a time, 78% of the monkeys (45/58) choose the bucket with four pieces of food over the bucket with two pieces. In contrast, in the two 2 vs. 4 conditions presented here in which objects move as a united set into the buckets, the success rate was 56% (18/32). The difference in results between these two presentation conditions is significant ($\chi^2(1) = 4.47, p < .04$). When data from the 2 vs. 3 comparisons reported here are also included (by grouping the 2 vs. 3 and 2 vs. 4 comparisons according to method of presentation), analyses reveal that 77% of the monkeys (57/74) succeeded when objects were presented one at a time, compared to 54% (26/48) when objects were presented as a united set ($\chi^2(1) = 6.99, p < .01$). These results indicate that differences in method of presentation described here play a significant role in determining whether PI or set-relational representations alone are activated.

The results of Experiment 3 replicate the findings of Experiments 1 and 2, and further indicate that discrimination of sets on the basis of one-to-one correspondence is elicited when objects are last seen as independently moving individuals, but not merely if objects have previously moved independently, prior to moving as united sets. The results also show that results for united sets do not change when subjects are given prior evidence that the objects are independent individuals, thus undermining the possibility that results for united sets are due to a failure to recognize the objects in these arrays as distinct individuals.

Finally, PI was used for set discrimination only when objects were last seen as independently moving individuals, whereas subjects distinguished between singular and plural sets (i.e., 1 vs. 2 and 1 vs. 5) under all conditions. These results suggest that set representations are activated whether objects are presented in static arrays, move together, or move independently, whereas PI is most readily activated for rhesus monkeys when objects move independently. Thus, for adult monkeys, unlike 22- to 24-month-old human infants, PI representations are preserved when set-relational representations are simultaneously activated.

5. General discussion

Rhesus monkeys have the capacity to distinguish between two sets without representing their absolute magnitudes and without comparing them on the basis of one-to-one correspondence. When objects are presented as united sets (Experiment 1), or they move one-by-one to join a single united set that is subsequently hidden as a whole (I–U condition of Experiment 3), rhesus monkeys distinguish between singular and plural sets (1 vs. 2 and 1 vs. 5), but not between two plural sets (2 vs. 3, 2 vs. 4, and 2 vs. 5).

This pattern of results cannot be explained by AM representations, since ratios of 2:4 and 2:5 are equally or more favorable than 1:2, and monkeys succeed only at the

1 vs. 2 comparison. Under conditions in which small sets were presented only once, AM representations were apparently not activated. This pattern of results cannot be explained by PI because monkeys failed at comparisons within their PI capacity (2 vs. 3 and 2 vs. 4), yet succeeded at 1 vs. 5, a comparison that involved one set beyond their PI capacity. Of course, these results do not mean that AM and PI are never deployed for exactly these same numerical comparisons; indeed, our experiments explored the conditions under which PI representations would be deployed. When objects are presented as independently moving individuals (Experiment 2), or when they are presented as a whole set and last seen as hidden one-by-one (Experiment 3), rhesus monkeys can distinguish between two sets containing up to 4 individuals. Under these conditions subjects succeeded at 2 vs. 3 and 2 vs. 4 but failed at 2 vs. 5. Further, subjects in Experiment 2 failed at a 3 vs. 5 comparison. These data thus replicate previous studies in which separately moving objects are placed, one at a time, into separate buckets for choice. These previous studies find success when both sets are within the range of PI (1 vs. 2, 2 vs. 3, and 3 vs. 4), in the face of failures when one set is outside that range (Hauser et al., 2000; see Feigenson & Carey, 2003, 2005; Feigenson et al., 2002, for parallel infant results). These data also suggest that the 3 vs. 5 success reported by Hauser et al. (2000) was an anomaly a conclusion which is also consistent with that study's finding that rhesus monkeys fail at even 3 vs. 8.

Although we explored some of the conditions that lead to the deployment of set-relational representations and PI, we did not explore here why monkeys did not deploy AM representations under the circumstances of our experiments. However, a wide range of non-human primate species certainly *can* deploy them for sets this size (Beran, 2007; Beran & Beran, 2004; Brannon & Terrace, 1998, 2000; Call, 2000; Cantlon & Brannon, 2006, 2007; Dehaene, 1997; Lewis, Jaffe, & Brannon, 2005). There were several significant differences between our study and these previous reports. In our work, animals were free-ranging, were tested in a single trial, and were exposed to sets (or members of sets) for very small durations. In most previous studies that find effects attributable to AM, animals have typically been tested in a laboratory setting in which all attentional resources can be assigned to the task at hand. Also, these animals have typically been given many training trials and have been exposed to sets for much longer durations and with greater numerical variation, perhaps priming AM representations. These, and other minor differences between methods (e.g., objects used, distinctness of individual set members, simultaneous presentation of compared sets, etc.) all likely contribute to creating conditions under which the signature of set representations can be isolated from AM. Thus, we believe that exploring methodological differences between various studies is valuable to uncovering the ways in which different mechanisms of quantification are triggered, and do not indicate inconsistencies in the primate number literature.

Although it is impossible in a single study to document all of the conditions under which various systems of representation are activated, the current study does allow us to state a number of observations regarding the activation of AM and PI, in addition to characterizing the computations that are available in their absence. We can safely conclude that AM is not obligatorily triggered under all circumstances, but

that AM representations are the output of optional computations. This conclusion is supported by our results, but also by previous studies of both non-human animals and human infants. This does not mean that the computation of number is a “last resort” for animals, but only that it is not automatic and obligatory. Thus we take a middle ground between those who suggest that the computation of number is laborious for animals, and those who argue that it is automatic (see Cantlon & Brannon, 2007, for review).

Our results are consistent with the idea that rhesus monkeys, and presumably many other species, have a limited working memory capacity: they cannot maintain parallel representations of an unlimited number of individuals. According to theories of object-based attention and working memory, independently moving individuals trigger the assignment of visual indexes to objects (Pylyshyn, 2003), which can then be represented in working memory (Kahneman, Treisman, & Gibbs, 1992; Luck & Vogel, 1997). These representations permit the comparison of sets (e.g., held in two working memory models) on the basis of one-to-one correspondence, as well as on the basis of summed continuous variables, so long as both sets are within the limits of PI (Feigenson & Carey, 2003, 2005; Feigenson et al., 2002). These facts regarding PI, in addition to the fact that AM representations are non-obligatory, allowed us to study the signatures of set-relational representations.

It is possible that the monkeys in Experiment 1 and Experiment 3 (U–I condition) did still engage representations of PI, but simply did not assign a distinct index to each object in a set. As mentioned in the introduction, it is known from studies of human adults that collections of objects that undergo common motion can be tracked by a single attentional index, permitting adults to track up to 3 or 4 collections at a time in a multiple object tracking paradigm (vanMarle & Scholl, 2003; see also Wynn et al., 2002). For the purposes of the visual system, collections – or pluralities – are *visual objects*. It is also known that visual objects permit feature binding, such that features are assigned to particular visual objects (Kahneman et al., 1992). In the current study, rhesus monkeys may have assigned a single visual index to united sets, and bound features like “single individual” and “set of individuals” as warranted. In turn, under these conditions, PI representations failed to assign indexes to individual objects within each set, and thus were incapable of resolving set-size differences on the basis of one-to-one correspondence. Based on this analysis, our results are consistent with previous findings in the literature on PI, but add to this the idea that indexed sets can be assigned singular–plural features.

These studies represent the first steps to investigating the conceptual foundations of set-relational representations needed for language, logic, and mathematics. They also constitute an effort to understand the set representations that are potentially necessary for organizing animals’ perception of individuals and sets for the deployment of AM and PI representations (e.g., by providing a mechanism for segregating sets, and determining the units over which each system operates). The results presented here suggest that rhesus monkeys, who lack natural language, nonetheless make a conceptual distinction between singular and plural sets.

How is this capacity related to set-relational quantification in natural language? Previous studies in our labs have found that, in children acquiring English, success

at 1 vs. 4 comparisons for independently moving objects is correlated with the emergence of explicit singular–plural morphology in language production. Barner et al. (2007) found that 18- and 20-month-old children, who mostly lacked plural nouns in their speech, failed at comparisons of 1 vs. 4. However, 22- and 24-month-olds, most of whom used plural nouns, succeeded at 1 vs. 4. Within these older groups there was a significant correlation between 1 vs. 4 success and production of plural nouns in speech. While this correlation is consistent with the hypothesis that language is causally implicated in the deployment of singular–plural knowledge, the present results suggest that acquiring singular–plural morphology depends on non-linguistic conceptual resources that predate language, at least in evolution. The evidence presented here suggests that the distinction between singular and plural sets does not depend on language, but can be elicited in its absence. Set-relational representations that form the foundation for semantic structures in language may exist prior to language acquisition in children, and may be shared by other species.

Acknowledgements

Thank you to Amanda Libenson and Aubrey Gibson for their help coding data. This investigation was supported under an NIH, NCRR Grant CM-5-P40RR003640-13 awarded to the Caribbean Primate Research Center and awards from the University of Puerto Rico-Medical Sciences Campus; its contents are solely the responsibility of the authors and do not necessarily represent the official views of NCRR or NIH. Additional funding was provided by a McDonnell grant to M.H., an NSF Grant BNS9012075 to S.C. and M.H., an NIH (NRSA) grant to J.N.W., an NSF Grant REC-0337055 to Elizabeth Spelke, M.H., and S.C. and by a fellowship from the National Sciences and Engineering Research Council of Canada to D.B. The authors would like to thank Dr. Melissa Gerald for facilitating the research on Cayo Santiago.

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