

RELATIVE NUMEROSITY DISCRIMINATION BY ORANGUTANS

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Abstract

Nonhuman primates' abilities to perform relative numerosity judgments (RNJ) have been well documented in the literature, although little research has been conducted on orangutans. In this study, two captive orangutans were trained and subsequently tested on RNJs presented in abstract format (i.e., as shapes), one with and one without previous experience in numerosity judgments. It was hypothesized that orangutans would successfully choose the larger of two arrays with differing numerosities and choices would follow patterns found in previous studies of other nonhuman primates (including orangutans), indicating evidence of analogue-magnitude representations in the form of numerical distance, numerical size, and ratio effects. In each trial, two arrays containing differing numerosities of blue squares (ranging 1-6) were presented on a touch screen monitor by computer experimental control. Orangutan participants were required to choose the array with the larger numerosity and the computer recorded their choices. Results showed that both orangutans reliably solved RNJs, based on % correct choices. Furthermore, results demonstrated the predicted influence of numerical difference, numerical size, and ratio between arrays on participants' accuracy. These results suggest that, as with other nonhuman primates, numerosity was used as the discriminative cue in RNJs and numerical representation in orangutans in this task is by approximation.

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Introduction

Interest in nonhuman animal numerical ability is not a recent phenomenon (Beran, 2007; Rilling, 1993). Although controversy continues over the existence of ‘true’ numerical ability in nonhuman animals (i.e., formal symbol processing, quantification, or approximation; Dehaene, 1992) and the experimental paradigms required to demonstrate it, it is generally agreed that many different taxa are able to discriminate differing numerosities in both natural and experimental settings (Davis & Perusse, 1988; Dehaene, 1992; Gallistel & Gelman, 1992). The ability to discriminate between differing numerosities can be relevant in various ecological contexts, such as reducing the risk of predators and improving foraging efficiency (Addessi, Crescimbene, & Visalberghi, 2008). Numerosity discrimination, therefore, can play a crucial problem-solving role for dealing with some of the daily problems encountered by many animals (Gallistel, 1989; Hanus & Call, 2007).

Findings from past research suggest elementary numerical ability (i.e., the ability to discriminate between differing numerosities) in several nonhuman primate species (e.g., Addessi et al., 2008; Call, 2000; Hanus & Call, 2007; Shumaker, Palkovich, Beck, Guagnano, & Morowitz, 2001; Tomonaga, 2008). Furthermore, despite the assumption that sophisticated numerical abilities such as counting and summation require language, both abilities have been demonstrated in nonhuman primates (e.g., Boysen, 1997; Cantlon & Brannon, 2007; Rumbaugh, Savage-Rumbaugh, & Hegel, 1987). The majority of nonhuman primate studies have been conducted with trained participants, but spontaneous counting without training has also been reported (e.g., MacDonald, 1994).

From an evolutionary perspective great apes are humans' closest existing taxonomic relatives and research conducted with them can offer special insights on human numerical cognition. Furthermore, because of the lack of investigation involving all great ape species, chimpanzees have become the standard for comparing human and great ape numerical abilities (Shumaker et al., 2001). Therefore, it is important to increase species breadth in this area of study in order to obtain a more complete picture of great apes' numerical abilities and to avoid *only* associating the numerical abilities of chimpanzees with the numerical abilities of humans.

The present study aimed to study numerical ability, specifically relative numerosity judgment (i.e., the ability to discriminate between differing numerosities) and its mental representation, in orangutans. Orangutans are of particular interest because they are an understudied great ape species in the area of numerical cognition – my literature review found only four published studies dealing with orangutan numerosity discrimination (Anderson, Stoinski, Bloomsmith, & Maple, 2007; Call, 2000; Hanus and Call, 2007; Shumaker et al., 2001) and four studies dealing with orangutan Piagetian volume conservation strategies (Call & Rochat, 1996, 1997; Suda & Call, 2004, 2005).

Relative numerosity judgment

To date, numerosity studies provide evidence for simple numerical abilities in both humans and nonhuman primates (Davis & Perusse, 1988). Dehaene (1992) suggested that animal recognition for an array of items might be related to the total collection of items in an array (i.e., the number of items in an array) and this was subsequently termed 'numerosity'. An understanding of numerical symbols (e.g., Arabic

symbols) and/or language is not requisite for basic numerical operations (Brannon & Terrace, 2002; Dehaene, 1992). Relative numerosity judgment (RNJ) - judgment of unequal numerosities - is one such basic numerical ability (Brannon & Terrace, 2002). For example, it is possible to discriminate, without symbols, that a group of four peanuts is larger in numerosity than a group of two apples (Brannon & Terrace, 2002). RNJs typically involve pairwise more-versus-less comparisons of items and, accordingly, RNJs occur when individuals reliably discriminate between differing numerosities (typically by choosing the larger, or, under reversed reinforcement contingencies, the smaller) (Anderson et al., 2005; Anderson et al., 2007; Davis & Perusse, 1988). RNJ is typically classified as a numerical-related cognitive ability; however some researchers argue that it may be in fact a perceptual ability (Davis, Albert, & Barron, 1985; Starkey, Spelke, & Gelman, 1983).

The ability to make RNJs has been explored in gorillas (Anderson et al., 2005), orangutans (Anderson et al., 2007; Call, 2000; Hanus & Call, 2007, Shumaker et al., 2001), chimpanzees (e.g., Boysen & Berntson 1995; Boysen, Berntson, & Mukobi, 2001; Menzel & Draper, 1965; Muncer, 1983; Rumbaugh, Savage-Rumbaugh, & Hegel, 1987; Rumbaugh, Savage-Rumbaugh, & Pate, 1988), and bonobos (Hanus & Call, 2007). RNJs have also been explored in several monkey species (e.g., Anderson, Awazu, & Fujita, 2004; Brannon & Terrace, 2000; Judge, Evans, & Vyas, 2005; Silberberg & Fujita, 1996; Washburn, 1994), in adult humans (e.g., Geary & Lin, 1998; Huntley-Fenner & Cannon, 2000; Thomas, Phillips, & Young, 1999), young children (e.g., Brannon & Van de Walle,

2001; Murray & Mayer, 1988), and human infants (Starkey & Cooper, 1980; Strauss & Curtis, 1981).

RNJ methods. RNJ research employs differing experimental paradigms to better understand RNJ ability in nonhuman primates. These include varying stimulus presentation through the use of simultaneous, sequential, and item-by-item presentations along with, in some cases, the use of reversed reinforcement contingencies.

Studies employing simultaneous presentation of stimuli present several discrete numerosities to be discriminated by participants concurrently, thereby enabling the discrimination of *all* numerosities at the time of choice (Hanus & Call, 2007). These tasks are said to be the most ‘basic’ of all presentation methods because they are thought not to affect working memory or at least to pose very low demands on working memory (Anderson et al., 2007). Conversely, sequential presentation of stimuli requires participants to discriminate discrete numerosities that are not all perceptually available to them at the time of choice (Call, 2000). From an evolutionary point of view, according to Call (2000), cognitive mechanisms that allow animals to represent and compare numerosities that are not all visually available at the time of choice may have important value in that they better simulate natural conditions. For example, it might be of interest for wild primates to track the numerosity of individuals in one’s own group versus that of a competitor group because it could be difficult to visibly keep track of all individuals at once.

In addition to simultaneous and sequential RNJ presentations, studies have demonstrated that nonhuman primates can cope with numerosities that are presented not

as whole sets, but item-by-item (e.g., Hanus & Call, 2007; Hauser, Carey, & Hauser, 2000). With item-by-item presentation, no pair of numerosities can be viewed as a group for comparison (Beran, 2001). In an example of item-by-item presentation, Hanus and Call (2007) asked participants to select between food numerosities (i.e., pellets), which were never presented together. The researchers placed pellets into one of two opaque cups, one by one. First, before dropping the pellets, the experimenter gave participants the opportunity to look into both cups to demonstrate that they were empty. Next, both cups were placed on a platform in an upright position. The food pellets were then dropped into the cups one by one, starting with the left cup and then the right cup. Once the last pellet was dropped into the right cup, both cups were placed within reach of the participant and participants were asked to make her choice of one of the two cups. The item-by-item task required participants to shift their attention back and forth between the two cups because the items placed into the first cup was separated in time by the placement of items into the second cup.

The last experimental paradigm to be explored is numerosity discrimination using reversed reinforcement contingencies. This paradigm has been used to examine whether or not participants can reliably discriminate numerosities given the chance to optimize their performance over time (Boysen & Berntson, 1995). Reverse reinforcement contingencies require a participant to select one of two numerosities, the chosen numerosity is removed, and the participant receives the contents of the non-selected numerosity (usually, food). For optimum performance, participants should pick the

smaller of two numerosities and subsequently be reinforced by receiving the larger numerosity (e.g., Shumaker et al., 2001).

Numerical Representation

Evidence suggesting that nonhuman primates have RNJ ability raises questions pertaining to the nature of their numerical representations. An important question is: if nonhuman primates have RNJ ability and form numerical representations, what form do their mental representations take? How are they organized? For humans, two systems of numerical representation are hypothesized: one dependent on language and another independent of language (Jordan & Brannon, 2006). Two models of nonverbal numerical representation have been proposed, based on evidence from human adults, human infants, and nonhuman primate research: the analogue-magnitude model and the object-file model (Addessi et al., 2008; Tomonaga, 2008).

Analogue-magnitude model. In the analogue-magnitude model (also known as the accumulator model, Meck & Church, 1983 or core system 1, Feigenson et al., 2004), numerical representation does not consist of precise integers but instead of mental magnitudes (Tomonaga, 2008). The model was originally proposed by Meck and Church (1983) to account for animal numerical abilities but was eventually applied to infant numerical abilities by Gallistel and Gelman (1992) as well. Here representation has the following characteristics: it is imprecise, independent of absolute magnitude, *can* be influenced by numerical distance and numerical size effects, and *always* demonstrates sensitivity to ratios (Addessi et al., 2008; Anderson et al., 2007).

The numerical distance effect is the phenomenon whereby individuals can better distinguish between numerical pairwise comparisons that are more disparate than ones that are closer together (Dehaene, Dehaene-Lambertz, & Cohen, 1998). This effect has been shown for RNJs (e.g., Addessi et al., 2008; Tomonaga, 2008). For example, under the numerical distance effect, it is easier to discriminate between an array composed of 4 items and an array of 9 items than it is to discriminate between an array composed of 4 items and an array of 5 items.

The numerical size effect is the phenomenon whereby if the distance between two numerical pairwise comparisons remains constant, an individual will experience more difficulty in distinguishing between a numerically larger in value pairwise comparison than a numerically smaller in value pairwise comparison (Dehaene et al., 1998). For example it would be easier to discriminate that an array composed of 3 items is larger than an array composed of 2 items than to discriminate that an array composed of 100 items is larger than an array composed of 99 items. This effect has been shown in RNJ research (e.g., Tomonaga, 2008).

In addition to numerical distance and numerical size effects, the predominant feature of the analogue-magnitude model is the ratio effect (Addessi et al., 2008; Tomonaga, 2008). According to the ratio effect, performances in numerosity discrimination decline as the ratio between two numerosities increases and approaches a value of 1 (Rouselle et al., 2004). Thus according to this effect, for example, it is easier to discriminate between the numerosities of 4 and 8 (ratio of 1:2) than to discriminate between the numerosities of 6 and 10 (ratio of 3:5). This is because a ratio of 1:2 is

equivalent in value to 0.5 and a ratio of 3:5 is equivalent in value to 0.6 and the latter ratio of 3:5 (0.6) is closer to a value of 1 than the former ratio of 1:2 (0.5).

The ratio effect, in essence, is a combination of both the numerical distance and numerical size effects because ratio co-varies simultaneously with both numerical distance and numerical size when discriminating between a pair of numerosities (Rouselle et al., 2004). For an equal numerical distance, the ratio approaches a value of 1 when the numerosities increase (4:8, 8:12, 12:16, 16:20,...) but also the ratio approaches a value of 1 when the distance between two numerosities decreases (1:10, 1:8, 1:6, 1:4,...) (Rouselle et al., 2004). Therefore, if numerical distance is kept constant and numerical size increases discrimination becomes more difficult due to the numerical size effect *and* the ratio effect since the ratio between the numerosity pairs approach a value of 1. Also, as the distance between two numerosities decreases, discrimination becomes more difficult due to the numerical distance effect but also the ratio effect because the ratio between the numerosity pairs approach a value of 1.

An important feature of the analogue-magnitude model of numerical representation is that it obeys Weber's law: in order for a constant level of discrimination to occur between two numerosities, an increase in the numerical distance between the two numerosities needs to be proportional to the numerical size of the numerosities (Beran et al., 2005). For example, Weber's law predicts that if one needs an increase or decrease of 4 pounds to detect a noticeable difference in a 20 pound sack of flour, then that same person would require an increase or decrease of 8 pounds to detect a noticeable difference in a 40 pound sack of flour (Jordan & Brannon, 2006). Thus, with respect to numerosity

discrimination, the accuracy of numerosity discrimination is inversely proportional to the numerosity considered (Anderson et al., 2007) and variability in numerosity discriminations occurs due to numerical distance and numerical size effects or the ratio effect, which combines the other effects (Rouselle et al., 2004).

Object-file model. Although some research suggests that nonhuman primates, including great apes, represent numerosities as mental magnitudes, there is also compelling evidence that, like some humans, some nonhuman primates may also employ an alternative method for the representation of small arrays of items: the object-file model. In the object-file model, representation is very precise, but pertains only to arrays composed of small numerosities (e.g., Xu, 2003). First, each item in an array is represented by a distinct symbol (the type of symbol is unknown) and corresponds to a memory file. Second, numerical correspondence occurs when one establishes a one-to-one correspondence between his/her memory files for the items and the items themselves (Addessi et al., 2008). For the object-file model, researchers hypothesize that numerical tasks are performed successfully due to general non-numerical abilities (Uller, Carey, Huntley-Fenner, & Klatt, 1999). Pylyshyn (1989) further hypothesized that one keeps track of items in the object-file model through a “pre-attentive individuation process.”

An important distinguishing feature of the object-file model is that discrimination is available only for arrays of up to three or four items; above this range, arrays of items cannot be discriminated (Anderson et al., 2007; Rouselle, 2004). Specifically, it has been found that for human infants, discrimination declines when array components exceed three items (Addessi et al., 2008) and that for nonhuman primates discrimination

declines when array components exceed four items (Addessi et al., 2008; Anderson et al., 2007).

RNJ findings

Relative numerosity judgments have been established in many humans and nonhuman primate species across differing presentation paradigms. However, many studies demonstrate more successful RNJ performance with food arrays than with non-food arrays (e.g., symbols) and when participants are rewarded in food items corresponding to the numerosity of their chosen array (e.g., Beran, 2001, 2004; Beran & Beran, 2004; Call, 2000; Hauser, Carey, & Hauser, 2000, Rumbaugh et al., 1987; Shumaker et al., 2001). For example, for the comparison of 2 grapes versus 5 grapes, it is predicted that participants will, overall, be more successful if their choice is rewarded by the food in their selected array choice rather than if they were rewarded one grape for choosing the correct answer. Furthermore, in these studies, nonhuman primates demonstrated RNJ success independent of the presentation paradigm (i.e., simultaneous vs. sequential presentation). In studies employing non-food arrays, RNJ success has been found to be contingent upon greater training (Beran et al., 2005). For example, Addessi and colleagues (2008) found that capuchin monkeys required more sessions to reach criterion for non-food arrays than food arrays and that the monkeys made more errors with token presentations than with food presentations. Beran et al. (2005) argue that non-food array numerical tasks require greater training than food array tasks because individuals need more time to learn to associate non-food items with a reward that is not obviously presented.

Food arrays also posed problems for chimpanzees under reversed reinforcement contingency presentation. For example, Boysen and Berntson (1995) presented two adult chimpanzees with a reverse contingency task in which two different numerosities were available in each trial, presented in the form of candies. The chimpanzees could choose one of the presented numerosities, which was then removed by the experimenter, and were then allowed to eat the remaining array of candies. Pairs of numerosities to be differentiated were: 1, 2; 1, 4; and 1, 6. Both chimpanzees consistently failed to select the smaller array, always selecting the larger numerosity array. The results of this study have been replicated with chimpanzees across hundreds of trials and several experiments (e.g., Boysen et al., 2001; Boysen, Berntson, Hannan, & Cacioppo, 1996).

Interestingly, within the same experiment, after substituting Arabic numerals for candies both chimpanzees (who were number symbol trained), immediately and reliably selected the smaller array. Boysen and Berntson (1995) suggest that using incentives typically desirable to chimpanzees (i.e., food) interferes with their ability to choose the smaller of two arrays. When ‘non-incentive stimuli’ (e.g., Arabic numerals) were used, the chimpanzees’ ability to employ their numeric training increased. Similarly, Carlson, Davis, and Leach (2005) found that when three and four-year-old children were given a comparable reverse reinforcement contingency task using candies, performance was not optimal. The three-year-old children (but not the four-year old children), like Boysen’s chimpanzees, were unable to reliably choose the smaller amount of candy. Conversely, when the children were presented with the same task but abstract symbols replaced the candy, both three and four-year old children performed similarly to Boysen’s

chimpanzees, reliably selecting the smaller array and thus performing optimally.

Carlson et al. proposed that abstract symbols produce “psychological distancing” which allows participants to hold back their primary response and is involved in the development of executive functioning (i.e., control over thought and action).

In contrast to chimpanzees, orangutans have demonstrated their ability to perform RNJs under the use of reversed reinforcement contingencies using normal incentive stimuli (i.e., food) (Shumaker et al., 2001). For the orangutans, the incentive value of food stimuli did not hinder their performance on RNJs. Instead, orangutans performed optimally on a significant number of trials. Consequently, the authors stated that their results suggest cognitive differences between chimpanzees and orangutans.

Many RNJ studies, further, have not dissociated confounding study elements with their RNJ tasks and researchers agree that one cannot conclude that RNJ discriminations are based on numerosity when there is lack of control of stimulus dimensions (Brannon & Terrace, 2000; Davis & Perusse, 1988). Shumaker et al. (2001) failed to control for non-numerical features by using various varieties of stimulus grapes. Furthermore, the use of food as stimuli in RNJ studies and especially orangutan RNJ studies (e.g., Anderson et al., 2007; Call, 2000; Hanus & Call, 2007; Shumaker, 2001) has limited exploration of confounding non-numerical features. That is, the use of non-food stimuli removes one non-numerical distractor (i.e., color, shape, taste) that could be highly salient.

Furthermore, the use of food as a discriminative stimulus causes “hedonic” value to covary with numerosity (Brannon & Terrace, 2000; Washburn & Rumbaugh, 1991), which plausibly contributes to findings of greater RNJ success with food arrays than with non-

food arrays. Furthermore, the hedonic value of food could be a contributor to unsuccessful chimpanzee RNJs, under reversed RNJ contingencies, due to food co-varying with what Carlson et al. (2005) call a primary response that inhibits “psychological distancing.”

In many situations, when numerosities are presented simultaneously, numerosity can also co-vary with numerical-related features such as the size of individual items, the density of items within an array (i.e., ‘sparseness’ or ‘closeness’ of items in an array) (Davis & Perusse, 1988), or total area (i.e., sum of the areas of all items in an array) (Tomonaga, 2008). For example, three cars, three circles, and three trees have a common numerosity, three, but differ on numerical-related features such as item size and total item area. Also under sequential and item-by-item presentation, stimuli can co-vary with time (i.e., rate and/or duration of stimulus presentation) (Brannon & Terrace, 2000). For example, if one does not control the duration of each array presentation or the rate of item-by-item presentation, either duration or rate could serve as a cue for the correct response thus eliminating the need to focus on numerosity (Beran, 2007).

Previous studies with chimpanzees have demonstrated the importance of numerical-related stimulus features when testing for RNJs. For example, Boysen et al. (2001) examined contributions of item size in their reversed reinforced contingency RNJ tasks. In each trial, chimpanzees were presented with arrays composed of small and large candies, ranging from 1 to 5 in numerosity. When arrays differed in both candy size and numerosity, over all trials, subjects selected arrays containing the larger candies on 66% of trials. Therefore item size in arrays biased choice, regardless of whether or not the

array with the larger candies had the larger or smaller numerosity. Davis and Perusse (1988) argue that in instances where food is used as the discriminative stimulus, the size of food items can greatly predict RNJ success because in many foraging situations the goal could be to maximize food in terms of total amount in contrast to numerosity.

In addition to confounding RNJs with non-numerical item features (i.e., food), *all* orangutan RNJ research to date has confounded RNJ tasks with numerical-related confounds. For example, Anderson et al. (2007), Call (2000), and Shumaker et al. (2001) failed to control item size, total area, and density in their studies. Many researchers have argued that even when stimulus dimensions are confounded, judgment is based on numerosity because rewards were given *only* when the larger (or smaller under reversed RNJ) numerosity was chosen (Beran, 2007). However, caution needs to be exercised in making that type of claim because, although it is possible that orangutans were solving the task based on numerosity, it is also possible that accuracy was based on other non-numerical or numerical-related confounds.

In contrast to studies that used food as their primary stimuli, Tomonaga (2008) used pre-programmed computer stimuli (i.e., computer generated red circles) for his experiment on chimpanzee RNJs. The computer stimuli were used to control for numerical-related features associated with his experimental stimuli. Accordingly, the basis for this experimental design was to examine whether or not the chimpanzees could reliably perform RNJs based on the larger numerosity even when in some cases the larger numerosity was presented as having smaller total area or less density. Total area refers to the sum of the areas of all the items in an array and density refers to the closeness or

sparseness of items within an array. For the total area conditions, Tomonaga examined the effects of pairing arrays with large total array area to arrays with small total array area. He arranged the stimuli (circles with different areas) so that in one condition the larger numerosity had the larger total area, but in another condition, the larger numerosity had the smaller total array area. For the density conditions, the author paired larger numerosities in a denser array presentation with smaller numerosities in a less dense array presentation. As well, Tomonaga paired larger numerosities in less dense presentations with smaller numerosities in more dense presentations. Overall, he found that the numerical-related stimulus features biased the chimpanzees' performances.

Beran (2007) established RNJ in rhesus monkey participants after controlling for rate, duration, and total area. In Beran's study (2007) two rhesus monkeys were presented with an item-by-item RNJ task on a computer monitor. Four experiments were conducted in which rate, duration, and total area for the numerosities 1-10 were controlled. One of the experiments did not have any controls for confounds. Results demonstrated that the rhesus monkeys performed RNJs successfully even when confound controls were applied.

In addition to establishing RNJ, for many researchers studying numerical abilities, the question of numerical representation is most pressing. The patterns of errors made by participants when discriminating numerosities allows for the examination of various models of the representations possibly underlying RNJs (Anderson et al., 2007). Characteristics of the analogue-magnitude model – numerical distance, numerical size, and ratio effects - have been reported for adult humans comparing abstract symbol

numerousities (Buckley & Gillaman, 1974; Van Oeffelen & Vos, 1982) and when working with Arabic numerals or numerical words (e.g., one, two, three, etc...) (Ashcraft & Battaglia, 1978; Buckley & Gillaman, 1974; Dehaene, Dupoux, & Mehler, 1990; Moyer & Landaeur, 1967). Distance effects and agreement with Weber's law have also been found in children as young as 6 years of age (Duncan & McFarland, 1980; Jordan & Brannon, 2006; Sekuler & Mierkiewicz, 1977). Even more interesting is the finding that preverbal human infants (6 months old) can discriminate large numerosities if the numerosities correspond to a ratio of 1:2 (e.g., Xu, 2003).

Furthermore, characteristics of the analogue-magnitude model have been found in nonhuman primates. A good example of numerical distance and numerical size effects can be found in Brannon and Terrace (2002) wherein both rhesus monkeys and college students were tested in an experiment requiring participants to touch the smaller of two paired numerosities (values 1-9) presented on a touch screen. For both species, markedly similar distance effects were found: participants were faster and more accurate as numerical disparity increased. Also, when distance between stimuli was held constant and numerical size increased both species made more errors – i.e., showed a numerical size effect. Distance effects have also been reported in many great ape RNJ studies (Anderson et al., 2007; Boysen et al., 1996; Boysen and Berntson, 1995; Hanus and Call, 2007; Tomonaga, 2008). For example in the reverse contingency task used by Boysen et al. (1996), for conditions using food as the stimulus, a greater degree of interference against optimal performance was apparent on trials in which there was a larger disparity between numerosities to be discriminated. As the distance between numerosities of real

food arrays increased, so did the chimpanzees' selection of the larger numerosity (i.e., the worse their performance); the distance effect was the main predictor for chimpanzees' performance. In Boysen and Berntson (1995), still under reverse contingency, for RNJ tasks with Arabic numerals and not food, the greater the difference between two arrays the better the performance was for chimpanzees; thereby demonstrating the distance effect.

Also, Anderson and colleagues (2007) found that accuracy of middle-aged (20-25 years old) and older (32-47 years old) orangutans on RNJ tasks was unaffected by numerosity differences in stimulus arrays; conversely, younger orangutans' (10-14 years old) performance was reliably affected by stimulus numerosity differences. Plausibly, for the orangutans, distance and size effects only occur at younger ages when learning might be most sensitive. However, for all age groups, RNJ accuracy declined as the ratio between numerosities increased. On a significant number of trials, middle-aged orangutans selected the larger numerosity when numerosities corresponded to ratios of 1:2, 1:3, 1:4, 1:5, 2:3, 2:4, 2:5, 3:4, 3:5, and 4:5. Older orangutans were able to choose the larger numerosity for all ratios, except when numerosities corresponded to the ratio of 2:3 and 3:4, when they failed to choose the larger numerosity. Similarly, younger orangutans were able to choose the larger numerosity for all ratios except when numerosities corresponded to a 3:4 ratio. Hanus and Call (2007), similarly found that ratio best predicted orangutan, gorilla, and bonobo RNJ performance and accounted for 81% of the variability in their data.

Call (2000) found that distance effects and the ratios between numerosities significantly affected orangutan RNJ performance for both simultaneous and sequentially presented stimuli. For two of the three participants, larger ratios (e.g., 5:6) led to worse performance and decreased accuracy but smaller ratios (e.g., 1:5) led to increased accuracy on RNJs. For the third participant, the distance effect best predicted RNJ accuracy. For example, when a large distance between numerosities was present (e.g., 1 vs. 5) fewer errors were made.

A critical characteristic for differentiating between the analogue-magnitude model and the object-file model is the numerosity of the items in a given array. Beran (2007) found that his rhesus monkey participants were able to discriminate arrays of up to 10 items. Furthermore, he found that performance was not disrupted when one array had fewer than four items and the other array had more than four items. Similarly, other studies have found the numerosity of array items to not influence RNJ performance. For example, Anderson et al. (2007) found that for their middle-aged and young orangutans, performance was unaffected when array items totaled nine.

There are some studies, however, that have found evidence in support of the object-file model and correspondingly a ceiling for RNJ ability when arrays were composed of more than three or four items for human infants and nonhuman primates, respectively. There are fewer of these studies than those in support of the analogue-magnitude model but they cannot be discounted because this model may describe numerical representations in nonhuman primates.

Evidence supporting the object-file model can be found in both human infant and rhesus monkey research. In one set of studies, 10 and 12 month old human infants watched as researchers placed different food items in opaque containers (Feigenson, Carey, & Hauser, 2002). The infants successfully crawled to the bucket containing the larger numerosity of graham crackers when the contrasts were 1 vs. 2 or 2 vs. 3 but failed to choose the larger numerosity with any contrast that included numerosities larger than 3, even when ratios were favorable (e.g., 2 vs. 4 –comparable to ratio 1 vs. 2). Similarly rhesus monkeys tested in the same two-container choice discrimination paradigm showed declining ability to discriminate numerosities that exceeded four items (Hauser et al., 2000). Specifically, the monkeys succeeded with contrasts such as 1 vs. 2, 2 vs. 3, and even 3 vs. 4, but failed with numerosities larger than 4 (e.g., 5 vs. 6 and 4 vs. 8).

Present Study

Because of the lack of orangutan RNJ data, the present study aimed to assess orangutan RNJs. This study used abstract stimulus presentation because the use of abstract, non-food stimuli removed one non-numerical distractor that is highly salient and could confound RNJ investigation. Given orangutans' previous RNJ success with food stimuli (Anderson et al., 2007; Call, 2000; Hanus & Call, 2007; Shumaker et al., 2001), it was valuable to see if they could perform RNJs with different stimuli and apparatus (i.e., abstract shape, computer responses). Furthermore, to add to the human and nonhuman primate literature, numerical representations in orangutans were investigated by examining numerical distance, numerical size, ratio, and total array item effects: the imprecise analogue-magnitude model vs. the more precise object-file model.

Based on previous research with other nonhuman primates, including great apes, I hypothesized that orangutans would choose the larger of two arrays with differing numerosities when presented in abstract form (i.e., as shapes). Second, I hypothesized that orangutan choices would follow patterns found by previous studies of other nonhuman primates (including orangutans), showing evidence of analogue-magnitude representations in the form of numerical distance, numerical size, and/or ratio effects. These expectancies were in accord with Tomonaga (2008) who demonstrated chimpanzees' ability to perform abstract RNJs on a computer, and with Addessi et al. (2008) and Tomanaga (2008) who found ratio but not total array items to be the best predictor of capuchin monkey and chimpanzee RNJ performance, respectively.

Method

Design

In the present study, two orangutan participants underwent two levels of acquisition training to become familiarized with RNJs: (1) numerosity versus blank and (2) small numerosity versus large numerosity. After meeting predetermined success criteria on acquisition training, participants proceeded to test trials to assess their RNJ abilities formally. In test trials, participants were introduced to all 15 possible pairwise comparisons of numerosities 1-6. In both acquisition training and test trials, orangutan choices were designated as correct if the array selected contained the larger numerosity of items.

Participants

Two adult orangutans (*Pongo pygmaeus*), Allie (female, age 14) and Azy (male, age 31) housed at Great Ape Trust of Iowa, voluntarily participated in this study. They were chosen from among the orangutans at the Trust because both had experience with cognitive experiments (joint attention tasks (Pitman & Shumaker, in press) and tool use (Shumaker, personal communication)). Furthermore, Azy had experimental experience with observational learning (Shumaker, 1997; Shumaker, Beck, Brown, & Taub, 1998), object permanence (deBlois, Novak, & Bond, 1998), spatial memory (Stoinksi, Shumaker, & Maple, 1999), visual perspective taking (Shillito, Shumaker, Gallup, & Beck, 1998), and symbol acquisition (Shumaker, 1997; Shumaker, unpublished data). Before this study Allie was, experimentally, numerically naïve whereas Azy had previously worked with Arabic numerals and numerosities in object (i.e., food) form (Shumaker et al., 2001, unpublished data).

During the course of this study, both Allie and Azy received a regular daily diet consisting of fresh vegetables, fruit, and monkey chow. Water was also available ad libitum. Thus, no orangutans were food or water deprived during the present study. The research protocol was approved by the York University Animal Care Committee and Great Ape Trust Institutional Animal Care and Use Committee.

Setting

All orangutans at the Trust live in an indoor residence (1274 m³) connected to an outdoor enclosure (1274 m³). Also, the orangutans have access to an environmentally rich

outdoor yard (12,141 m²). For additional interest, Great Ape Trust provides a virtual tour of the orangutan building at <http://www.greatapetrust.org/player/video.php?vid=21>.

Orangutans had free access to all areas within the indoor residence, including a research room for orangutans, except the observation room from which human observations occurred. The research room for orangutans and the observation room were separated by a heavy glass observation window. A section of the observation window could be opened so that researchers and/or caretakers could deliver food rewards during research. This window was opened during study with Azy but not with Allie. Allie suffers from limited mobility due to an unexplained neurological event and, as such, she performed research tasks with caretakers in close proximity (i.e., caretakers went inside the research room with Allie during research) who delivered rewards by hand.

Apparatus

Acquisition training and test trials were conducted inside the research room for orangutans. For the orangutans, the main experimental apparatus was a 42-in infrared touch screen monitor (NEC PX-42VP4PA) permanently positioned in the research room. The resolution of the monitor was 853 x 480 pixels. One hundred pixels corresponded to 108mm. The touch screen monitor was connected to a personal computer system (Dell Pentium 4 Desktop and NEC Multisync LCD 2080UX+ monitor) that controlled stimulus display on and data collection from the touch screen monitor. Software was designed for the experiment using Java and was installed on the personal computer system to control stimulus display and data collection. A Sanyo Xacti HD 7.1-megapixel video camera was used to record all acquisition training and test trials.

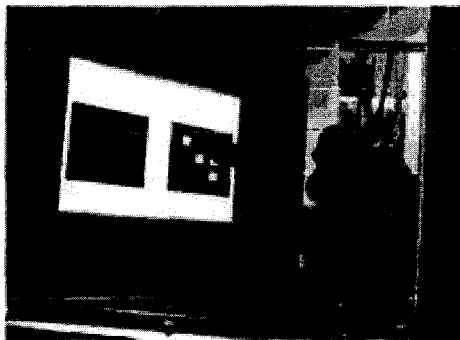
Stimuli

As shown below in Figure 1, for each trial, two side-by-side arrays were presented on the touch screen monitor. Each array was composed of blue squares (35mm base length each) displayed on a black background (315mm by 315mm; i.e., 992.25cm²). All remaining area on the screen outside of the black background was gray. The distance between the centers of the arrays was 210mm. Array square arrangement varied randomly from trial to trial within a 9 x 9 virtual matrix in which squares could be presented. For numerosity versus blank and small numerosity versus large numerosity trials, pairwise comparisons and the position of the correct array within each pair (left versus right on the computer screen) were randomly presented. For test trials, pairwise comparisons and the position of the correct array within each pair were randomly presented but appeared with equal frequency.

Numerosity versus blank. Numerosities of each of the two arrays varied from b (i.e., b = blank) to 6 and six possible pairwise comparisons (i.e., b vs. 1, b vs. 2, b vs. 3, b vs. 4, b vs. 5, b vs. 6) were presented.

Small numerosity versus large numerosity. Numerosities of each of the two arrays varied from either 1 to 3 and 4 to 6 respectively, and all nine possible pairwise comparisons (i.e., 1 vs. 4, 1 vs. 5, 1 vs. 6, 2 vs. 4, 2 vs. 5, 2 vs. 6, 3 vs. 4, 3 vs. 5, 3 vs. 6) were presented.

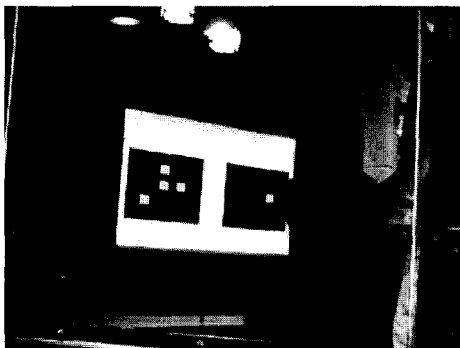
Test trials. Numerosities of each array varied from 1 to 6 and all 15 possible pairwise comparisons (i.e., 1 vs. 2, 1 vs. 3, 1 vs. 4, 1 vs. 5, 1 vs. 6, 2 vs. 3, 2 vs. 4, 2 vs. 5, 2 vs. 6, 3 vs. 4, 3 vs. 5, 3 vs. 6, 4 vs. 5, 4 vs. 6, 5 vs. 6) were presented.



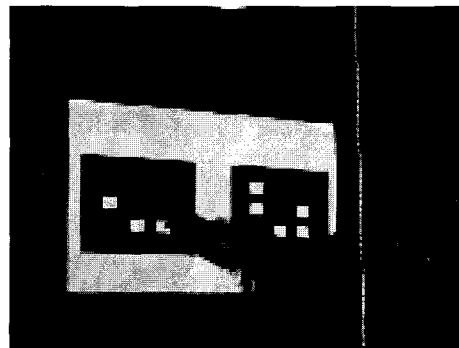
a.



b.



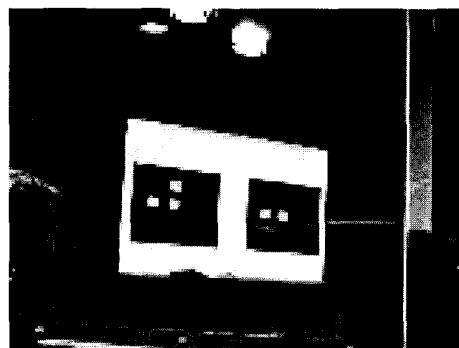
c.



d.



e.



f.

Allie

Azy

Figure 1. Orangutan participants (Allie and Azy) performing numerosity versus blank (a, b), small numerosity versus large numerosity (c, d), and test trials (e, f).

Measures

An orangutan response indicated orangutan choice and was operationally defined as a computer registered touch to the monitor surface by any part of the participants' finger(s) or hand. Accuracy on RNJs was used to assess orangutan success (i.e., accuracy measured by percent correct) on abstract RNJs.

Measures used to assess orangutan numerical representation were as follows.

A. Analogue-magnitude model:

1. Numerical difference: The larger numerosity minus the smaller numerosity (Addessi et al., 2008), ranged from 1 (for pairwise comparison of numerosities 1 vs. 2, 2 vs. 3, 3 vs. 4, 4 vs. 5, 5 vs. 6) to 5 (for pairwise comparison of numerosities 1 vs. 6)
2. Numerical size: The larger numerosity of a pairwise comparison (Dehaene et al., 1998), ranged from 2 (for pairwise comparison of numerosities 1 vs. 2) to 6 (for pairwise comparison of numerosities 1 vs. 6, 2 vs. 6, 3 vs. 6, 4 vs. 6, 5 vs. 6).
3. Ratio: The smaller numerosity divided by the larger numerosity (Addessi et al., 2008), ranged from 0.17 (for pairwise comparison of numerosities 1 vs. 6) to 0.83 (for pairwise comparison of numerosities 5 vs. 6).

B. Object-file model:

1. Total array items: The addition of the smaller and the larger numerosity from a pairwise comparison (Addessi et al., 2008), ranged from 3 (for pairwise comparison of numerosities 1 vs. 2) to 11 (for pairwise comparison of numerosities 5 vs. 6).

Procedure

Testing began with either RD (principal investigator), RS (Azy's primary researcher and GAT staff) or GAT caretakers asking either Allie or Azy if they would like to do some work with RD in the case of Allie or RS in the case of Azy. Allie had worked with various researchers but Azy had a long history of working solely with RS on numerical types of research. Therefore, Allie was deemed able to work with a new researcher, RD, but RS conducted work with Azy. RS was unavailable for a period of time during the course of this study and during his absence, Azy worked with GAT caretakers and RD. Due to caretaker and building scheduling, Allie participated early in the day and Azy later in the afternoon.

Once the participant voluntarily moved into the research room and in front of the touch screen monitor, testing began. Participants sat ~45-60 cm away from the monitor surface. Each trial began with the presentation of a start key (i.e., plus sign) in the middle of the touch screen. When the participant touched the start key, two arrays of differing numerosities of squares (i.e., a pairwise comparison) were simultaneously presented on the touch screen.

In all trials, participants were required to choose the array with the larger numerosity of squares (any numerosity was treated as larger than blank). If the participant selected the correct array a positive sound (i.e., tone) played and they were rewarded with a food item (i.e., small pieces of sugar free jello, peanuts, Brazil nuts, or grapes). Both participants were given food rewards by either the principal investigator or Great Ape Trust staff. If participants selected the incorrect array a negative sound (i.e., buzzer)

played and participants were not rewarded with a food item. Once a choice was made, both arrays disappeared and the touch screen monitor returned to presentation of the start key. Testing stopped when the participant demonstrated lack of interest, such as not attending to study tasks, or moving away from the touch screen computer.

Acquisition training: Each session in the acquisition training consisted of 30 trials. Numerosity versus blank trials were presented first, followed by small numerosity versus large numerosity. In numerosity versus blank trials, orangutans were rewarded for choosing the array containing any square(s), when presented with one array that contained no squares (blank) and the other that contained some (1, 2, 3, 4, 5, or 6) square(s). In small numerosity versus large numerosity trials, orangutans were rewarded for choosing the array containing the larger numerosity of squares when one array contained either 1, 2, or, 3 square(s) and the other array contained 4, 5, or 6 squares.

Typically Allie and Azy participated in one acquisition training session a day, however, when extra time was available throughout the day, either orangutan could participate in a second or third session if they chose to do so. For both levels of acquisition training, orangutans were required to achieve a minimum accuracy of 80% on 3 consecutive sessions before moving on to subsequent phases of study.

Test trials: Each participant was presented with arrays that included all 15 pairwise comparisons of 1-6 squares. Each of the 15 possible pairwise comparisons was presented 56 times for a total of 840 trials. For test trials, orangutans were rewarded for choosing the array containing the larger numerosity for all possible pairwise comparisons of numerosities ranging from 1-6 square(s). Data collection typically consisted of 15-60

trials in a period of 5-20min and was termed a 'sitting' (i.e., sitting 1, sitting 2, sitting 3....). The duration and number of trials performed at each 'sitting' were determined by the orangutan's interest and willingness to participate in the task. Typically Allie and Azy participated in one 'sitting' of test trials a day, however, when extra time was available throughout the day, either orangutan could participate in a second or third 'sitting'.

Results

Research commenced on October 18, 2008 and lasted until December 14, 2008. Typically, testing occurred every day. Prior to data collection and during mid data collection, orangutan introductions were conducted in the orangutan building. The Great Ape Trust had recently acquired two new orangutans and, at the time, they were being introduced to the existing orangutans at the Trust. It is important to note that these introductions might have hindered orangutan concentration levels during testing, therefore affecting orangutan RNJ choices. Furthermore, during RS' absence, Azy worked with other GAT caretakers. This may have impeded his performance, as Azy was used to only working with RS on numerical types of research especially when a computer interface was involved.

Acquisition training

Both participants demonstrated very good accuracy on the numerosity versus blank training trials. Allie reached criterion (i.e., 80% on three consecutive sessions) in five 30 trial sessions and performed with 90%, 100%, and 83% accuracy in her last three sessions. Azy reached criterion in 3 sessions and performed with 90%, 93%, and 100% accuracy. For small numerosity versus large numerosity training, Allie reached criterion

in 8 sessions whereas Azy reached criterion in 30 sessions. For their last three sessions of small numerosity versus large numerosity training, Allie performed with 80%, 83%, and 83% accuracy and Azy performed with 97%, 90%, and 97% accuracy. Average performance, across sessions, on both numerosity versus blank and small numerosity versus large numerosity is shown in Figure 2.

Test trials

Pairwise comparisons were designed for presentation 56 times each, however, due to technical problems, presentations of some pairwise comparisons were not fully balanced. As a result, for Allie, 116 trials were unbalanced and for Azy 48 trials were unbalanced. That is, for Allie, 116 trials consisted of pairwise comparisons that were presented more or less than 56 times and for Azy, 48 trials consisted of pairwise comparisons that were presented more or less than 56 times. These trials were still considered valuable; thus, they were included in (rather than deleted from) the analyzable data set. Upon consultation with statisticians, it was decided that the loss of a ‘fully’ balanced data set would not affect results given the number of total data points. Additionally, upon viewing video recordings, invalid trials were identified (i.e., hand touching screen when not looking). Of Allie’s 840 data points, 16 trials were invalidated due to inadvertent touch screen. Of Azy’s 840 data points, one trial was invalid due to an inadvertent touch screen trigger. Thus data for these trials were discarded. Analyses were based on the remaining 824 and 839 trials for Allie and Azy, respectively.

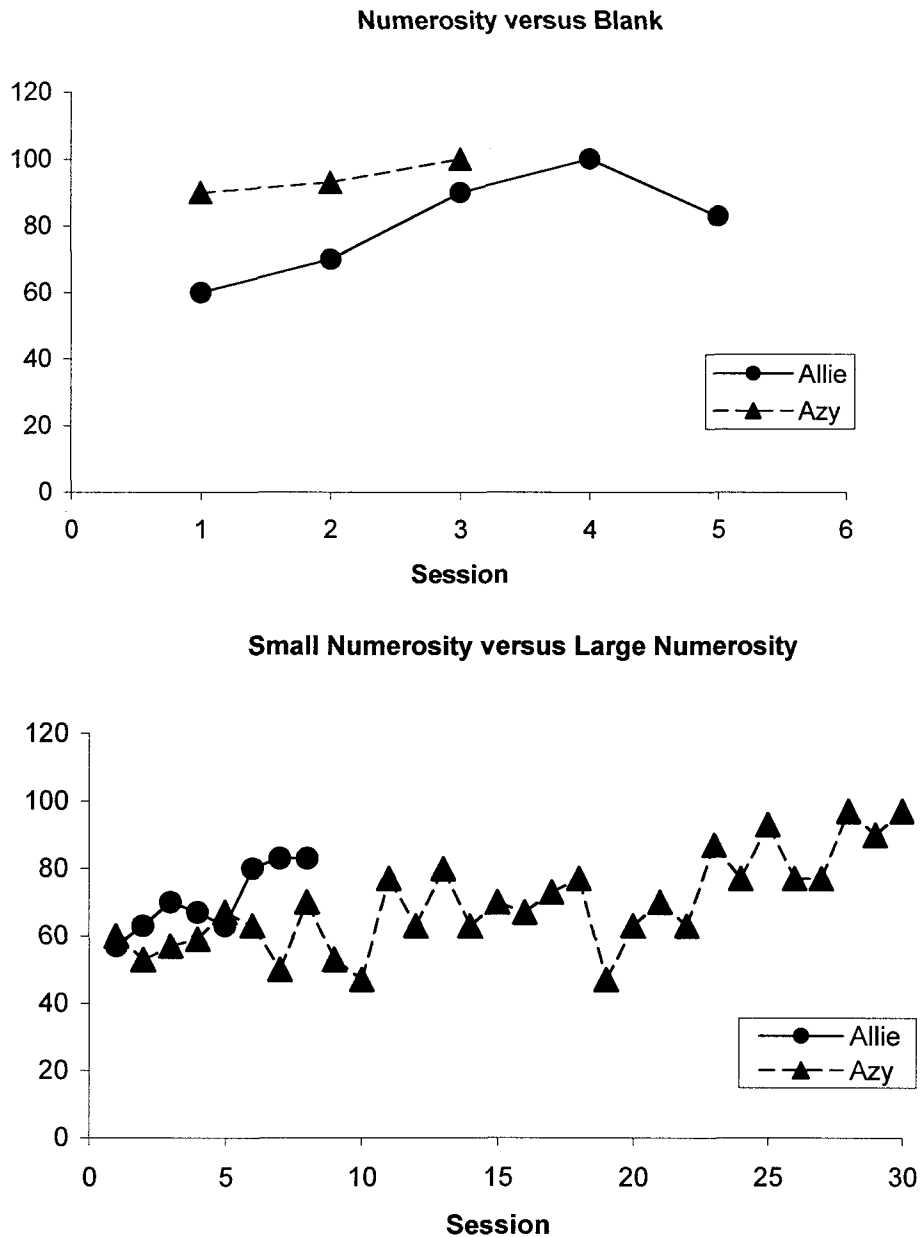


Figure 2. Average percent of correct choices made by Allie and Azy on numerosity versus blank (top panel) and small numerosity versus large numerosity (bottom panel) across sessions.

The accuracy scores on test trial RNJs for Allie ranged from 59% to 87% with a mean of 73% ($SD = 7.85$). For Azy, accuracy scores ranged from 45% to 93% with a mean of 70% ($SD = 13.58$). As seen in Figure 3 both participants demonstrated variability in their accuracy.

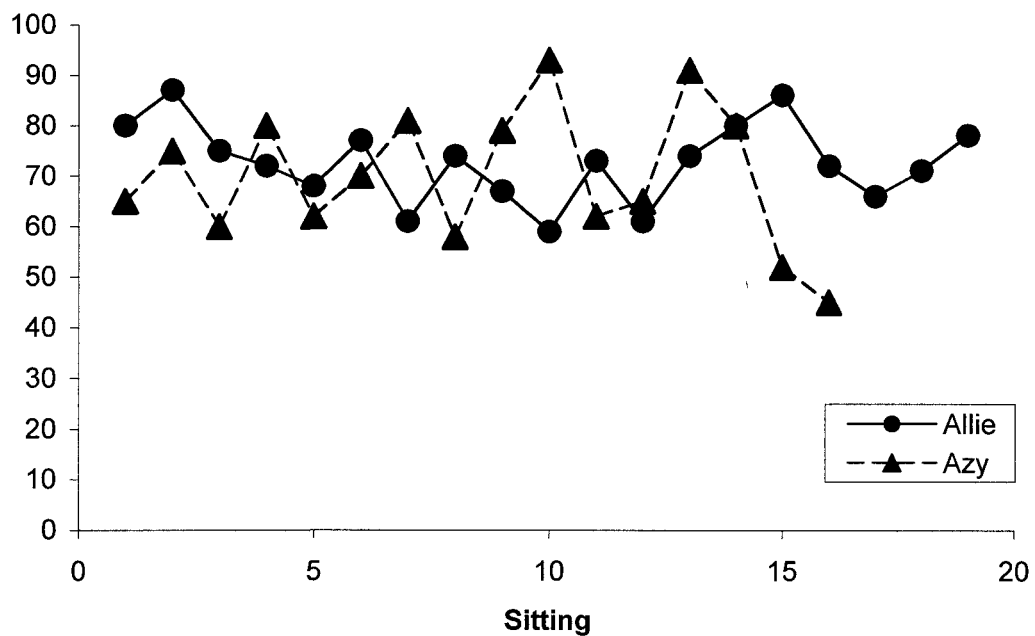


Figure 3. Average percent of correct choices made by Allie and Azy on RNJ test trials across sittings.

For each participant, incorrect and correct RNJ frequencies were calculated and analyzed in a chi-square goodness-of-fit test. Expected values (i.e., success rates by chance) were calculated by dividing the observed test trial frequencies by two because for

each pairwise comparison orangutans had a 50% chance of choosing the correct array.

These frequencies are shown in Table 1. As expected, chi-square analyses revealed that

RNJ accuracy for both orangutans was significantly higher than predicted by chance

(Allie, $\chi^2(1, N = 1) = 152.08, p < 0.001$; Azy, $\chi^2(1, N = 1) = 136.97, p < 0.001$). These

results were consistent with other investigations of RNJs wherein nonhuman primates

demonstrated RNJ ability. Although Allie made more incorrect RNJ choices than Azy, a

chi-square test of independence revealed that there was no significant difference between

their RNJ performance, $\chi^2(1, N = 2) = 0.329, p > 0.05$.

Table 1

Response Accuracy Frequencies for Orangutans (Allie and Azy) on Test Trials

	Correct (Observed)	Incorrect (Observed)	Expected	Invalid
RNJ Frequencies				
Allie	589	235	412	16
Azy	589	250	419.50	1

Figure 4 shows the accuracy scores for each pairwise comparison for each participant as a function of the *numerical difference* between the larger and smaller pairwise comparison and *numerical size*. For example, accuracy for the pair 5 vs. 3 is plotted at “2” along the horizontal scale. The graphs show not only the effect of

numerical difference but also of *numerical size* on both participants' accuracy scores.

To test the effects of numerical difference and numerical size on accuracy, multiple regression analyses were conducted using the numerical size and the numerical difference of the pairwise comparisons as the predictor variables and accuracy scores as the criterion variable.

For Allie, a significant multiple R-squared was obtained ($F(2,12) = 40.024, p < 0.001$; Adjusted $R^2 = 0.848$) (see Table 2). The Adjusted R^2 value informs us that 84.8% of the variability in the criterion variable (i.e., accuracy scores) was accounted by the predictor variables (i.e., the numerical size and the numerical difference). Also the regression coefficient for each independent variable was significantly different from 0 (numerical difference, unstandardized $B = 9.743, \beta = 1.042, p < 0.001$; numerical size, unstandardized $B = -2.657, \beta = -0.284, p < 0.05$). Therefore, an increase in numerical difference of 1 was associated with a 9.743% increase in percent correct, after controlling for numerical size. Furthermore, an increase in numerical size of 1 was also associated with a 2.657% decrease in percent correct, after controlling for numerical difference.

For Azy, a significant multiple R-squared regression was also obtained ($F(2,12) = 20.493, p < 0.001$; Adjusted $R^2 = 0.736$) (see Table 2). The Adjusted R^2 value informs us that 73.6% of the variability in Azy's accuracy scores was accounted by numerical size and numerical difference. Further, the regression coefficient for numerical difference was significantly different from 0 (numerical difference, unstandardized $B = 9.686, \beta = 0.988, p < 0.001$) but the regression coefficient for numerical size was not (numerical size, $B = -2.857, \beta = -0.292, p = 0.091$). Therefore, an increase of numerical difference by 1 was

associated with a 9.686% increase in accuracy, controlling for numerical size but an increase in numerical size of 1 was not associated with an increase or decrease in percent correct, after controlling for numerical difference.

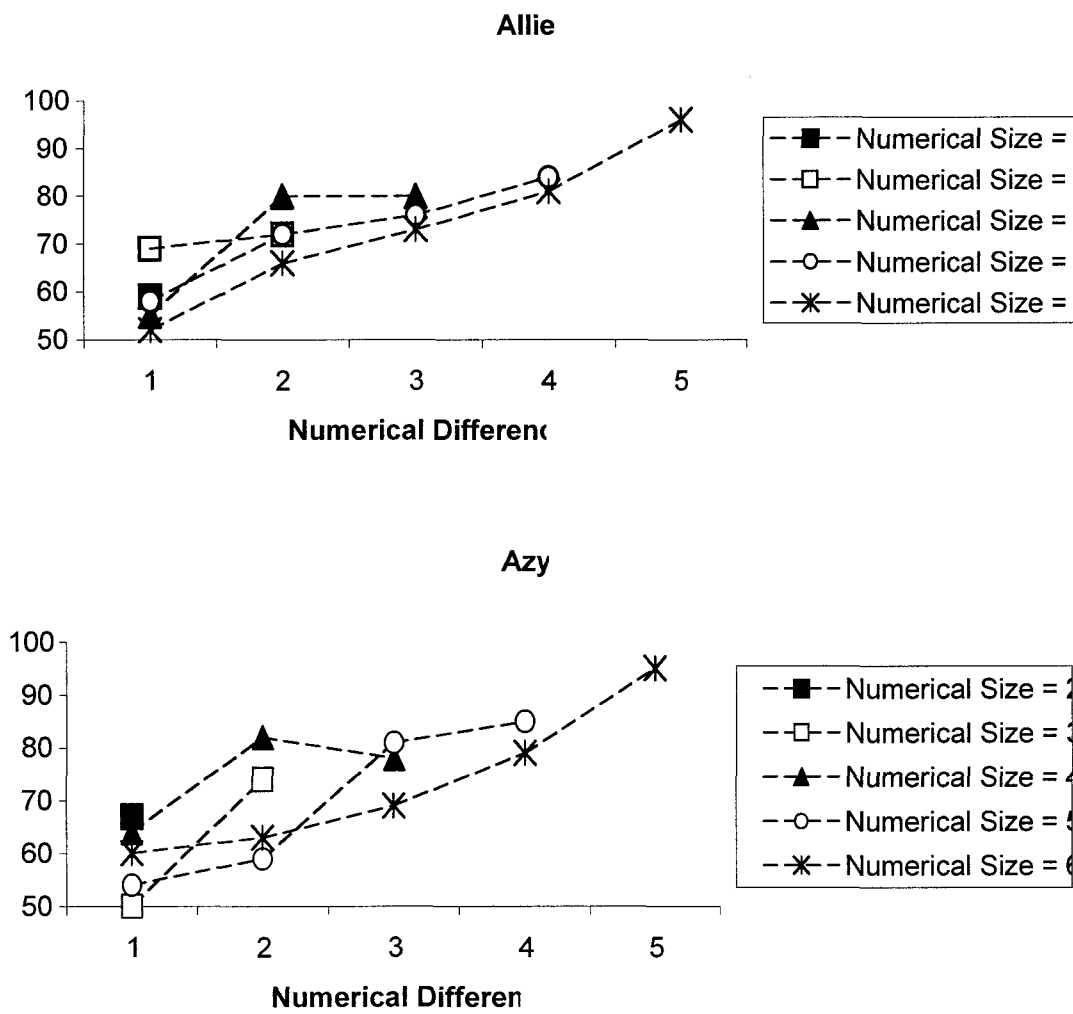


Figure 4. Accuracy for each pair of numerosities for Allie (top panel) and Azy (bottom panel) as a function of numerical difference and numerical size.

Table 2

Multiple Regression Analyses for Numerical Difference and Numerical Size on Accuracy

Participant	Coefficients					
	numerical difference	numerical size	Intercept	Adj R^2	β for numerical difference	β for numerical size
Allie	9.743***	-2.657**	61.200	0.848***	1.042***	-0.284**
Azy	9.686***	-2.857 ns	61.400	0.736***	0.988***	-0.292 ns

ns not significant

*** $p < 0.001$

** $p < 0.05$

If orangutan performance was based on the analogue-magnitude model, results should show a significant effect of ratio for pairwise comparisons. To evaluate this effect, simple regression analyses were conducted using the ratio of pairwise comparisons as the predictor variable and accuracy scores as the criterion variable (see Table 3). Figure 5 shows the average percent of correct choices made by Allie and Azy on pairwise ratios.

For both participants significant simple regressions were obtained (Allie, $F(1,13) = 41.893$, $p < 0.001$; Adjusted $R^2 = 0.745$; Azy, $F(1,13) = 39.780$, $p < 0.001$; Adjusted $R^2 = 0.735$). For Allie, 74.5% of the variability in her accuracy scores can be accounted for by the ratio of the

pairwise comparisons. For Azy, 73.5% of the variability in his accuracy scores can be accounted for by the ratio of the pairwise comparisons. Furthermore, for both participants, the regression

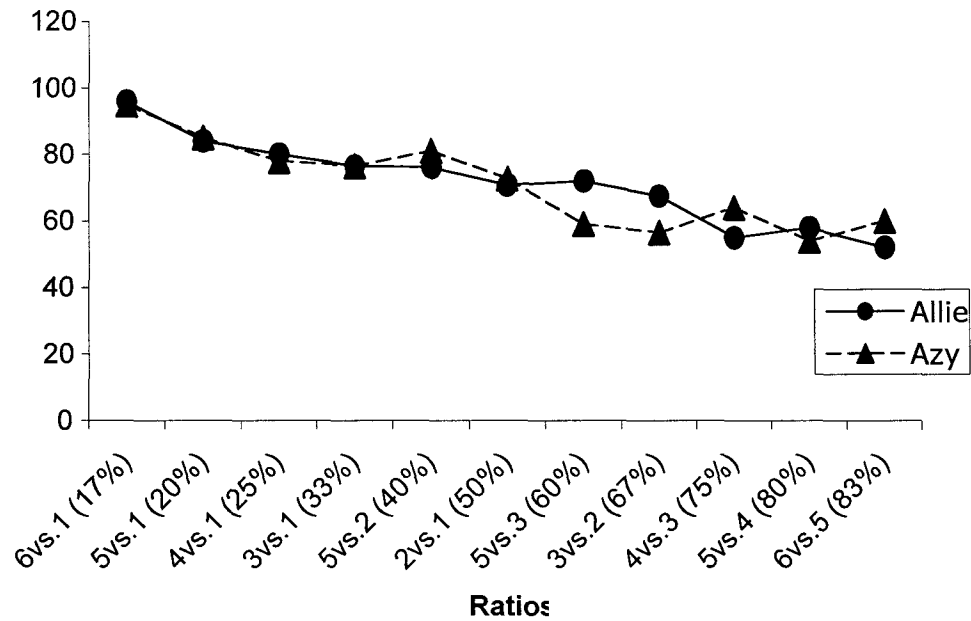


Figure 5. Average percent of correct choices made by Allie and Azy on RNJ ratios across sittings.

coefficient for the ratio was significantly different from 0 (Allie, unstandardized $B = -48.648$, $\beta = -0.874$, $t(13) = -6.472$, $p < 0.001$; Azy, unstandardized $B = -50.653$, $\beta = -0.868$, $t(13) = -6.307$, $p < 0.001$). Therefore for Allie, an increase of ratio by 1 was associated with a 48.648% decrease in percent correct and for Azy an increase of ratio by 1 was associated with a 50.653% decrease in percent correct.

Table 3

Simple Regression Analyses for Ratio on Accuracy

Participant	Coefficients			
	ratio	Intercept	Adj R^2	β
Allie	-48.648***	95.857	0.745***	-0.874***
Azy	-50.653***	95.993	0.735***	-0.868***

ns not significant

*** $p < 0.001$

** $p < 0.05$

If orangutan performance was based on the object-file method, results should show a significant effect of total array items for pairwise comparisons. To evaluate this effect, simple regression analyses were conducted using total array items for pairwise comparisons as the predictor variable and accuracy scores as the criterion variable (see Table 4).

For both participants, simple regressions for total array items on accuracy were non-significant (Allie, $F(1,13) = 0.837, p > 0.10; R^2 = 0.061, \text{Adjusted } R^2 = -0.012$; Azy, $F(1,13) = 0.885, p > 0.10; R^2 = 0.064, \text{Adjusted } R^2 = -0.008$). Furthermore, for both participants, the regression coefficient for total array items was not significantly different from 0 (Allie, unstandardized $B = -1.329, \beta = -0.246, t(13) = -0.915, p > 0.10$; Azy,

unstandardized $B = -1.429$, $\beta = -0.252$, $t(13) = -0.941$, $p > 0.10$). Therefore, these results suggest that object-file representation was not present in orangutan RNJs and that numerical representation, in the present study, was best explained by the analogue-magnitude model.

Table 4

Simple Regression Analyses for Total Array Items on Accuracy

Participant	Coefficients			
	Total array items	Intercept	Adj R^2	β
Allie	-1.329 ns	80.833	-0.012 ns	-0.246 ns
Azy	-1.429 ns	80.667	-0.008 ns	-0.252 ns

ns not significant

Discussion

Previous research on orangutan numerical ability has explored orangutan RNJ ability with the use of food arrays during simultaneous presentation, sequential presentation, and reversed reinforcement contingencies. RNJs without food arrays have received less attention. The goal of the present research was to assess RNJs with simultaneously presented non-food arrays, specifically abstract arrays (i.e., squares on a computer), and to assess numerical representation (i.e., analogue-magnitude model vs.

object-file model) based on numerical distance, numerical size, ratio, and total array item effects. Orangutans trained on simple simultaneously presented RNJs were tested for their RNJ abilities on all possible pairwise comparisons of numerosities from 1-6.

Consistent with the nonhuman primate literature, the results showed that the two orangutan participants successfully performed RNJs. Allie had relatively little difficulty during acquisition training but Azy took much longer to reach criterion than Allie. This is interesting given that Allie, prior to this study, had no numerical experimental experience. In contrast, Azy had participated in several projects regarding numerosities and Arabic numerals. Despite their different numerical experience, Allie and Azy had similar accuracy rates and showed few other differences in performance during test trials, thereby demonstrating that, after acquisition training, both had a similar understanding of RNJs. Throughout test trials, however, Azy demonstrated much more variability than Allie in performance. It is plausible that Azy's previous experience with reversed reinforced contingencies (Shumaker et al., 2001) was a source of confusion and delayed his understanding of straightforward RNJs (i.e., *not* reversed reinforced). Furthermore, several caretakers were involved in running and distributing rewards in the present study, which Azy had not experienced in his earlier numerical work. As such, Azy's previous experience with a single researcher in numerical studies may have been an additional source of confusion on the present tasks.

Analysis of the nonhuman primate literature has suggested that RNJ performance is more successful with food arrays than with non-food arrays and when participants are rewarded with food items corresponding to the numerosity of their chosen array (Beran et

al., 2005). In the current study, both participants successfully performed RNJs when arrays were not food related *and* also when rewards did not correspond to the exact array numerosities. This study cannot and did not aim to verify whether orangutan choices on abstract RNJs are more or less reliable than choices made on food RNJs. An understanding of this would require a study using the same paradigm to directly compare RNJ performance with food arrays and non-food arrays. However, Azy has previously participated in a study on reversed contingencies using food arrays and performed successfully (Shumaker et al., 2001). Therefore, for Azy, the use of food arrays (as in Shumaker et al., 2001) and the use of non-food arrays (abstract symbols used in the present study) seemed to pose him little difficulty. Furthermore, Azy, in the present study did not have problems when rewards did not correspond to the numerosity of his choices and previously did not have problems when rewards did correspond to the numerosity of his choices (as in Shumaker et al., 2001). Thus, for orangutans, the use of food arrays versus that of non-food arrays and rewards directly corresponding to orangutan choices versus rewards not directly corresponding to orangutan choices may not be important factors in predicting orangutan RNJ ability.

Consistent with previous reports in the literature (e.g., Addessi et al., 2008; Tomonaga, 2008), for both participants, patterns of choice were mainly affected by numerical differences and ratios present among pairwise comparisons. For both orangutan participants, numerical difference significantly contributed to RNJ choices. Specifically, as the numerical difference increased between pairwise comparisons, orangutans had greater RNJ success. In particular, as seen in Figure 2, both Allie and Azy

demonstrated greater accuracy when the numerical difference was greater than 1. With numerical differences of 1 (e.g., pairs 3 and 2, or 6 and 5), both orangutans' choices were only 50% accurate. In comparison, with numerical differences of 5, both orangutans' choices were 90% accurate. This finding contrasts with Tomonaga's (2008): his chimpanzees RNJs were 90% correct even when numerical differences equaled 2. It is plausible that more training sessions and a higher success criterion on training would have resulted in greater accuracy for the orangutans during test trials with smaller numerical differences. For example, Tomanaga's success criterion during acquisition was 90% whereas this study used a criterion of 80% for all phases of acquisition training.

Furthermore, for Allie but not Azy, an increase in numerical size was associated with a decrease in percent correct. That is, her accuracy was influenced by the magnitude of the larger of the two numerosities being compared, irrespective of the numerical difference between array pairs. For both apes, however, numerical size contributed to performance when combined with numerical difference to assess ratio effects. For Allie and Azy, 74.5% and 73.5% of the variability in their RNJ performances, respectively, can be attributed to the ratios among pairwise comparisons. Specifically, as ratios of pairwise comparisons approached 1, accuracy decreased. For example, pairwise comparisons of 5 vs. 6 proved more difficult than 1 vs. 4. Therefore the orangutans in this study had more difficulty making RNJs when ratios were large than those that were small. These results are consistent with previous reports in nonhuman primates including orangutans (e.g., Anderson et al., 2007; Hanus & Call, 2007), in which ratio was the best predictor of RNJ performance.

As previously mentioned, there is an ongoing debate centered on the main system for numerical representation used by humans and nonhuman animals: approximate representation (i.e., analogue-magnitude model) and the precise representation of distinct items (i.e., object-file model) (Tomonaga, 2008). In the present study, total array items were used to measure the presence of object-file representation, and there was no significant effect for total array items on accuracy. Both orangutans were able to reliably choose the array containing the larger numerosity even when both array items totaled more than 4 (the maximum limit for total array item representation under the object-file model). This is in line with other studies that have also failed to find the total items of two arrays to affect RNJ choices (e.g., Addessi et al., 2008; Anderson et al., 2007; Hanus & Call, 2000).

Previously, in the literature, some nonhuman primates have demonstrated certain characteristics of the analogue-magnitude model but numerical size is one such effect that has not always been documented in the literature. However, both numerical difference and ratio has been predominantly found to affect nonhuman primates' RNJ choices. In the present study, similarly, numerical difference and ratio best explain orangutan choices. There was no effect found for total array items on accuracy, thereby making it unlikely that orangutans represent numerosity by way of the object-file model. The analogue-magnitude model best explains numerical representation in orangutans in the present study.

Conclusion

Orangutans reliably made correct RNJs, by selecting the larger numerosity of two paired arrays, when numerosities were presented in the form of abstract stimuli. This suggests that orangutans have numerical ability and further adds to the wealth of research indicating that nonhuman animals have numerical ability. Furthermore, the pattern of results gives support to the analogue-magnitude model of numerical representation. This pattern of representation, also found in human preverbal infants and adults, adds strength to the argument that great apes and, plausibly, other species of animals may use approximate numerical representation.

These findings contribute to the existence of non-verbal numerical representation and add to the existence of numerical ability and numerical representation in other species that do not possess language. Many researchers have argued that numerical ability requires language and that it is not independent of language (Hurford, 1987). However, the current results, in agreement with previous findings of non-verbal numerical representation, suggest that, in fact, numerical ability may not require an understanding of language. As some researchers argue for humans' predisposed ability to learn language, numerical ability may also be a predisposed ability. This suggests potential evolutionary aspects of numerical ability. I am not arguing that numerical abilities such as counting or multiplication are instinctive, however, there is the possibility that a basic elementary numerical ability such as relative numerosity judgment is a natural ability. As previously stated, there are quite possibly many advantages for being able to succeed on RNJs such that one is more equipped in the wild in terms of

foraging or for tracking opponents. Therefore, RNJs may be closer to an evolutionary ability while counting, or multiplication, could be more ontogenetically set because humans *must* learn to count in order to survive in most societies and cultures. Thus numerical ability may be ‘portioned’ in that it may include both developmental verbal symbolic types of abilities, required for higher-level numerical ability (e.g., arithmetic) as well as evolutionary preverbal abilities such as numerosity tasks that have even been demonstrated in human infants.

Although the present study examined the use of abstract stimuli it did not examine the effects of other numerical-related factors such as area or density. It is possible that such factors could be more salient than the numerosities themselves, in orangutans. Because previous research has yet to systematically look at these factors, it is important that these be considered in future designs. Future studies should also use paradigms in which both the use of food arrays and non-food arrays are used so that direct comparisons between the two types of stimuli can be directly assessed.

Lastly, to really assess numerical ability or more so a predisposition in nonhuman primates for numerical ability, it is suggested that less training is provided before data is collected (Tomonaga, 2008). It is possible that extensive training may impede performances on certain types of numerical ability (e.g., Azy on straightforward RNJs after being trained on reversed reinforced RNJs) and that learning may override numerical abilities with similar goals but studied under different paradigms (e.g., Azy on straightforward RNJs after being trained on reversed reinforced RNJs). Therefore more effort should be made to collect data on spontaneous exhibits of numerical ability in

“untrained” situations because, to date, there still exist inconsistent results in the “untrained” situations (e.g., Lewis, Jaffe, & Brannon, 2005). Even more, it may be worth testing infant nonhuman primates with less experience for a better understanding of instinctive ability versus developed ability, something not researched.

More studies of this nature are very important in understanding numerical ability evolutionarily and developmentally: a field with the potential to link human numerical cognition to that of animal numerical cognition. These in result may shed light on the origins of human numerical ability as well as the importance for having numerical ability.

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