SYMBOLIC QUANTITY DISCRIMINATION AND SUMMATION IN WESTERN LOWLAND GORILLAS

by

TORI L. VRATANINA

(Under the Direction of Irwin S. Bernstein)

ABSTRACT

Some non-human primate species have demonstrated the capacity for quantity discrimination and summation with symbolic representation in the form of tokens. I examined this capacity in seven Western lowland gorillas (*Gorilla gorilla gorilla*). In Phase I of the experiment, the gorillas were asked to make a choice between two unequal values (e.g. 1 cylinder token = 5 blueberries vs. 1 cube token = 1 blueberry). In Phase II, two subjects were presented with homogeneous choice combinations (e.g. 2 pyramid tokens = 6 blueberries vs. 4 cube tokens = 4 blueberries). Three of the gorillas performed successfully in Phase I while one performed successfully in Phase II, utilizing the strategy of 'choose the larger sum,' under some conditions, over the alternative strategies of 'choose the larger number of tokens' or 'choose the higher value token.' This research demonstrates that gorillas have the capacity to perform symbolic quantity discriminations and summation judgments.

INDEX WORDS: quantity discrimination, summation, symbolic representation, *Gorilla*, token

SYMBOLIC QUANTITY DISCRIMINATION AND SUMMATION IN WESTERN LOWLAND GORILLAS

by

TORI L. VRATANINA

BS, Michigan State University, 2007

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2009

SYMBOLIC QUANTITY DISCRIMINATION AND SUMMATION IN WESTERN LOWLAND GORILLAS

by

TORI L. VRATANINA

Major Professor: Irwin S. Bernstein

Committee: Jonathon L. Crystal
Dorothy M. Fragaszy

Electronic Version Approved:

Maureen Grasso
Dean of the Graduate School
The University of Georgia
August 2009

ACKNOWLEDGEMENTS

There are many individuals I would like to thank for their encouragement and assistance on this project. First, I am grateful to my major advisor, Dr. Irwin Bernstein. His patience, support, and advice have been instrumental in the development and completion of this project. I also would like to thank my committee members, Dr. Dorothy Fragaszy and Dr. Jonathon Crystal, for their support in the completion of my thesis. It was greatly improved by their suggestions. Finally, I would like to thank the Zoo Atlanta staff—Charles Horton, Curator of Primates; Dr. Tara Stoinski, Manager of Conservation Partnerships; and the primate keepers: Bernie Gregory, Jodi Carrigan, Kristina Krickbaum, and Michele Dave—for their advice and assistance. This project would not have been possible without their flexibility and support.

I also am indebted to my friends and family who offered their time and advice in the implementation and completion of my Master's thesis. This project would not have been possible without the help of my research partner, Desiree Sharpe. I am especially grateful to Desiree for helping me develop and carry out the project.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

The ability to understand ‘number,’ particularly the concepts of ‘less’ and ‘more,’ has significant ecological relevance for animals when engaging in behaviors such as foraging and predator avoidance (i.e. reducing the risk of predation by choosing to live in a larger group), as well as social interactions, such as aggressive encounters (i.e. identifying the number of potential opponents) (Agrillo, Dadda, & Bisazza, 2007). Numerical competence has been investigated and demonstrated in a variety of non-human primate species in both laboratory and field settings (for reviews see Boysen & Hallberg, 2000; Gallistel & Gelman, 2000). Specifically, non-human primates have demonstrated the capacity to choose the larger of two unequal choice options (i.e. a relative numerousness judgment, or RNJ) in a variety of contexts, such as straightforward quantity discrimination tasks, reversed contingency tasks, and tasks in which items are presented sequentially rather than simultaneously or item-by-item rather than whole sets.

Quantity Discrimination in Non-human Primates

In straightforward quantity discrimination tasks, subjects are presented with a choice between a larger and a smaller quantity. The subject is then given the chosen quantity. To perform optimally on this task and demonstrate RNJ, the subject must choose the larger quantity. Many non-human primate species have performed successfully on this type of task, as demonstrated in the great apes (*Pan paniscus, Pan troglodytes, Gorilla gorilla, Pongo pygmaeus*), capuchin monkeys (*Cebus apella*), cotton-top tamarins (*Saguinus oedipus*), common marmosets (*Callithrix jacchus*), and rhesus macaques (*Macaca mulatta*) (Anderson, Stoinski, Bloomsmith, Marr, Smith, & Maple, 2005; Anderson, Stoinski, Bloomsmith, & Maple, 2007; Boysen & Berntson, 1989; Call, 2000; Flombaum, Junge, & Hauser, 2005; Hanus & Call, 2007; Stevens, Wood, & Hauser, 2007; Tomonaga, 2008). For example, Anderson et al. (2007) investigated RNJs in nine orangutans. The orangutans were presented with a choice between two trays, each with one food well baited with 1 to 5 grapes so that they received 10 quantity comparisons (1:2, 1:3, 1:4, 2:3, 2:4, 2:5, 3:4, 3:5, and 4:5). For instance, in the 4:5 comparison one tray was baited with 4 grapes and the other tray was baited with 5 grapes. Seven of the nine orangutans performed RNJs above chance, selecting the larger quantity, after receiving 130 trials.

In reversed contingency tasks, subjects are once again presented with a choice between a larger food array and a smaller food array. However, in order to perform optimally in this task the subject must choose the smaller array in order to receive the larger array. Reversed contingency tasks are typically used to study self-control but also can reveal nuances between non-human primates' perceptual and cognitive approaches to RNJs. Some non-human primates perform well on this task (see Shumaker, Palkovich, Beck, Guagnano, & Morowitz, 2001; Vlamings, Uher, & Call, 2006) while for others the task can be challenging. Two chimpanzees (Sheba and Sarah) in Boysen and Berntson's (1995) study were unable to perform successfully on a reversed contingency task despite their extensive experience in counting and number comprehension tasks. The chimpanzees were asked to choose between two quantities of candies (ranging from 1 to 6 pieces). The selected quantity was given to a passive 'observer' chimpanzee while the 'selector' received the remaining quantity. The 'selector' was unable to suppress choosing the larger quantity despite displaying behavioral distress which demonstrated an appreciation of the response consequences. Sarah and Sheba had previously learned an association between Arabic numerals and a corresponding, equivalent food reward (i.e. the Arabic numeral 2 = 2 pieces of candy). Unsurprisingly, when the choices were presented as Arabic numerals both chimpanzees began choosing the smaller quantity and thus receiving the larger candy quantity. Successful performance occurred immediately following the introduction of the Arabic numerals, indicating that the chimpanzees had learned the contingencies of the task but were unable to apply them when presented with food arrays. In another study by Boysen, Berntson, Hannan, and Cacioppo (1996), chimpanzees were tested on the reversed contingency task without the presence of an 'observer' chimpanzee. The chimpanzees were tested on rock arrays (i.e. 3 rocks = 3 pieces of candy) in addition to the candy and Arabic numeral arrays. They performed similarly to Sheba and Sarah on the candy and Arabic numeral array trials, replicating Boysen and Berntson's (1995) previous findings. The chimpanzees' performance on the rock array trials was below chance although better than their performance on the candy array trials. Overall, these findings indicate that quantity discriminations in non-human primates can be accomplished at different levels of cognition.

Further experiments have examined how the presentation of the choice stimuli, and therefore the cognitive difficulty of the task, influences non-human primates' performance on quantity discrimination tasks. In particular, Hanus and Call (2007) investigated the effect that a whole set presentation versus an item-by-item presentation would have on great apes' performance on a quantity discrimination task. In one task (whole set presentation), subjects were given a choice between two unequal food quantities under two conditions: a low-quantity test and a high-quantity test. The choice options were presented in two separate dishes either simultaneously or sequentially. For the low-quantity test they received all possible combinations ranging from 0 to 6 pellets (i.e. 0:1, 1:2, 1:3, 1:4, 1:5, 1:6, 2:3, 2:4, 2:5, 2:6, 3:4, 3:5, 3:6, 4:5, 4:6, 5:6). For the high-quantity test they received all possible combinations ranging from 4 to 10 pellets (i.e. 1:2, 2:3, 3:6, 4:6, 5:6 3:9, 4:8, 4:10, 5:8, 5:9, 6:8, 6:9, 6:10, 7:8, 7:9, 7:10, 8:10, 9:10). All of the great ape species performed successfully on this task by choosing the larger quantity regardless of the combination presented (e.g. performed equally well on the low-quantity and high-quantity presentations) or whether the quantities were presented simultaneously or sequentially. In the second task (item-by-item presentation), subjects were given a choice between the same food quantities as listed above that were dropped sequentially into two opaque cups. All of the great ape species selected the larger quantity in the low-quantity but not the high-quantity presentations; however, only chimpanzees and orangutans performed significantly above chance. These results demonstrate that great apes are able to manage complex representations of different quantities even when the task becomes more cognitively difficult.

Summation in Non-human Primates

In addition to demonstrating non-human primates' capacity for RNJs, work with non-human primates also has yielded evidence for 'summation,' as defined by the ability to correctly choose the pair of quantities that have an overall sum that is larger than the sum of the other pair option(s) (Anderson et al., 2005, 2007; Otlhof, Iden, & Roberts, 1997; Pérusse & Rumbaugh, 1990; Rumbaugh, Savage-Rumbaugh, & Hegel, 1987). Rumbaugh et al. (1987) examined summation in two chimpanzees, by asking them to choose between two trays, each containing two food wells baited with 0 to 4 chocolates (i.e. 4 and 1 versus 4 and 0). In order to perform successfully on this task, the subjects had to combine the quantities presented in each tray to choose the tray with the larger overall sum. The chimpanzees showed a significant preference for the larger sum, regardless of which tray had the largest amount of food in a single well or the geometry of the food placement in each well. Subsequent studies with the same two chimpanzees (Pérusse & Rumbaugh, 1990) also revealed that the subjects were not using the strategy of avoiding the trays with wells containing 0 or 1 chocolate to perform successfully on the summation task. These results indicate that chimpanzees are capable of performing basic summation operations.

Numerical Competency Tasks with Symbolic Representation

A large body of research also has been devoted to investigating quantity discriminations and summation with symbolic representation (Addessi, Crescimbene, & Visalberghi, 2007, 2008; Beran, Beran, Harris, & Washburn, 2005; Olthof et al., 1997). Beran et al. (2005) trained two chimpanzees and a rhesus macaque to associate different food quantities with a particular colored container. In a quantity discrimination task, subjects were presented with trials consisting of three or more containers during which they could select one at a time. All three subjects were able to use the color representations to choose the correct ordinal sequence of containers, from those holding the largest food quantity to those holding the smallest food quantity. Olthof et al. (1997) investigated summation in two squirrel monkeys (*Saimiri sciureus*) using combinations of Arabic numerals (0, 1, 3, 5, 7, and 9) which corresponded to an equivalent food reward. The subjects were presented with choice options containing more than one number (e.g. 9 + 0 versus 7 + 5). Both monkeys exhibited an immediate, strong preference for the larger sum on most choice combinations.

Tokens also have been successfully used as symbolic representations of food, specifically as secondary reward items, in cognitively difficult tasks (see Sousa & Matsuzawa, 2001). Recent research directly comparing RNJs with food and tokens indicates that capuchin monkeys are more successful at numerical competence tasks involving primary reinforcement (Addessi et al., 2008). The monkeys were presented with a choice between two unequal quantities, ranging from 0 to 5 items, of either peanuts or tokens. Although the monkeys were able to make RNJs in both conditions, their performance was higher when peanuts were the choice stimuli. These results may be explained by the fact that token tasks are more cognitively difficult as they require that the monkeys both estimate the quantity of food the token represents as well as remember what the tokens stand for. Additionally, Addessi et al. (2007) found that some capuchin monkeys displayed a capacity for summation using token choices representing different amounts (e.g. token 'A' = 1 peanut, token 'B' = 3 peanuts). Four of ten monkeys tested reliably chose the larger sum when given a choice between 1 'B' token and 1 to 5 'A' tokens. Furthermore, two of six monkeys tested reliably chose the larger sum when offered a choice between 1 or 2 'B' tokens and 3 to 6 'A' tokens. Taken together, these studies demonstrate that capuchin monkeys are able to use tokens flexibly to both represent and combine quantities to maximize their payoffs.

Numerical Competence in Gorillas

Gorillas are traditionally thought of as being less intelligent than the other great ape species (Attenborough, 1979 as cited by Byrne, 1996). Research investigating gorillas' cognitive and social complexity may dispel this stereotype (for a review see Byrne, 1996). The present study builds upon previous work demonstrating RNJs and summation in Western lowland gorillas (*Gorilla gorilla gorilla*). Anderson et al. (2005) investigated RNJs in 11 gorillas. The gorillas were presented with a choice between two trays, each with a food well baited with 0 to 4 grapes.

They were given ten quantity comparisons: 0:1, 0:2, 0:3, 0:4, 1:2, 1:3, 1:4, 2:3, 2:4, and 3:4 (i.e. in the 1:4 comparison one tray was baited with 1 grape and the other tray was baited with 4 grapes). Four of the eleven gorillas reliably performed RNJs, selecting the larger quantity, before receiving any specific training to do so. All eleven gorillas were able to perform RNJs after receiving specific training which involved a correction procedure (no reinforcement and a 30 second inter-trial interval following selection of the smaller quantity). In the same study, the gorillas were tested on a summation task involving primary reinforcement. They were presented with a choice between two trays, each with two food wells baited with 0 to 4 grapes resulting in 27 possible choice combinations (i.e. in the choice combination of 2:3 one tray could be baited with 1 grape in one well and 1 grape in the second well and the other tray could be baited with 2 grapes in one well and 1 grape in the other well). Each of the eleven gorillas performed successfully on this task, choosing the tray with the larger sum significantly more often than chance would predict. Additionally, the gorillas' performance on the summation task was similar to that of chimpanzees and orangutans that had more experience with numerical competency tasks (Call, 2000; Pérusse & Rumbaugh, 1990; Rumbaugh et al., 1987).

Predictions

The present study examined Western lowland gorillas' success on a quantity discrimination task and a summation task with secondary reinforcement (tokens). In doing so I added greater cognitive difficulty to the summation task by asking the gorillas to use tokens flexibly as symbols to represent and to combine quantities to maximize their payoffs. The gorillas were trained to associate three tokens with a corresponding food reward of 1, 3, or 5 blueberries. Next, they were tested on a quantity discrimination task in which they had to remember what each token stands for as well as to estimate the amount of food the token represents in order to choose the larger quantity. Finally, they were tested on a summation task in which they had to combine token quantities in order to choose the larger sum. I also assessed which of three possible strategies the gorillas could be using on the summation task: (i) choose the higher value token, (ii) choose the larger physical number of tokens, or (iii) choose the larger sum. I predicted that (i) subjects would choose the larger quantity of two choices (e.g. choosing one 5-blueberry token instead of one 1-blueberry token) and (ii) subjects would choose the larger sum of two choices (e.g. choosing two 3-blueberry tokens rather than four 1-blueberry tokens).

CHAPTER 2

METHOD

Subjects

Seven captive Western lowland gorillas were tested. They ranged in age from 10 to 47 with an average age of 21.3. The gorillas were housed in three social groups at Zoo Atlanta, Atlanta, Ga. The gorillas were not food or water deprived during testing. Four of the seven gorillas had participated in quantity discrimination and summation tasks involving primary reinforcement prior to this study (see Anderson et al., 2005). See Table 1 for a detailed description of the test subjects.

Table 1
Test Subject Information

Subject	Sex	Age	Social Grouping	Prior Experience in Numerical Competency Tasks
Ozzie	M	47	Single male, multi-female	Yes
Machi	F	32	Single male, multi-female	No
Kekla	M	19	All male bachelor group	Yes
Stadi	M	17	All male bachelor group	Yes
Charlie	M	12	All male bachelor group	Yes
Olympia	F	12	Single male, multi-female	No
Kidogo	M	10	All male bachelor group	No

Tokens and Apparatus

The tokens consisted of wooden objects similar in dimensions (approximately 1” x 1” x 1”) which differed in shape and color. They included a blue or green cylinder worth a 5-blueberry food reward, an orange or purple pyramid worth a 3-blueberry food reward, and a red or yellow cube worth a 1-blueberry food reward (Figure 1). Two experimenters worked simultaneously with different subjects. In order to facilitate this, the token colors were arbitrarily chosen based on the number of each particular token available. Therefore, Olympia, Charlie, and Kidogo were tested with the green, purple, and yellow tokens while Machi, Ozzie, Stadi, and Kekla were tested with the blue, orange, and red tokens.

Figure 1: Example of Tokens: cylinder, pyramid, and cube tokens (equivalent to a 5-blueberry, 3-blueberry, and 1-blueberry food reward respectively).

The apparatus was the same as that used by Anderson et al. (2005). The plastic, rectangular tray (59.7cm x 24.1cm x 2.5cm, Figure 2) had two circular wells where the tokens and food rewards could be placed for presentation to the gorillas. The tray also had a handle and plastic rectangular stop which allowed the tray to be placed within the gorilla’s reach and prevented the subject from being able to pull the tray into the cage.

Figure 2: Tray Apparatus with Tokens

Procedure

Zoo Atlanta generously made their gorillas available from August to December, 2008 to participate in this study. The study could not be extended, however, beyond this time period as the gorillas were committed to participating in another study starting in January, 2009. Even so, we have been assured that the gorillas will be available for further testing following the completion of the studies in which they are currently participating. Testing took place three days a week from 4:00-5:30 pm (immediately after the gorillas were brought indoors for the night). Since testing took place in their indoor cages, the gorillas could not be completely isolated for testing. We were able to move Charlie, Stadi, Ozzie, and Kekla to their own cages for the duration of testing although they still had visual access to gorillas from both their own and other social groups. Machi and Olympia were tested in separate cages but still had access to each other as the doors could not be closed between their cages. Kidogo was the only test subject that could not be isolated from his social group members in any way during testing.

Pretrial Training: Token Association

One cylinder token was placed in one well while the other well was left empty. This design forced the subject to choose the cylinder token. The gorillas were required to point in order to indicate their choice (Figure 3). Once they pointed to the cylinder, the token was removed and replaced with 5 blueberries. The food reward was administered by pushing the well portion of the tray into the gorilla's cage. This process was repeated, with the token being presented in the right or left well an equal number of times, for 40 trials spread over two days. The procedure was then repeated for the cube token and its 1-blueberry food reward following the association training with the cylinder token. The pyramid token was not introduced until the subjects had successfully completed the cylinder versus cube quantity discrimination (discussed below). We then repeated the procedure for the pyramid/3-blueberry food reward association.

Figure 3: Kidogo Indicating His Choice by Pointing

Phase I: Quantity Discrimination

The gorillas were given the cylinder token (5) versus the cube token (1) quantity discrimination task first. One cylinder was placed in a well and one cube was placed in the other well; token placement was pseudo-randomized, with the criterion that a token could not be placed on the left or right side more than three consecutive times to reduce the development of a side preference (if a side preference did occur the lesser value token was repeatedly placed in the preferred well until the subject chose the token in the opposite well). The tray was pushed to the front of the subject's cage which prompted them to choose a token. The chosen token was rewarded with the corresponding number of blueberries. Choices were recorded for two blocks (per day) of 12 trials, with the cylinder token recorded as the correct choice. Criterion was successfully met when the subject made at least 10 of 12 correct choices in two consecutive blocks. This procedure was repeated for the pyramid token (3) versus the cube token (1) quantity discrimination task and the cylinder token (5) versus the pyramid token (3) quantity discrimination task (for an example of token placement see Figure 4). The experimenters wore dark sunglasses to avoid giving the test subjects any inadvertent cues.

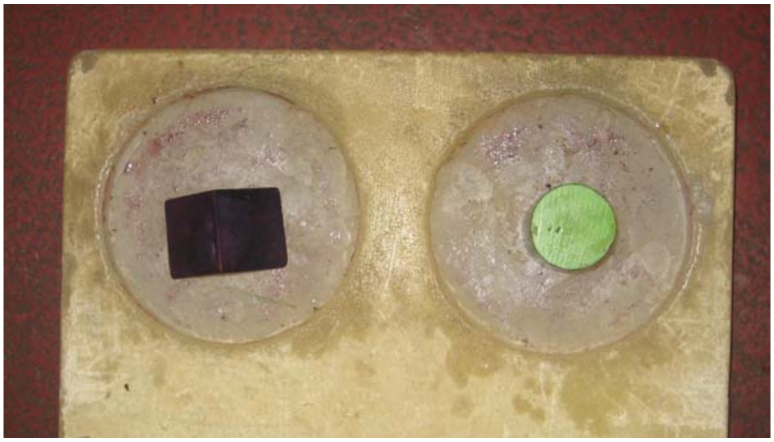

Figure 4: Illustration of Token Placement for Quantity Discrimination Trials: Token placement for pyramid (3) vs cylinder (5) quantity discrimination trial.

Phase II: Summation

The same procedure for presenting tokens used in Phase I of testing was used in Phase II. The gorillas were presented with homogeneous token combinations ranging in sum from 1 to 6. Choice combinations included: one cylinder token (5) versus two cube tokens (2); one cylinder token (5) versus three cube tokens (3); one cylinder token (5) versus four cube tokens (4); one cylinder token (5) versus two pyramid tokens (6); one pyramid token (3) versus two cube tokens (2); one pyramid token (3) versus four cube tokens (4); two pyramid tokens (6) versus three cube tokens (3); two pyramid tokens (6) versus four cube tokens (4) (see Table 2 for a summary and Figure 5 for an example of token placement). Choices were recorded for blocks of eight trials over 10 days, one block of trials per day. Each choice combination was presented once per block of trials.

Table 2
Summary of Summation Token Conditions

Token Choice Options	**Numerical Comparison**
1 cylinder vs 2 cubes	5 vs 2
1 cylinder vs 3 cubes	5 vs 3
1 cylinder vs 4 cubes	5 vs 4
1 cylinder vs 2 pyramids	5 vs 6
1 pyramid vs 2 cubes	3 vs 2
1 pyramid vs 4 cubes	3 vs 4
2 pyramids vs 3 cubes	6 vs 3
2 pyramids vs 4 cubes	6 vs 4

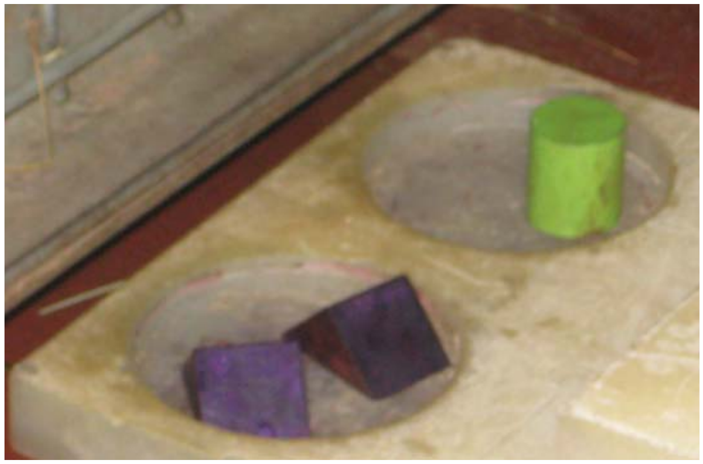

Figure 5: Illustration of Token Placement for Summation Trials: Token placement for two pyramid (6) vs one cylinder (5) summation trial.

Data Analysis

A binomial test was conducted to analyze the frequency of choosing the cylinder token or pyramid token (i.e. choosing the higher value token) during the following trials, in which the higher value token was the incorrect choice: one cylinder (5) versus two pyramid (6) condition and one pyramid (3) versus four cube (4) condition. A binomial test also was used to analyze the frequency of choosing the larger physical number of tokens during the following trials, in which the larger number of tokens was the incorrect choice: one cylinder (5) versus two cube (2) condition, one cylinder (5) versus three cube (3) condition, one cylinder (5) versus four cube (4) condition, one pyramid (3) versus two cube (2) condition, two pyramid (6) versus three cube (3) condition, and two pyramid (6) versus four cube (4) condition. The data also was analyzed with a G-test to determine if Charlie and Olympia's performances overall on the summation conditions were significantly different from chance (see McDonald, 2008).

CHAPTER 3

RESULTS

Phase I: Quantity Discrimination

Three of the seven gorillas completed the symbolic quantity discrimination task (see Table 3). Stadi completed the cylinder (5) versus cube (1) discrimination task in 384 trials, the pyramid (3) versus cube (1) discrimination task in 324 trials, and the cylinder (5) versus pyramid (3) discrimination task in 60 trials. Charlie completed the cylinder versus cube discrimination task in 468 trials, the pyramid versus cube discrimination task in 168 trials, and the cylinder versus pyramid discrimination task in 24 trials. Olympia completed the cylinder versus cube discrimination task in 408 trials, the pyramid versus cube discrimination task in 276 trials, and the cylinder versus pyramid discrimination task in 48 trials. Machi completed the cylinder versus cube discrimination task in 408 trials but did not complete the pyramid versus cube task before the end of the study period (after receiving 372 trials). Thus, she was unable to participate in the remainder of the study. Ozzie and Kekla did not complete the cylinder versus cube discrimination task after 516 trials and 384 trials respectively. Additionally, Kekla never made more than 6 out of 12 correct choices within the 384 trials he received and Ozzie developed a strong side preference during his last 72 trials. Kidogo completed 300 trials but was prevented from participating further in the study by the dominant male in his social group. Therefore, Ozzie, Kekla, and Kidogo were not included in the remainder of the study.

Table 3
Summary of Quantity Discrimination Data

	Number of Trials to Reach Criterion		
Subject	*Cylinder vs Cube (5 vs 1)*	*Pyramid vs Cube (3 vs 1)*	*Cylinder vs Pyramid (5 vs 3)*
Stadi	384	324	60
Charlie	468	168	24
Olympia	408	276	48

Phase II: Summation

Two of the three remaining subjects completed the summation phase of the experiment. Stadi completed the quantity discrimination phase of testing on the final day of the study and, therefore, was unable to participate in the summation phase. Charlie and Olympia received a total of 10 trials, spread across 10 days, for each token condition.

A binomial test was conducted to analyze the frequency of choosing the higher value token (either the cylinder or pyramid depending upon the trial condition) during those trials where choosing the higher value token would be incorrect. As shown in Table 4, both Olympia and Charlie chose the higher value token significantly less than chance for both token conditions (one cylinder (5) vs two pyramid (6) condition and one pyramid (3) vs four cube (4) condition; $p<.05$). Both subjects chose correctly upon initial presentation of these token conditions, when the token conditions were still novel. An additional binomial test was conducted to analyze the frequency of choosing the larger physical number of tokens during those trials where choosing the larger number of tokens would be incorrect. As shown in Table 5, both subjects chose the larger number of tokens significantly less than chance for some token conditions ($p<.05$). Charlie chose correctly on the one cylinder (5) versus two cube (2) condition and one pyramid (3) versus two cube (2) condition the first time these conditions were presented. Olympia chose correctly on the one cylinder (5) versus two cube (2) condition the first time this condition was presented. The remaining conditions did not differ significantly from chance in either direction. These trials also were analyzed using a G-test which revealed that Charlie's performance (i.e. his accuracy on these token conditions) differed significantly from chance ($G(1) = 13.17$, $p<.001$) while Olympia's did not ($G(1)=1.81$, NS).

Table 4
Do Gorillas Prefer the Higher Value Token? Frequency of choosing (a) cylinder token or (b) pyramid token over 10 trials for each condition; *p<.05 (binomial test)

Subject	**(a)** *1 cylinder vs 2 pyramid (5 vs 6)*	**(b)** *1 pyramid vs 4 cube (3 vs 4)*
Charlie	1*	0*
Olympia	0*	0*

Table 5
Do Gorillas Prefer the Larger Number of Tokens? Frequency of choosing the larger number of tokens over 10 trials for each condition; *p<.05 (binomial test)

Subject	*1 cylinder vs 2 cube (5 vs 2)*	*1 cylinder vs 3 cube (5 vs 3)*	*1 cylinder vs 4 cube (5 vs 4)*	*1 pyramid vs 2 cube (3 vs 2)*	*2 pyramid vs 3 cube (6 vs 3)*	*2 pyramid vs 4 cube (6 vs 4)*
Charlie	1*	3	7	2*	5	5
Olympia	2*	7	7	5	6	7

CHAPTER 4

DISCUSSION

On the basis of past studies examining numerical competencies in great apes, and RNJ and summation capabilities in capuchin monkeys utilizing tokens, I expected the gorillas to select both the larger of two unequal quantities and the larger of two sums. Although not in reversed contingency tasks, tokens inherently increase the cognitive difficulty of numerical competency tasks. This study demonstrates that Western lowland gorillas have the capacity (i.e. it is within the range of the species) to perform quantity discriminations and summation judgments using symbolic representation, specifically in the form of tokens.

Symbolic Quantity Discrimination in Gorillas

In Phase I of the study, three of the seven gorillas completed the symbolic quantity discrimination task when presented with one cylinder token (5) versus one cube token (1), one pyramid token (3) versus one cube token (1), and one cylinder token (5) versus one pyramid token (3). The number of trials necessary to meet criterion drastically declined from one quantity discrimination task to the next, as the gorillas gained more experience with the task (see Table 2). By performing successfully on this task Olympia, Stadi, and Charlie demonstrated that they could remember what each token stood for as well as estimate the amount of food the token represents when making their choice.

Why Do Some Gorillas Fail on the Quantity Discrimination Task?

Two of the four gorillas that failed on the symbolic quantity discrimination task had previously been successful on quantity discrimination tasks where the stimuli consisted of grapes. Both Ozzie and Kekla had successfully participated in Anderson et al.'s (2005) study but could not consistently choose the cylinder token in the cylinder (5) versus cube (1) discrimination task in our study, even after having received over 350 trials. The four gorillas may have failed at the token quantity discrimination task for several reasons. For example, the gorillas could have failed because the task may have been too cognitively difficult for some individuals and not others. Anderson et al. (2005) used a correction procedure for the gorillas that were unable to initially choose the larger of two quantities significantly above chance. Perhaps the gorillas that failed in Phase I of this study could perform successfully if given a similar correction procedure.

Another possible explanation for the gorillas' poor performance could have been that those subjects did not find the food reward motivating enough to stay attentive to the task. I was limited to using those foods that were part of the gorillas' regular diet as rewards (tokens corresponded to 1, 3, or 5 apple or banana pieces at the beginning of the study). Initially, this was a problem for the gorillas that completed Phase I and may have inflated the number of trials necessary to reach criterion for the cylinder (5) versus cube (1) discrimination task. When I implemented frozen blueberries as the food reward I saw an immediate improvement in performance in the three successful gorillas, indicating that they knew what quantities the tokens stood for but were inattentive to the task until the food reward was more motivating.

Finally, the gorillas may have been too distracted by their conspecifics to remain attentive to the task. We tested the gorillas in their indoor cages where they could not be completely isolated from the rest of the gorillas. The subjects still had visual access to gorillas from both their own and other social groups, even in those instances where we were able to move the subjects to their own cage for the duration of testing. This was especially a problem in the instance of Kidogo. Kidogo could not be physically isolated in any way from the rest of his social group. His group members would either passively observe, while sitting right next to Kidogo, or actively interfere during testing. I cannot definitively say that Kidogo is incapable of making symbolic quantity discriminations because the dominant male in his social group prevented Kidogo from working with us partway through the cylinder (5) versus cube (1) quantity discrimination task.

Symbolic Summation in Gorillas

Only two gorillas participated in Phase II of the study. Stadi completed Phase I on the final day of the study and therefore could not participate in the next phase. I believe that if Stadi had been tested on the summation task he would have performed similarly to Charlie, given their common background in numerical competence tasks. It is important to note that one of the subjects that did participate in Phase II was choosing the larger sum for some token combinations on the first presentation of summation trials (see Charlie, Tables 4 & 5 for the token combinations). Unlike in the quantity discrimination trials, the gorilla's ability to combine tokens appeared spontaneously and without any specific training to do so.

Olympia received 10 blocks of summation trials. Her performance on the one cylinder (5) versus two pyramid (6) condition and the one pyramid (3) versus four cube (4) condition indicated that she was not just choosing the higher value token during the summation trials (see Table 4). The data also demonstrated that her performance during Phase I could not be attributed to a simple object preference (i.e. preference for the cylinder over the cube and pyramid; preference for the pyramid over the cube). Olympia's performance on the remaining summation trials does not allow for any clear distinction between the strategies of 'choose the larger physical number of tokens' and 'choose the larger sum'. Although she did choose the larger number of tokens significantly less than chance on the one cylinder (5) versus two cube (2) condition, which would indicate the use of a summation strategy on that condition, her choices on the remaining conditions did not differ significantly from chance in either direction (see Table 5). One possible explanation for Olympia's performance on the remaining trials is that she was influenced to some degree by both strategies causing her to choose randomly. It is important to note that prior to this study Olympia had no experience in numerical competency tasks, unlike the other successful gorilla, Charlie. Therefore, her performance could improve with experience on the task if given more trials. No definitive answers can be provided, however, without further testing.

Charlie also received 10 blocks of summation trials. Similar to Olympia, his performance on the one cylinder (5) versus two pyramid (6) condition and the one pyramid (3) versus four cube (4) condition indicated that he was not just choosing the higher value token during the summation trials (see Table 4). The data also demonstrated that Charlie's performance during Phase I could not be attributed to a simple object preference (i.e. preference for the cylinder over the cube and pyramid; preference for the pyramid over the cube). His performance on the remaining summation trials indicates that, on some token conditions, Charlie made a summation judgment. Although his performance on four of the six conditions was not significantly above chance in either direction, Charlie's performance on two of the conditions (one cylinder (5) vs two cube (2) and one pyramid (3) vs two cube (2); see Table 5) was significantly below chance for the strategy of ‘choose the larger number of tokens’ indicating the alternative of ‘choose the larger sum’. A G-test also demonstrated that Charlie was not choosing randomly on these conditions ($G(1) = 13.17$, $p<.001$). His successful performance on the one pyramid (3) versus four cube (4) condition and one pyramid (3) versus two cube (2) condition, taken together, indicates that he was using the summation strategy on at least some token conditions during the summation task. Therefore, in addition to remembering what the tokens denoted and estimating the quantities of food represented by the tokens, Charlie also was combining those representations and comparing them before making a choice under some conditions of this study. It is important to note that Charlie, like Olympia, was likely influenced by a combination of the physical number of the tokens as well as their representative sum in the remaining trials of the summation task. Further testing is required to determine the degree of interaction between these two strategies.

Conclusion

In summary, at least three of the gorillas were able to use tokens flexibly as symbols to represent quantities in order to maximize their payoffs. Additionally, at least one gorilla was able to perform successfully on a summation task by using the strategy of ‘choose the larger sum’ over the alternative strategies of ‘choose the higher value token’ or ‘choose the larger physical number of tokens’ under some conditions of this study. These results build upon previous research examining quantity discriminations and summation in both great apes and monkeys, particularly Anderson et al.’s (2005) and Addessi et al.’s (2007, 2008) studies, and add to the body of evidence discrediting the traditional view that gorillas are less intelligent than the other great ape species. I conclude that Western lowland gorillas have the capacity to perform quantity discriminations and summation judgments using symbolic representation.

REFERENCES

Addessi, E., Crescimbene, L., & Visalberghi, E. (2007). Do capuchin monkeys (*Cebus apella*) use tokens as symbols? *Proceedings of the Royal Society B, 274*, 2579-2585.

Addessi, E., Crescimbene, L., & Visalberghi, E. (2008). Food and token quantity discrimination in capuchin monkeys *(Cebus apella)*. *Animal Cognition, 11,* 275-282.

Agrillo, C., Dadda, M., & Bisazza, A. (2007). Quantity discrimination in female mosquitofish. *Animal Cognition, 10,* 63-70.

Anderson, J. R., Awazu, S., & Fujita, K. (2000). Can squirrel monkeys (*Saimiri sciureus*) learn self control? A study using food array selection tests and reverse-reward contingency. *Journal of Experimental Psychology, 26*, 87-97.

Anderson, U. S., Stoinski, T. S., Bloomsmith, M. A., Marr, M. J., Smith, A. D., & Maple, T. L. (2005). Relative numerousness judgment and summation in young and old western lowland gorillas. *Journal of Comparative Psychology, 119,* 285-295.

Anderson, U.S., Stoinski, T.S., Bloomsmith, M.A., & Maple, T.L. (2007). Relative numerousness judgment and summation in young, middle-aged, and older adult orangutans (*Pongo pygmaeus abelii* and *Pongo pygmaeus pygmaeus*). *Journal of Comparative Psychology, 121*, 1-11.

Beran, M.J., Beran, M.M., Harris, E.H., & Washburn, D.A. (2005). Ordinal judgments and summation of nonvisible sets of food items by two chimpanzees and a rhesus macaque. *Journal of Experimental Psychology: Animal Behavior Processes, 31*, 351-362.

Boysen, S. T., & Berntson, G. G. (1989). Numerical competence in a chimpanzee (*Pan troglodytes*). *Journal of Comparative Psychology, 103*, 23-31.

Boysen, S. T., & Berntson, G. G. (1995). Responses to quantity: Perceptual versus cognitive mechanisms in chimpanzees (*Pan troglodytes*). *Journal of Experimental Psychology: Animal Behavior Processes, 21,* 82-86.

Boysen, S. T., Berntson, G. G., Hannan, M. B., & Cacioppo, J. T. (1996). Quantity-based interference and symbolic representations in chimpanzees (*Pan troglodytes*). *Journal of Experimental Psychology: Animal Behavior Processes, 22,* 76-86.

Boysen, S.T., & Hallberg, K.I. (2000). Primate numerical competence: Contributions toward understanding nonhuman cognition. *Cognitive Science, 24,* 423-443.

Byrne, R.W. (1996). The misunderstood ape: Cognitive skills of the gorilla. In A.E. Russon, K.A. Bard, & S.T. Parker (Eds.), *Reaching into thought: The minds of great apes* (pp. 111-130). New York: Cambridge University Press.

Call, J. (2000). Estimating and operating on discrete quantities in orangutans (*Pongo pygmaeus*). *Journal of Comparative Psychology, 114,* 136-147.

Flombaum, J.I., Junge, J. A., & Hauser, M.D. (2005). Rhesus monkeys (*Macaca mulatta*) spontaneously compute addition operations over large numbers. *Cognition, 97,* 315-325.

Gallistel, C.R., & Gelman, R. (2000). Non-verbal numerical competence: From reals to integers. *Trends in Cognitive Sciences, 4,* 59-65.

Hanus, D., & Call, J. (2007). Discrete quantity judgments in the great apes (*Pan paniscus, Pan troglodytes, Gorilla gorilla, Pongo pygmaeus*): The effect of presenting whole sets versus item-by-item. *Journal of Comparative Psychology, 121,* 241-249.

McDonald, J.H. 2008. *Handbook of Biological Statistics*. Baltimore: Sparky House Publishing.

Olthof, A., Iden, C.M, & Roberts, W.A. (1997). Judgments of ordinality and summation of number symbols by squirrel monkeys *(Saimiri sciureus)*. *Journal of Experimental Psychology: Animal Behavior Processes, 23,* 325-339.

Pérusse, R., & Rumbaugh, D. M. (1990). Summation in chimpanzees (*Pan troglodytes*): Effects of amounts, number of wells, and finer ratios. *International Journal of Primatology, 11,* 425-437.

Rumbaugh, D. M., Savage-Rumbaugh, S., & Hegel, M. T. (1987). Summation in the chimpanzee (*Pan troglodytes*). *Journal of Experimental Psychology: Animal Behavior Processes, 13,* 107-115.

Shumaker, R. W., Palkovich, A. M., Beck, B. B., Guagnano, G. A., & Morowitz, H. (2001). Spontaneous use of magnitude discrimination and ordination by the orangutan (*Pongo pygmaeus*). *Journal of Comparative Psychology, 115,* 385-391.

Sousa, C., & Matsuzawa, T. (2001). The use of tokens as rewards and tools by chimpanzees (*Pan troglodytes*). *Animal Cognition, 4,* 213-221.

Stevens, J.R., Wood, J.N., & Hauser, M.D. (2007). When quantity trumps number: Discrimination experiments in cotton-top tamarins (*Saguinus oedipus*) and common marmosets (*Callithrix jacchus*). *Animal Cognition, 10*, 429-437.

Tomonaga, M. (2008). Relative numerosity discrimination by chimpanzees (*Pan troglodytes*): evidence for approximate numerical representations. *Animal Cognition, 11*, 43-57.

Vlamings, P. H. J. M., Uher, J., & Call, J. (2006). How the great apes (*Pan troglodytes, Pongo pygmaeus, Pan paniscus,* and *Gorilla gorilla*) perform on the reversed contingency task: The effects of food quantity and food visibility. *Journal of Experimental Psychology: Animal Behavior Processes, 32,* 60-70.