The Pennsylvania State University

The Graduate School

College of the Liberal Arts

PLANNING A COORDINATED SEQUENCE OF ACTIONS: COTTON-TOP

TAMARINS (*SAGUINUS OEDIPUS*) STICK TO THE PLAN

A Thesis in

Psychology

by

Kate M. Chapman

Submitted in Partial Fulfillment
of the Requirements
for the degree of

Master of Science

May 2010

The thesis of Kate M. Chapman was reviewed and approved* by the following:

Daniel J. Weiss
Associate Professor of Psychology
Thesis Adviser

David A. Rosenbaum
Distinguished Professor of Psychology

William J. Ray
Professor of Psychology

Susan Mohammed
Associate Professor of Psychology
Director of Graduate Training

*Signatures are on file in the Graduate School.

ABSTRACT

Cotton-top tamarins have demonstrated sophisticated anticipatory motor planning when performing a single grasp (Weiss, Wark & Rosenbaum, 2007). The present study extends this work by investigating a task that requires a coordinated series of manual motor actions. We presented tamarins with a tape measure that contained a food reward located at a near or far distance that could be reeled in. In Experiment 1, subjects viewed the reward as they pulled. In Experiment 2, subjects received no visual feedback during pulling. In Experiment 3, the amount of rope pulled in both near and far conditions was equated. In Experiment 4, the physical forces on the rope were equated and visual feedback was removed. Tamarins typically used a hand-over-hand method to reel in the food and the dependent variable was the distance between grasps (cm) on the tape measure. In Experiment 1, the inter-grasp distance in the near condition was significantly smaller than in the far condition, an effect evidenced in all subjects. This significant difference was found in Experiments 2, 3, and the trend, although not significant, appeared in Experiment 4 as well. These results demonstrate that tamarins prospectively scale their pulls as a function of goal-distance, representing multiple-action planning. To the best of our knowledge, these results are the first empirical demonstration of nonhuman primates' ability to plan an *untrained* sequence of actions without requiring on-going visual feedback.

TABLE OF CONTENTS

LIST OF FIGURES

INTRODUCTION

The ability to plan multiple actions in anticipation of a goal appears to be a requirement for many behaviors noted in humans and nonhumans. Humans, both adults and children, also display behaviors indicative of multiple-action planning. Some examples include language, tool-use, dancing, and making a grocery list. Nonhuman primates display behaviors such as climbing trees, building sleeping nests, displaying predator avoidance, hunting, and others that likely require the ability to plan sequences of actions in advance. Studies of natural food processing behaviors in nonhuman primates (e.g. gorillas, Ross, 2009) provide evidence for coordinated sequences of actions that often involve nested hierarchies of action sets. These studies, however, do not necessarily address if this sequences is *planned* from the start, or if the primates are constantly updating their actions independent of a sequence, using feedback. Laboratory studies with nonhuman primates have shown that they are capable of learning ordinal lists of items (Terrace, 2005). These studies appear to involve planning, but require extensive operant training procedures.

Recent evidence has shown that nonhuman primates (cotton-top tamarins; Weiss, Wark & Rosenbaum, 2007, lemurs; Chapman, Weiss & Rosenbaum, in press) are capable of basic anticipatory motor planning, as indexed by the end-state comfort effect. This effect is robust in human adults (Rosenbaum, Marchak, Barnes, Vaughan, Slotta, & Jorgensen, 1990) and appears to various degrees in children between the ages of 2 and 9 years of age. The end-state comfort effect is the tendency to deploy a distinct initial position or posture in the service of a later position or posture. This ability, however, does not appear with adult levels of consistency in children until roughly 9 years of age

1

(Stoeckel, Weigelt, Hagen & Thomas, 2009). Anticipatory motor planning abilities are hypothesized to scaffold to higher level cognition, as seen in tool-use (Johnson-Frey, 2004). Children are capable of tool-use, language, and other complex cognitive processes by 5-7 years of age, but do not show robust levels of end-state comfort until age 9. Tamarins and lemurs, however, are not capable of tool use and yet they demonstrate anticipatory planning abilities, indexed by the end-state comfort effect, hypothesized to scaffold complex-cognition (Johnson-Frey, 2004). If higher-level cognition does depend on anticipatory planning, then this type of planning should be considered necessary, but not sufficient. Perhaps the scope of anticipatory planning abilities differentiates tool users and non tool users. This scope could include the number of actions planned and how far in advance an action can be planned. It is also possible that humans' ability to coordinate *multiple* actions (instead of a single action) is the critical basis for complex cognition. The investigation of multiple-action planning is the focus of the present study. The comparative literature investigating serial list learning and food processing suggests that nonhuman primates are capable of coordinating multiple actions. However, the serial ordinality experiments are heavily trained and the food processing behaviors are able to inform when this coordination, or planning, begins. The goal of the present study is to investigate whether nonhuman primates are capable of spontaneously planning a coordinated sequence of actions in advance of a goal. The present study does not employ operant procedures, and further asks when this planning occurs, and what factors may constrain multiple-action planning.

This paper will begin by briefly describing major motor planning phenomena of interest in human adults and review what is known about this type of planning in infants

and children. This will be followed by a review of the recent findings regarding anticipatory motor planning in nonhuman primates from our laboratory. I will then provide examples of coordinated sequences of actions observed in the natural food processing behavior of wild nonhuman primates, behavior thought to require multiple-action planning. Finally, I will discuss examples of what may be considered multiple-action planning in other areas of comparative cognition laboratory research; hierarchical structure learning serial ordering, and ordinal position sequencing. Following this discussion, I will present a series of four experiments designed to investigate goal-directed, multiple-action planning in cotton-top tamarins (*Saguinus oedipus*). The results of each experiment will be presented and discussed briefly prior to a general discussion of the findings and their theoretical implications.

Motor Planning in Adults

Human adults plan their motor behaviors in anticipation of a goal state, which is observed across a variety of reaching and grasping behaviors. One clear example of this type of anticipatory motor planning is demonstrated in the end-state comfort effect, which can be defined as the tendency to deploy an initially distinct posture or position in the service of a later posture or position (Rosenbaum, Marchak, Barnes, Vaughan, Slotta, & Jorgensen, 1990). An important distinction regarding end-state comfort is that adults typically adopt these initially distinct grasps or postures *only* when they will result in a final posture that is canonical or allows better precision (Rosenbaum et al., 1990). The end-state comfort effect is an example of anticipatory motor planning; the initial non-canonical grasp is deployed in anticipation of the final action.

In a seminal study investigating the end-state comfort, Rosenbaum and colleagues (1990) asked participants to pick up a horizontally-oriented dowel with a white end and a black end and place it vertically in a disk-shaped holder. Critically, the participants were instructed to place either the black or white end into a disk to the left or right of the dowel's starting position (See Figure 1).
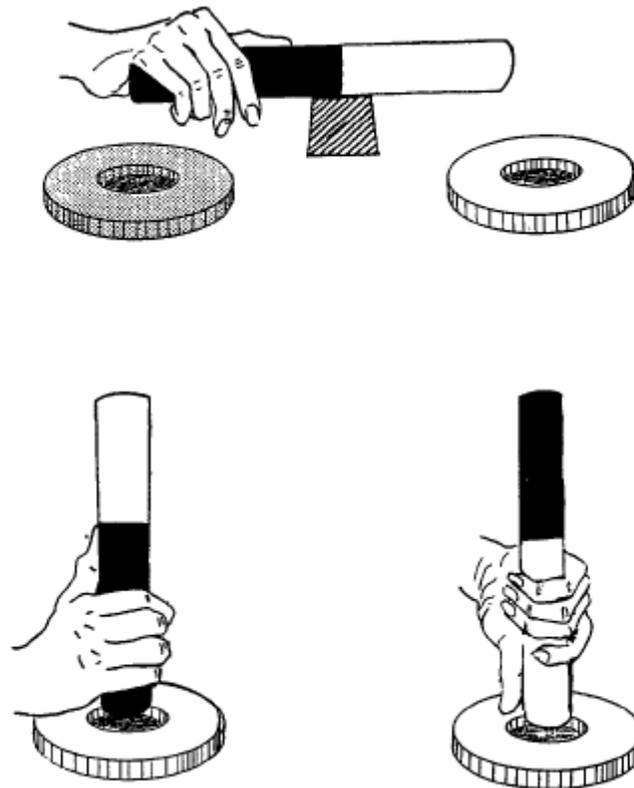
Figure 1. Illustration of the dowel task as used in Rosenbaum et al.'s (1990) study (Reproduced from Hughes, 1996).

The variables of interest were the initial grasping posture used to pick up the dowel and the ending position of the hand once the dowel was inserted in the disk. Examining only the participants who used their right hand on every trial, all used a canonical, overhand grasp when the right end of the dowel was to be placed in either the left or right

disk. On these trials, their final hand position showed the thumb pointing upward in a canonical grasp. However, when the left end of the dowel was to be placed in either disk, the same participants *always* adopted a non-canonical, underhand grasp when initially picking up the dowel, and ended with a thumb-up, canonical grasp on the dowel. Participants never deployed the underhand grasp, however, when the right side of the dowel needed to be inserted into the disks. The finding that participants adopted initially non-canonical grasps in the service of a final hand position indicates that they were choosing their grasp in the dowel in anticipation of their final posture. Coined the end-state comfort effect (Rosenbaum et al., 1990), this tendency was later explored in depth and demonstrated in tasks involving grasp height (see Cohen & Rosenbaum, 2004; see also Rosenbaum, Halloran & Cohen, 2006) and speed of rotation (Rosenbaum, van Heugten & Caldwell, 1996). Despite many empirical demonstrations of motor planning in human adult behavior, the ontogenetic trajectory of such behavior in our species is still under investigation. The phylogeny of this type of planning behavior is even less well understood, but recent studies with nonhuman primates have begun to elucidate its evolutionary origins. The below sections review what is known about the ontogeny and phylogeny of anticipatory motor planning.

Motor Planning in Infants and Children

The field of developmental psychology encompasses research regarding typical motor development in children, especially infant locomotion (see Adolph & Berger, 2006 for a review, see also Adolph, 2008). McCarty, Clifton, and Collard (1999) examined planning behavior in infants reaching for a spoon containing food. The spoon was presented to the child in the center of their body, but the spoon's handle either pointed right or left. The

most efficient manner to bring the food to the mouth was to use the hand (right or left) that corresponded with the direction the spoon handle was pointing (right or left). Twelve-month-old infants tended to reach with their dominant hand on all trials, which brought the spoon-handle to the mouth instead of the food bowl on 50% of all trials. However, 19-month-old infants appeared to reach with the hand that corresponded to the spoon handle, functionally bringing the food to their mouth. This finding indicates that as of 19-months, infants can switch hands on a simple task based on a goal, thereby exhibiting some degree of advance planning

McCarty and Keen (2005) investigated the possibility of facilitating 9- and 12-month-old infants' performance on the above spoon-reaching task. They administered the same basic task to infants. In this case, however, two innovations were implemented in effort to facilitate performance. In the first condition, spoons were presented in the same right/left orientation for several successive trials, in an attempt to allow the infants to learn from recent feedback. In the second condition, two spoons were presented, one in each orientation, to allow the infants to choose between two options (and perhaps recognize the affordances of each). The investigators found that the 12-month olds benefited from the first intervention (repeated trials of the same type) but that 9-month olds did not. Neither age group appeared to benefit from the second intervention (two spoons in different orientations), and infants of both ages did not appear willing to reach across their midline to take hold of the spoon in the correct orientation.

Claxton, Keen, and McCarty (2003) asked whether infants act differently on an object initially, based on what they planned to do with it subsequently, a tendency indexing anticipatory motor planning that has previously been demonstrated in human

adults (see Martenluk, MacKenzie, Jeannerod, Athenes & Dugas, 1987). Ten-month old infants were observed when their either threw a ball or put it into a tube. It is important to note that the action of putting a ball into the tube required more precision than throwing the ball. Claxton and colleagues measured the kinematic features of the infants' hand approaching the ball prior to the action of throwing or placing. Infants approached the ball faster before they threw the ball, compared to their approaches before placing the ball in a tube, which indicates that 10-month olds are capable of planning for both parts of the action; approaching the object and subsequently acting on it. These results demonstrated a more sophisticated level of goal-directed planning in younger infants than had been previously documented.

Recent research has investigated the end-state comfort effect, specifically, in children at various developmental stages. These studies have tested typically developing children between 3- and 8-years old and some have even compared their performance to disordered child populations. While most of the researchers have used similar tasks to measure end-state comfort proportions, their findings have been mixed. Some are in agreement, others are contradictory, but all suggest that children do not resemble adults in terms of their anticipatory motor planning behavior until at least 9 years of age.

Weigelt and Schack (in press) employed a version of Rosenbaum et al.'s (1990) dowel rod task with young children, and also failed to find a consistent end-state comfort effect in 3-, 4- and 5- year olds. They found significant age differences on critical trials (trials that required children to deploy noncanonical grasps to achieve end-state comfort); 3 year-olds chose the underhand grasp on 18% of trials, 4-year olds on 45% of trials, and 5-year olds on 67% of trials. This pattern of results demonstrates that there is

developmental trend for the emergence of end-state comfort, with each age range showing larger and larger proportions of trials in accordance with end-state comfort. Weigelt and colleagues also noted that 3-year olds appeared to be learning throughout the course of the experiment; none of these children deployed the underhand grasp on Trial 1, but 29% of children adopted the underhand grasp on Trial 3. Experience with motor planning tasks and different grasp deployments may allow children to learn avoid uncomfortable final positions, which could explain the ESC difference between 3-, 4- and 5-year olds. While this set of findings begins to elucidate the developmental trajectory of end-state comfort, the results do not answer the question of when children begin to *resemble adults* in terms of consistent end-state comfort in reaching tasks.

Adalbjornsson, Fischman and Rudisill (2008) used a different task to investigate the same research question about the ontogeny of end-state comfort. Two- to 3- year olds and 5- to 6-year olds were tested on a bimanual task requiring children to fill an overturned glass with water from a pitcher. Of the 40 children tested in this experiment, only 11 demonstrated grasps in accordance with end-state comfort and there were no systematic differences between the age groups. Overall, children exhibited no standard procedure for achieving the goal, using as many as 5 different strategies across individuals, none of which were in alignment with end-state comfort.

Stoeckel, Weigelt, Hagen and Thomas (2009) recently expanded this literature by testing 7-, 8- and 9-year old children with the same dowel rod task to determine whether older children's resemble adults in proportions of end-state comfort achieved. The authors found a developmental trajectory across age groups, but overall, these older children showed much higher proportions of trials in accordance with end-state comfort

8

than groups tested in the above studies. Respectively, 7-, 8- and 9-year olds chose grips facilitating end-state comfort on 75.9%, 82.1% and 95.5% of trials. The authors conclude that by age 9, the end-state comfort effect is fully in place, comparable to the proportions of which it has been observed in adults (Rosenbaum et al., 1990).

A small body of literature has compared the motor performance (including end-state comfort tasks) of typically developing children to atypically developing children. These studies provide more data on the typical ontogeny of motor planning and also provide evidence addressing delays in this ability. Hughes (1996) compared differences in motor behavior in preschoolers that were either diagnosed as 'low' or 'high' autistic, 'low' or 'high' mildly learning disabled, and typically developing age-matched controls. This experiment contained a very similar dowel task to Rosenbaum and colleagues' (1990) original task. Results regarding the typically developing children indicated that only 14.3% of 3-year olds deployed the underhand grasp when it would result in a thumb-up position on the dowel, whereas 71.42% of 4-year olds deployed the underhand grasp in the service of a thumb-up final grasp. This large gap may indicate that sensitivity to end-state comfort starts to develop between ages 3 and 4 in typically developing children. The results for 3-year olds appear in line with Weigelt and Schack's (in press) findings, but the 4-year olds here appear to outperform those in Weigelt and Schack' study.

Hughes' (1996) results for the atypically developing populations also inform the discussion of motor planning development. Overall, the atypically developing children performed less successfully than typically developing controls, and autistic children were, on average, less successful than the learning disabled children (despite their higher-rated 'mental age'). In the autistic population, 27.70% of children in the 'high' group deployed

9

the underhand grasp when it would result in a thumb-up position on the dowel, whereas only 5.50% of children in the 'low' group deployed the underhand grasp in the service of a thumb-up final grasp. For the learning disabled population, 50% of children in the 'high' group deployed the underhand grasp when it would result in a thumb-up position on the dowel and 41.67% of children in the 'low' group deployed the underhand grasp in the service of a thumb-up final grasp. These results support previous findings that autistic children show impairments in goal-directed motor behavior on simple tasks, and perform differently than typical controls and learning disabled children. Hughes suggests that the poor performance observed is likely due to failure to predict outcomes of an action as well as deficits in sequencing motor actions. It is also possible that these individuals struggle with impaired visual control of movement, and cannot use external feedback to guide their motor actions. While the results of this study cannot distinguish between these possible accounts for the cause, it is clear that autistic individuals demonstrate impairment in their motor behaviors, even for simple actions that require basic anticipatory planning.

Smyth and Mason (1997) used a similar dowel task to compare children diagnosed with Developmental Coordination Disorder (DCD) to typically developing children of various ages. These authors studied 4- to 8-year old children, who were either typically developing or diagnosed with DCD. The investigators found that the two groups of children did not differ significantly in the proportion of trials in which end-state comfort was followed, and there was also no effect of age for either group. The control group demonstrated some improvement from age 4 through 8, but the DCD group showed little to no improvement as age advanced. It is surprising that the DCD children did not differ

from the controls, but the ASD children in Hughes' (1996) study were less successful than controls. One might expect children with a motor coordination disorder to struggle more with this task than an autism spectrum disordered child. Figure 2 shows that for controls subjects, 5- to 6-year olds actually demonstrated a *larger* proportion of trials in accordance with end-state comfort than 7- to 8-year olds. Overall, the oldest children do not act in accordance with end-state comfort even 75% of the time, indicating that none of the children tested in this study even approach an adult proportion of end-state comfort achieved. These results, however, contract those of Stoeckel et al. (2009), whose 7-, 8-, and 9-year olds all achieved ESC at on75% or greater proportion of trials. As a result, it is unclear at what age children begin to show adult-like behavior in end-state comfort tasks.
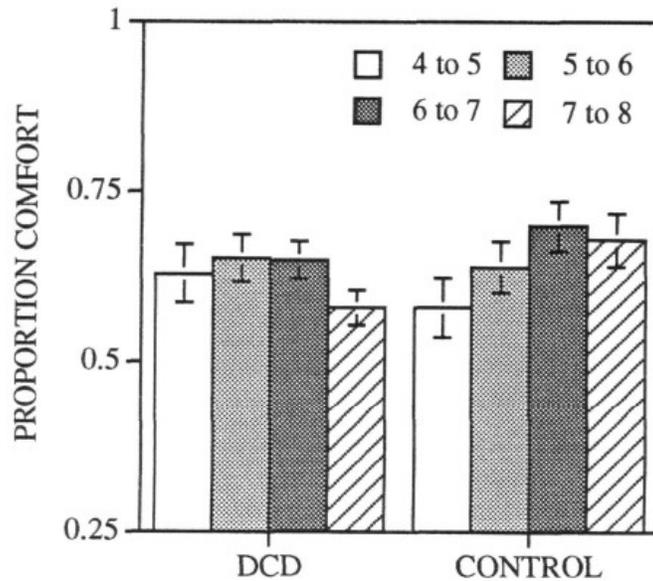
Figure 2. Proportion of grasps in accordance with end-state comfort for DCD and Control children. (Reproduced from Smyth & Mason, 1997.)

The above set of findings highlights what appear to be inconsistencies in the developmental trajectory of motor planning. While some children appear to behave like adults in terms of end-state comfort behavior by age 9, various studies examining 7- to 8-year olds fail to find the same levels of end-state comfort achieved. Taken together, this literature suggests that children do not develop adult-like anticipatory motor planning behaviors until *at least* 9 years of age. However, there is evidence of motor planning in the reaching behaviors of human infants as young as 10-months old. Infant studies have also demonstrated differences between the planning abilities of close developmental groups (9- to 12-months old, 12- to 19-months old), suggesting an early ontogenetic trajectory of this kind of planning. Some studies of older children have shown differences in end-state comfort proportions in developmental groups (e.g. 3- to 5-year olds; Weigelt & Schack, in press) but others have failed to detect differences across similar age gaps (e.g. 5- to 8-year olds; Smyth & Mason, 1997). Studies of disordered populations have shown that autism spectrum disordered individuals show delays in motor development, but this is not true of mildly learning disabled individuals. More research is warranted for the question of how and why developmental disorders are manifested in motor planning delays.

We can conclude that the literature concerning motor development contains a paradox. Older children do not reach adult levels of anticipatory motor planning until age 9, but infants' planning for a goal is clearly evident in their reaching behavior as of 10 months. These findings provide evidence from an early, but protracted developmental trajectory of the ability to plan one's motor actions for a future state or goal. The contrast between infants and children, and children and adults is particularly surprising given that

children are using tools and interacting with many objects in their environment by age 8. The source of this initially early but then extended course of development is not yet known. Inhibition may play a role, but infants can inhibit a dominant hand reach, whereas children struggle with consistently inhibiting a particular hand posture. Whatever the cause, the ontogeny of anticipatory motor planning warrants, and requires further investigation.

Motor Planning in Nonhuman Primates

One way to better understand anticipatory planning abilities and their ontogenetic development is to investigate the phylogeny of such behavior. The phylogenetic approach to understanding these abilities focuses on when in our evolutionary history these planning abilities developed. Until recently, there had been no systematic investigation addressing this question. In the first study of its kind, Weiss, Wark and Rosenbaum (2007) asked if nonhuman primates demonstrated anticipatory motor planning, as indexed by the end-state comfort effect. They provided a simple reaching motor task to cotton-top tamarins (*Saguinus oedipus*), arboreal, new-world primates that are a non-tool using species in the wild. Tamarins were given small champagne glasses with an extended stem, baited with a marshmallow. In each trial, the cup was presented in an upright or inverted orientation within an apparatus that was designed to constrain reaching behavior. The cup could only be removed from the apparatus if the tamarin grasped the stem and pulled the cup forward. When the cup was upright, tamarins always deployed a canonical, thumb-up grasping posture to remove the cup from the apparatus and extract the marshmallow. However, when the cup was inverted, tamarins typically deployed a non-canonical, thumb-down grasp which resulted in a final thumb-up grasp

for food retrieval. This tendency to use the non-canonical thumb-down grasp occurred only in the inverted condition and provided the first reported evidence for end-state comfort in a nonhuman species.

In addition, this finding provided evidence contrary to a hypothesis suggesting that anticipatory planning abilities may serve as the cognitive underpinning for tool use in humans (Johnson-Frey, 2004). Johnson-Frey hypothesized that these sophisticated forecasting abilities may scaffold to more complex cognition (i.e. tool use). Depending on your interpretation, this hypothesis could predict that the motor planning abilities apparent in humans would not be found in non tool-using, nonhuman primate species. However, as tamarins are a non-tool using species (Santos, Rosati, Sproul, Spaulding, & Hauser, 2005), and act in accordance with end-state comfort, we can conclude that non-tool using primates are capable of anticipatory motor planning. What remains unclear, then, is how humans and nonhuman primates may differ in their forecasting abilities, and if this difference can explain tool-use (and other cognitive) differences.

To further investigate the phylogeny of these planning behaviors, a recent study replicated the above experiment with six species of lemur, another non-tool using primate (Weiss, Chapman & Rosenbaum, in press). Lemurs are prosimian primates, the most distant living primate relatives of humans, thought to have diverged from the common primate ancestor of humans roughly 50 million years ago (Glaser, Myrtek, Rumpler, Schiebel, Hauwy, Rappold & Schempp, 1999). Lemurs are reported to have poor grasping abilities and primarily use their mouth to grasp objects, including food (Jolly, 1964). Further, lemurs are only capable of the power grip, which means that they do not have any independent digit control (with the exception of the opposable thumb), which

differs from both tamarins and humans (Bishop, 1962). Consequently,, lemurs were an ideal group to test for the presence of end-state comfort as a gauge of the likelihood that homologous motor planning abilities are common to all primates. Overall, the lemurs exhibited the end-state comfort effect; the majority of individuals inverted their hand at least once in the inverted cup condition, but never inverted their hand when reaching for the upright cup. This finding indicates that motor planning capabilities have a lengthy evolutionary history in primates and cast further doubt on the hypothesis (Johnson-Frey, 2004) that anticipatory planning abilities are sufficient for tool-use.

The end-state comfort tasks described above demonstrates that tamarins can plan at least one action in advance. While these studies only tested a single action, nonhuman primates' motor behaviors appear to be subject to similar effects to humans in experiments requiring multiple actions. Cotton-top tamarins were tested in a reaching task requiring them to reach for small pieces of marshmallow in a semicircular arrangement (Weiss & Wark, 2009). Tamarins could use either hand, but were constrained to using one hand to grasp a marshmallow. Tamarins' pattern of arm choice in behavior demonstrated that they are subject to a hysteresis effect, a phenomenon of human motor planning in which previously used grasps are more likely to be used on following grasps. Like humans, tamarins appear to be subject to perseverative effects that guide their motor behavior.

Tamarins and lemurs demonstrate anticipatory motor planning abilities, indexed by the end-state comfort effect, similar to humans. This finding helps elucidate the phylogeny of motor planning, suggesting that all extant primates may share these abilities. This finding, however, was contrary to a hypothesis posited by Johnson-Frey

(2004), who suggested that tool-use in humans may rely on the ability to plan in advance. Expanding upon his initial hypothesis, our finding of anticipatory planning abilities in non-tool using primates allowed us to rule out the most extreme version of this account; anticipatory planning may be necessary but not sufficient for the development of tool use. However, the studies in our lab concerned motor actions were confined to tasks involving a single action or multiple actions performed individually. We are uncertain as to the *scope* of motor planning in nonhuman primates. Perhaps the ability to plan *sequences* of actions in advance (instead of just a single action) is a critical ability for the development of tool use and other complex cognition in humans. While Johnson-Frey did not posit this, we extend his hypothesis to suggest that we may find planning differences between humans and nonhumans in terms of the ability to coordinate multiple motor actions in anticipation of a future state or goal. We have shown that both tamarins (Weiss, Wark & Rosenbaum, 2007) and lemurs (Chapman, Weiss & Rosenbaum, in press) are capable of anticipating a forthcoming goal at least one motor action in advance. The present study asks if nonhumans can coordinate sequences of actions in advance of a goal. While we are unaware of any formal investigations of sequential motor action planning in nonhuman primates, there are several comparative findings (reviewed below) that may contribute valuable insight to this question.

Natural Food Processing Behavior

There is ecological reason to believe that nonhuman primates are capable of planning a coordinated sequence of actions. Even before considering comparative laboratory studies, naturalistic observations of nonhuman primate behavior can inform the main research question in this paper. Various food processing and extraction behaviors of wild

16

primates appear to consist of a specific sequence of actions, some of which may demonstrate hierarchically nested subsequences. Whiten (1988) provided observational evidence of multiple action coordination in olive baboons during food processing behavior. In order to consume sedges, baboons completed 5 to 6 sequential actions, which included repetitions of a sub-sequence of these actions (removing segment, biting off sheath, and so on). Sub-sequence repetition is taken to reflect hierarchical nested actions.

A similarly sequential process appears to be used by mountain gorillas when consuming wild celery, bedstraw and nettles (Byrne, 1995; see also Byrne & Byrne, 1993). Bedstraw, celery and nettle processing typically appear to consist of four, six, and eight sequential actions, respectively. An example of steps in celery processing include: pull a stem, bite a segment from the stem, remove the segment's casing, and so on (Whiten, 1998). As in baboon feeding behavior, some of these food processing sequences involve hierarchically nested subsequences (specifically in the case of nettles and celery).

Not surprisingly, some of our most closely related primate relatives also display sequential actions in foraging behavior. Wild chimpanzees (*Pan troglodytes*) demonstrate specific sequences of actions that are apparent in behaviors such as termite and ant fishing. Boesch and Boesch (1990) described Tai chimpanzees' actions of digging out the opening of an ant nest, inserting their arm inside, removing the arm, and finally eating the larvae and pupae from their hands. They further describe an ant fishing technique using a twig, which appears to consist of at least three steps; inserting the twig into a nest, waiting for the ants to crawl on the twig, removing the twig, and swiveling the ants on their lips from the twig's surface. Ant fishing employed by Gombe chimpanzees involves

a similar set of distinct stepped actions. The above descriptions of naturalistic food processing behavior in baboons, chimpanzees, and gorillas appear to highlight the sequential aspects of primates' wild consummatory behavior. Given the potential for nested hierarchical structure and the specific ordinal requirements of these processes, these action sequences are likely suggestive of goal-directed multiple action planning. However, these observations do not provide clear evidence of how these actions may be planned and how far in advance this sequential planning may occur, which highlights the need for more controlled laboratory studies.

Hierarchical Organization

Similar to the nested hierarchies present in natural food processing behaviors, the concept of learning hierarchical structure has been examined in nonhuman primates and children in a more controlled laboratory setting. Greenfield, Nelson and Saltzman (1972) provided 11- to 26- month old infants with a game of seriated nesting cups. Three strategies were examined: pairing method, pot strategy and subassembly strategy, each of which increases in complexity (see Figure 3). Eleven-month olds used the pairing method, 21-month olds employ the pot strategy, and children demonstrate the subassembly method which is hierarchical in nature by 36 months of age.
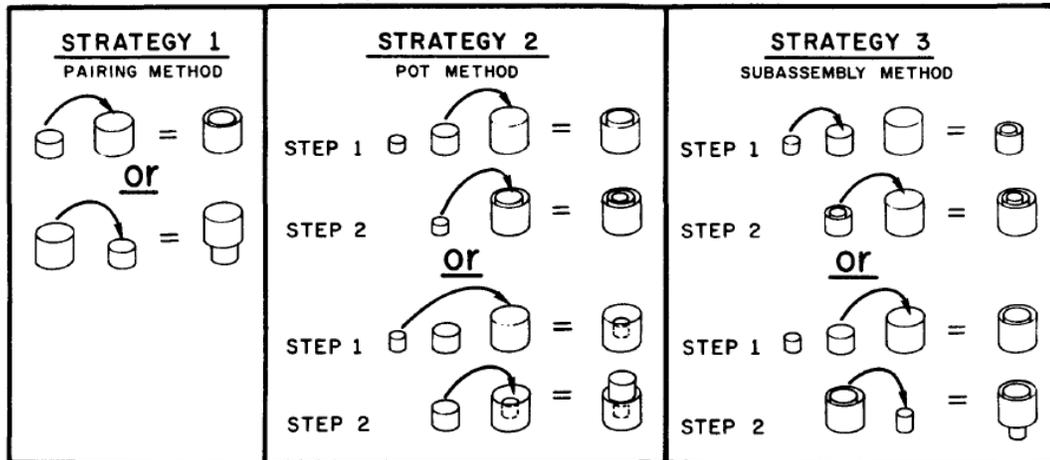
Figure 3. Three cup strategies (Reproduced from Johnson-Pynn et al., 1999)

Johnson-Pynn and colleagues (1999) replicated the above nested cups method with three species of nonhuman primate; chimpanzees, bonobos, and capuchin monkeys. A human experimenter demonstrated how to nest the cups and primates were then tested, although capuchins required a training phase. At initial test, both chimpanzees and bonobos demonstrated more hierarchical nesting (using the subassembly method) than capuchins, who appeared to struggle with nesting in general. After the capuchins were trained, their performance was similar to the apes', showing evidence of pairing, potting and sub-assembling. However, unlike the children in Greenfield et al.'s (1972) study who acquired a dominant subassembly strategy by 36 months, the nonhuman primates never used subassembly as their dominant strategy. This indicates that bonobos, chimpanzees and capuchin monkeys can learn hierarchical structure and ordering, but may be more cognitively limited than children in their capacity for hierarchical organization.

Sequential learning, Serial List Learning and Ordinality

Sequential learning can be understood as the ability to represent the order of elements in a given sequence, and is present in a variety of complex human behaviors (i.e. learning a dance routine, language processing). Sequential learning, depending on the complexity and number of elements, is thought to imply anticipatory planning (Conway & Christiansen, 2001). A sequence of behaviors or actions may be planned well in advance, and does not necessarily involve planning after each individual element. Serial list learning, which requires sequential learning abilities, is another rich domain of cognition that may yield insight into the planning underlying coordinated action sequences. Various species of nonhuman primates have proved capable of learning ordered sequences of images and Arabic numerals. Ross (2009) taught a single lowland gorilla (*Gorilla gorilla gorilla*) to select a specific sequence of seven numerals on a touch screen. While the gorilla required a training period (starting with two items, moving up to seven), her performance was indicative of serial learning. She consistently performed better on earlier items in a list, and her longest latencies to choose appeared at the first item. Her latencies declined over the course of a list, and her shortest latencies occurred for the last item. This pattern of latencies is taken as evidence of pre-planning; the first item is processed for a longer time because the individual is planning for a multiple-item sequence instead of a single choice. Although gorillas are great apes, they are not wild tool-users, which makes this finding of serial list learning particularly interesting with regards to the idea that planning abilities may scaffold tool use.

Similar serial ordering has been observed in a chimpanzee subject (Biro & Matsuzawa, 1999; see also Matsuzawa, 1985). A female chimpanzee, Ai, was trained to select three numerals at various positions on a computer screen in ascending order (Biro

& Mastuzawa, 1999). In order to ensure that she was planning the sequence from the outset and using a collective search strategy instead of using a serial search strategy. Ai was tested with switch trials. On these trials, the order of the second two stimuli was switched on the screen after a first numeral selection was made. Her performance on these switch trials dropped sharply, indicating that she had been planning for a sequence and the switch of the stimuli disrupted her coordinated plan. Ai's hand movement trajectories were also analyzed and indicated that she corrected hand movements during these switch trials. The authors concluded that her behavior is evidence of three processing stages also seen in humans; planning, executing and monitoring.

Oshiba (1997) compared the performance of humans, chimpanzees and Japanese macaques on a serial ordering task, again using visual stimuli. Two to four colored circle stimuli were presented on a touch screen and subjects were trained to select items according to a specific order. In one test, the items would disappear after they had been touched. Monkeys, but not humans, showed decreased reaction times for each item, indicating that they were using a serial search strategy. The human reaction time was longest for the first item and then relatively stable for the remaining items, indicating a collective search strategy. Chimpanzees demonstrated a collective search strategy on the monotonic list (size order) but switched to a serial search strategy for a non-monotonic list. This indicates that humans and chimpanzees, but not macaques, can learn the ordinal sequence of the circles. This type of sequencing indicates planning is present in the beginning of a trial.

In the past, chaining theory has been used to describe how animals learn serially organized behaviors (Ebbinghaus, 1964). Chaining theory explains serial actions as a set

of stimulus-response chunks, with associations between two items at a time. Research on list-learning with nonhuman primates, however, has revealed that chaining theory cannot explain the performance of many subjects trained and tested with ordinal lists (Terrace, 2005). Chen, Swartz and Terrace (1997) studied rhesus monkeys' ability to order four novel visual photographic stimuli on a touch screen. Their goal was to distinguish between potential strategies subjects may use; learning adjacent-item associations or learning ordinal position information. Rhesus monkeys were trained on four-item lists using the simultaneous chaining paradigm (all items are displayed simultaneously on each trial). They learned to respond to a specific order regardless of where on the screen each item occurred. Monkeys were then trained on derived lists, in which two of the times were from the first list and two items were new. Some derived lists retained the old items ordinal position and other lists had new ordinal positions. If the macaques were using item-item associations then the ordinal position should not impact learning the derived lists. Monkeys learned lists with maintained ordinal position very quickly with little errors. The changed ordinal lists, however, needed extensive training for the monkeys to learn. In addition, errors were most often noted based on an items' original ordinal position. Based on the pattern of errors and training needed for the derived list learning, the authors conclude that the monkeys were able to acquire and use knowledge of the ordinal positions of items in the lists. They also suggest that chaining theory (item to item associations) cannot be used to explain their pattern of results. This indicates that monkeys are not merely learning item to item singular associations, but instead, can learn a sequence of items and maintain a representation of their ordinality.

There are many instances of list learning and performance that cannot be explained by chaining theory and must invoke understanding of ordinal positions (see Terrace, 2005 for a review). This body of literature can be used to inform the current research question. Ordinal list learning studies have shown that nonhuman primates are capable of representing the ordinal position of items in a list, and do not rely on item to item or stimulus-response associations alone. This suggests that these primates are capable of anticipatory planning in a coordinated sequence of actions. However, these studies did not specifically address when in the sequence the planning begins. In addition, the above reviewed studies all relied heavily on training paradigms and required a minimum of hundreds of trials and more typically thousands of trials for the subjects to learn a sequence of four items (Chen et al., 1997). None of the action sequences described above (pressing items on a touch screen) can be considered spontaneous. As a result, we cannot be sure if these animals can coordinate a sequence of actions, planned in advance, without training.

The Present Study

The present study aims to empirically determine if nonhuman primates are capable of planning a sequence of coordinated actions without training or conditioning. The below set of four experiments provided cotton-top tamarins (*Saguinus oedipus*) tamarins with a simple tape-measure pulling task. Tamarins were required to reel in a food reward located at various distances on the tape measure. I measured the distances between grasps on the tape to determine if tamarins changed their pulling behavior according to the location of the food reward. If tamarins plan sequences of multiple actions in anticipation of a goal, one would predict systematic differences in the distances between grasps in the near

23

versus far food-location. However, if tamarins do not plan sequences of actions in a pulling task, one would expect to see an average distance between grasps when the food is located near and far. Alternatively, based on Hull's (1934) research with rats, one might expect to see successively smaller distances between grasps as the food approaches, regardless of where the food is located (see also Drew, 1939).

EXPERIMENT 1: Coordinating Multiple Manual Actions

Pulling with Visual Feedback

Methods

Subjects

Four female and three male captive cotton-top tamarins (*Saguinus oedipus*) participated in this experiment. The monkeys were born at the New England Regional Primate Research Center in Southborough, MA and were transferred to the Pennsylvania State University in June, 2005. The tamarins are housed in mated pairs in a single colony room. All tamarins tested in this experiment have previously participated in behavioral experiments investigating motor planning (e.g., Weiss, Wark & Rosenbaum, 2007; Weiss & Wark, 2009). However, none of the tamarins have participated in any experiments involving the method employed in the current series of experiments. Throughout the course of the experiments, the tamarins were maintained at 95% of their free feed weight and had ad libitum access to water. Use and care of the tamarins conformed to the rules and regulations of the IACUC at the Pennsylvania State University.

Stimuli and Apparatus

All test sessions were conducted in an experimental procedure room with each monkey tested individually. Trials were recorded with two digital camcorders (JVC Everio hard-disk and Sony Handycam DCR-HC21) simultaneously, each located on either side of the testing apparatus. At the start of a trial, tamarins were located in a transport box (12" high x 9.25" wide x 12" deep) with 2 Plexiglas walls, one wall and a

ceiling made of wire mesh caging, and a metal front door, that could be removed to allow

the tamarins to see into the test chamber (see Figure 4 for transport box).

Figure 4. Cotton-top tamarin in transport box.

The transport box was located directly behind the testing chamber, and the metal door

was aligned with a Plexiglas door of identical size in the back side of the testing chamber.

The testing chamber (2.5 cm tall x 40.75 cm wide x 30.5 cm deep) was constructed of

four Plexiglas walls and a Plexiglas ceiling, supported by a wooden frame (see Figure 5).

The floor was made of plywood covered with Plexiglas. The back wall of the testing

chamber contained a Plexiglas door (32.5 cm long x 21.5 cm wide) in tracks that could be

lifted and lowered to allow the tamarins access to the chamber. The front wall of the

testing chamber contained a small central hole (2.75 cm diameter) located 12 cm above

the floor of the chamber (See Figure 6). On the opposite side of the testing chamber's

back Plexiglas wall, a long wooden table (60.5 cm long x 18.75 cm wide) was placed

with the edge directly against the bottom of the hole in the Plexiglas back wall. This

table was centrally located with respects to the testing chamber and central hole in the

chamber's Plexiglas back wall. The tape measure was stretched out on top of this table

for all trials.

Figure 5. Front (left) and rear (right) views of the testing chamber and apparatus.

A tape measure (150 cm long x 1 cm wide) labeled with inch measurements on one

side and centimeter measurements on the opposite side was stretched out flat on the

surface of the table, in line with the hole in the Plexiglas wall of the testing chamber. The

tape measure was placed on the table, extending 65cm. The remaining 85 cm of the tape was draped over the far end of the table, obscured from the monkeys' view in the testing chamber. The tape measure was consistently presented such that the white side (cm) was visible, and the yellow side (inch) was face down against the wooden table. The initial 3 centimeters of the tape measure was threaded into the testing chamber through the hole in the Plexiglas wall (see Figure 3). The remainder of the tape measure was located outside of the testing chamber. The tape measure contained a set of sealed metal discs serving as a weight (4 in diameter x 49.56 grams) located between the 60.5 and 65 cm mark. This weight was always at the far end of the wooden table relative to the subject. The weight was used to create a standard amount of resistance on the tape across all trial types. When subjects pulled the rope, the weight slid forward along the table.

A Plexiglas disc, designed to hold and deliver food to the tamarin, was also affixed to the tape measure. This disc (3.7 cm diameter) contained a central hole (1 cm diameter) that allowed the end of the tape measure to be fed through the center. The disc was designed to slide along the tape measure and was secured at various locations with a small piece of transparent tape. This disc rested on the wooden table with the tape threaded through its central hole during test sessions.

Half-raisin pieces were placed on the half of the disc closest to the tamarin (Figure 3). When the tape slid forward (due to tamarin's pulling) the disc would eventually strike the Plexiglas wall, thereby presenting the raisin to the tamarin via the central hole in the wall.

Figure 6. Tape measure and Plexiglas disc containing a raisin, as used in experimental sessions.

Procedure

Each focal tamarin was tested individually in an experimental testing room. The tamarin was transported from their home cage in the colony room to the experimental room in a transport box. The food (a piece of raisin) was either located at near, intermediate or far distances (13, 26 or 52 cm). Focal tamarins were tested in two test sessions, each consisting of two near, two intermediate and two far trials, a total of six trials. The order of trial type in a given session was pseudo-randomized and counterbalanced across individuals.

At the start of each trial, the focal tamarin was located in the transport box, the door of which was aligned with the door of the testing chamber. Out of the view of the tamarins, the experimenter affixed the Plexiglas disc and placed the raisin at the appropriate location on the tape measure. The metal transport box door was then removed

so the subjects could see the table, tape measure and the location of food on the tape

measure. An experimenter lifted the sliding Plexiglas door to allow the tamarins to enter

the testing chamber and access the tape measure. Once inside the testing chamber, the

tamarins could pull the tape measure by grasping the first three cm fed into the chamber.

They could pull in any manner they chose and the trial lasted until the disc was pulled

against the Plexiglas barrier and the food was accessible to the subject. Figure 7 shows a

tamarin pulling the tape measure in a test trial. Once the tamarin consumed the food, the

experimenter lifted the sliding door and allowed the tamarin to shift back into the

transport box. At this point, the tape measure was reset and baited with food for the next

trial.

Figure 7. Cotton-top tamarin participating in Experiment 1 pulling the tape measure with

a hand-over-hand method.

Data Analysis

All trials were coded by an experimenter using both video camera angle recordings. Using Adobe Premiere Elements, an experimenter viewed both the right and left camera angles for a given trial, moving through the file frame-by-frame. The dependent variable of interest was the distance between hand grasps on the tape measure. This was defined as the number of centimeters of tape between a tamarin's hands when both hands were on the tape at the same time. To achieve consistency in measurement across trials, sessions and subjects, the experimenter always measured the location of the *front* of each grasp on the tape; the foremost part of the hand, typically the thumb or the forefinger, depending on the hand grasp. This ensured that the experimenter measured the part of each hand that was closest to the food at any given point on the trial. Locations of the hand on the tape were recorded in half-centimeter units as this was the smallest reliable unit of measurement based on the markings on the tape measure and the video quality. Thus, the dependent variable was the distance between the two hand grasps (see Figure 8).

Figure 8. A cotton-top tamarin grasping the tape measure with both hands during pulling behavior. The blue arrow shows the dependent variable of interest, the distance between grasps.

In order to record this measure, the tamarin needed to grasp the tape with one hand and then the other. In instances in which the tamarin dropped the tape measure, the distance between the hand grasps prior and subsequent to the drop were not included in the analysis. Trials, in which the experimenter could only see the location of one hand grasp, but not the preceding or subsequent hand grasp, were also excluded. Trials in which the tamarins only used one hand repeatedly or used their mouth were also excluded.

The experimenter also coded videos for two other variables of interest: number of manual pulls in each trial, and the distance the tape traveled for each manual pull. They calculated the number of manual pulls by simply counting each individual pull. In order

to code for the distance traveled, the experimenter observed the location of the tape at the round hole in the Plexiglas barrier. When a pull occurred, they noted what centimeter measurement was aligned with the hole when the pull stopped. The experimenter then calculated the difference between the two measurements, thereby providing an estimate of how many centimeters of the tape had travelled for a given pull.

Some trials were not included due to problems revealed in data coding. Several individual trials did not produce data for the following reasons: lack of hand-over hand pulling, monkeys pulling outside of the view of the camera, camera malfunctions or blurry images, and pulling the length of tape with either one pull or using mouth. The results section (below) explains how many trials were removed, and for what reasons they were removed.

If tamarins can plan a sequence of actions in anticipation of a goal, one would expect to see systematic differences in their pulling behavior when the food reward is at different distances away from them (across the three conditions). However, if tamarins do not plan sequences of actions in advance of a goal, one would not expect to see any systematic differences in their pulling behavior based on distance to the food reward. If the tamarins do not plan their pulls as a sequence of actions, one might expect to see a default pulling behavior (e.g. the tamarin exhibits a default distance between grasps, regardless of food location.) In the absence of planning, one might also observe tamarins planning for each individual pull. In this case, subjects might modify each pull individually based on the current location of the food, evidenced by varying distances between grasps as the trial progressed in both near and far conditions.

Results

33

Eight monkeys participated in Experiment 1 but one female was excluded from analysis due to the consistent use of her mouth to pull the tape measure. Data collection was designed to include twelve trials per subject across two separate sessions (four trials of three trial types, as described above). Data coding, however, revealed that several individual trials did not produce data. Of the seven monkeys retained in analysis, five monkeys completed two sessions of 6 trials as planned. Two subjects required two additional trials because two trials from their first sessions could not be included in analysis. One individual used his mouth to pull on his two excluded trials, and the other individual used her mouth to pull on one excluded trial and refused to pull at all on her second excluded trial. Consequently,, the minimum number of trials needed for a subject was 12 (n = 5) and the maximum was 14 (n= 2).

A within-subjects ANOVA was conducted to compare the distance between grasps in the near, intermediate and far conditions. There was no significant main effect of condition, Wilks' Lambda=.322, $F(2,5) =$ 5.27, $p =$.059. Three paired-samples t-tests were used to conduct post-hoc comparisons because the p value closely approached significance. These tests compared the distance between grasps in the near and intermediate, intermediate and far, and near and far conditions. On average, the distance between grasps in the near condition (M=5.00, SD=1.37) was significantly smaller than distances between grasps in the intermediate condition (M=6.03, SD=1.55); $t(6)$= -3.35, p=.015. On average, the distance between grasps in the near condition (M=5.00, SD=1.37) was significantly smaller than distances between grasps in the far condition (M=6.34, SD=1.40); $t(6)$= -2.92, p=.027. However, there was no significant difference between the scores for the intermediate (M=6.03, SD=1.55) and far (M=6.34, SD=1.40)

conditions; $t(6) = -.82$, $p=.44$. Consequently,, data from the intermediate and far

condition was collapsed into one category (subsequently referred to as *far*) for all

remaining analyses for Experiment 1.

 A paired-samples *t*-test was used to compare the distance between grasps in the near

and far conditions. On average, the distance between grasps in the near condition

($M=5.00$, $SD=1.37$) was significantly smaller than the distance between grasps in the far

condition ($M=6.23$, $SD=1.38$); $t(6)= -3.24$, $p=.018$. See Figure 9 for graphic

representation of the distance between grasps across conditions. In addition, all seven

individual tamarins displayed the same trend, which can be seen in Figure 10.
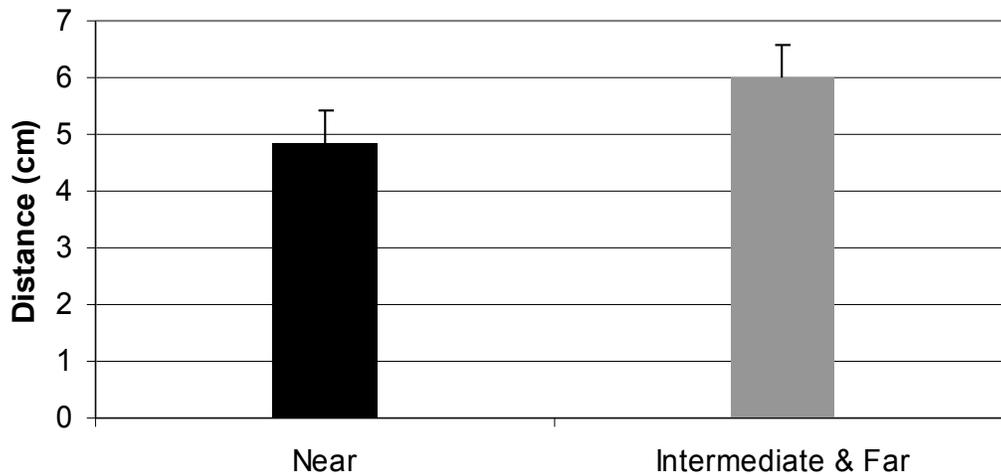

Figure 9. Experiment 1: Average distance between grasps in near and far conditions.
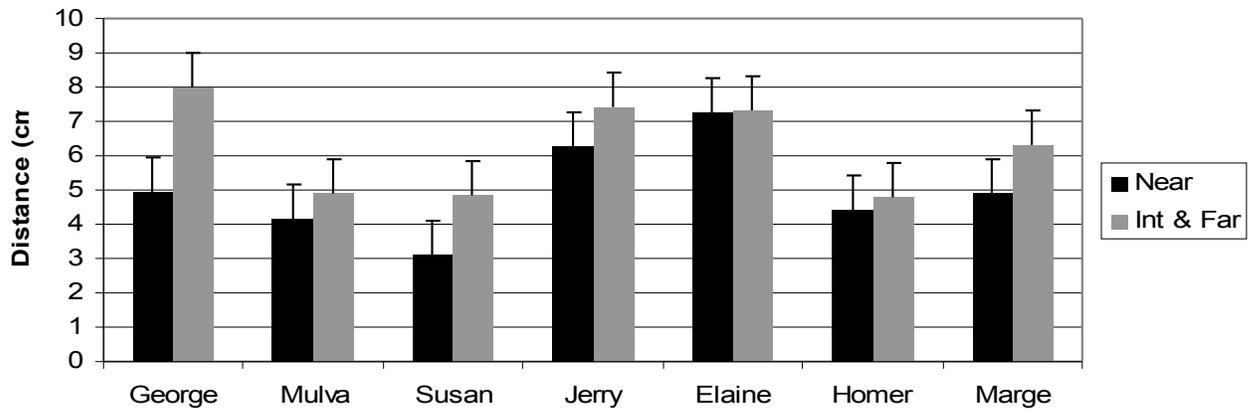
Figure 10. Experiment 1: Average distance between grasps for each individual subject.

To ensure that the observed difference between grasps was systematic over the course of a trial, it was necessary to determine that the scaling behavior started at the outset of the trial. It was possible that the scaling behavior was an artifact of the tape's momentum. In the far trials, a longer distance of tape was available to pull. With more distance to move forward, it is possible that the tape measure could gain more momentum over time. In the event that the momentum increased over the course of a far trial, it may have been possible to take larger distances between grasps due to the tape moving faster. In the near trials, however, the length of tape measure available was likely too short to allow as much momentum to build. If true, this could account for the larger distances between grasps in the far condition compared to the near condition. To rule out this confound, I compared the first two distances between grasps in the near condition to those in the far condition. I focused on the first two pulls on the tape because these pulls should not be subject to any momentum. On the first pull, the tape is at rest, so the physical forces on tape for near and far trials are equated. If the tamarins show differences in the distances between grasps on these first two pulls, this would indicate that momentum is not causing

36

this difference. A paired-samples *t*-test was conducted to compare the first two data points in the near and far conditions. On average, the distance between grasps in the near condition (*M*=5.00, *SD*=1.37) was significantly smaller than the distance between grasps in the far condition (*M*=5.83, *SD*=1.35); *t*(6)= n -2.46, *p*=.049 (see Figure 11). Five of 7 monkeys demonstrated this same trend (see Figure 12).
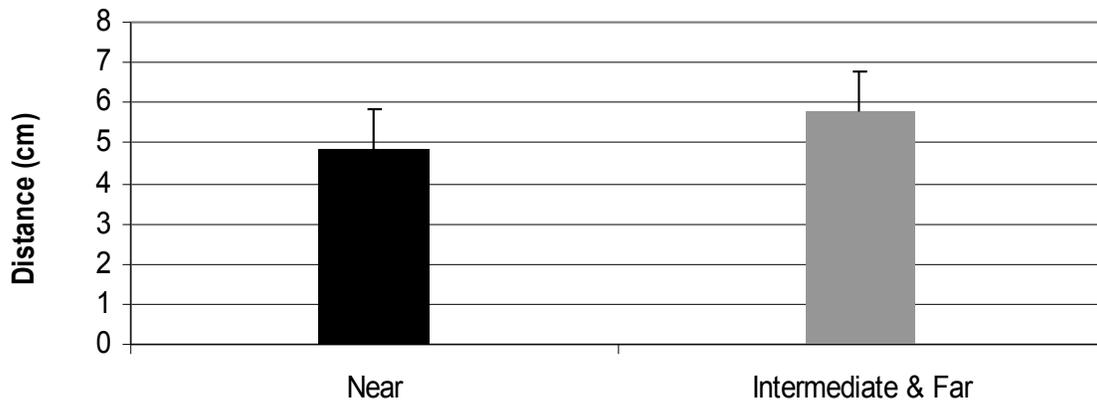

Figure 11. Experiment 1: Average distance between grasps for first 2 distances across near and far conditions.
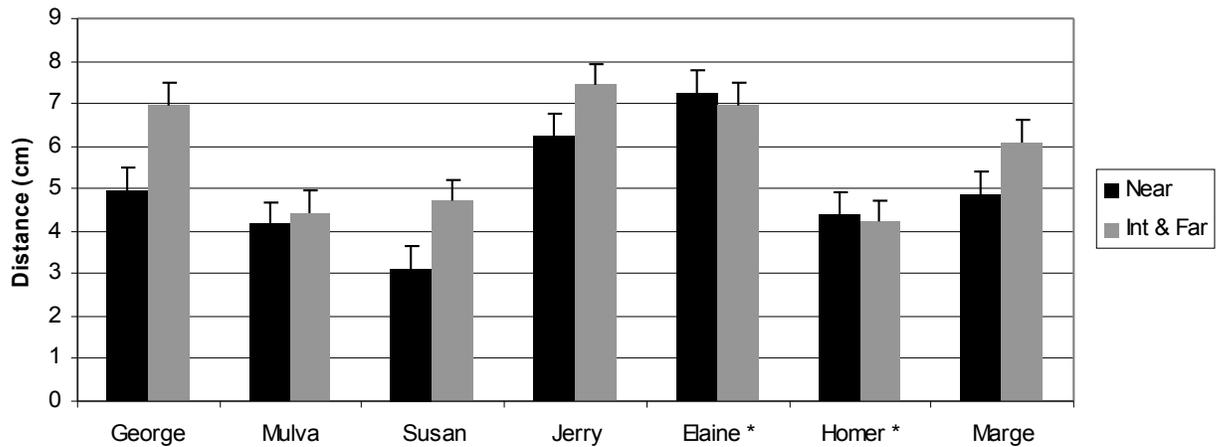

Figure 12. Experiment 1: Average distance between grasps for each individual including first two distances only.

A within-subjects ANOVA was conducted to examine the number of manual pulls in the near, intermediate and far conditions. There was a significant effect of condition, Wilks' Lambda=.067, $F(2,5)=34.71$, $p=.001$. Three paired-samples t-tests were used to conduct post-hoc comparisons because the p value was significant. There were significantly fewer pulls in the near condition ($M=1.96$, $SD=.34$) than the intermediate condition ($M=4.04$, $SD=.88$); $t(6)=-6.44$, $p=.001$. There were significantly fewer pulls in the near condition ($M=1.96$, $SD=0.34$) than number of pulls in the far condition ($M=5.96$, $SD=1.25$); $t(6)=-8.369$, $p < .0001$. Finally, there were significantly fewer pulls in the intermediate condition ($M=4.04$, $SD=.88$) than the far condition ($M=5.96$, $SD=1.25$); $t(6)= -8.99$, $p < 0001$.

A paired-samples t-test was used to compare the distance the tape measure traveled during each pull in the near and far conditions. There was no significant difference between the distance the tape measure traveled in the near condition ($M=7.03$ $SD=1.60$) than the far condition ($M=6.91$ $SD=1.50$), $t(6) = .203$, $p=.846$. Consequently, this variable was not coded for or used in analyses for subsequent experiments.

Discussion

The main variable of interest was the distance between grasps on the tape. In Experiment 1, there were no significant differences between the intermediate and far conditions for this variable. However, once the data from intermediate and far conditions were collapsed, a significant pattern emerged. The distances tamarins took between grasps on the tape in the near condition, when the food was closer, were systematically smaller than those in the far condition, when the food was farther away. The tamarins in

Experiment 1 appeared to be scaling their pulling behavior according to the distance to the food.

The initial analysis for Experiment 1 considered the average distance between grasps over the course of entire trials. This method of analysis did not examine whether the distances between grasps were relatively uniform over the course of an individual trial, or if instead, they increased or decreased as the food drew nearer. As a result, it was possible that a momentum-based account could explain the scaling effect without invoking planning. It is possible that distances between grasps were larger in the far condition because the last few pulls yielded larger distances between grasps than the initial pulls, as a result of momentum. Over the course of a trial, the momentum of the tape measure may have increased with each successive pull. If the momentum increased and the tape measure was easier to pull, the distance between the tamarins' grasps may also have increased as the food drew nearer. This account would indicate that the pattern of results was due to the physical properties of the tape in motion instead of anticipatory planning on the tamarins' part.

To rule out the above momentum-based explanation, I examined the initial pulling behavior at the outset of the trial for near and far conditions. At the beginning of each trial, the physical forces on the tape measure were equated across conditions; the tape was not in motion and had no momentum. Thus, I compared the average distance between grasps for the first two data points of each trial and found that the distance between grasps was still smaller in the near condition than the far condition. Five of the seven monkeys displayed this pattern. For both individual subjects, and at a group level, we continue to see a systematic difference in pulling behavior between the near and far

conditions as early as the first two pulls. We can conclude that the difference between pulling behavior (as demonstrated by distance between manual grasps) in the near and far conditions was not caused by momentum of the tape's forward movement.

Before concluding that the results are based on planning, several additional confounding factors must be ruled out. Over the course of a trial, the tamarins had full visual access to the tape moving toward them with each successive pull. Thus, the tamarins could visually track the location of the *food* (goal) on the tape while pulling. Given that they had visual feedback of the food moving with each manual action, one cannot definitively determine when planning began. It is possible that the tamarins noted the location of the food before each individual manual pull and re-evaluated their pulling strategy, updating a plan with each manual action. In this case, the series of actions would not be considered coordinated or planned in advance. Experiment 2 (below) was designed to address this issue.

Another possible confound relates to the method of data analysis used to compare near and far trials. As noted in the data analysis section above, any trials with less than two pulls did not yield data that could be analyzed. It was possible for tamarins to obtain the food with a single pull in the near condition but not in the far condition, especially because the plastic stopper caused the tape to stop moving as soon as the food was within reach. Because the Plexiglas disc caused the tape to stop moving artificially in Experiment 1, we do not know if tamarins would have demonstrated larger distances between grasps in the near condition if they had a longer distance of tape available to pull, regardless of food location. In addition, we don't know if the tamarins would have demonstrated smaller distances between grasps if the tape had suddenly stopped moving

at 13 cm while the food was located at 52 cm. Perhaps the artificial nature of the tape stopping at 13 cm caused the pulling behavior to manifest itself differently in the near condition. A second problem related to this issue arises in our data filtering and analysis. As a result of the trials with one large pull, a larger number of near condition trials needed to be removed from analysis than far condition trials. Specifically, five near trials (from four individuals) contained a single pull, whereas none of the far trials were completed with a single pull. Experiment 3 (below) was designed to ensure that Experiment 1's experimental method and data filtering process were not contributing to the systematic difference in distance between grasps.

A final question remaining about Experiment 1's results concerns the role of physical differences in the near and far conditions. While the two conditions were equated for the weight of objects on the tape measure (washer weight, Plexiglas disc, and raisins), the Plexiglas disc and raisin were placed at different locations on the tape in each condition. While the weight of the disc (2.65 grams) seemed negligible to a human experimenter, it is possible that our 400-500 gram tamarin subjects could detect the physical difference of this small weight located at 13 cm or 52 cm. If the tamarins could detect this subtle difference, their pulling behavior may have been influenced by the physical feedback of the tape in motion, instead of resulting from planning based on the goal location. Experiment 4 was designed to address this potential confound by removing any physical weight differences on the tape in the near and far conditions.

Overall, the pattern of results from Experiment 1 demonstrate a systematic difference in distance between grasps across near and far conditions (near < far), apparent as early as the first two pulls in a trial. However, we cannot conclude that tamarins coordinated a

41

sequence of pulling actions with respect to distance to the goal without ruling out the

above confounds.

EXPERIMENT 2: No Visual Feedback

During Experiment 1, the tamarins received visual feedback from the food moving towards them with each successive pull. In order to conclude that the tamarins planned a sequence of actions in Experiment 1, we need to rule out the possibility that the tamarins evaluated the distance to the food before each pull and planned only for one action at a time. The goal of Experiment 2 was to rule out this type of intermittent planning by preventing continuous visual feedback throughout the trial. The following questions were addressed with Experiment 2. Do tamarins require visual feedback in order to scale their behavior to the distance to a goal? In the absence of visual feedback during the course of a trial, do tamarins scale their manual pulling behavior to the distance from the reward in a similar manner to that observed in Experiment 1?

Method

Subjects

Four female and three male captive cotton-top tamarins (*Saguinus oedipus*) participated in Experiment 2. These individuals also participated in Experiment 1 prior to this experiment.

Stimuli and Apparatus

The apparatus was identical to the apparatus described in Experiment 1, except for the addition of a tunnel that covered the tape measure to prevent monkeys from viewing the movement of the food while they were pulling the tape (see Figure 13). The tunnel was triangular in shape, measuring 54 cm long. The triangular opening at each end measured 7 cm wide and 5.5 cm high (at the apex). The tunnel was constructed of thin metal bars covered in brown paper on the outside. The front opening of the tunnel (end closest to the

tamarins) was covered with a gray cotton curtain to preclude the subjects from viewing the tape measure. The 7.5 cm long curtain was hung from the top of the tunnel so that it covered the entire width of the opening, as well as the length.

Figure 13. Experimenter view (top) and subject view (bottom) of the tape measure apparatus used in Experiment 2.

Procedure

In Experiment 2, the location and transport procedures were identical to what was described above for Experiment 1. Test sessions consisted of four trials; two near trials (13cm) and two far trials (52cm). The order of these trial types was randomized and counterbalanced across individuals.

The experimental procedures were similar to those described for Experiment 1. The tamarins began in the transport box with only a Plexiglas door separating them from the inside of the testing chamber. Through this transparent door, the tamarin watched the experimenter bait the tape with food at either a near or far location. The experimenter tapped the back Plexiglas wall of the testing chamber to focus the attention of the monkey before sticking the raisin on the Plexiglas disc at either 13 or 52 cm. The experimenter then lowered the tunnel over the tape measure on the table. A second experimenter then lifted the sliding Plexiglas door to allow the tamarins to enter the testing chamber. Test sessions continued in the same manner as in Experiment 1.

Data Analysis

Data analysis procedures were the same as described above for Experiment 1, except that we restricted our analyses to the distance between grasps.

Results

Seven monkeys participated in the experiment, but one was excluded from analysis and further experimental conditions due to 'cheating' behavior; reaching through the hole in the Plexiglas wall of the chamber to grasp the tape while it was still on the table outside of the chamber instead of pulling it from inside the chamber.

Data collection was designed to gather four trials of each type (near and far) across two separate test sessions of four trials each (a total of 8 trials across two sessions). Data coding, however, revealed that some trials did not produce data (i.e. lack of hand-over hand pulling, monkeys pulling outside of the view of the camera, pulling the length of tape with either one pull or using mouth.) The minimum number of trials needed for a subject was 8 and the maximum was 14. Four subjects were tested on more than 8 trials each due to some of their trials' failure to yield data that could be included in analysis. Over all four individuals, 8 trials were discarded and re-run, due to the following reasons: lack of hand-over-hand pulling (n=4), tamarins' body blocking video (n=2), and camcorder recording malfunction (n=2).

A paired-samples t-test was used to compare the distance between grasps in the near and far conditions. On average, the distance between grasps in the near condition (*M*=4.02, *SD*=1.05) was significantly smaller than the distance between grasps in the far condition (*M*=6.65, *SD*=1.53); $t(5)$=-4.99, *p*=.004. See Figure 14 for graphic representation of the distance between grasps across conditions. In addition, all six individual tamarins displayed the same trend, which can be seen in Figure 15.
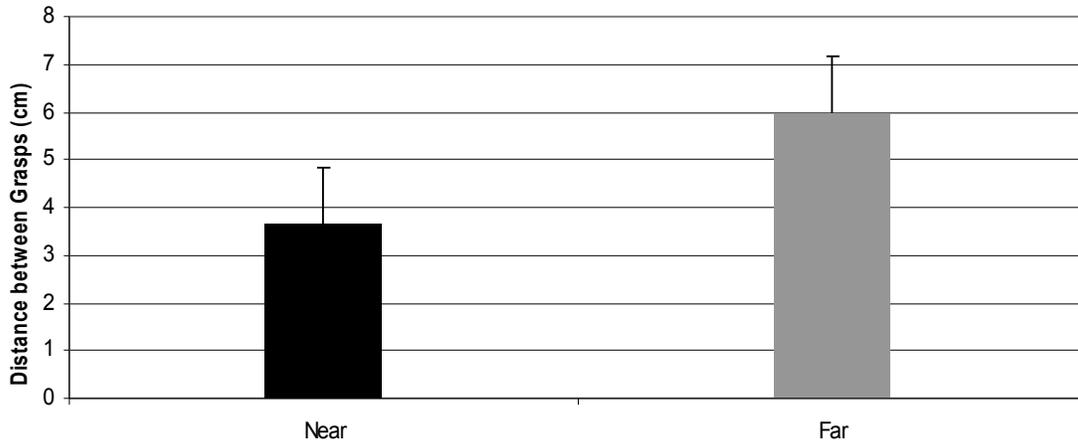
Figure 14. Experiment 2: Average distance between grasps in near and far conditions.

Figure 15. Experiment 2: Average distance between grasps for each individual subject.

A paired-samples *t*-test was conducted to compare the first two data points in the near and far conditions. On average, the distance between grasps in the near condition (*M*=4.02, *SD*=1.05) was significantly smaller than the distance between grasps in the far condition (*M*=6.04, *SD*=1.71); *t*(5)= -4.629, *p*=.006. See Figure 16 for graphic

representation of the distance between grasps for the first two data points across

conditions. When examining individual performance for the same analysis, all six

monkeys demonstrated this same trend, as shown in Figure 17.
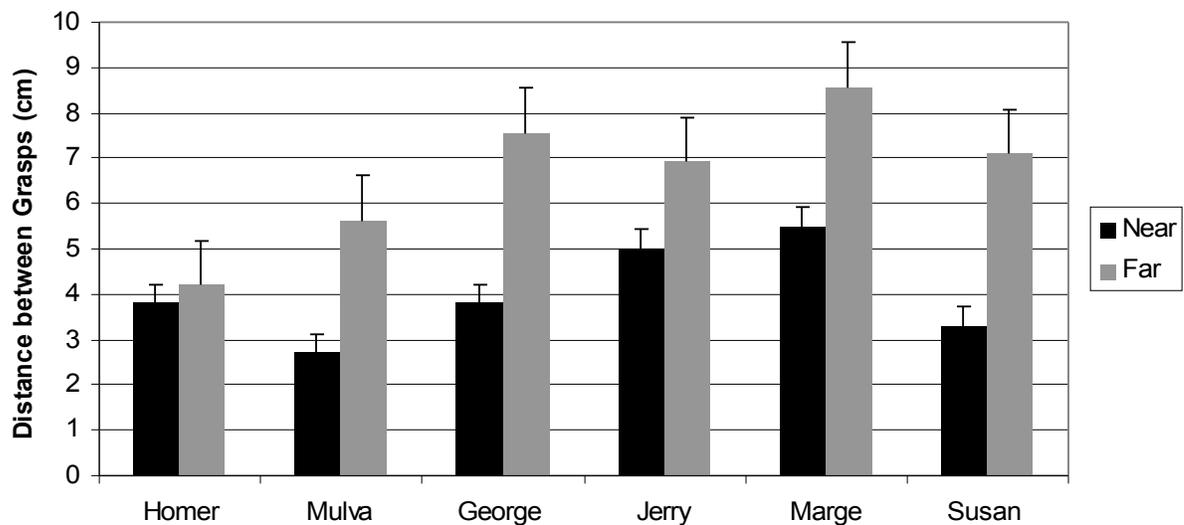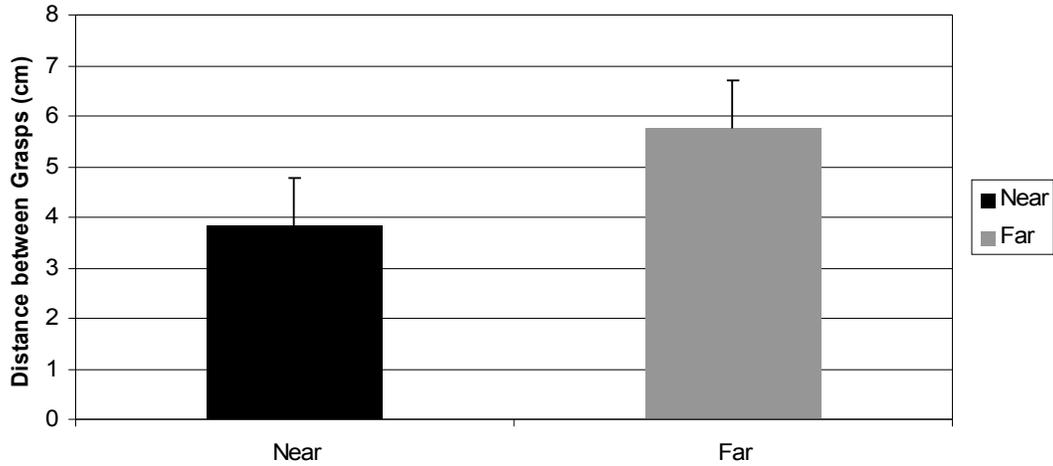

Figure 16. Experiment 2: Average distance between grasps for first two data points in
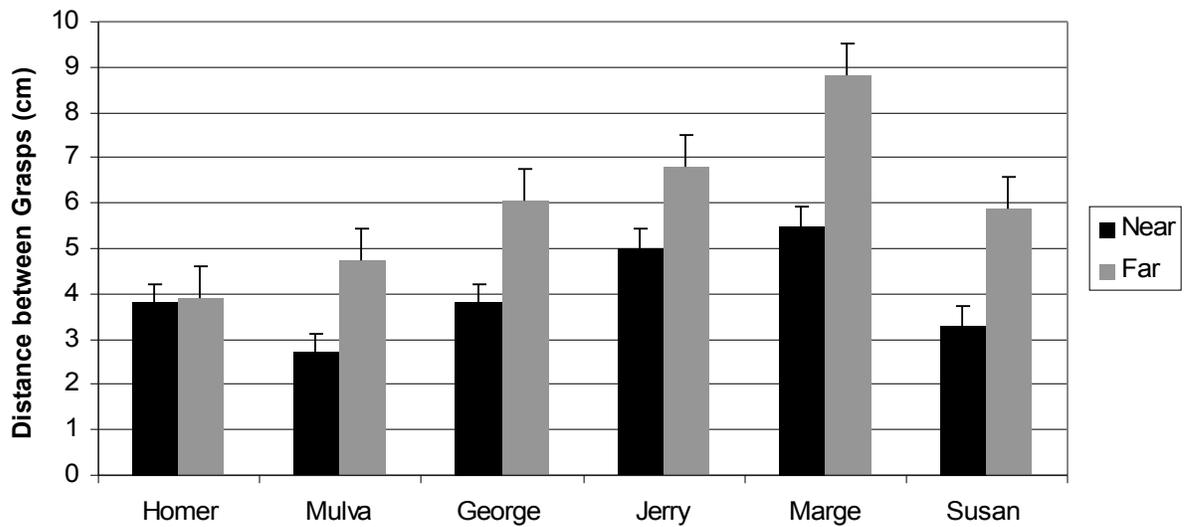
near and far conditions.

Figure 17. Experiment 2: Average distance between grasps for first two data points for

each individual subject in near and far conditions.

Discussion

The results of Experiment 2 indicate that tamarins persist in demonstrating a systematic difference in their manual pulling behavior in near and far conditions in the absence of visual feedback, with smaller distances between grasps for the near condition relative to the far condition. All subjects evidenced this pattern. As in Experiment 1, we examined the distance between the first two grasps in order to determine whether the effect took hold at the onset of motor sequence. In these trials, the distances were also smaller for the near trials than the far trials, a pattern which was also evidence by all individuals.

Experiment 2 served to rule out the possibility that the visual feedback was responsible for the pattern of results observed in Experiment 1. Since the tamarins could not see the food travel closer with successive pulls, they could not have altered their behavior by visually re-evaluating the distance to the food. This experiment replicated the effects from Experiment 1 and provided further evidence that tamarins may plan multiple action sequences in anticipation of a goal.

EXPERIMENT 3: Artificially Stopped Tape

Experiment 3 served to rule out confounds related to our experimental methods and data analysis procedures. Specifically, it was possible that the Plexiglas disc, serving as a stopper to artificially cease forward movement, contributed to the scaling we observed. When the food was in the near position, the tamarins only had 13 cm of tape available to pull and manipulate, whereas 52 cm of tape was available in the far condition. It is possible that the tamarins would have exhibited larger distances between pulls in the near condition if the tape had not artificially stopped moving at 13 cm. Further, our coding system posed another concern. In near trials, but not far trials, it was possible for a monkey to pull the tape measure once and bring the food and disc within reach. Consequently, the near condition of Experiments 1 and 2 yielded trials that could not be included in data analysis due to one pull instead of multiple pulls. The far condition did not yield trials that were discarded for this reason. Thus, Experiment 3 employed a different methodology to eliminate the possibility that our experimental method or data analysis techniques were responsible for the results observed in Experiments 1 and 2. This was accomplished by artificially stopping the rope at 13cm regardless of where the food was located on the tape measure.

Method

Subjects

Four female and three male captive cotton-top tamarins (*Saguinus oedipus*) participated in Experiment 3. These individuals also participated in Experiments 1 and 2 prior to this experiment.

Stimuli and Apparatus

The apparatus was identical to the apparatus described in Experiment 1, except that the Plexiglas disc was not used as a food-holder and stopper on the tape. In addition, marshmallows were used instead of raisins as the food reward, as they remained affixed to the tape more easily. The half-marshmallow pieces were stuck directly onto the tape. In Experiment 3, the tape measure was taped to the underside of the table, allowing so only 13 cm of tape to be pulled forward during a trial. Because the tamarins were unable to see that the end of the tape measure was affixed to the table, Experiment 3 was visually identical to Experiment 1.

Procedure

In Experiment 3, the location and transport procedures were identical to what was described for Experiments 1 and 2. Test sessions consisted of four trials. The marshmallow was either located at near or far distances (13 or 52 cm). Each session consisted of four trials (two near, two far), the order of which was randomized and counterbalanced across individuals.

The procedure of Experiment 3 was similar to the procedure described above for Experiment 1. The tamarin viewed the experimenter place the food on the tape at a near or far location before they were given access to the chamber. However, because the end of the tape measure was taped to the underside of the table, the tamarins were only able to pull a maximum of 13 cm. On the near (13 cm) trials, the tape measure could only be pulled 13 cm, but food was available at the 13 cm location. Likewise, on the far (52 cm) trials, the tape stopped at 13 cm, but the food remained out of the tamarins' reach. Thus,

far trials were unreinforced and ended when the tape measure was pulled to the 13 cm mark.

Tamarins were tested in only one session of 4 trials; 2 near and 2 far. Because half of the trials in this condition were unreinforced, subjects were not tested in additional sessions of this method, even if a given trial did not yield data. This was done to avoid extinguishing the manual pulling behavior.

Data Analysis

In Experiment 3, the experimenter coded data for the distance between grasps, as in previous experiments. However, the far trials were coded for the pulls on the tape before the 13 cm mark. Thus, distance between grasps that occurred as a result of manual pulls anywhere on the tape between 0 and 13 cm were retained for analysis. In both near and far conditions, the tape measure stopped moving forward automatically, due to the stopper at the 13 cm location. On far trials, the food was not within reach of the tamarins but was still visible, so they often continued to try to pull the tape. None of these pulls were included in analysis, as they were not functional (e.g. did not move the tape forward).

Results

Seven monkeys participated in this experiment, but one monkey was excluded from analysis due to lack of useable trials (due to dropping the tape, or reaching the food with one pull). Data collection was designed to gather two trials of each type (near and far) in one test session. Data coding, however, revealed that some trials did not produce data (i.e. lack of hand-over hand pulling, monkeys pulling outside of the view of the camera,

pulling the length of tape with either one pull or using mouth.) The minimum number of successful trials by a subject was 2 and the maximum was 4.

A paired-samples *t*-test was conducted to compare the distance between grasps in the near and far conditions. On average, the distance between grasps in the near condition (M=3.83, SD=0.80) was significantly smaller than in the far condition (M=5.42, SD=1.11); $t(5)$= -2.960, p=.032. See Figure 18 for graphic representation of the distance between grasps across conditions. In addition, all 5 of 6 individual tamarins displayed the same trend, which can be seen in Figure 19.
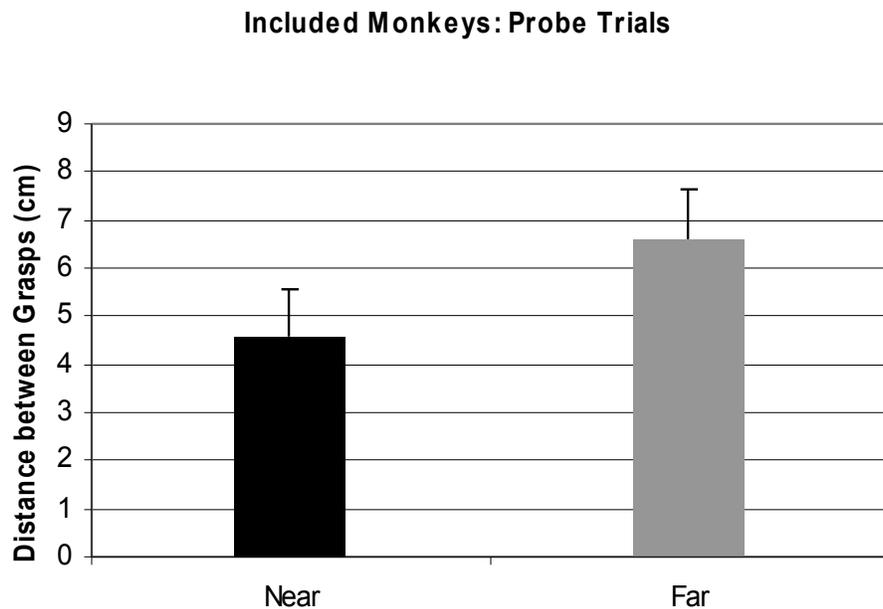
Included Monkeys: Probe Trials

Figure 18. Experiment 3: Average distance between grasps in near and far conditions.
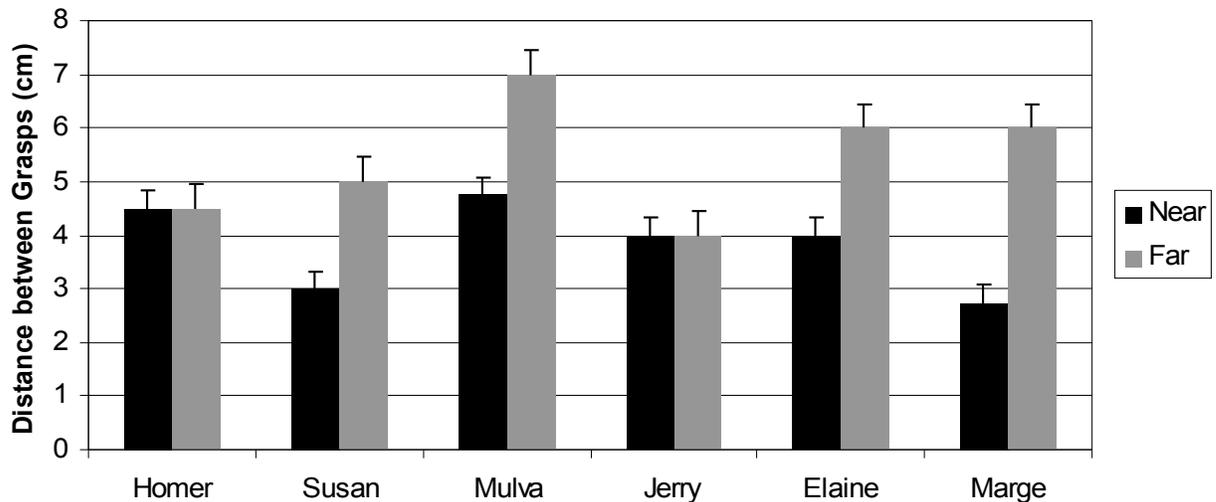
Figure 19. Experiment 3: Average distance between grasps for each individual subject.

Because only 13 cm of the tape was available, there was no need to compare the first 2 distances between grasps. In fact, the maximum number of pulls on any trial (near or far) was 3 and the minimum was 1. The average number of pulls in the near condition was 1.71 and 1.86 in the far.

Discussion

Experiment 3's results demonstrate that the systematic difference between the near and far conditions remained when the tamarins had access to only 13 cm of the tape, regardless of condition. The tape measure stopped artificially at 13 cm in both conditions, regardless of the food's location. On average, trials in the near condition continued to yield smaller distances between grasps than trials in the far condition. Five of the six participating tamarins demonstrated this trend. These results eliminate the possibility that the food presentation method or data analysis techniques used in Experiments 1 and 2 (Plexiglas disc causing an artificial stop of the tape measure) were responsible for the results. Given that the subjects continued to demonstrate smaller distances between

grasps in the near condition than in the far condition indicates that they were coordinating their pulls at the start of the trial. Because the only information the tamarins could use to distinguish the two conditions was the placement of the food, we suggest that the systematic difference between grasps reflects goal-directed planning of an action sequence.

EXPERIMENT 4: Unreinforced Probe Trials

No Physical or Visual Feedback

Experiment 4 investigated the possibility that the results from previous experiments were due to subtle, yet detectable physical differences on the tape measure across conditions (physical feedback). It is conceivable that the tamarins participating in Experiment 2 were not planning for the distance to the food, but instead were able to detect different weight and or resistance forces on the tape measure during the pulling sequence. Even though the near and far trials in Experiment 2 contained the same objects on the tape (Plexiglas disc, raisin pieces and metal weight), the Plexiglas disc and raisin were not located in the same place. The Plexiglas disc was located either close to the tamarins (13 cm) or four times as far away. While the weight of the Plexiglas disc, 2.65 grams, feels negligible to the human experimenter, the tamarins weigh between 400 and 500 grams. The weight of the disc, then, may be detectable to these small primates. The physical sensation of pulling a tape measure with a small amount of weight located near versus far may have been enough for the tamarins to use to distinguish between the two trial types in Experiment 2. If this is true, the tamarins may not have been planning their pulling sequences based on the distance to the food, but may instead have been responding to the way the tape felt as they pulled. As a result, Experiment 4's first goal was to rule out this explanation of our effect by equating the physical properties of the tape measure across near and far trials.

Even if physical feedback differences are ruled out as an explanation of the effect which would, thus, implicate planning, we have not demonstrated *when* the planning begins. The second goal of Experiment 4 was to ask when the tamarins' planning may

start in a given trial. This experiment's method combines the no-visual-feedback apparatus from Experiment 2 and unreinforced probe trials in which the tamarins see the food at a near or far location, but it is surreptitiously removed before they pull. Thus, Experiment 4's method removes all weight differences on the tape, thereby confining the difference between the near and the far condition to only one variable; where the tamarins *believe* the food is located. Any systematic differences in pulling in Experiment 4 must be due to planning. If tamarins continue to scale their pulling behavior on unreinforced probe trials with no ongoing visual feedback, we may conclude that planning began at the start of a trial.

Method

Subjects

Four female and three male captive cotton-top tamarins (*Saguinus oedipus*) participated in Experiment 4. These individuals also participated in Experiments 1, 2 and 3 prior to this experiment.

Stimuli and Apparatus

The apparatus was identical to the apparatus described in Experiment 2, except that the Plexiglas disc was not used as a food-holder and stopper on the tape during Experiment 4. In addition, marshmallows were used instead of raisins as the food reward. The tunnel used to cover the food was identical to the one used in Experiment 2.

Procedure

In Experiment 4, the location and transport procedures were identical to what was described above for Experiments 1, 2 and 3. Each 6-trial session consisted of three near and three far trials, the order of which was pseudo-randomized and counterbalanced

across individuals. Within a session, four of these trials were reinforced (monkeys could obtain and eat the food). However, two trials (one near and one far) were unreinforced probe trials. The order of these trials in the session was randomized across individuals. These 2 probe trials did not contain any food on the tape. Each tamarin only participated in one test session.

The initial procedure for Experiment 4 was similar to the procedures described above for Experiments 1, 2 and 3. The tamarin viewed the experimenter place the food on the tape at a near or far location before they were given access to the chamber. In the reinforced trials, a fresh, sticky marshmallow half was stuck securely to the tape. Once the experimenter was sure the tamarin attended to the location of the food, they covered the tape measure with the tunnel used in Experiment 2. The tamarins were then able to enter the chamber and commence pulling. In the probe trials, however, dry marshmallow halves were used. These marshmallows were dry enough that they did not stick to the tape. On these unreinforced trials, the experimenter allowed the monkey to observe the location of the food, and then surreptitiously removed the marshmallow from the tape while simultaneously lowering the tunnel over the tape measure. The monkey was only able to see the tunnel being lowered over the tape measure but could not see the hand actions behind the tunnel. The experimenter also took steps to ensure that the duration of the tunnel lowering movement was the same in reinforced and unreinforced trials. This eliminated any physical differences on the tape that could be caused by the marshmallow being located at a near versus far location. After the tunnel was placed over the tape measure, a second experimenter lifted the sliding Plexiglas door to allow the tamarins to enter the testing chamber and begin pulling. Test trials in Experiment 4 ended when the

tamarins had obtained the food (in the reinforced trials) or when the tape measure was pulled until it stopped and could be pulled no farther (in the probe trials).

Data Analysis

Data analysis procedures were similar to what was described above for Experiment 2 with distance between grasps as the variable of interest. The experimenter coded both reinforced and unreinforced probe trials. However, only data from the unreinforced probe trials were included in analysis. The experimenter coded every pull on these probe trials, but only included the pulls that contacted the tape before reaching the 'shown' food location (13 cm in the near trials, and 52 cm in the far trials). These distances between grasps were retained for analyses.

Results

Four female and three male monkeys participated in the experiment but three were excluded from analysis. One monkey was excluded due to cheating behavior (lifting curtain to view food and tape measure underneath the tunnel and two monkeys were excluded due to failure to contribute data to both near and far probe conditions. The remaining four monkeys completed one near and one far unreinforced probe trial with distance between grasp data that could be used.

This experiment was designed to collect data from 6 trials in one session, although the two trials of interest were the unreinforced probe trials. Data coding, however, revealed that two subjects only completed five (instead of six) reinforced trials that produced data. For each monkey, a single reinforced trial did not contribute data due to reaching outside of the chamber to grab the marshmallow (n=1) and lack of hand-over-hand pulling (n=1). None of the reinforced trials were included in analysis, so this did not

59

factor into our data. All four monkeys successfully completed one near and one far probe

trial with useable data. Because 33% of the trials in this condition were unreinforced,

subjects were not tested in additional sessions of this method. We wanted to avoid

extinguishing the manual pulling behavior.

A paired-samples *t*-test was conducted to compare the distance between grasps in the

near and far conditions. On average, the distance between grasps in the near condition

(*M*=5.69, *SD*=1.41) was less than the distance between grasps in the far condition

(*M*=6.99, *SD*=1.16) but this difference was not significant; *t*(3)= -1.98, *p*=.142. See

Figure 20 for graphic representation of the distance between grasps across conditions. In

addition, all four individual tamarins displayed the same trend, which can be seen in
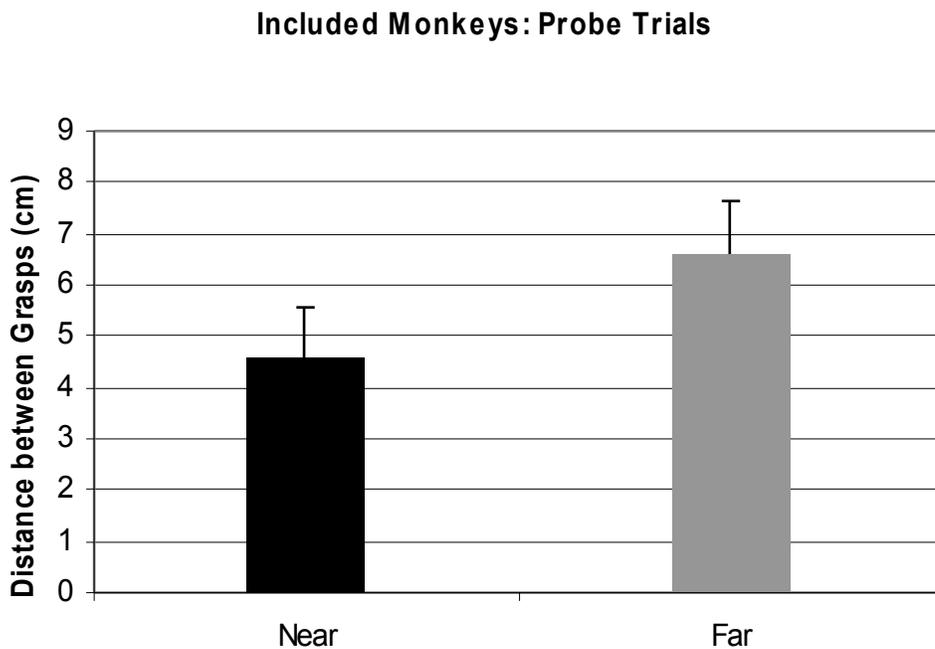
Figure 21.

Included Monkeys: Probe Trials

Figure 20. Experiment 4: Average distance between grasps in near and far conditions, on

unreinforced probe trials.
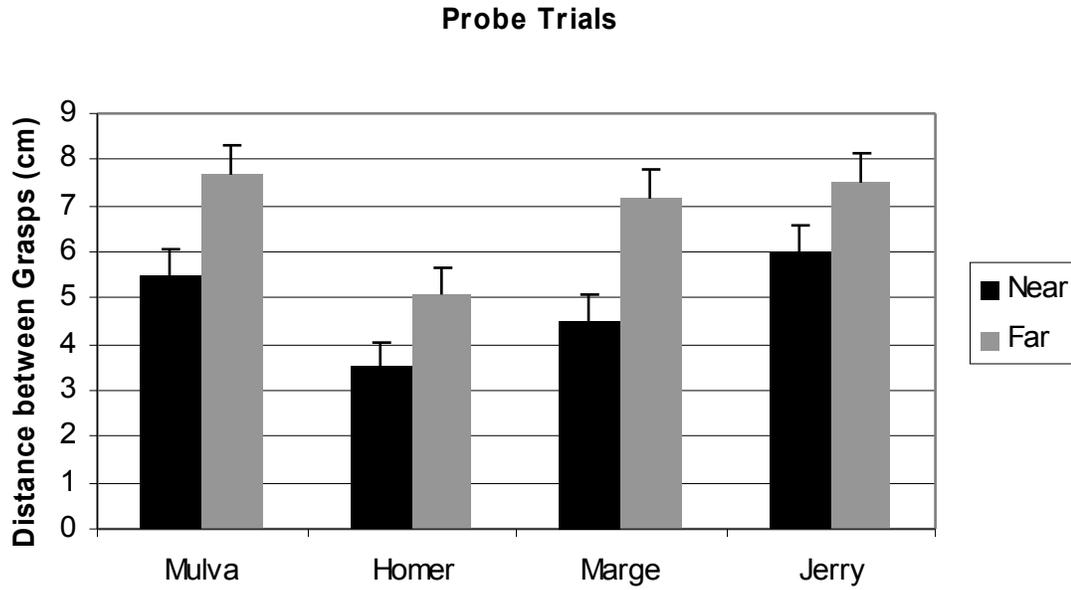
Probe Trials

Figure 21. Experiment 4: Average distance between grasps for each individual subject on unreinforced probe trials.

A paired-samples *t*-test was conducted to compare the first two data points in the near and far conditions. On average, the distance between grasps in the near condition (*M*=4.94, *SD*=1.01) was smaller than the distance between grasps in the far condition (*M*=5.44, *SD*=1.85), but this difference was not significant; *t*(3)= -.75, *p*=.509. See Figure 22 for graphic representation of the distance between grasps across conditions for the first two data points. When examining individual performance for the first two distances between grasps, 3 out of 4 monkeys demonstrated this same trend, as shown in Figure 23.

Figure 22. Experiment 4: Average distance between grasps for first two data points in near and far conditions, on unreinforced probe trials (ns).
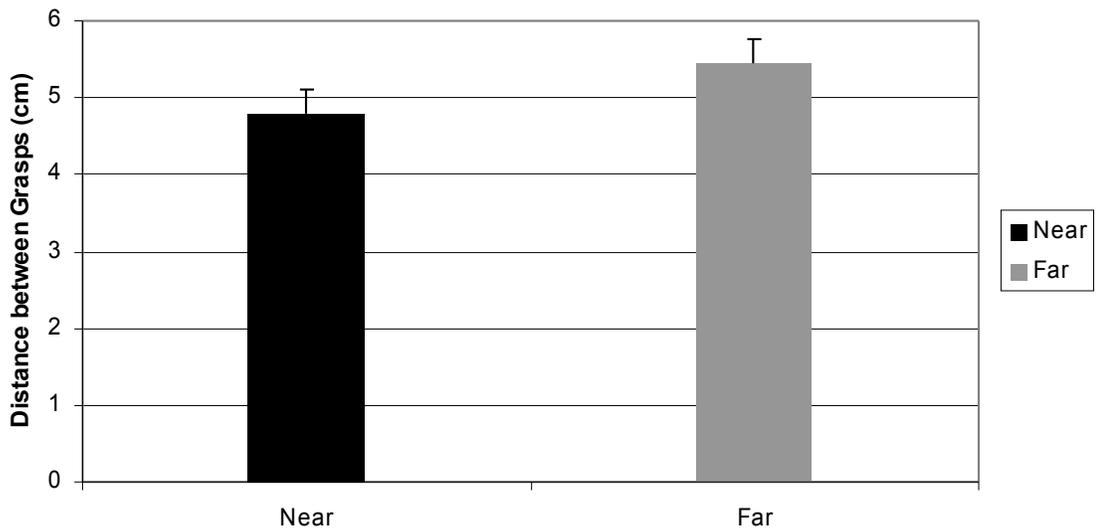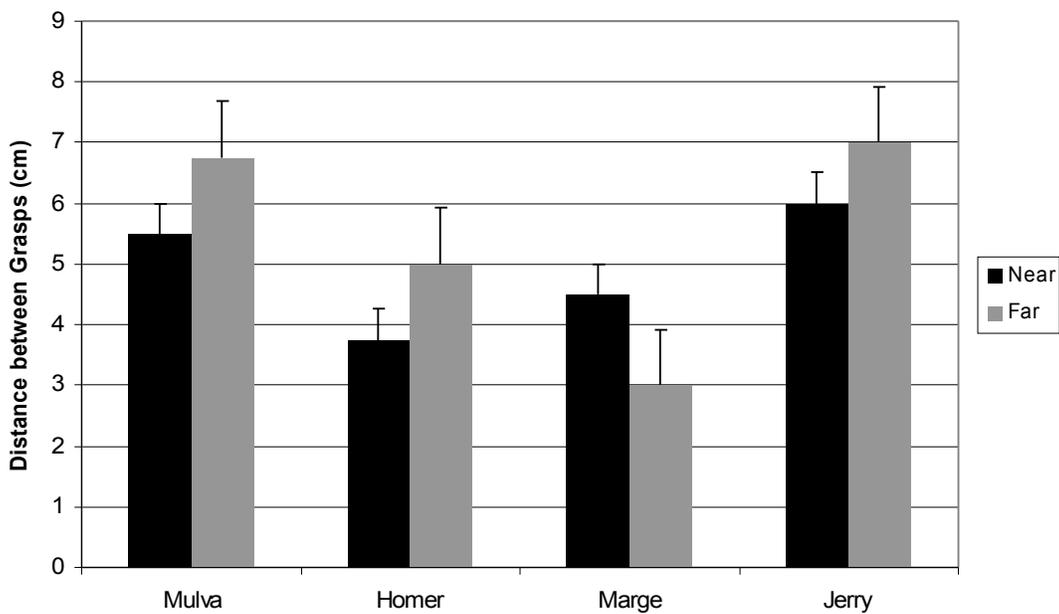

Figure 23. Experiment 4: Average distance between grasps for first two data points for each individual subject on unreinforced probe trials.

Discussion

In Experiment 4, tamarins continued to demonstrate systematic differences in the distance between grasps in the near and far condition. On unreinforced probe trials during which the tape contained no food and the tamarins could not see the tape's movement, subjects still took smaller distances between grasps in the near condition than in the far condition. All four subjects demonstrated this same pattern of performance. Importantly, the near and far conditions only varied based on where the tamarins *thought* the food was located. The near and far conditions were identical except for the location of food that the tamarin viewed prior to pulling in the absence of visual feedback. Because the food was surreptitiously removed, there was no opportunity for any subtle, detectable, weight differences on the tape at various locations to alter tamarins' pulling behavior (either consciously or subconsciously). In Experiment 4, the first two distances between grasps in the near condition did not significantly differ from the far condition. However, the trend remained (near < far) when averaged over all trials, and three out of four monkeys demonstrated the same pattern in their individual data. We hypothesize that the result was not significant due to lack of statistical power. We only had four individuals in Experiment 4, compared to 6 and 7 individuals in previous experiments. In addition, because data analysis included only probe trials, each tamarin only contributed two trials of each type instead of the four used in previous experiments. Without weight differences, and in the absence of visual feedback, the tamarins demonstrate systematic differences in their manual pulling based on where they saw the food, alone. Based on apparent trend, Experiment 4 also indicates that this planning begins at the beginning of a trial. The presence of the distance between grasps effect in Experiment 4's probe trials

replicates the same effect observed in Experiments 1, 2, and 3. We conclude that the

tamarins do not rely on physical differences to scale their behavior, and that they are

capable of multiple-action planning.

GENERAL DISCUSSION

This set of experiments was designed to ask if cotton-top tamarins can plan a coordinated sequence of actions in anticipation of a goal. The results of Experiment 1 demonstrated that tamarins' manual pulling behavior differs when the goal is near versus far, as evidenced by the tamarins scaling their pulling behavior relative to the distance to the food. That this scaling behavior was evident on the first two pulls of a trial suggests that this was not an epiphenomenon due to differences in momentum between the conditions. Experiment 2 asked if tamarins would continue to scale their pulling behavior in the absence of visual feedback. The tamarins persisted in using smaller distances between grasps in the near condition than in the far condition, and this effect was also present as of the first two distances of each trial. Thus, Experiment 2 ruled out the possibility that tamarins were modifying or updating their pulling plan based on watching the food's movement. Experiment 3 asked if the scaling effect could be explained by the tape measure's manner of stopping or by the data filtering and analysis needed due to the stopping. By equating the two conditions in terms of how far the tape measure could travel, Experiment 3's results demonstrated that tamarins continue to scale their pulling behavior (as evidenced by smaller distances between grasps when the food was near compared to far), even when they only were able to pull the initial 13 cm of tape forward. Experiment 4 asked if the scaling effect could be due to subtle physical differences on the tape due to the weight of the Plexiglas disc and food at near and far distances. Further, this experiment included the use of the no-visual-feedback method (from Experiment 2). It would not have been possible to insert unreinforced probe trials into a session with a method that allowed for visual feedback during the trial. In Experiment 2, we ruled out

the role of visual feedback on the tape as an explanation for our scaling effect, but we could not rule out the role of physical feedback from the objects' weights. Preventing both physical feedback and visual feedback in Experiment 4 allowed us to draw more certain conclusions about the tamarins' pulling behavior. On unreinforced probe trials in which the food was surreptitiously removed from the tape, tamarins continued to scale their pulling behavior according to the distance to the initial food location they had been shown. The results of Experiment 4 suggest that the tamarins are planning a set of actions in advance of a goal, and do not require *either* type of feedback in order to scale their pulls.

Taken together, the results from all experiments demonstrate that tamarins appear capable of planning for a sequence of connected actions in anticipation of a goal. While previous results from our laboratory have demonstrated that cotton top tamarins (Weiss, Wark & Rosenbaum, 2007) and various species of lemur (Chapman, Weiss & Rosenbaum, in press) are capable of planning a single action in advance, this study provides the first evidence of anticipatory multiple-action motor planning in a nonhuman primate species, to the best of our knowledge. As far as we know, this study is also the first of its kind to demonstrate planning in the context of coordinated sequences of actions on an *untrained*, laboratory task. Several studies have demonstrated that nonhuman primates are capable of learning ordinal sequences of numerals or other visual stimuli and are capable of reproducing these sequences on touch screen monitors (lowland gorillas, Ross, 2009; chimpanzees, Biro & Matsuzawa, 1999; Japanese macaques, Oshiba, 1997; rhesus macaques, Chen et al, 1997, see also Terrace, 2005). The error and latency rates observed during many of these serial ordering tasks (e.g. Ross,

2009) indicate that subjects planned for the entire list (collective strategy) instead of using an item by item strategy (serial strategy). Although the data from serial order experiments can start to inform the question of multiple-action planning, our experiments differ on a number of levels. In each of the aforementioned studies, all subjects required extensive training to learn the sequences, often resulting in hundreds or thousands of trials. The subjects appeared to plan a sequence of ordered actions, but we are not certain of the basic abilities before training. Due to these extensive training sessions, we cannot be certain that the subjects did not learn to use a collective strategy instead of a serial strategy over the course of these training sessions. Our experiments, however, tested tamarins in a spontaneous, unlearned task. The planning we found in Experiments 1 through 4 can be considered untrained behavior, especially given the small number of trials per individual, per condition. Consequently,, our results are free from the potential confound of learning a planning strategy based on experience.

In addition, our experiments provided a task that was directly connected to obtaining food. The tamarins pulled a tape measure toward them that contained food, making this task more similar to natural food processing. Primates participating in the serial ordering tasks underwent operant conditioning before any testing could occur. The subjects performed a sequence of actions (touching items on a screen) and then were given food based on their performance. Critically, regardless of how the tamarins manipulated the tape, they received food. Tamarins who pulled with their mouth, pulled with a single hand over and over again, or used hand-over –hand pulling all were reinforced with the same food reward.

Although the sequential behaviors in the serial order experiments described above were heavily trained, there is also evidence for untrained, coordinated sequences of actions when considering natural food processing behaviors in wild nonhuman primates. Various food processing behaviors observed in mountain gorillas (Byrne & Byrne, 1993) chimpanzees (Boesch & Boesch, 1990) and olive baboons (Whiten, 1998) appear to consist of sequences containing between three and eight (and potentially more) distinct actions. Critically, the actions must be performed in a specific order to yield the desired result, and some of the subsequences are repeated several times for optimality, which are thought to function as nested hierarchies. These behaviors, and their constraints (i.e., specific order of actions), appear to suggest that nonhuman primates do plan goal-directed sequences of actions without extensive training, but we cannot be sure of when the planning begins in these cases. The documented cases of food processing do not provide information to address if the primates are using feedback from the current action to modify their plan for the subsequent action. The current set of experiments provided stringent control procedures not available in wild food processing behaviors that allow us to assess when the planning started and under what conditions it appears. Our experiment also more closely represents these types of wild food processing behaviors because the behavior being examined can be considered spontaneous and does not require operant conditioning. Consequently, Experiments 1 through 4 provide data that address an area of the literature that has not yet been explored.

Evidence for multiple action planning in a non-tool using species of new world monkey also indicates that while anticipatory planning abilities may be necessary for the development of tool use, they are not sufficient. If anticipatory motor planning abilities

do serve as the cognitive underpinning of tool-use in humans (Johnson-Frey, 2004), humans and non-tool using primates are expected to vary on the scope of planning outside of the capacity to plan multiple actions as a sequence. It is possible that humans may be able to plan longer sequences of actions, or plan sequences of actions farther in advance than nonhuman primates. The current study rules out the possibility that humans and nonhumans differ in their ability to plan goal-directed sequences of actions. The scope of these sequences, however, is not yet know.

I conclude that cotton-top tamarins are capable of planning a sequence of actions in anticipation of a goal, and that this plan is not subject to modification based on visual or physical feedback over the course of the sequence. This finding may inform our understanding of the phylogeny of motor planning in primates. Because I demonstrate evidence of multiple-action advance planning in a nonhuman primate, I suggest that these abilities were present in a primate ancestor common to humans and new-world monkeys. These findings also provide evidence for anticipatory, multiple action planning in a non-tool using species of primate, demonstrating that this type of planning is not unique to tool-using species alone.

Future Directions

Despite the stringent control procedures employed in Experiments 2, 3 and 4, unanswered questions remain from this experiment. Future studies should be designed to address how far in advance (temporally) nonhuman primates can plan a sequence of actions, and how many actions can be planned in a sequence. We are also interested in examining the role of precision in this type of multiple-action planning. In Experiments 1 through 4, the tamarins were not required to use precision in their pulling behavior; they

received the food regardless of how they pulled (with the exception of unreinforced trials). It is valuable to consider whether precision requirements for a given action, or set of actions, alters the planning observed. The serial ordering tasks and food processing tasks discussed above require ordinal precision. The ordering tasks, in particular, required that subjects learn each element's order in relationship to an entire sequence of other elements. In order to be rewarded, their sequence required precision of element selection on the screen. In natural food processing, order of the separate action elements was more flexible, but still required some ordinal precision. For example, in the case of wild celery processing by gorillas, the outer casing must be removed before any of the internal pith can be eaten (Byrne, 1995). Our tape-measure pulling task did not require ordinal precision. The tamarins could complete any number of behaviors related to the tape measure, and assuming they brought the tape forward, they would obtain the food reward. One could envision a task in which tamarins had to pull several ropes in a specific order to obtain a food reward. This type of experiment could inform what we know about ordinal precision in tamarins' multiple-action planning behavior.

Future studies could also address the physical precision requirements of the final movement in a task. In our experiments, the tamarins obtained the food via pulling regardless of how their final pull was performed. The food arrived at the hole in the testing chamber as long as the tamarins pulled the entire length of tape between their bodies and the food. No manual precision was required; the tamarins were not required to pull carefully on any of the pulls, nor the final pull. We could examine whether imposing a precision requirement on the final action may change their multiple-action planning. Rosenbaum (in review) recently examined step length as human adults walked across a

room towards a target on the ground. This task required precision in the final movements, as participants needed to end their last step directly on the target. Rosenbaum found that the step lengths decreased as they neared the target, which appears to be a form of scaling similar to what we observed with our tamarins' pulling behavior. In this case, step length is analogous to distance between grasps as measured in the current experiments. One could ask if tamarins, like humans, show a decrease in distance between grasps if they are required to end their final pull in a precise manner (i.e. stop pulling before the tape passes a certain point). If tamarins do show this decrease in distance between grasps, then we could conclude that they are able to plan for a final action in the context of multiple-action planning.

The findings from Experiments 1 through 4 could also be expanded to include various types of actions instead of a single class of action. Our experiments required tamarins to pull a tape measure forward, and while we did not restrict how they accomplished this task, they tended to use manual grasps to pull. The serial ordinality experiments also required a single action; touching a computer monitor with a hand or a finger. .However, the naturalistic food processing behaviors observed in wild primates tend to include sequences of different actions. For example, olive baboons use the following actions when processing a sedge: yank, hold, remove, drop, and so on (Whiten, 1998). By testing tamarins on a task that involves them to perform multiple *types* of action in a sequence, we may learn more about the scope of their ability to plan coordinated sequences in advance. For example, to create a task comparable to food processing requirements, one could ask tamarins to pull a tape measure to gain access to a box, which would then require them to open a lid, reach in, and grasp a food item. This type of sequence would

require not only multiple types of actions, but would also address the idea of ordinal precision, as the tape would need to be pulled before they could open the box.

Future studies should also include various species of primate to determine if the same scaling behavior is noted in all groups. It may be valuable to examine both humans and prosimians, as these two groups span the entirety of evolutionary time for extant primates. A final consideration would be to examine how ontogeny factors into this type of planning. Investigating anticipatory, multiple action planning in developing humans and nonhuman primates may inform our understanding of the ontogenetic trajectory of these motor planning abilities. As discussed above, the developmental trajectory of motor planning, as indexed by the end-state comfort effect, appears to be very protracted in children. Human infants display evidence of some motor planning in inhibition of dominant hand reaches as early as 12 months (Claxton et al., 2003, McCarty et al., 1999), but children do not appear to show end-state comfort in grasping behaviors at an adult level until roughly 9 years of age (Stoeckel et al., 2009). This finding is in striking contrast to the recent evidence of end-state comfort in a developing, 4-month old infant lemur (Chapman, Weiss & Rosenbaum (in press). While this infant lemur did not show end-state comfort at the same level as adult lemurs, and her manual actions were clumsy, she did act in accordance with end-state comfort on two out of three test trials. This was the first evidence, to our knowledge, documenting anticipatory motor planning in a developing nonhuman primate. Future studies should address why the ontogenetic development of motor planning in humans is both early and protracted, whereas some anticipatory planning skills indexed by the end-state comfort effect are present in infant nonhuman primates. Because the ontogeny of motor planning in nonhuman primates is

remains largely unknown, studying single- and multiple-action planning in these primates

may inform our understanding of this trajectory, both in humans and nonhumans

REFERENCES

Adalbjornsson, C.F., Fischman, M.G., & Rudisill, M.E. (2008) The end-state comfort effect in young children. *Research Quarterly for Exercise and Sport,* 79, 36-41.

Adolph, K. E. (2008). The growing body in action: What infant locomotion tells us about perceptually guided action. In R. Klatzky, M. Behrmann, & B MacWhinney (Eds.), *Embodiment, ego-space, and action* (pp. 275-321). Mahwah, NJ: Erlbaum.

Adolph, K.E. & Berger, S.E. (2006). Motor Development. In W. Damon & R. Lerner (Series Eds.) & D. Kuhn & R.S. Siegler (Vol. Eds.) *Handbook of Child Psychology: Vol 2: Cognition, Perception, and language (6th ed.)* (pp 161-213). New York: Wiley.

Biro, D. & Mastuzawa, T. (1999). Numerical ordering in a chimpanzee (*Pan troglodytes*): Planning, executing, and monitoring. *Journal of Comparative Psychology, 113,* 178-185.

Bishop, A. (1962) Control of the hand in lower primates. *Annals of the New York Academy of Science*, 102, 316-337.

Boesch, C. & Boesch, H. (1990). Tool use and tool making in wild chimpanzees. *Folia Primatologica, 54,* 86-99.

Byrne, R.W. (1995*). The thinking ape*. Oxford, England: Oxford University Press.

Byrne, R.W., & Byrne, J.M.E. (1993). Complex leaf-gathering skills of mountain gorillas (*Gorilla g. beringei*): Variability and standardization. *American Journal of Primatology, 31,* 241-261.

Chapman, K.M., Weiss, D.,J., & Rosenbaum, D.A. (in press). The evolutionary roots of motor planning: The end-state comfort effect in lemurs. Jo*urnal of Comparative Psychology.*

Chen, S., Swartz, K.B., Terrace, H.S. (1997). Knowledge of the ordinal position of list items in rhesus monkeys. *Psychological Science, 8*, 80-86.

Claxton, L.J., Keen, R., & McCarty, M.E. (2003). Evidence of motor planning in infant reaching behavior. *Psychological Science,* 14, 354-356.

Cohen, R. G. & Rosenbaum, D. A. (2004). Where objects are grasped reveals how grasps are planned: Generation and recall of motor plans. *Experimental Brain Research, 157*, 486-495.

Conway, C.M. & Christiansen, M.H. (2001). Sequential learning in non-human primates. *TRENDS in Cognitive Sciences, 5,* 539-546.

Drew, G. C. (1939). The speed-of-locomotion gradient and its relation to the goal gradient. *Journal of Comparative and Psychology, 27*, 333-372.

Ebbinghaus, H. (1964). *Memory: A contribution to experimental psychology*, New York, New York: Dover.

Glaser, B., Myrtek, D., Rumpler, Y., Schiebel, K., Hauwy, M., Rappold G.A., & Schempp, W. (1999). Transposition of SRY into the ancestral psuedoautosomal region creates a new psuedoautosomal boundary in a progenitor of simian primates. *Human Molecular Genetics, 8*, 2071-2078.

Greenfield, P.M., Nelson, K., & Saltzman, E. (1972). The development of rulebound strategies for manipulating seriated nesting cups: a parallel between action and grammar. *Cognitive Psychology, 3*, 291-301.

Hughes, C. (1996). Planning problems in autism at the level of motor control. *Journal of Autism and Developmental Disorders,* 26, 101-109.

Hull, C. (1934). The rat's speed-of-locomotion gradient in the approach to food. *Journal of Comparative and Psychology, 41*, 393-422.

Johnson-Frey, S.H. (2004). The neural bases of complex tool use in humans. *Trends in Cognitive Sciences*, 8, 71–78.

Johnson-Pynn, J., Fragaszy, D.M., Hirsh, E.M., Brakke, K.E., & Greenfield, P.M. (1999). Strategies used to combine seriated cups by chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*) and capuchins (*Cebus apella*). *Journal of Comparative Psychology, 113*, 137-148.

Jolly, A. (1964). Prosimian's manipulations of simple object problems. *Animal Behavior,* 12, 560-570.

Martenluk, R.G., MacKenzie, C.L., Jeannerod, M., Athenes, S., & Dugas, C. (1987). Constraints on human arm movement trajectories. *Canadian Journal of Psychology, 41*, 365-378.

Matsuzawa, T. (1985). Use of numbers by a chimpanzee. *Nature, 315*, 57-59.

McCarty, M.E., Clifton, R.K., Collard, R.R. (1999). Problem solving in infancy: The emergency of an action plan. *Developmental Psychology,* 35, 1091-1101.

McCarty, M.E., Clifton, R.K., Collard, R.R. (2001). The beginnings of tool use by infants and toddlers. *Infancy,* 2, 233-256.

McCarty, M.E. & Keen, R. (2005) Facilitating problem-solving performance among 9- and 12- month old infants. *Journal of Cognition and Development, 6*, 209-228.

Oshiba, N. (1997). Memorization of serial items by Japanese monkeys, a chimpanzee, and humans. *Japanese Psychological Research, 39*, 236-252.

Rosenbaum, D. A., Cohen, R. G., Meulenbroek, R. G., & Vaughan, J. (2006). Plans for grasping objects. In M. Latash & F. Lestienne (Ed.), *Motor Control and Learning Over the Lifespan* (pp. 9-25). New York: Springer.

Rosenbaum, D. A. (in review). Stepping onto targets. *Experimental Brain Research.*

Rosenbaum, D.A., Halloran, E.S., & Cohen, R.G. (2006). Grasping Movement Plans. *Psychonomic Bulletin and Review, 13*(5), 918-922.

Rosenbaum, D. A., Marchak, F., Barnes, J., Vaughan, J., Slotta, J., & Jorgensen, M. (1990). Constraints for action selection: Overhand versus underhand grips. In M. Jeannerod (Ed.), *Attention and performance XIII*, (pp. 321–342). Hillsdale, NJ: Lawrence Erlbaum Associates.

Rosenbaum, D.A., van Heugten, C.M., & Caldwell, G.E. (1996). From cognition to biomechanics and back: the end-state comfort effect and middle-is-faster effect. *Acta Psychologica, 94*, 59-85

Ross, S.R. (2009). Sequential list-learning by an adolescent lowland gorilla (*Gorilla gorilla gorilla*) using an infrared touchframe apparatus. *Interaction Studies, 10*, 115-129.

Santos, L.R., Rosati, A., Sproul, C., Spaulding, B., & Hauser, M.D. (2005). Means-end tool choice in cotton-top tamarins (*Saguinus oedipus*): Finding the limits on primates' knowledge of tools. *Animal Cognition, 8,* 236-246.

Smyth, M.M. & Mason, U.C. (1997). Planning and execution of action in children with and without developmental coordination disorder. *Journal of Child Psychology and Psychiatry, 38*, 1023-1037.

Stoeckel, T., Weigelt, M., Beeger, H., & Schack, T. (2009, June). The developmental nature of representing comfortable end-states in long-term memory. Paper presented at the meeting of the International Society of Sport Psychology (ISSP), Marrakesh, Morocco.

Terrace, H. (2005). The simultaneous chain: a new approach to serial learning. *TRENDS in Cognitive Sciences, 9,* 204-210.

Weigelt, M. & Schack, T. (in press). The developmental nature of the end-state comfort effect in pre-school children. *Experimental Psychology.*

Weiss, D. J., Wark, J. D., & Rosenbaum, D. A. (2007). Monkey see, monkey plan, monkey do: The end-state comfort effect in cotton-top tamarins (*Saguinus oedipus*). *Psychological Science,* 18, 1063-1068.

Weiss, D.J. & Wark, J.D. (2009). Hysteresis effects in a motor task with cotton-top tamarins (*Saguinus oedipus*). *Journal of Experimental Psychology: Animal Behavior Processes, 35*, 427- 433.

Whiten, A. (1998). Imitation of the sequential structure of actions by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology, 112*, 270-281.

Yoder, A. (2007). Lemurs. *Current Biology,* 17, R866-R868.