

FACTORS AFFECTING SPATIAL ABILITIES OF  
CAPTIVE WESTERN LOWLAND GORILLAS:  
AGE, GENDER, AND EXPERIENCE

A Dissertation  
Presented to  
the Academic Faculty

By

Christopher W. Kuhar

In Partial Fulfillment  
of the Requirements for the Degree  
Doctor of Philosophy in the  
School of Psychology

Georgia Institute of Technology  
December, 2004

Factors Affecting Spatial Abilities of  
Captive Western Lowland Gorillas

Approved by:

Dr. Terry L. Maple, Advisor  
School of Psychology

Dr. M. Jackson Marr  
School of Psychology

Dr. Anderson D. Smith  
School of Psychology

Dr. Mollie A. Bloomsmith  
Georgia Institute of Technology, Center for  
Conservation and Behavior

Dr. James G. Herndon  
Yerkes National Primate Research Center

Dr. Tammie L. Bettinger  
Disney's Animal Kingdom

Date Approved:  
October 25, 2004

## ACKNOWLEDGEMENTS

It is with great appreciation that I acknowledge the contributions of many individuals. I thank my academic advisor Dr. Terry Maple for the opportunities afforded me throughout my graduate school career at Georgia Tech. Additionally, I acknowledge the participation of my dissertation committee: Drs. Jack Marr and Andy Smith of the Georgia Tech Department of Psychology, Dr. Mollie Bloomsmith of the Georgia Tech Center for Conservation and Behavior, Dr. Jim Herndon of Yerkes National Primate Research Center, and Dr. Tammie Bettinger of Disney's Animal Kingdom.

I acknowledge the assistance of Dr. Dwight Lawson, Charles Horton, Bernie Gregory, Jody Kissinger, and Kristina Krickbaum at Zoo Atlanta without whose patience and cooperation this study could not have been completed at Zoo Atlanta. I thank Joe Christman, Hollie Colahan, Rebecca Sellin, Beth Richards, Linda Cory, Monica Chaplin, Wendy Crofut, and the entire Primate Team at Disney's Animal Kingdom who accepted an unusual research idea with enthusiasm and enabled me to complete the task.

It is with extreme gratitude that I thank Pei Sun for her assistance in data collection. Without her help, I could not have completed this study. I thank my fellow lab mates, past and present, which made the graduate school experience one of the best periods of my life, even in the bad times. I thank my parents and family for teaching me that something is worth achieving if you want it bad enough, even when it's hard. Finally, I thank my best friend Gayle Albers who started this journey as my friend and completed it as my wife. Without her support I surely would have failed.

## TABLE OF CONTENTS

|   |      |
|---|------|
| Acknowledgements  | iii  |
| List of Tables  | vi   |
| List of Figures   | vii  |
| Summary   | viii |
| Chapter 1 Age-related Differences in Human and Nonhuman Memory                          | 1    |
| 1.1 Human Cognitive Aging Research  | 2    |
| 1.2 Nonhuman Cognitive Aging Research   | 6    |
| 1.2.1 Rats  | 6    |
| 1.2.2 Nonhuman Primates   | 8    |
| 1.2.3 Ape Research  | 14   |
| Chapter 2 The Delayed Response Task in the Gorilla: Age, Gender, and Experience Effects | 17   |
| 2.1 Introduction  | 17   |
| 2.2 General Methods   | 20   |
| 2.2.1 Subjects  | 20   |
| 2.2.2 Behavioral Testing  | 20   |
| 2.2.3 Data Collection and Analysis  | 24   |
| 2.3 Experiment One: Zero-Second Delay   | 25   |
| 2.3.1 Methods   | 25   |
| 2.3.2 Results   | 27   |
| 2.3.3 Discussion  | 29   |
| 2.4 Experiment Two: One-Second Delay  | 30   |
| 2.4.1 Methods   | 30   |
| 2.4.2 Results   | 32   |
| 2.4.3 Discussion  | 35   |
| 2.5 Experiment Three: Five-Second Delay   | 36   |
| 2.5.1 Methods   | 36   |
| 2.5.2 Results   | 37   |
| 2.5.3 Discussion  | 40   |
| 2.6 Experiment Four: Increasing Delay Intervals   | 41   |
| 2.6.1 Methods   | 41   |
| 2.6.2 Results   | 44   |
| 2.6.3 Discussion  | 49   |
| 2.7 Experiment Five: Increasing Choice Sites  | 51   |
| 2.7.1 Methods   | 52   |
| 2.7.2 Results   | 54   |

|   |    |
|---|----|
| 2.7.3 Discussion                          | 59 |
| 2.8 General Discussion                    | 59 |
| 2.8.1 Impact of Experience and Gender     | 60 |
| 2.8.2 Impact of Age                       | 61 |
| 2.8.3 The Delayed Response Task           | 62 |
| 2.8.4 Response Rigidity and Perseveration | 66 |
| 2.9 Conclusions                           | 67 |
| Appendix A: Tables                        | 69 |
| References                                | 78 |

## LIST OF TABLES

|         |  |    |
|---------|--|----|
| Table 1 | Demographic Attributes of Subjects   | 70 |
| Table 2 | Regression Results for Experiment One Examining Trials to Criterion and Errors to Criterion  | 71 |
| Table 3 | Regression Results for Experiment Two Examining Trials to Criterion and Errors to Criterion  | 72 |
| Table 4 | Regression Results for Experiment Three Examining Trials to Criterion and Errors to Criterion  | 73 |
| Table 5 | Repeated-measures ANOVA Results for Experiment Four Examining Within-subjects Effects of Delay Interval and Between Subjects Effects of Age, Gender, and Experience on Performance         | 74 |
| Table 6 | Regression Results from Experiment Four Examining the Effects of Age, Gender, and Experience on Side Bias  | 75 |
| Table 7 | Repeated-measures ANOVA Results for Experiment Five Examining Within-subjects Effects of Number of Choice Sites and Between Subjects Effects of Age, Gender, and Experience on Performance | 76 |
| Table 8 | Repeated-measures ANOVA Results for Experiment Five Examining Within-subjects Effects of Number of Choice Sites and Between Subjects Effects of Age, Gender, and Experience on Side Bias   | 77 |

## LIST OF FIGURES

|           |   |    |
|-----------|---|----|
| Figure 1  | Diagrammatic Representation of the Trays of the Modified WGTA   | 23 |
| Figure 2  | Plots of the Relationship between Age and Performance in Experiment One for Trials to Criterion and Errors to Criterion   | 28 |
| Figure 3  | Plots of the Relationship between Age and Performance in Experiment Two for Trials to Criterion and Errors to Criterion   | 34 |
| Figure 4  | Plots of the Relationship between Age and Performance in Experiment Three for Trials to Criterion and Errors to Criterion | 39 |
| Figure 5  | Performance as a Function of Increasing Delay Intervals in Experiment Four  | 45 |
| Figure 6  | Performance as a Function of Age for 30-, 60-, and 90-sec Delay Intervals in Experiment Four                              | 46 |
| Figure 7  | Side Bias as a Function of Age in Experiment Four with All Subjects Represented   | 47 |
| Figure 8  | Side Bias as a Function of Age in Experiment Four with only Inexperienced Subjects Represented                            | 48 |
| Figure 9  | Performance as a Function of the Number of Potential Choice Sites in Experiment Five                                      | 56 |
| Figure 10 | Performance as a Function of Age for 2, 3, and 4 Choice Sites in Experiment Five  | 57 |
| Figure 11 | Side Bias as a Function of Age in Experiment Five with All Subjects Represented   | 58 |

## SUMMARY

With the increase in research on age-related declines in human cognitive capabilities has come an increased demand for a nonhuman cognitive aging model that controls for confounds in the human research, including education, socio-economic class, and language abilities. A nonhuman primate model of cognitive aging is particularly attractive given the similarities in physiology and behavior between nonhuman primates and humans. The rhesus macaque has proven to be a highly effective model of human aging, but apes, the closest genetic relatives to humans, are virtually unstudied. Only three studies have examined age-related changes in cognitive abilities in apes, and all three studies were conducted using tasks that have had relatively little success in revealing age-related performance decline in monkeys. Sixteen gorillas housed at Zoo Atlanta and Disney's Animal Kingdom underwent five experiments to determine the effects of age, gender, and previous research experience on performance. When delay intervals were increased from zero to 90 seconds performance decreased in a two choice delayed response task. However, there was no effect of age, gender, or experience. Similarly, when the number of potential choice sites was increased from two to four there was a decrease in performance, but again there was no effect of age, gender, or experience. However, older subjects were more likely to have a response bias and choose a single side, irrespective of where the reward was located. This effect was more pronounced in inexperienced subjects. As a result, age does not appear to affect performance accuracy in the delayed response task in gorillas, but there may be an effect on response rigidity. Further research on cognitive aging in gorillas should utilize a

research naïve population and use a titrated experimental protocol to gradually increase delay intervals to a point where age-related differences are apparent.

## CHAPTER 1

### AGE-RELATED DIFFERENCES IN HUMAN AND NON-HUMAN MEMORY

“This increase in the life span and in the number of our senior citizens presents this Nation with increased opportunities: the opportunity to draw upon their skill and sagacity – and the opportunity to provide the respect and recognition they have earned. It is not enough for a great nation merely to have added new years to life – our objective must also be to add new life to those years.”

- John F. Kennedy, 1963

Over forty years ago, John F. Kennedy spoke to the U.S. Congress on the needs of the senior citizens in the United States. Forty years have magnified the importance of those words. The average life expectancy has increased by nearly ten years to 77.2 (Arias & Smith, 2003) since President Kennedy spoke to the needs of increasing the quality of life for senior citizens. The increase in life expectancy, along with the slow march of baby boomers to old age fuels a demand for information on aging.

Many issues have been explored since Kennedy urged Congress to not only explore the opportunities that an aged population provides, but aid them in their later years. Aging and the aging population have caught the attention of the academic community in a variety of disciplines. The questions examined over the decades have ranged from the biological causes and interventions of aging to the psychological effects and the sociological and economic impacts of an aging population. The literature from each of the disciplines is vast. As a result of the interest in the aging mind and body,

psychology has evolved a sub-discipline: cognitive aging. In fact, cognitive aging research had developed even further into subdisciplines focusing on attention, memory, language, emotion, social cognition and metacognition (Craik & Salthouse, 2000). Of these, memory remains a focus and has been the dominant subject of presentations at the Cognitive Aging Conference since 1987 (A.D. Smith, personal communication, 2002).

The interest in aging and memory is not surprising given the popular opinion that older adults are prone to forgetfulness and memory lapses. However, upon examination the relationship is less straightforward. Each type of memory, i.e. declarative, implicit, sensory, is affected differently by aging and many other factors can moderate these effects. As a result, the study of aging and memory in humans is a vigorous field, with various research groups tackling a different set of variables using a particular methodology. In fact, to control for the large number of human demographic variables, some researchers have undertaken studies on nonhumans, primarily rodents and primates, to help untangle the factors. While this research has been productive, no strict evolutionary relationship between cognitive decline and aging has been found. An overview on aging and memory research is presented here, with particular emphasis on the evolutionary relationship between humans and non-humans and the explanatory power of non-human studies.

### **Human Cognitive Aging Research**

One of the largest sub-disciplines in the field of gerontology has been cognitive aging. Many older adults have reported increased memory failures with increased age. As a result, much research has been conducted on aging and memory. Today, the study of age-related changes in memory dominates cognitive aging research.

Colloquially, memory is viewed as a single entity, but in fact, memory is not a single entity or process, but actually a multi-faceted phenomenon (Graf & Schacter, 1985; Baddeley, 1986). Human memory has conceptually been divided into sensory, short-term or working memory, and long-term memory. Dissociations between these types, and their neurological substrates provide support for these divisions. The effects of aging have been explored for each of these memory types.

Overall there is research on the relationship between sensory memory and age (Whitbourne, 2001). While older adults may be limited in the information they are able to process due to deterioration of the sensory modalities, the information that enters the sensory store is just as accessible for older adults as it is for younger adults and decays at essentially the same rate. However, recent research has implied that older adults may be limited in their short-term memory span (Verhaeghen, Marcoen, & Goosens, 1993). Research on short-term, or working memory, has shown many more age-related differences than seen with sensory memory. Older adults are impaired in the amount of material they are able to hold in working memory (Salthouse & Babcock, 1991), particularly when that information needs to be manipulated or processed (Engle, Cantor, & Carullo, 1992). Research on long-term memory is divided between implicit and explicit memory. Whereas tasks of explicit declarative memory show age differences, implicit memory, as measured by repetition priming tasks reveal few age-related differences (Howard & Howard, 1989).

Many theories have been proposed to explain these memory differences. Some have postulated that aged individuals are deficient in some resource, such as working memory or attention (Hasher & Zacks, 1979), or are limited by a lack of environmental

support (Craik, 1983; 1986; Craik & Byrd, 1982). Others have suggested that age-related differences are caused by a decrease in cognitive processing speed (Cerella, 1985; Salthouse, 1991; 1996). Older adults with decreased processing speed show a general slowing of information processing and as a result sensory input is encoded or processed more slowly than in younger adults. Thus, information is not available to be used by a later process or there may not be enough time to complete the component processes of cognitive function when there are time constraints associated with the task.

Alternatively, it has been suggested that older adults are not able to inhibit responses or attention and as a result more information, even information that is irrelevant to the task, is encoded (Hasher & Zacks, 1988; Zacks & Hasher, 1994; 1997). The excess of goal irrelevant information in working memory prevents efficient processing and results in memory errors.

Despite disagreements over the source of cognitive decline, one thing is certain: cognitive decline is much less structured than cognitive development. Whereas cognitive development follows a standard trajectory, advancing age does not guarantee cognitive decline and many older adults perform at or above the level of younger adults (Craik, Byrd, & Swanson, 1987; Shimamura, 1993). Consistent patterns of age-related decline are not always evident. As a result, chronological age is merely a proxy for the aging phenomenon. Some individuals are more affected by age and show the signs of aging, mentally and physically, much earlier than other individuals. Therefore, chronological age, in and of itself, is not indicative of cognitive decline.

If not chronological age, what then can be used to predict cognitive decline?

With an increased focus on cognitive aging, why haven't the questions associated with

the phenomenon been answered? Many other factors including genetics and ontogenetic differences can have a strong impact on the aging process. Derenne and Baron (2002) have proposed that developmental factors, including diet, exercise, education, socio-economic status, medications, drug and alcohol use, hobbies, etc., have the largest impact on cognitive aging. Without controlling for these factors, we are unable to learn much about aging, its causes, or its impacts.

It is precisely this lack of control over developmental experiences that fueled the meteoric rise to psychological superstardom of the laboratory rat and pigeon in the early part of the 1900s. The behaviorist school of psychology emphasized the importance of a homogeneous rearing environment and the use of laboratory animals to uncover basic processes of learning and memory that could be applied to humans in a much more heterogeneous environment. The potential control over developmental phenomena in captive animals allows for these phenomena to be factored out and general rules of psychology to be developed and applied. Because aging in humans can be influenced by life experiences some have called for the development of animal models of aging (Elias & Elias, 1976; Gallagher & Rapp, 1997; Lane, 2000). These models would be advantageous in that education, hobbies, socio-economic status, drug use, gender roles, etc. would not effect performance. Additionally, a non-human model possesses many advantages for neurobiological analyses, including surgical alteration studies, short post-mortem delays for tissue analysis, and no inclusion of undiagnosed Alzheimer's patients in aged samples (Peters et al., 1996; Gallagher & Rapp, 1997).

## **Non-human Cognitive Aging Research**

The superiority of the human species has been in question since the writings of Darwin, who attempted to demonstrate the continuity between animal species and humans. While humans stand alone in their ability to change and control their environment, the uniqueness of the species is less obvious when compared to non-human primates, particularly the great apes with whom humans share many derived as well as conserved characteristics (Erwin, Hof, Ely, & Perl, 2002). This fact, along with an explosion in research examining the psychological aging process in humans over the past two decades (i.e. Baltes, 1987), has inspired non-human research that attempts a comparative assessment of aging.

### Rats

Research on non-humans has focused on spatial abilities for two reasons: 1) spatial abilities are paramount to the success of every living organism and may be evolutionarily selected for, and 2) specific methodologies have been developed to assess spatial abilities in those that do not possess language skills (i.e. Morris, 1981; Spetch & Edwards, 1986). Early research found age-related differences in maze performance of laboratory rats, but these differences were often attributed to response rigidity or the complexity of the task (Goodrick, 1975). However, as multiple strategies for spatial navigation were defined, it became clear that aged rats were impaired in a type of learning known as place learning. Place learning relates to the concept of cognitive maps, and is a flexible form of learning that allows an animal to navigate to a goal from a number of novel starting positions (O'Keefe & Nadel, 1978). Aged rats are impaired not only in the acquisition of tasks that require place learning (Barnes, McNaughton, &

O'keefe, 1983; Gage, Dunnett, & Bjorklund, 1984), but rely on local cues instead of place cues when motor strategies are ineffective (Rapp, Rosenberg, & Gallagher, 1987).

In recent years, research on spatial memory decline in the aged rat has shifted toward specific aspects of the tasks that impact performance, such as delay interval (Dunnett, Evenden, & Iversen, 1988), attention deficits (Muir, Fischer, & Bjorklund, 1999), or strain effects (Wyss, Chambless, Kadish, & van Groen, 2000). More prominently, there has been an emphasis on age-related declines and physiologic changes, such as neural deterioration (i.e. Poe, Teed, Insel, White, McNaughton, & Barnes, 2000; Rogers, Zornetzer, Bloom, & Mervis, 1984). While the use of the rat model has proved effective as a neurological aging model, other interesting findings have developed from the rat research.

Rats are often used for comparative research because they are relatively easy to care for, but they are often held in small enclosures with a minimal amount of stimulation and resources. Research has revealed that isolated rats lived approximately 20% shorter lives than their counterparts housed in social conditions (Menich & Baron, 1984). Additionally, enrichment provided to middle aged rats has been shown to decrease age-related impairment in spatial memory (Frick, Stearns, Pan, & Berger-Sweeney, 2003). Indeed, rearing history, social housing, and general motivational differences have been noted to impact the performance of aged rats on spatial task and their impact must be assessed before statements about the impact of aging can be made (van der Staay, 2002). Given the environmental condition in which many laboratory rats are kept one must consider the number of observed age-related detriments that can be attributed to lack of social or environmental stimulation and not natural aging effects. Many of the findings

with rats may be attributed to a general lack of stimulation or the interaction between the sterile environment and age.

In addition to shortcomings in how captive rats are housed, the laboratory rat lacks physiological and behavioral similarity to humans, and some have called for increased aging research on non-human primates in order to bridge the developmental gap between rats and humans (Erickson & Barnes, 2003). Non-human primates share many more features, behaviorally, anatomically and in terms of lifespan, with human than do rats. One of the criticisms of non-human models of aging is that they often use tasks, such as the Morris water maze, that are not directly comparable to tasks used with humans. The behavioral repertoire and neurological development of rats is such that they are unable to perform many of the same tasks as humans and, while informative, the results are not directly comparable. Alternatively, non-human primates share morphological features at the cortical and sub-cortical level, and there is a tremendous amount of research on CNS lesions and the resulting structure-function relationships. Thus, while the rat model of aging has been informative, the non-human primate model may be more effective due to the higher degree of similarity between them and humans.

### Nonhuman Primates

The majority of the cognitive aging research on non-human primates has focused on the rhesus macaque, primarily due to its availability in the national primate research centers (Roberts, 2002). Rhesus macaques have been tested for age-related deficits in a variety of cognitive components, but the most commonly tested is recognition memory. Recognition memory is a broad term encompassing all tasks in which subjects are required to choose between stimuli based on their ability to “recognize” or “remember” a

previously presented stimulus. There are a number of tasks designed to measure recognition memory and, depending on the design of the task, these tasks assess different components of memory.

The type of recognition memory most closely related to long-term or declarative memory in humans is centered in the medial temporal lobe. This area has been implicated in anterograde amnesia in humans (Corkin, 1984), and is thought to be involved in long-term retention of new material (Gallagher & Rapp, 1997; Squire, 1992). Many lesioning studies have been conducted on monkeys to explore the role of particular medial temporal regions, particularly the hippocampus, in memory (Alvarez, Zola-Morgan, & Squire, 1995; Wilner, Otto, Gallagher, & Eichenbaum, 1993; Zola-Morgan, Squire, & Amaral, 1989). The most commonly used behavioral test with lesioning studies is the delayed non-matching-to-sample task (DNMS).

The DNMS contains not only a memory component, imparted by the delay interval, but also a discrimination and learning component. The subject must learn the relationship between the sample and the choice stimuli, remember the item to be avoided (the sample) over the delay interval, and discriminate between the choice stimuli to make a correct selection. As a result, aging studies have examined all portions of this task. For example, while examining discrimination learning, Voytko (1999) found that older monkeys required more trials to learn object discriminations, and made more errors in learning pattern discriminations. However, Voytko (1999) and others found no age differences in the ability to learn spatial discriminations (Bachevalier et al., 1991; Lai, Moss, Killiany, Rosene, & Herndon, 1995; Rapp, 1990). Thus, it appears that older

animals are capable of learning spatial discriminations as well as younger animals, but they may be impaired in the learning of pattern and object discriminations.

Given that there may be age-differences in the acquisition of a discrimination task, subjects in a DNMS task are trained to a discrimination criterion prior to the manipulation of delay intervals. While some studies have shown age-related differences in the acquisition of DNMS (Herndon, Moss, Rosene, & Killiany, 1997; Herndon, Lacreuse, Ladinsky, Killiany, Rosene, & Moss, 1999; Lacreuse, Herndon, Killiany, Rosene, & Moss, 1999; Moss, Rosene, & Peters, 1988), others have shown no differences (Rapp, 1990). Regardless of the acquisition rate, nearly all aged subjects are able to reach criterion in the training portion of the DNMS provided they are given enough trials (Gallagher & Rapp, 1997). So despite differences in the speed an aged monkey can learn discriminations, they are capable of performing the task when given enough training. However, once delay intervals are imposed the performance ability of aged animals drops off. Virtually all studies have shown that older monkeys are more impaired by longer delay intervals between the presentation of the sample and the choice stimuli (Herndon et al., 1997; 1999a; Killiany, Moss, Rosene, & Herndon, 2000; Rapp, 1990; Lacreuse et al., 1999). These differences begin to show at 60-sec delays (Killiany et al., 2000), but are much more pronounced at delays of 120 seconds or more (Herndon et al., 1997). It should be noted that several old monkeys in most of these studies performed as well or better than the younger monkeys. This follows with the human literature in that behavioral deterioration is not dependent on chronological age, but highly variable, and the range of performance increases with age. However, it should be noted that without a longitudinal assessment it is not possible to determine whether some of the older subjects

did not decline or whether they declined from a higher initial performance level than other aged subjects.

A variation of the DNMS that has become increasingly popular is the delayed recognition span task (DRST). Since, the use of the DRST to quantify memory performance following hippocampal removal in monkeys (Rehbein, 1985), it has been used to assess memory performance in aged monkeys as well as humans (Herndon et al., 1997; Lange, Robbins, Marsden, James, Owen, & Paul, 1992; Moss, Albert, Butters, & Payne, 1986). Successful performance on the DRST requires the ability to select a novel stimulus (i.e. color, object, spatial location) as in the DNMS. However, in the DRST stimuli are presented serially, such that the subject is required to remember an increasing number of stimuli in order to discriminate correctly on the next trial. The DRST appears to be more sensitive than the DNMS, as all published studies have shown aged monkeys to be impaired on some form of this task (Herndon et al., 1997; 1999a; Killiany et al., 2000; Lacreuse et al., 1999). This impairment is detectable in monkeys as young as 19-years-old, considered early old age in the rhesus monkey (Killiany et al., 2000). This age sensitivity is supported by the fact that DRST was most strongly correlated to chronological age when compared to some other recognition memory measures (Herndon et al., 1997).

While spatial impairments are thought to reflect deterioration of the hippocampus (Gallagher & Rapp, 1997), the DRST seems to have a greater demand for temporal ordering of stimuli, in addition to the spatial demands, than the DNMS, where performance can be based on paired associations and familiarity (Killiany et al., 2000). Tests of the influence of gender and age on spatial abilities in rhesus macaques revealed

that the DRST detected gender differences, but these gender differences disappeared with age (Lacreuse et al., 1999). While the hippocampus in the medial temporal lobe is thought to deteriorate with age, resulting in lower spatial performance in both males and females, this study implies a greater decline in older male monkeys than in older females. Interestingly, spatial reversals, a task that requires on-line manipulation of information and is based in other brain structures, did not show any age-related or gender differences. Thus, the DRST appears to be highly sensitive to MTL deterioration, probably due to the high memory demands of the task.

Alternatively, cognitive tasks that require temporal ordering of information and on-line manipulations of this information utilize the prefrontal cortex and the frontal lobe systems (Moscovitch & Umlita, 1991). While neurological research is less plentiful for the prefrontal cortex than the medial temporal lobe, research indicates that humans show impairments in temporal ordering as they age (Parkin, Walter, & Hunkin, 1995) and these impairments comprise a separate factor from those of declarative memory (Glisky, Polster, & Routhieaux, 1995). Thus, cognitive decline may be attributed to either medial temporal lobe deterioration or prefrontal cortex deterioration and these declines need not be related (Gallagher & Rapp, 1997).

Reversal tasks require processing of response-reward contingencies and therefore online adaptation of response strategies. These tasks are thought to rely heavily on the prefrontal cortex, as the PFC has been hypothesized to support a variety of organizational processes that influence the strategic use of memory (Gallagher & Rapp, 1997). These functions are commonly referred to as central executive capacity. Discrimination reversals have shown mixed results for age-related differences in monkeys. Some studies

have found differences in oddity, pattern, color and spatial discrimination reversals (Davis, 1978; Herndon et al., 1997; Voytko, 1999), while other studies found no differences in pattern (Rapp, 1990), spatial location (Voytko, 1999), or object discrimination reversal (Herndon et al., 1997; Rapp, 1990; Voytko, 1999). Thus the task demands of discrimination reversal may not be sufficient to reliably produce age-related impairments.

A recognition memory task with sufficient task demands to specifically assess performance based in the prefrontal cortex is the delayed response task (DR). No complex associations need be created for these tasks, only the recognition and selection of a baited site after a specified delay. By manipulating the delay interval the demands on memory can be increased to reveal age-related differences in performance. Direct baiting, in which the animal watches food placed in a site (i.e. Bachevalier et al., 1991), and indirect baiting, in which the subject is signaled via a light stimulus as to where the reward can be found (i.e. Bartus & Johnson, 1976), have been used with similar results. There appear to be no age differences in learning the procedural aspects of the task (Bachevalier et al., 1991; Bartus, Fleming, & Johnson, 1978; Roberts, Gilardi, Lasley, & Rapp, 1997). While delays as short as 1-sec have revealed age-related differences in performance (Roberts et al., 1997), performance declines become more obvious as delay intervals are increased to 15-sec and beyond (Bachevalier et al., 1991; Bachevalier, 1993; Lacreuse, Wilson, & Herndon, 2002). The relative lack of differences in performance with short or no delays indicates that the difference is not due to motivation or sensory deficiencies in the older animals, but is related to memory performance.

Impaired delayed response performance is among the earliest age-associated cognitive deficits to appear. Studies have revealed that delayed response performance is not necessarily related to performance on recognition memory tests, such as DNMS, or other tests that are affected by medial temporal lobe lesions (Bachevalier et al., 1991; Rapp & Amaral, 1989), indicating performance is based in a separate brain region. DR requires the subject to recall the most recently baited site, thus creating a temporal demand and forcing subjects to rely on an on-line processing function similar to the central executive function found in the prefrontal cortex in humans. Longer delay intervals create a larger demand on this “working memory” function, and the failure of older monkeys on this task resembles the short-term memory performance of aged humans and may indicate true memory dysfunction (Flicker, Bartus, Crook, & Ferris, 1984; Medin, 1969).

Thus, both the human and monkey research show that age effects are not uniform across information-processing domains and that MTL processing dysfunction may not wholly account for cognitive aging (Glisky et al., 1995). Additionally, both the human research and the monkey research show an increase in performance variability in older subjects (i.e. Bachevalier et al., 1991). The similarities in the pattern of decline with age for monkeys and humans indicate similar biological processes may be involved (Albert & Moss, 1996), and further development of a non-human primate model may be fruitful.

### Ape Research

While the monkey research continues to thrive, there is a surprising gap in the non-human primate aging literature. Only three studies that specifically addressed the cognitive performance of aged apes have been conducted; all were conducted on

chimpanzees (Bernstein, 1961; Bloomsmith, Anderson, Smith, & Maple, in review; Riopelle & Rogers, 1965). Despite studies showing a decline in brain volume with age (Herndon, Tigges, Anderson, Klump, & McClure, 1999), these studies have revealed few age-related decreases in cognitive performance.

Bernstein (1961) conducted four tasks: 1) object discrimination, 2) discrimination reversal, 3) conditional (signaled) discrimination reversal, and 4) a problem solving task in which subjects rotated a wheel to retrieve a food reward. No age differences in performance were found for any of these tasks. Riopelle and Rogers (1965) conducted a delayed response task with 0-, 5-, and 10-sec delay intervals. Older subjects performed more poorly than younger subjects at 0- and 5-sec delays, but showed equivalent performance at 10-sec delays. Age-related differences were found in a four-choice oddity test, but not in pattern discriminations or concurrent object discriminations. In a replication of these tests twenty years later (Bloomsmith et al, in review), no age differences were found for object discriminations, object reversal, or the delayed response at delays of 0- and 5-sec. Older subjects performed more poorly than younger subjects on the 10-sec delayed response task, but better than the younger subjects on the four-choice oddity test, presumably due to familiarity with this and other rule-based tasks.

While these findings seem to indicate few age-related differences in cognitive performance in apes, the tasks employed may not have contained sufficient demands to reveal age-related differences. Discrimination and reversal tasks have since been shown to exhibit conflicting results in the rhesus monkey even though cognitive decline has been clearly documented in other tasks. Additionally, the 10-sec retention interval used

in the delayed response tasks is less than the 15-sec retention intervals shown to produce reliable age differences in monkeys (Bartus et al., 1978; Bachevalier et al., 1991). Given the performance levels of aged rhesus macaques and the greater cortical development in chimpanzees, it is not surprising that few age-related differences were revealed in these early studies. Despite the potential shortcomings of these tasks, no attempts have been made to reexamine the cognitive abilities of any aged ape species using tasks with more demanding components. Thus, the species with the closest relationship to humans, and therefore the greatest biological similarity and potential to serve as a model for human cognitive processes, have yet to have their memory abilities appropriately studied. Additionally, gorillas and orangutans have been sparsely used as cognitive research subjects (but see MacDonald, 1994; MacDonald & Agnes, 1999; Rumbaugh, 1970; Taylor Parker, Mitchell, & Miles, 1999), and never in studies of cognitive aging. Finally, although the research on monkeys continues to be productive, the criticism of rat research can also be applied to monkey research. The monkeys used in these tasks are housed in biomedical facilities. Due to the demands of biomedical research protocols, these animals are often housed solitarily. Although attempts to provide environmental enrichment are made, these animals may be showing cognitive deficits due to an effect of their living environment or an interaction between aging and their living environment. Animals housed in complex social environments with many enrichment opportunities may provide a better indication of the environmental effects on these animals. Further research will determine if and how non-human animals should be used as models of human cognitive aging.

## CHAPTER 2

### THE DELAYED RESPONSE TASK AND THE GORILLA: AGE, GENDER, AND EXPERIENCE EFFECTS

#### **Introduction**

The number of studies of age-related changes in cognitive processes, such as attention, learning, and memory, has increased rapidly over the past forty years. Cognitive aging has developed sub-disciplines, which seek to explore specific causes of and preventions against certain types of cognitive decline. While developmental change is well structured in childhood and adolescence, the changes associated with old age are much less rigid. In fact, it has been shown that chronological age is not directly related to developmental change. While the cognitive capabilities of a three-year-old are quite predictable, the capabilities of an eighty-three-year-old are much less so. Many more factors are associated with cognitive capabilities in adulthood.

While genetics and biology play a large role in age-related cognitive decline, other factors associated with an individual's experiences may also be important. Education level, socio-economic status, exercise, health, drug and alcohol use, occupation, and hobbies can influence how quickly a person's cognitive capacities will decline with age. Many psychologists seek to separate these factors with complicated multivariate statistics, including structural equation modeling. These studies may not be practical in all cases due to the costs associated with the large number of subjects required for such studies. Human studies also rely on personal reporting of socially undesirable factors, including drug use and other potentially harmful behaviors. The reports from these individuals may not always be accurate (Whitley, 1996).

The branch of psychology known as behaviorism has traditionally used laboratory animal models of learning in an attempt to control for developmental and genetic factors associated with cognitive task performance. Recently, Derenne and Baron (2002) called for the return to use of nonhuman subjects in the study of human cognitive aging. They argued that many of the factors associated with age-related cognitive decline are precisely the ontogenetic factors that are uncontrolled when research is conducted on human subjects. By using nonhuman subjects reared in a captive environment, it is possible to control for developmental factors that may influence the results instead of relying on personal report of historical information, which can be inaccurate. Additionally, some species can allow for the study of the longitudinal changes associated with aging during the period of a grant, instead of relying on cross-sectional information from differing cohorts.

For nearly one hundred years, nonhuman primates have been used as research subjects in the fields of biology and psychology. While these species can be long-lived and do not provide the time-related convenience that smaller species, such as rats provide, development of the neocortex allows for tasks with nonhuman primates to more closely resemble human tasks.

Over the years, laboratory and zoo primates have been used in a variety of learning experiments utilizing a variety of experimental paradigms (i.e. Schrier, Harlow, & Stollnitz, 1965; Taylor Parker et al., 1999). The most prevalent research subject in studies examining age-related change is the rhesus macaque (i.e. Bachevalier et al., 1991; Bartus et al., 1978; Herndon & Lacreuse, 2002; Zola-Morgan et al., 1989). This is due in

part to the behavioral complexity of the species, the relatively short lifespan, and the large numbers available for research in biomedical facilities.

While rhesus macaques and humans share many behavioral features and neurological structures, apes are more similar to humans neurologically and share many derived characteristics with humans that monkeys do not (Erwin et al., 2002). Relatively few studies have examined age-related differences in learning and memory in apes (but see Bernstein, 1961; Bloomsmith et al., in review; Riopelle & Rogers, 1965) despite the fact that apes are neurologically and behaviorally more similar to humans than are monkeys. These studies have found limited age-related impairments in the cognitive abilities of chimpanzees. This is surprising given the widespread study of cognitive impairments in aged monkeys and humans.

While chimpanzees are still housed in two of the federally funded primate research centers (Yerkes National Primate Research Center and Southwest Foundation for Biomedical Research), the majority of the other great apes are housed in zoological parks. Erwin et al. (2002) noted that the captive aging ape population continues to grow as the care and husbandry of these animals continues to improve. The current study was designed to capitalize on the large gorilla populations at Zoo Atlanta and Disney's Animal Kingdom. Zoo Atlanta holds the largest number of gorillas over the age of 30 in North America, as well as younger animals that can serve as controls. The goal of this study was to increase the difficulty of traditional nonhuman primate cognitive tasks used on apes to more closely match the large volume of research being conducted on monkeys to determine if age-related impairments exist.

## General Methods

### Subjects

Nine western lowland gorillas (*Gorilla g. gorilla*) at Zoo Atlanta and seven at Disney's Animal Kingdom served as subjects. These subjects ranged in age from 6 to 43 years, and included seven females and nine males. All subjects were housed in social groups ranging in size from three to eight individuals. Subjects housed at Zoo Atlanta had experience in at least one cognitive study (Anderson, 2003), and many have extensive experience in cognitive testing (Yerkes National Primate Research Center, unpublished records). As a result, these animals were considered to have research experience, while subjects housed at Disney's Animal Kingdom were considered to be research naïve. Specific coding of demographic information is presented in Table 1 in Appendix A.

Unfortunately, the available subjects presented several confounds among the independent variables. For instance, most of the aged subjects were female and experienced, while most of the young subjects were male and inexperienced. While separation of the effects of each independent variable is difficult, this sample is based on the animals available at the time of the study.

### Behavioral Testing

A delayed response (DR) task was used to assess spatial recognition memory in gorillas. While using a relatively simple methodology, DR tasks have been highly effective in uncovering age-related differences in recognition memory in monkeys (Bachevalier et al., 1991; Bartus et al., 1978; Roberts, 1997), and have been used on chimpanzees at short delay intervals (Bloomsmith et al., in review; Riopelle & Rogers,

1965). The methodology employed here was based, in part, on the methodology used by Bachevalier and colleagues. This simple procedure was thought to be effective with gorillas, which have proven to be easily distracted in the zoo-testing environment.

When possible, subjects were physically separated from other group members during testing. During separations, the test subject remained in auditory and in many cases visual contact with other group members. Subjects were tested four to six days per week. Due to management issues, i.e. space availability and time restrictions, it was not possible to test all animals simultaneously, nor was it possible to test animals daily. Therefore animals were tested in batches, with a batch composed of animals that meet management criterion for being tested on the same days.

While food deprivation has been shown to increase motivation in many animal studies, previous cognitive studies with gorillas at Zoo Atlanta have shown that attempts to test these animals prior to the afternoon feeding negatively affected results. When food was withheld, the animals were distracted and looked around, presumably for the keepers with their meal, and did not attend to the task reliably. Additionally, the exhibit design and operating procedures of Disney's Animal Kingdom made food deprivation impractical. Therefore, all tests were conducted following the normal feeding session, but the normal diets were used as rewards whenever possible.

### Test Apparatus

The test apparatus was a modified Wisconsin General Test Apparatus (WGTA). The WGTA consisted of 5 cm foodwells, with each foodwell set into a plastic board that could be slid forward under the gap at the bottom of the cage mesh to allow the subject to remove the food reward. A stopper on the backside of each board prevented it from

being pulled into the exhibit with the gorillas (Figure 1). The apparatus was placed 15 cm in front of the gorilla's cage during baiting, but was pushed to within 2 cm of the cage to allow the subjects to reach out and make a selection. Once a subject selected a foodwell the board was pushed forward under the mesh so the subject could retrieve any reward that was present. Rewards consisted of a preferred but infrequently provided food item, such as grapes, raisins, orange slices, or peanuts. Overturned opaque plastic cups covered the wells during trials and a wooden screen prevented visual access to the WGTA during trials. A translucent plastic shower curtain mounted on a PVC frame prevented subjects from taking visual cues from the experimenter during testing sessions.

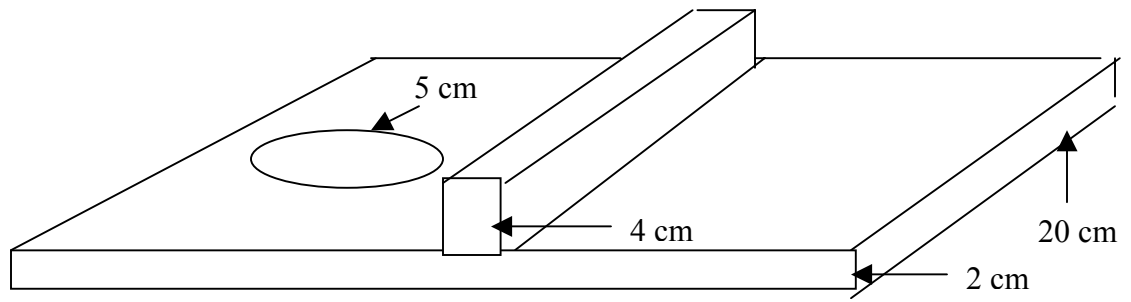


Figure 1. Diagrammatic Representation of the Trays of the Modified WGTA.

### Initial Training

For initial training, the WGTA contained 2 foodwells, spaced 10 cm apart. While the subject watched, a food reward was placed in a foodwell and the trays were pushed to within 2 cm of the front of the cage. To respond, the subject was required to reach under the mesh and touch a board or to place its hand through the mesh over a single reward. Attempts to simultaneously select both foodwells and ambiguous selections were ignored and only a single selection was acknowledged. Once a foodwell was selected the tray was pushed to the cage mesh to allow the subject to obtain the reward, if present. This process continued until each subject received a minimum of 20 rewards from each well and made the correct selection in 18 of the previous 20 presentations. This method of selection was similar to the methodology used by Anderson (2003) to assess quantity discrimination in gorillas at Zoo Atlanta, but the methodology was novel to gorillas housed at Disney's Animal Kingdom. A 30-sec inter-trial interval and a non-correction procedure were utilized for this and all subsequent phases. Additionally, the well to be baited was randomly determined prior to the administration of each phase.

### **Data Collection and Analysis**

All data were collected using paper datasheets. The data were then entered into a Microsoft Excel® spreadsheet for manipulation. SPSS for Windows Version 11.5 was used to analyze all data.

Regression and repeated-measures GLM tests were run to test hypotheses in the experiments. Normality of the residuals was tested with P-P plots and Q-Q plots. VIF statistics were conducted to test for multicollinearity within each model. In all multiple

regression models, VIF statistics indicated the variables were not sufficiently correlated to violate assumptions.

### **Experiment One: Zero-Second Delay**

Trials in Experiment One consisted of a 0-sec delay between the baiting of the tray and the selection opportunity for the subjects. No visual barrier between the selection sites and the subjects was utilized.

#### **Methods**

##### Subjects

All 16 subjects completed the experiment.

##### Test Methodology

On each test day the experimenter set up the foodwells in front of the animal at the front of the cage. The experimenter called the subject's name while holding the food up and moving the food around for the subject to see. Once the animal appeared to look at the food, it was placed in one of two lateral foodwells. Then, both wells were covered simultaneously with plastic cups and immediately pushed to within 2 cm of the subject to allow them to make a selection. Once the selection was made, the cup was removed from that well and the board was pushed under the mesh to allow the subject to obtain the reward, if present. Following the opportunity to retrieve the reward a 30-sec inter-trial interval was imposed prior to the start of the next trial. Twenty trials per day were conducted until the subject reached a criterion of 18 correct responses out of the previous 20 presentations. The major hypotheses of this experiment were:

**H<sub>1A</sub>: No age-related differences were expected with the 0-sec delay.** The findings of many monkey studies indicate that no age-related differences are found in studies with extremely low cognitive demands. Due to the very low memory demands of this phase, no differences were expected

**H<sub>1B</sub>: No gender-related differences were expected for the 0-sec delay.** While Lacreuse and colleagues (1999) found gender differences in the spatial DRST, they did not find differences in the spatial reversal task. As the DRST is thought to assess medial temporal lobe performance, and DR and reversal tasks are thought to assess prefrontal cortex function, no gender-related differences in performance in this phase were expected.

**H<sub>1C</sub>: Subjects with little or no experimental task background were expected to require more trials and commit more errors to reach criterion in the 0-sec delay.**

Due to the novelty of the testing situation, subjects with little or no experience were expected to require more trials and commit more errors to reach criterion in this phase because they were less practiced in the methodology and may still be learning the parameters of the testing situation.

### Data Analysis

The primary dependent variables for this task were the number of trials to criterion and the number of errors to criterion. Age, gender, and research experience were independent variables. Gender and experience were dummy coded for regression

analyses (gender: male = 1, female = 0; experience: yes = 1, no = 0). Separate multiple regression analyses were run for trials and errors to criterion with the three independent variables as predictors. Separate analyses were run because the data did not meet the assumptions for multivariate regression analysis (Stevens 2002).

## **Results**

The model including all three independent variables was a significant predictor for trials to criterion ( $R^2 = 0.597$ ,  $F_{3,12} = 5.926$ ,  $P = 0.010$ ). However, only experience was a significant individual predictor (Table 2 in Appendix A). Research naïve subjects required more trials to reach the criterion than did experienced subjects (mean: Inexperienced = 58.1, Experienced = 23.2). Younger subjects required more trials to reach criterion (Figure 2) and males required more trials than females (mean: Male = 44.7, Female = 30.6), but neither was a significant individual contributor to the model (Table 2 in Appendix A).

The model including all independent variables was also a significant predictor of errors to criterion ( $R^2 = 0.618$ ,  $F_{3,12} = 6.458$ ,  $P = 0.008$ ), but as with the trials model, only experience was a significant individual predictor (Table 2 in Appendix A). Subjects with previous research experience made fewer errors before reaching the 80% criterion (mean: Inexperienced = 17.4, Experienced = 2.4). Younger subjects made more errors (Figure 2), and males made more errors than females (mean: Male = 11.0, Female = 6.4), but these values were not significant individual predictors (Table 2 in Appendix A).

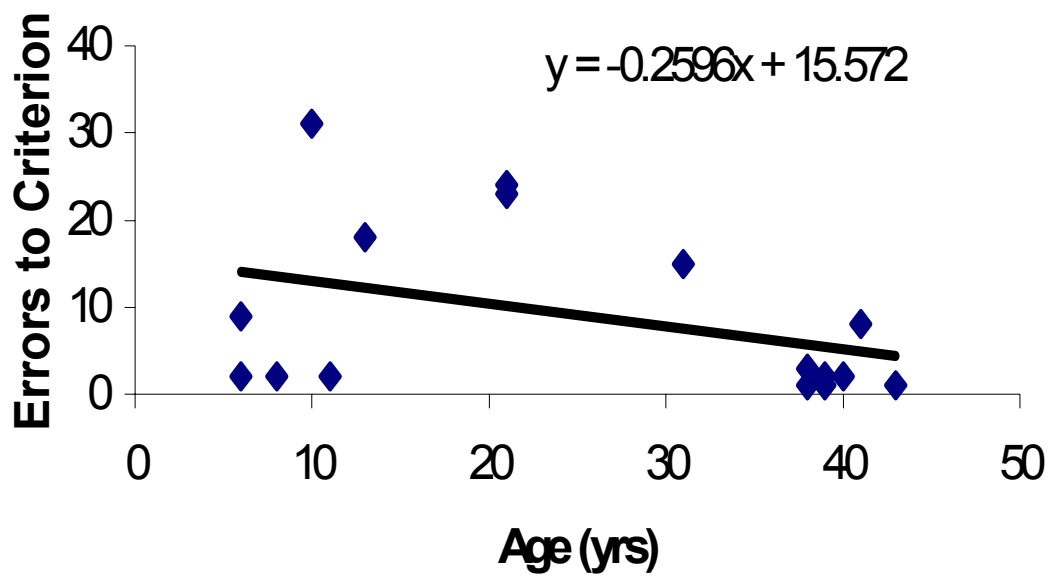
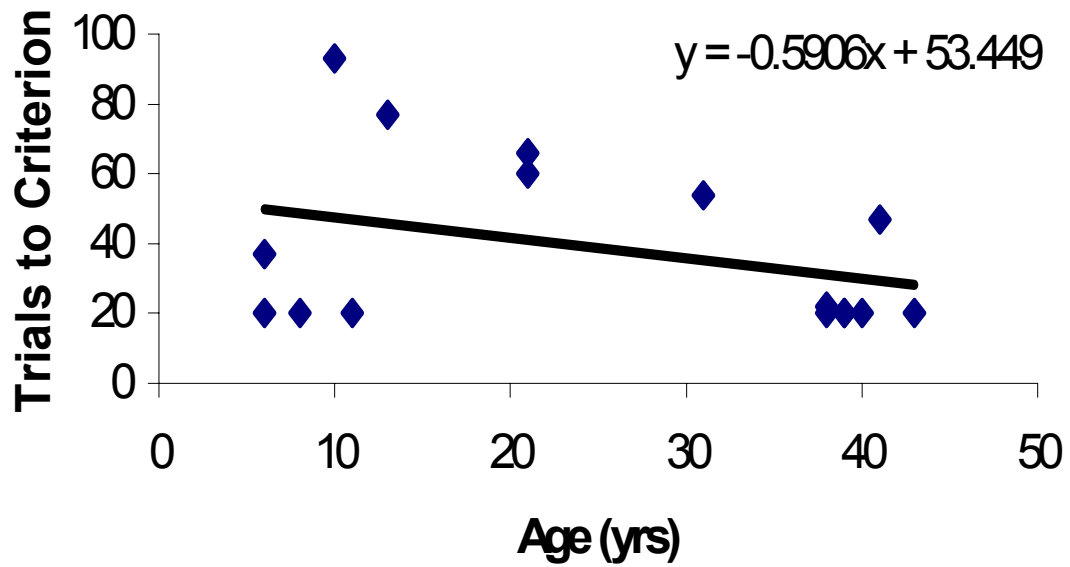


Figure 2. Plots of the Relationship between Age and Performance in Experiment One for Trials to Criterion and Errors to Criterion.

## **Discussion**

While the independent variables in Experiment One combined to create a significant regression model for both trials and errors to criterion, only experience was a significant univariate predictor. This is not surprising considering the research history of the subjects. All of the experienced subjects had completed a quantity discrimination task within the past year and as a result were familiar with the choice methodology used in this experiment. Additionally, in most zoological parks that house apes, animals are discouraged from sticking their hands through the mesh for the safety of the keeper staff. As a result, this methodology may have placed these subjects at an even greater disadvantage.

Components of the WGTA may have been confusing for naïve subjects as well. Although the methodology in this experiment utilized a modified WGTA, subjects were not able to displace the cups to retrieve their own reward. Such a design would be impractical in a zoo setting; it would require subjects to reach their entire hand through the caging and, given the standard of two-inch mesh for housing primates in most North American zoos, this would require major exhibit modifications in order to ensure safety. Presumably, displacing the cover and obtaining the reward would be easier to learn than the cause and effect relationship involved with an abstract pointing behavior and the delayed reinforcement of the experimenter removing the cup and sliding the tray underneath the mesh. Many of the older subjects had participated in as many as eight different cognitive research protocols during the time they were housed at Yerkes National Primate Research Center (unpublished records). As a result, it should not be surprising that these subjects would have little trouble adapting to the cognitive

methodology presented here, while subjects that had never been exposed to such a paradigm would require a few more trials and errors to reach the 80% criterion.

Similarly, the lack of significant relationships between age and gender and performance are not surprising. The task merely required subjects to point to where they had seen food placed only moments before. Such a task resembles assessment of sensory memory in humans and research with both humans and animals has shown that such immediate recall tasks often show no age-related differences or gender-related differences. Only when the demands of the task are increased, by adding delays, interference or creating more complicated tasks do these differences become apparent. The non-significant trends for males and younger animals to require more trials to reach criterion may be attributed to the unequal subject distribution in the current study. More of the young subjects were male and inexperienced. This potential confound will be discussed further within the context of later experiments.

### **Experiment Two – One-Second Delay**

In Experiment Two a visual barrier was briefly introduced. This brief “1-sec” delay served to desensitize subjects to the visual barrier and disrupt visual access to the baited site, which provides the foundation to build longer delays to impact memory.

#### **Methods**

##### Subjects

All 16 subjects completed the experiment.

## Test Methodology

In Experiment Two, the baiting of the wells proceeded as in Experiment One. However, after baiting and covering the wells, a brief “1-sec” delay interval was imposed by placing a 1m<sup>2</sup> wooden screen between the subject and the wells. This was done to disrupt visual access to the baited site (Meyer & Harlow, 1952). Once the screen was put into place it was immediately removed and the wells were pushed forward to allow the subject to make a selection. As in Experiment One, twenty trials per day were conducted using this procedure with a 30-sec inter-trial interval until the subject correctly responded to 18 out of the previous 20 presentations. The major hypotheses of this experiment were:

**H<sub>2A</sub>: No age-related differences were expected in the “1-sec” delay.** Although Roberts et al. (1997) found age-related impairment at a brief delay in monkeys, many studies have shown no age differences at short time intervals. The low cognitive demands on this task suggested there would be no age-related differences in performance.

**H<sub>2B</sub>: No gender-related differences were expected for the “1-sec” delay.** As the task demands were low for the “1-sec” delay no gender differences in performance were expected.

**H<sub>2C</sub>: No experience-related differences were expected for the “1-sec” delay task.** Although the demands of the task were low, the introduction of the wooden screen was thought to disrupt the performance of inexperienced subjects more than that of the more

experienced subjects. As a result, experienced subjects were expected to require fewer trials and errors to reach criterion in this phase.

### Data Analysis

As in Experiment One, the primary dependent variables for this task were the number of trials to criterion and the number of errors to criterion. Age, gender, and research experience were coded as before and incorporated in the regression models. Again, separate multiple regression analyses were run for trials and errors to criterion with the three independent variables as predictors.

### **Results**

In Experiment Two none of the factors were related to performance, as neither model was significant when the three independent variables were included. Trials to criterion could not be predicted with the combination of independent variables used ( $R^2 = 0.326$ ,  $F_{3,12} = 1.934$ ,  $P = 0.178$ ). A slight tendency for older subjects to require more trials to reach criterion is visible in Figure 3. Females required slightly more trials to reach criterion than did males (mean: Male = 26.7, Female = 29.0) and experienced subjects required more trials than did inexperienced subjects (mean: Inexperienced = 24.1, Experienced = 30.6), but none of these factors reached significance as independent predictors (Table 3 in Appendix A).

Similarly, errors to criterion could not be predicted by the independent variables ( $R^2 = 0.344$ ,  $F_{3,12} = 2.100$ ,  $P = 0.154$ ). While older animals (Figure 3), females (mean: Male = 3.4, Female = 6.3), and experienced animals (mean: Inexperienced = 4.4,

Experienced = 4.9) made more errors before reaching criterion, none of the Beta coefficients in the model reached univariate significance (Table 3 in Appendix A).

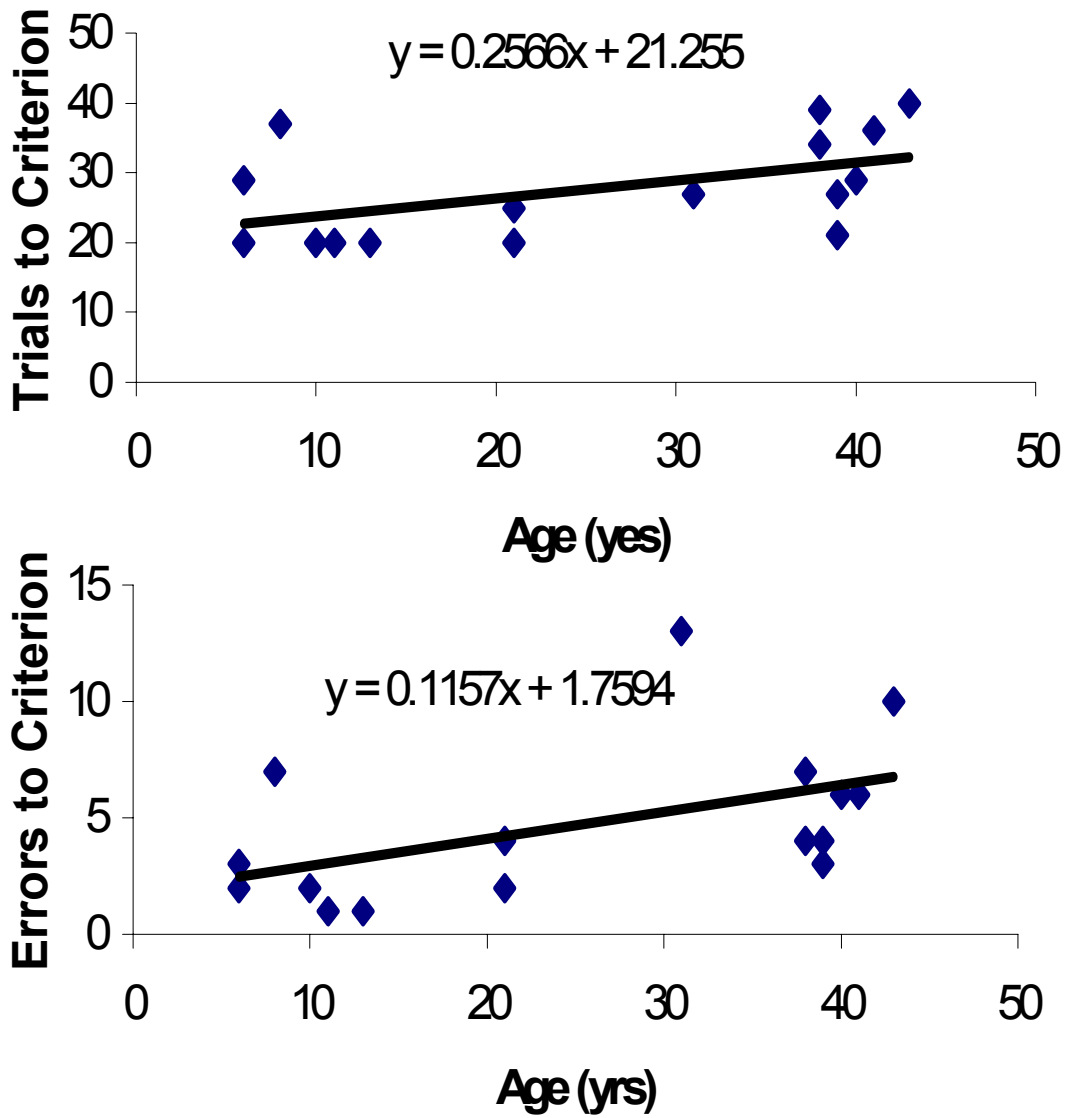


Figure 3. Plots of the Relationship between Age and Performance in Experiment Two for Trials to Criterion and Errors to Criterion.

## **Discussion**

As opposed to the regression models for Experiment One, regressions for Experiment Two did not result in significant models for either trials or errors to criterion using the independent variables provided. Beta coefficients revealed no significant trends for older animals, females, and experienced animals to require more trials and errors to reach significance.

Experiment Two required subjects to remember the location of the baited location for only a short period of time, probably less than five seconds from the time the food was placed on a tray until the time a choice was permitted. However, a wooden screen was introduced briefly to disrupt visual access to the baited site. Some of the subjects reacted negatively to the introduction of the screen, i.e. threatening the experimenter by banging their hand against the mesh, barking, or baring their teeth. However, this behavior did not occur on every trial and there was no discernible relationship between reacting negatively to the barrier and the independent variables. Nor was there an obvious relationship between negative reaction to the barrier and performance on the task. No subjects were reacting negatively to the barrier by the end of Experiment Two, indicating that desensitization to the barrier had occurred. However, individual reactions to the barrier may have driven the slight, nonsignificant correlations between the factors in such a small sample size.

As in Experiment One, the cognitive demands of the experiment were fairly low, and as a result no age- or gender-related differences were expected. Despite the low cognitive demands of the task, research naïve subjects were hypothesized to require more trials and errors to reach criterion because of the introduction of a new element (the

wooden screen) in the methodology. However, the wooden screen did not appear to have an effect, but as mentioned above, the screen did create issues for individual subjects that may have affected performance on this task.

### **Experiment Three – Five-Second Delay**

In Experiment Three a 5-sec delay was imposed between the baiting of the site and the time when the subject was permitted to make a selection. This relatively small delay was used to increase the time the subjects participated in the experiment and to increase the memory demands of the task.

#### **Methods**

##### Subjects

All sixteen subjects completed the experiment.

##### Test Methodology

In Experiment Three the trials proceeded as in the preceding experiments, but the wooden screen was left in place for five seconds before it was removed and the subject was permitted to make a selection. As in the preceding experiments, twenty trials per day were conducted with a 30-sec inter-trial interval until the subject made 18 correct selections out of 20 consecutive presentations. The major hypotheses of this experiment were:

**H<sub>3A</sub>: Age-related differences were expected for the 5-sec delay task, with younger animals requiring fewer trials and making more errors prior to reaching the criterion.** Riopelle & Rogers (1965) but not Bloomsmith et al. (in review) found old

subjects to be impaired at this delay. In monkeys, Bachevalier et al (1991) found an age-related impairment that fell just short of significance. Therefore, older subjects in this study were expected to require more trials and errors to reach criterion.

**H<sub>3B</sub>: No gender-related differences in trials or errors to criterion for the 5-sec delay interval were expected.** As the demands of the task, particularly the spatial demands, were low, no gender-related differences were expected for this phase.

**H<sub>3C</sub>: No experience-related differences in trials or errors to criterion for the 5-sec delay were expected.** At this point in testing, inexperienced subjects had received a minimum of 80 trials and as a result were expected to perform at the level of experienced subjects.

### Data Analysis

Data analysis proceeded as in the previous experiments with separate regression models run for trials to criterion and errors to criterion. All three independent variables were included in the model and coded as in previous experiments.

### **Results**

As in Experiment Two, neither model was a significant multivariate predictor of performance. Trials to criterion could not be predicted by the independent variables ( $R^2 = 0.155$ ,  $F_{3,12} = 0.732$ ,  $P = 0.552$ ). Age was positively related to number of trials necessary to reach the criterion (Figure 4). Females (mean: Males = 29.6, Females = 38.1) and inexperienced individuals (mean: Inexperienced = 34.0, Experienced = 32.8)

required slightly more trials. However as in previous experiments, none of the individual factors was a significant univariate contributor to the model (Table 4 in Appendix A).

Errors to criterion also could not be predicted by the independent variables ( $R^2 = 0.110$ ,  $F_{3,12} = 0.495$ ,  $P = 0.692$ ). Age was positively related to number of errors (Figure 4). Females (mean: Males = 5.2, Females = 6.7) and inexperienced individuals (mean: Inexperienced = 6.4, Experienced = 5.4) made more errors before reaching the criterion, but none of the factors was significant (Table 4 in Appendix A).

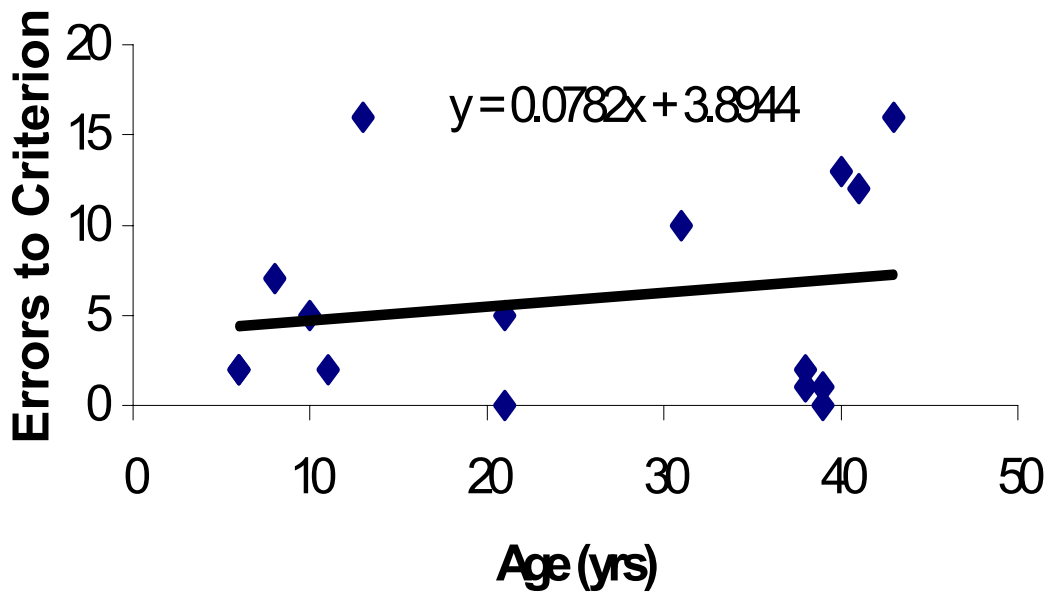
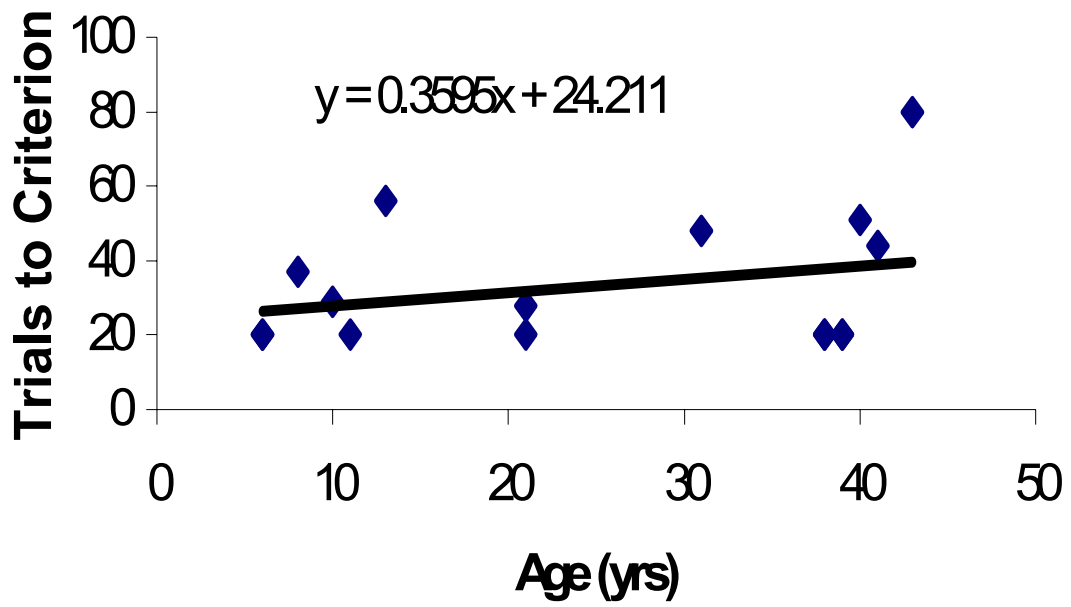


Figure 4. Plots of the Relationship between Age and Performance in Experiment Three for Trials to Criterion and Errors to Criterion.

## **Discussion**

As in Experiment Two, the regression models from Experiment Three did not result in a significant prediction of performance. The individual predictors again showed no significant trends for older subjects and females to require more trials and errors to reach criterion, but the very slight trend this time was for inexperienced subjects to perform more poorly than experienced subjects.

While no differences were predicted for gender or experience, older subjects were predicted to be impaired at the five-second delay in this task. While only a nonsignificant trend for older subjects to be more impaired was found, graphical representation of performance shows increased variation in performance of older subjects. Four of the aged subjects (Benga, Katie, Shamba, and Ozzie) performed more poorly than all but one of the younger subjects (Kejana), while four of the older subjects (Banga, Choomba, Paki and Ivan) and three of the younger subjects (Hasani, Jabari, and Kekla) required the minimum number of trials. Only 38-year-old Choomba made no errors during her series of trials. This increase in performance variability associated with increased age is a hallmark of cognitive aging research, both in humans (Craik et al, 1987; Shimamura, 1993) and nonhumans (Herndon et al., 1997), and there is a tendency for some old subjects to perform at or better than their younger counterparts. Although the statistical results from this experiment were not significant, the results illustrate how a small sample may lead to either a significant age-related difference or a nonsignificant result based entirely on the performance of a particular individual.

## **Experiment Four – Increasing Delay Intervals**

In Experiment Four, the delay interval was significantly increased and three different delays were used to test memory performance. These are the longest delays used to assess age-related differences in memory in apes to date. As such, they are expected to reveal age-related differences in performance, should they exist.

### **Methods**

#### Subjects

In Experiment Four only 14 of the 16 total subjects are included in the analyses. The two youngest subjects at Disney's Animal Kingdom left the testing area at delays longer than five seconds. Testing will be resumed on these subjects when they can be separated from other group members routinely, whereupon their attention to the task is expected to improve. Additionally, a third subject (Katie at Zoo Atlanta) died during the experiment. Katie was an old subject and showed no signs of illness during testing. Data from her 12 days of trials are included, as these are the number of days completed before she became ill.

#### Test Methodology

The baiting of the well proceeded as in previous experiments, but the screen remained in place for one of three different delay intervals: 30-sec, 60-sec, or 90-sec. Pilot studies revealed that delays that exceeded 90 seconds using this methodology resulted in decreased motivation and performance at the chance level. With delays longer than 90-sec subjects often would leave the testing area and not return. Extended delay intervals have been achieved by using a titrated procedure in which the delay interval is gradually increased (i.e. in three second intervals) only when a subject performs at a high

level (i.e. 95% correct) at the previous delay interval. The non-titrated methodology used in this study was an effort to maximize the number of subjects without the complications and time consumption of titration techniques in the zoo environment.

Nine trials per day were conducted and the delay intervals were presented in a pseudorandom order such that each delay interval was used prior to a second presentation of that delay interval in a session. Thus, three rounds of the delay intervals were presented in a random order three times during a session. This phase continued for 20 days and each subject received 60 trials at each delay interval. The major hypotheses for this experiment are:

**H<sub>4A</sub>: Age-related differences were expected in the percent of correct responses for each delay interval with younger animals correctly answering more trials at all delay intervals.** Despite the lack of information on age-related differences at these time intervals for apes, the monkey literature shows age differences at these intervals and that the differences are larger at the longer delay intervals.

**H<sub>4B</sub>: No gender-related differences were expected for any of the delay intervals.**

While the cognitive demands of this experiment were significantly higher than those of previous experiments, time alone was not expected to create performance differences in this task with relation to gender. Thus, no gender-related differences were expected for any of the delay intervals.

**H<sub>4c</sub>: No experience-related differences were expected for any of the delay intervals.**

As subjects had all received many trials by this point in testing, no experience-related differences were expected at any of the delay intervals.

### Data Analysis

The proportions of correct responses for each delay interval were used as dependent variables. The General Linear Model command in SPSS was used to create a repeated-measures ANOVA model for each independent variable. Differences between the within-subjects factor were assessed with Difference contrasts. A single multivariate model could not be utilized because the data violated the assumption of multivariate normality, as indicated by the Shapiro-Wilks test (Stevens, 2002), and the assumption of equality of covariance matrices, as indicated by Box's Test.

Gender and experience were coded as independent variables as in previous experiments. However, age was categorized as young and old in order to be used as a between-subjects variable in the repeated-measures analyses. Subjects older than 30 years were categorized as old, and subject younger than 30 years were categorized as young (old = 1; young = 0).

Response rigidity was assessed by calculating a Chi-square value for each subject from the observed and expected values of side selections. Subjects with high Chi-square values chose a specific side despite the fact that each side was baited the same number of times. A multiple regression analysis was run with the Chi-square values as the dependent variable and the three independent variables as predictors as in previous experiments.

## Results

For all three repeated-measures tests (Table 5 in Appendix A), performance declined with increasing delay interval (Figure 5), but only the 90-sec delay showed a significant decline in performance ( $P < 0.05$ ). No interactions were observed between delay and any of the between subjects factors (age, gender, experience), and no univariate between-subjects effects were observed for these factors (Table 5 in Appendix A).

Additionally, when equations from univariate regression models for age are compared at each delay interval there is little change in the slope of the regression function (Figure 6)

Side bias, as measured by the chi-square value, was not significantly correlated with mean performance in Experiment Four ( $r = -0.292$ ,  $F_{1,12} = 1.116$ ,  $P = 0.312$ ). When side bias was assessed using the regression model, the three independent variables were not able to predict the Chi-square score ( $R^2 = 0.221$ ,  $F_{3,10} = 0.944$ ,  $P = 0.456$ ). Males, experienced subjects, and older subjects all tended to show more of a side bias, as indicated by Beta coefficients (Table 6 in Appendix A). However, upon further examination of the plot for the relationship between age and Chi-square score (Figure 7) it is visible that a single young animal with a high Chi-square value and two old animals with extremely low values prevent an extremely strong linear correlation. Additionally, all but these two low scoring older subjects had Chi-square scores greater than the single outlying young subject. Furthermore, when only inexperienced subjects are included in a regression analysis examining the relationship between age and Chi-square score the model is significant ( $R^2 = 0.970$ ,  $F_{1,3} = 97.052$ ,  $P = 0.002$ ) and the linear relationship between the variables is quite clear (Figure 8).

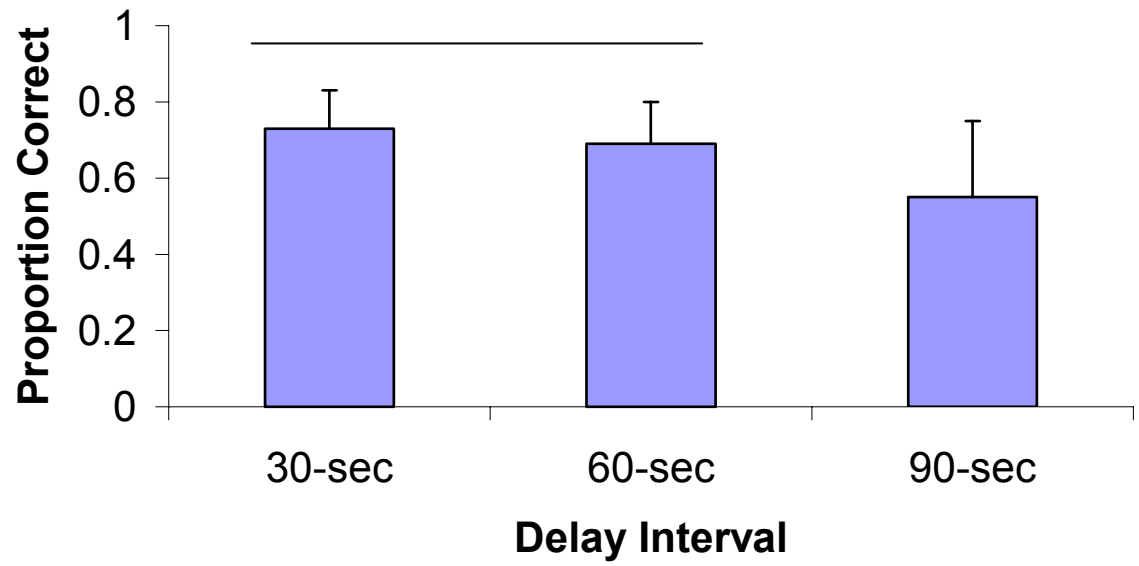


Figure 5. Performance as a Function of Increasing Delay Intervals in Experiment Four.

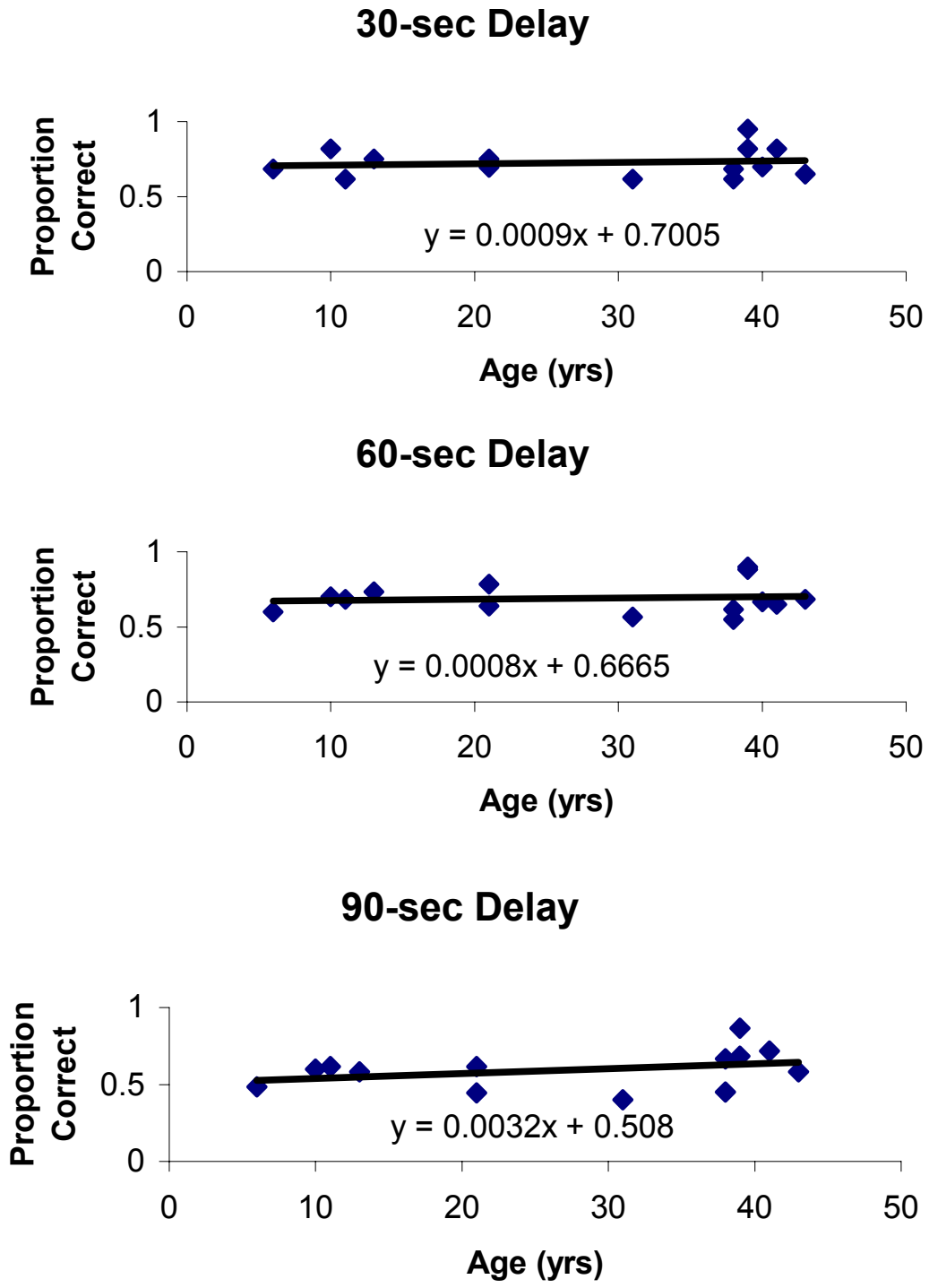


Figure 6. Performance as a Function of Age for 30-, 60-, and 90-sec Delay Intervals in Experiment Four.

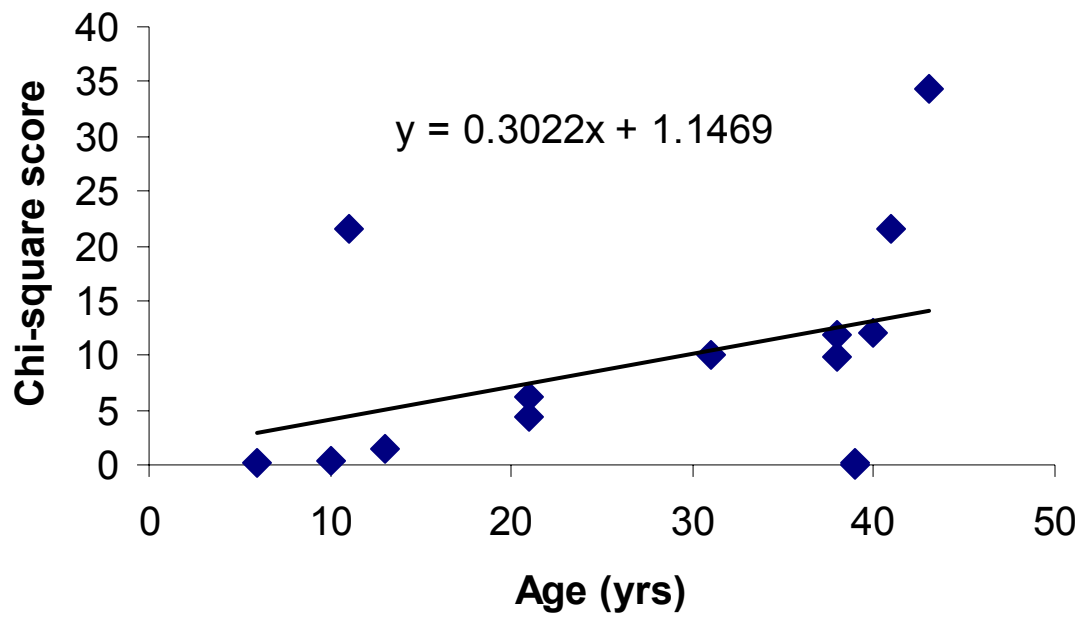


Figure 7. Side Bias as a Function of Age in Experiment Four with All Subjects Represented.

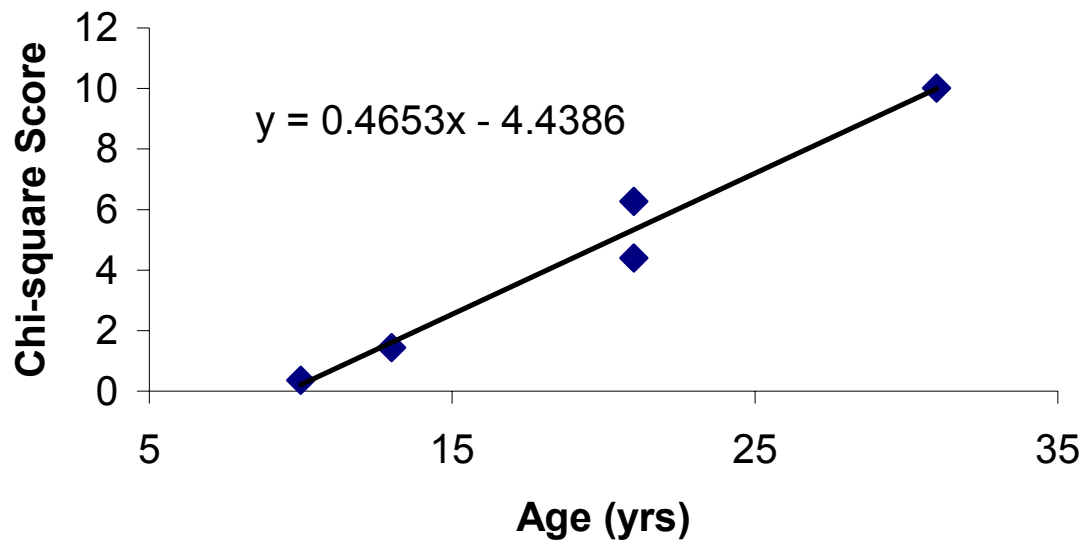


Figure 8. Side Bias as a Function of Age in Experiment Four with only Inexperienced Subjects Represented.

## **Discussion**

Repeated-measures models revealed that performance decreased with increasing delay, but only the 90-sec delay showed a significant decrease. Additionally, no interaction effect was found for any of the between-subjects factors and the delay.

While no effects were expected for gender or experience, age-related differences were predicted. If older subjects were differently affected by the increasing delay interval a delay by age interaction should have been apparent. This is not the case. Results from Experiment Three indicated that the increased variability in the performance of older individuals may decrease the effectiveness of statistical analysis, so individual plots of performance at the three delay intervals were visually examined for trends. The finding of no age-related effects on performance does not appear to be related to the statistical power of the regression because the slope of the regression line for age-effects is near zero for all subjects. This finding is surprising given the vast literature on the effects of age on cognition in primates. Several explanations exist for the lack of findings with the long delay intervals. First, the experience of older subjects moderated the cognitive decline. By participating in similar tasks the older subjects may have been more comfortable, familiar and prepared to participate (Botwinick, 1984). Second, although the delay intervals were longer than any previously used with apes, they may not be sufficiently long to reveal age effects. Attempts at delay intervals of 180- and 300-sec were unsuccessful because subjects often refused to participate or did so at random. This is not surprising given the methodology of including multiple long delays in a single session (Fletcher, 1965). Future attempts at longer delay intervals should employ a titrated procedure to maintain the interest and performance of the subjects. Finally, there may simply not be age-related decreases in performance in apes. This

explanation seems unlikely given the widespread findings of age-related impairments in other species within the same class.

Increasing delay intervals does not result in age-related differences in cognitive function as measured by proportion correct. However, a second measure of cognitive function, Chi-square values, was calculated for each subject. It is expected that responses should be distributed equally between the two sites because they were baited equally. The Chi-square value is a measure of deviation from that pattern. Low chi-square values are indicative of a subject that responds to both sites equally, while high values indicate a side preference. Although this value is not completely independent of performance as measured by the proportion of correct responses, the two measures are not significantly correlated. For example, Choomba performed extremely well in both performance and Chi-square measures, whereas Kekla scored decently on performance but showed the highest side bias of any subject.

Side bias could not be effectively predicted by the independent variables used here, but the regression analysis may have been compromised by the high degree in variance of performance. One younger subject (Kekla) was considerably left side biased and scored a Chi-square value of 21.52. The next highest young subject scored a Chi-square of 6.27, and the average score for young subjects was 5.69. Alternatively, the average score for older subjects was 12.5, but the two lowest scores were 39-year-old females who scored less than 0.2. Although all older subjects except the two low scoring individuals scored higher for side bias than all the younger subjects except the young outlier, these outliers prevented a significant relationship between side bias and age. As

mentioned above, the variation in performance of older individuals can make statistical analysis with small sample sizes extremely difficult to interpret.

Experience may also have influenced performance on this task. As all three outliers were experienced subjects, a regression was run on only the inexperienced subjects to determine if age had an effect on these subjects. Despite very limited statistical power due to the few inexperienced subjects in the sample, age was a significant predictor of side bias. While perseveration or response rigidity is common in cognitive aging research, we cannot determine whether response rigidity is a useful strategy for this sort of task. For example, side bias may be a useful strategy with 50% of rewards being achieved until the task can be mastered after years of experience with cognitive testing. Alternatively, side bias may be the result of the failure of inhibitory control with age (Zacks & Hasher, 1994), and few aged individuals have the capabilities to perform the cognitive tasks as they were intended. The two older females that performed well with little side bias may be the only subjects that have received enough practice to develop a response strategy beyond simple side preference, or they may be the only subjects that have not deteriorated and are still able to employ more complex frontal lobe capacities to solve the tasks. Further research with response rigidity and side bias may illuminate the difference.

### **Experiment Five – Increasing Choice Sites**

As an alternative to increasing the delay to increase task complexity, the number of potential sites was increased from two to four to determine whether this had an effect on performance.

## **Methods**

### Subjects

In Experiment Five, 11 subjects completed all of the trials. Three subjects did not participate, as in Experiment Four, and two additional subjects at Disney's Animal Kingdom were not completed due to difficulties with management of the task.

### Test Methodology

In Experiment Five, the number of sites that require monitoring was increased incrementally from two wells to four wells. Baiting of the wells proceeded as in previous experiments. The wells were covered in simultaneous pairs, starting with the outside wells and moving toward the inside wells in all presentations. After the wells were covered the screen was placed between the subject and the wells for a delay interval of 30-sec.

Twenty trials per day were conducted, and each subject received five days of testing (100 total trials) with each combination of choice sites. Testing began with subjects receiving five days of trials with two wells at the 30-sec delay interval. Following completion of those trials, a third well was added and subjects received five days of testing with a 30-sec delay. Upon completion of those trials a fourth well was added and subjects received five days of testing with four possible choice sites and a 30-sec delay. Throughout testing wells were maintained at 10 cm apart. Due to space limitations for some subjects, adding additional wells would have required decreasing the spacing between wells or would not have been possible. To maintain consistency across subjects a maximum of four wells was used. Major hypotheses for the study were:

**H<sub>5A</sub>: As the number of baited sites was increased, performance was expected to decrease, with a more rapid decline seen in the performance of the older animals.** As with increasing the time interval, adding additional sites to be monitored increased the cognitive demand of the task. As a result, older animals were expected to perform less well than younger animals.

**H<sub>5B</sub>: Gender-related differences were expected in the younger animals, with males performing better. However, no gender-related differences were expected with older individuals.** Lacreuse et al (1999) found that male superiority in spatial tasks declined with age, such that no performance differences were found in old age with monkeys. As such, no age-related differences were expected.

**H<sub>5C</sub>: No differences related to experience were expected at any of the number of wells.** Experience was not expected to increase performance in this task due to the high numbers of trials already completed.

### **Data Analysis**

The proportion of correct responses for each individual at each set of choices was used as the dependent variable. A repeated-measures ANOVA model was created using the General Linear Model command in SPSS for each independent variable. As in Experiment Four a single multivariate model could not be utilized because the data violated the assumption of multivariate normality, as indicated by the Shapiro-Wilks test (Stevens, 2002), and the assumption of equality of covariance matrices, as indicated by

Box's Test. Differences between the within-subjects factor were assessed with Difference contrasts.

Gender and experience were coded as independent variables as in previous experiments, and age was categorized as young and old as in Experiment Four. All independent variables were used as between-subjects factors in the repeated-measures analyses.

Response rigidity was also assessed by calculating a Chi-square value for each subject from the observed and expected values of selections at each number of choices. Separate repeated-measures ANOVAs were run with choice sites as the within-subjects factors and the independent variables as the between-subjects factors as above.

## **Results**

For all three repeated-measures tests (Table 7 in Appendix A), performance significantly decreased as the number of choice sites was increased (Figure 9). Individual contrasts revealed that although there appears to be a linear decrease in performance across sites, the only significant difference is when two-sites are compared to four-sites ( $P < 0.05$ ). No interactions were observed between delay and any of the between subjects factors (age, gender, experience), and only experience showed a univariate effect for the between subjects factors (Table 7 in Appendix A). Inexperienced subjects performed better than experienced subjects at all delay intervals. When regression lines for the three delay intervals are examined graphically, it is apparent that there is no relationship between performance and age (Figure 10). Finally, males performed better than females across all delay intervals (mean: Males = 0.54, Females = 0.51).

When side bias was assessed using repeated-measures models, neither the within-subjects factor for side bias, the interaction with the independent variables, nor the between-subjects effect of the independent variables was significant (Table 8 in Appendix A). Older subjects tended to have more of a side bias (Figure 11), while males (mean: Males = 7.22, Females = 5.85) and experienced subjects (mean: Inexperienced = 2.62, Experienced = 8.26) tended to be more side biased.

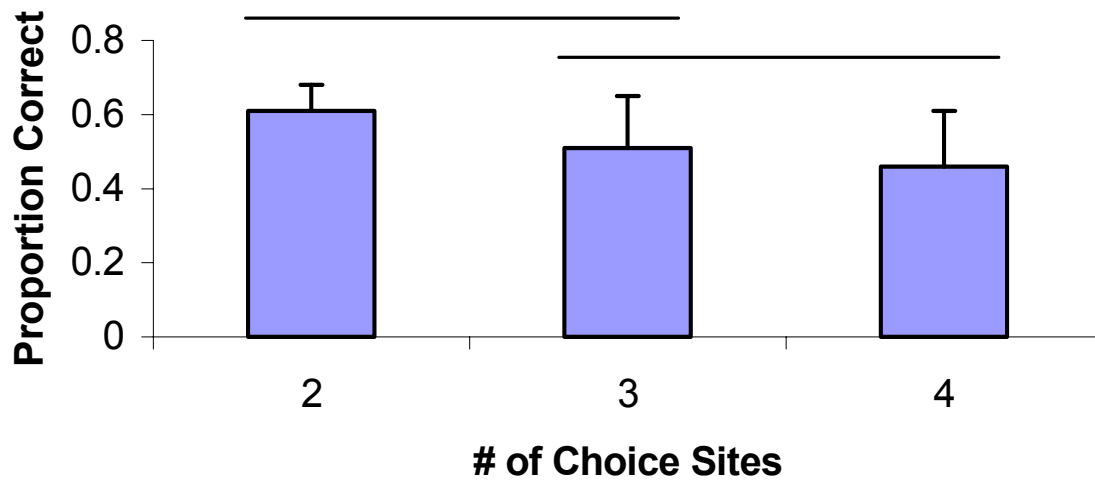
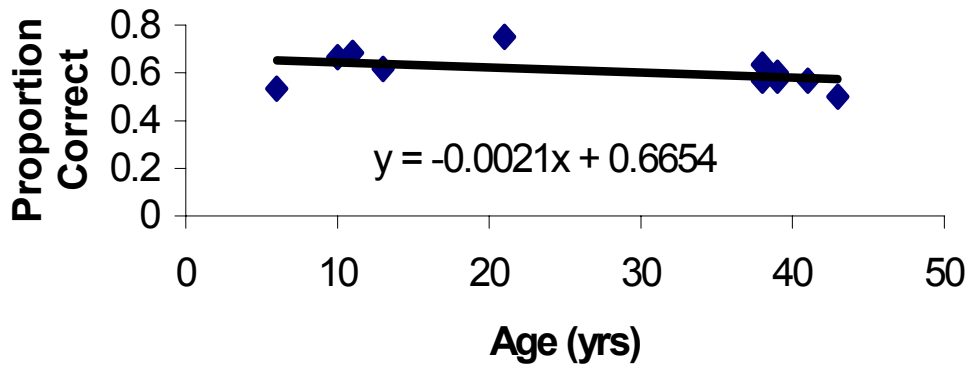
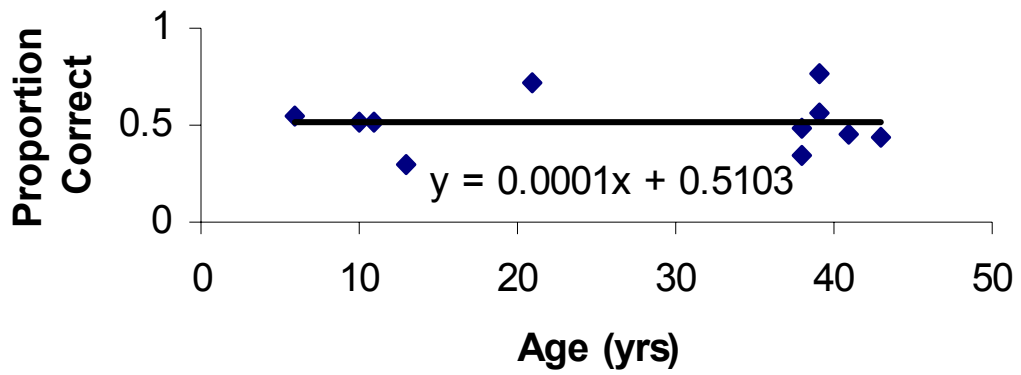


Figure 9. Performance as a Function of the Number of Potential Choice Sites in Experiment Five.

### Two Choice Sites



### Three Choice Sites



### Four Choice Sites



Figure 10. Performance as a Function of Age for 2, 3, and 4 Choice Sites in Experiment Five.

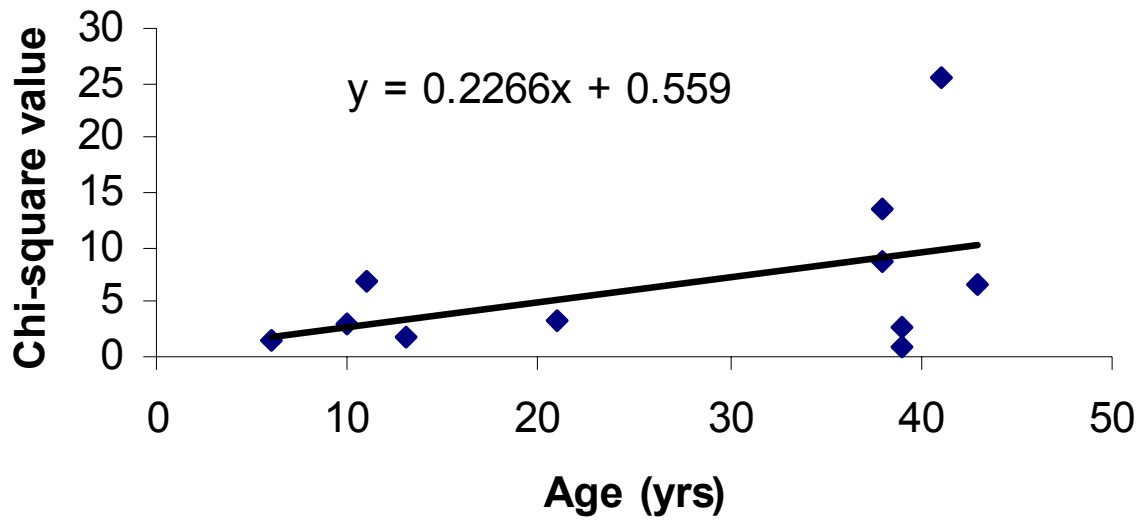


Figure 11. Side Bias as a Function of Age in Experiment Five with All Subjects Represented.

## **Discussion**

Repeated measures ANOVAs revealed that with an increasing number of choice sites the performance decreased, but there was no interaction with any of the independent factors, indicating that older subjects, different sexes and different experience levels did not react differently to the increased complexity of the task. Experience was the only independent factor to show a significant univariate effect as inexperienced subjects outperformed experienced subjects. As with Experiment Four, performance did not seem to be effected by age. Even when the results were graphed separately, there was no discernible pattern when performance was compared to age. While males performed slightly better than females the difference was not significant and probably related to the finding that inexperienced subjects performed better than experienced subjects. Whether that finding is an artifact of the study design (i.e. small sample size) is not known at this time.

No significant effects were found for the independent variables to effect side bias. As with Experiment Four, there did appear to be a trend for older subjects to show more side bias, but the depleted sample in Experiment five prevented further analysis of the data.

## **General Discussion**

Like other ape aging studies, the findings in the present study fail to show group wide impairments related to age for cognitive tasks. While no significant trends appear in the data during the acquisition of tasks and in tasks with low cognitive demands, these trends are not statistically significant.

## **Impact of Experience and Gender**

Due to logistical constraints the subject pool in this study was highly confounded. Although the correlation among age, experience, and gender did not mathematically impact statistical analyses (i.e. VIF statistic diagnosis of multicollinearity), it does affect the interpretation of the independent variables, particularly gender. Gender and age are highly correlated in the current sample with older subjects tending to be female and to a lesser degree experienced and younger subjects tending to be male and to a lesser degree inexperienced.

Research with monkeys has indicated a male superiority in spatial tasks that disappears with increasing age (Herndon & Lacreuse, 2002; Lacreuse et al., 1999). While the nonhuman model of gender-related differences in humans is extremely valuable because of its ability to control for socio-cultural factors (Herndon & Lacreuse, 2002), the subject is virtually untouched within the confines of age-related impacts with apes. Despite the high degree of confound, the analyses were run for gender-effects with the hope of a clear finding, but due to the limitations of the dataset any additional interpretation would be unwise.

Experience, although less confounded with age than gender, is also a major confound in the study design. All of the aged females and one of the aged males at Zoo Atlanta were found to have extensive cognitive research experience at Yerkes National Primate Research Center prior to coming to the zoo. Documentation of specific studies these individuals were used in and the number of trials is impossible because many were reported in book chapters where information on subjects is limited. However, institutional records indicate these individuals participated in anywhere from four to 10

different cognitive protocols. These individuals are expected to be more familiar with the testing procedure, and research with humans has indicated aged humans benefit from testing with familiar materials or in a familiar environment (Botwinick, 1984). Thus, as age and experience are somewhat confounded, it is possible that age-related decline is moderated by experience. The lack of sufficiently aged, inexperienced subjects prevents separation of these variables in the current analysis, but future research should focus on research naïve subjects to eliminate this confound.

### **Impact of Age**

In two previous assessments of cognitive capacity using the delayed response tasks in chimpanzees, age-related impairments were equivocal. Riopelle and Rogers (1965) found a trend for age-related decline in performance with 18 chimpanzees between 6 and 40 years while using 0- and 5-sec. However, this difference was less pronounced when a 10-sec delay was employed. Alternatively, Bloomsmith et al. (in review) found no age-related differences at 0- and 5-sec delays while comparing two aged and two young chimpanzees, but did find age-related impairments when using a 10-sec delay. Unfortunately, these samples sizes are relatively small, particularly given that only four of the 18 subjects in the Riopelle and Rogers study were over 30 years of age and only two were over 35, the benchmark used to define old age in chimpanzees by Tarou, Bloomsmith, Hoff, Erwin, and Maple (2002).

The current study design differs from previous ape aging studies in two important ways. First, the number of aged subjects is twice that used by Riopelle and Rogers and four times that used by Bloomsmith and colleagues. Second, the 10-sec delay interval used in previous ape aging studies is shorter than the 15-sec delay interval required to

produce reliable age-related differences in the delayed response task in monkeys (Bachevalier et al., 1991; Bachevalier, 1993; Lacreuse et al., 2002). The current study employed delay intervals up to 90 seconds, well within the range that would be expected to reveal age differences in monkeys, and much longer than those previously used with apes. Despite these advantages, no age-related differences were apparent. Even though the increasing delay interval did decrease performance the decrease was seen equally across all ages.

The delayed response tasks used in the Riopelle and Rogers (1965) and Bloomsmith et al (in review) studies employed five choice sites at all delay intervals. The current study employed only two choice sites in the assessment of the effects of increasing delay, but added up to four choice sites in Experiment Five. Again, no age-related differences were evident with increasing number of choice sites despite an overall decrease in performance. Due to space limitations for some of the subjects the number of choice sites was restricted to four. Additional sites would have required the spacing to be decreased between foodwells and decreasing distance between foodwells can negatively impact performance (Fletcher, 1965). It may be that the number of choice sites in this and previous ape studies were not sufficiently complex to reveal age-related differences in performance. Additionally, the combination of increasing delay interval with a minimum of five choice sites should be examined.

### **The Delayed Response Task**

Beside the lack of complexity in the tasks what else could explain the lack of age-related differences in apes when differences exist for humans, which could arguably be classified as an ape, and monkeys? One of the possibilities lies in the delayed response

task itself. Harlow once wrote, “Psychologists have often been at a loss as to how to classify the delayed response. It has been variously considered as a learning problem, attention problem, memory problem, and thinking problem” (Harlow, Harlow, Reuping, & Mason, 1960, p. 120). Fletcher (1965) elaborated on the issues with the delayed response problem stating there were four fundamental phases, three of which are important in the current context: baiting, delay, and response. In the baiting phase there is no guarantee that the subject attended to the baiting of the foodwell. In the current study, the subject’s name was called, the food was waved, and it was only placed when the observer “thought” the subject was attending to the food item. With this methodology, as in all direct-baiting delayed response tasks, there is never a confirmation of attention as there is in a matching to sample study or when using an automated apparatus like the AGED device (Bartus, Dean, & Fleming, 1979). Additionally, when the direct baiting procedure is used, the subject is permitted to see the reward and evaluate its intrinsic value. This has the potential to decrease the motivation of the subjects to participate.

Subjects in the current study were not food restricted in part because previous work at Zoo Atlanta has revealed the gorillas do not attend to tasks until after their afternoon feeding. More importantly, the outdoor habitats at Zoo Atlanta and Disney’s Animal Kingdom make it impossible to completely restrict all food items because many browse items grow in the exhibits where the animals spend their day. The lack of food deprivation may have resulted in decreased motivation. While Riopelle and Rogers (1965) noted that their chimpanzees were highly motivated to participate, some of the subjects had to be coaxed to the testing apparatus and many would leave the testing areas

during some of the delays. Whether species differences between gorillas and chimps caused this difference in motivation or whether it is due to the lack of food restriction is difficult to determine.

During the delay interval, orienting behaviors can confound results in the delayed response task because the subject knows the location of the correct answer. Overt body orientation did not appear occur in these gorillas during the tasks, as subjects would frequently change positions or get up and walk around during the delay. However, a few subjects attempted to “placeholder” by making a selection prior to being allowed to touch the cups and continuing to hold their hand in that spot during the delay interval. Not all subjects attempted this behavior, but those that did were asked to place their hands on the mesh between the cups and hold them there during the delay interval. This behavior was requested only once per trial and subjects would either hold their hands in place on the mesh or engage in other behaviors, but they would not return their hand to “placeholder” once they removed them from the spot. While this technique may have prevented overt orientation, there is really no control for covert orientation, such as visual gaze. While an intervening behavior could be requested to combat covert orientation behaviors, this would require all subjects to be equally trained to perform a behavior that they would willingly engage in for hundreds of trials. This is probably not practical.

Another issue during the delay is distractibility. During the delay interval, the experimenter has little control over distractions. While large-scale behavioral changes can be noted and separated during later analyses, there are no operational definitions that can accurately detect all distractions. Finally, the sequence of delay presentation can lead to inconsistent results. The standard procedure, which is to incorporate multiple trials of

multiple delay intervals in a single testing session, may lead to inconsistent results. Riopelle (1959) suggested that incorporating multiple long duration trials in a single session might lead to frustration that affects performance on short intervals. In fact, titrated procedures can increase performance levels by up to 20% or more. The standard procedure was utilized in the current study to enable the testing of a larger number of subjects.

Finally, during the response phase the outcomes of prior responses can influence performance. As there is a great deal of trial-to-trial interference, reinforcement on a particular side can influence future responses by making subjects more likely to choose that side. Stanley and Jaynes (1949) posited a “cortical act-inhibition hypothesis” whereby the frontal cortex was responsible for suppressing responses that are inappropriate. This hypothesis exists today in a modified format. The prefrontal cortex is often viewed as the locus of executive function, responsible for decision-making and allocation of resources (Gallagher & Rapp, 1997), but the basal ganglia are attracting more attention for their role in activating and inhibiting motor responses (Alexander, Crutcher, & DeLong, 1990). Moreover, the basal ganglia seem to be involved in perseverative responding in cognitive tasks, as well as stereotyped behavior in captive animals (Garner & Mason, 2002; Garner, Meehan, & Mench, 2003). Individuals who respond perseveratively in a 2-choice ‘gambling task’ are more likely to engage in stereotypic behavior and it appears that the inhibitory capacity of the basal ganglia is the neurological substrate for this lack of behavioral inhibition. Individuals who are unable to inhibit the motor response of selecting a previously rewarded location may be likely to show biased responding in the delayed response task.

## **Response Rigidity and Perseveration**

While Fletcher (1965) views the propensity for stereotyped responding in the delayed response procedure as a negative component of the task, it may be a useful feature for aging research. It may be that the delayed response task, or indeed any two-choice cognitive task, may create a situation in which perseverative responding is more likely. Perseveration is a feature of normal human aging (Foldi, Helm-Estabrooks, Redfield, & Nickel, 2003). It is the continued selection of a previously rewarded location despite the current inappropriate nature of the response. A large number of studies have shown age-related perseveration with impairment in various types of reversal learning in rhesus macaques (Bartus et al., 1979; Herndon et al., 1997; Voytko, 1990). However, in aged chimps Bernstein (1961) reported no response rigidity, while Bloomsmith et al (in review) reported that one of two aged subjects showed high response rigidity during a reversal-learning task.

In the current study, response bias was evaluated with Chi-square scores. Three outliers (one young subject and two old subjects) prevent a strong relationship with age for response rigidity, a finding supported by many nonhuman primate studies (Bartus et al., 1979; Herndon et al., 1997, Voytko, 1999). Many aging studies report some aged subjects maintaining performance at or better than the performance of younger subjects even when age-related difference exist (Craik et al., 1987; Herndon et al., 1997; Killiany et al., 2000; Shimamura, 1993; Voytko, 1999). This can make it difficult to assess with small sample sizes (Bloomsmith et al., in review), particularly if the subjects are mixed with respect to their research history.

Thus, while the statistical and methodological challenges prevent definitive statements about the relationship between age and side bias, side bias in choice tasks and response rigidity and perseveration may be features of increasing age in gorillas, particularly gorillas without extensive testing histories. Future studies that are specifically designed to examine response rigidity will further illuminate the relationship between these variables.

### **Conclusions**

In the largest study of age-related changes in gorilla cognition to date, few age-related detriments in performance could be found. Although increases in delay interval and the number of choice sites negatively impacted performance, older subjects were not more severely impacted. When using the proportion of correctly answered trials as the dependent measure, performance is virtually unchanged with increasing age. However, there is some indication that older gorillas are more likely to develop a side bias and choose that side more often regardless of whether it is baited or not.

Additionally, the delayed response task as employed here may not be appropriate for detecting age-related impairment. Future use of the delayed response task should include some degree of automation to determine attention to the baiting and employ a titration procedure instead of massing long delay trials into a single session.

Finally, not all zoo-housed subjects are equal in their usefulness to understanding cognitive aging in humans or nonhuman primates. Previous research experience was documented to impact performance during the acquisition of the tasks and it may impact performance in more complicated task by mediating cognitive decline or providing a

more familiar research environment for subjects with extensive testing history. Until a large enough sample, which is free from confounds associated with experience and gender, is assembled, apes will not be useful models for assessing human cognitive aging.

## APPENDIX A

### TABLES

Table 1. Demographic Attributes of Subjects.

| <b>Gorilla</b> | <b>Institution</b> | <b>Age<br/>(yrs)</b> | <b>Gender</b> | <b>Research<br/>Experience</b> |
|----------------|--------------------|----------------------|---------------|--------------------------------|
| Shamba         | Atlanta            | 43                   | F             | Yes                            |
| Ozzie          | Atlanta            | 41                   | M             | Yes                            |
| Katie          | Atlanta            | 40                   | F             | Yes                            |
| Choomba        | Atlanta            | 39                   | F             | Yes                            |
| Paki           | Atlanta            | 39                   | F             | Yes                            |
| Banga          | Atlanta            | 38                   | F             | Yes                            |
| Ivan           | Atlanta            | 38                   | M             | Yes                            |
| Benga          | DAK                | 31                   | F             | No                             |
| Hope           | DAK                | 21                   | F             | No                             |
| Gus            | DAK                | 21                   | M             | No                             |
| Kejana         | DAK                | 13                   | M             | No                             |
| Kekla          | Atlanta            | 11                   | M             | Yes                            |
| Spike          | DAK                | 10                   | M             | No                             |
| Hasani         | DAK                | 8                    | M             | No                             |
| Jabari         | DAK                | 6                    | M             | No                             |
| Charlie        | Atlanta            | 6                    | M             | Yes                            |

Table 2. Regression Results for Experiment One Examining Trials to Criterion and Errors to Criterion.

| <b>Trials to Criterion</b> |                  |             |          |          |
|----------------------------|------------------|-------------|----------|----------|
|                            | <i>Predictor</i> | <i>Beta</i> | <i>t</i> | <i>P</i> |
|                            | Age              | 0.377       | 1.256    | 0.233    |
|                            | Gender           | 0.308       | 1.235    | 0.241    |
|                            | Experience       | -0.874      | -3.728   | 0.003    |
| <b>Errors to Criterion</b> |                  |             |          |          |
|                            | <i>Predictor</i> | <i>Beta</i> | <i>t</i> | <i>P</i> |
|                            | Age              | 0.263       | 0.899    | 0.386    |
|                            | Gender           | 0.171       | 0.702    | 0.496    |
|                            | Experience       | -0.881      | -3.856   | 0.002    |

Table 3. Regression Results for Experiment Two Examining Trials to Criterion and Errors to Criterion.

| <b>Trials to Criterion</b> |                  |             |          |          |
|----------------------------|------------------|-------------|----------|----------|
|                            | <i>Predictor</i> | <i>Beta</i> | <i>t</i> | <i>P</i> |
|                            | Age              | 0.589       | 1.515    | 0.156    |
|                            | Gender           | 0.279       | 0.866    | 0.403    |
|                            | Experience       | 0.164       | 0.542    | 0.598    |
| <b>Errors to Criterion</b> |                  |             |          |          |
|                            | <i>Predictor</i> | <i>Beta</i> | <i>t</i> | <i>P</i> |
|                            | Age              | 0.639       | 1.668    | 0.121    |
|                            | Gender           | -0.106      | -0.333   | 0.745    |
|                            | Experience       | -0.342      | -1.144   | 0.275    |

Table 4. Regression Results for Experiment Three Examining Trials to Criterion and Errors to Criterion.

| <b>Trials to Criterion</b> |                  |             |          |          |
|----------------------------|------------------|-------------|----------|----------|
|                            | <i>Predictor</i> | <i>Beta</i> | <i>t</i> | <i>P</i> |
|                            | Age              | 0.474       | 1.088    | 0.298    |
|                            | Gender           | -0.021      | -0.057   | 0.955    |
|                            | Experience       | -0.325      | -0.957   | 0.357    |
| <b>Errors to Criterion</b> |                  |             |          |          |
|                            | <i>Predictor</i> | <i>Beta</i> | <i>t</i> | <i>P</i> |
|                            | Age              | 0.451       | 1.010    | 0.333    |
|                            | Gender           | 0.072       | 0.195    | 0.849    |
|                            | Experience       | -0.340      | -0.975   | 0.349    |

Table 5. Repeated-measures ANOVA Results for Experiment Four Examining Within-subjects Effects of Delay Interval and Between Subjects Effects of Age, Gender, and Experience on Performance.

| <b>Between-Subjects Factor</b> | <b>Delay</b>                         | <b>Delay X Between-Subjects Factor Interaction</b> | <b>Between-Subjects Effect</b>  |
|--------------------------------|--------------------------------------|--|---------------------------------|
| Age                            | Wilks $\lambda = 0.473$<br>P = 0.016 | Wilks $\lambda = 0.990$<br>P = 0.944               | $F_{1,12} = 0.000$<br>P = 0.998 |
| Gender                         | Wilks $\lambda = 0.433$<br>P = 0.010 | Wilks $\lambda = 0.823$<br>P = 0.343               | $F_{1,12} = 0.262$<br>P = 0.618 |
| Experience                     | Wilks $\lambda = 0.469$<br>P = 0.015 | Wilks $\lambda = 0.989$<br>P = 0.943               | $F_{1,12} = 0.045$<br>P = 0.835 |

Table 6. Regression Results from Experiment Four Examining the Effects of Age, Gender, and Experience on Side Bias.

| <b>Side Bias (<math>X^2</math>)</b> |             |          |          |  |
|-------------------------------------|-------------|----------|----------|--|
| <i>Predictor</i>                    | <i>Beta</i> | <i>t</i> | <i>P</i> |  |
| Age                                 | 0.389       | 0.951    | 0.364    |  |
| Gender                              | 0.156       | 0.433    | 0.674    |  |
| Experience                          | 0.214       | 0.650    | 0.530    |  |

Table 7. Repeated-measures ANOVA Results for Experiment Five Examining Within-subjects Effects of Number of Choice Sites and Between Subjects Effects of Age, Gender, and Experience on Performance.

| <b>Between-Subjects Factor</b> | <b>Choice Sites</b>                  | <b>Choice Sites X Between-Subjects Factor Interaction</b> | <b>Between-Subjects Effect</b> |
|--------------------------------|--------------------------------------|---|--------------------------------|
| Age                            | Wilks $\lambda = 0.313$<br>P = 0.010 | Wilks $\lambda = 0.861$<br>P = 0.550                      | $F_{1,9} = 0.786$<br>P = 0.399 |
| Gender                         | Wilks $\lambda = 0.336$<br>P = 0.013 | Wilks $\lambda = 0.845$<br>P = 0.509                      | $F_{1,9} = 0.135$<br>P = 0.721 |
| Experience                     | Wilks $\lambda = 0.385$<br>P = 0.022 | Wilks $\lambda = 0.622$<br>P = 0.150                      | $F_{1,9} = 6.588$<br>P = 0.030 |

Table 8. Repeated-measures ANOVA Results for Experiment Five Examining Within-subjects Effects of Number of Choice Sites and Between Subjects Effects of Age, Gender, and Experience on Side Bias.

| <b>Between-Subjects Factor</b> | <b>Choice Sites</b>                  | <b>Choice Sites X Between-Subjects Factor Interaction</b> | <b>Between-Subjects Effect</b> |
|--------------------------------|--------------------------------------|---|--------------------------------|
| Age                            | Wilks $\lambda = 0.653$<br>P = 0.181 | Wilks $\lambda = 0.8641$<br>P = 0.558                     | $F_{1,9} = 2.340$<br>P = 0.160 |
| Gender                         | Wilks $\lambda = 0.696$<br>P = 0.235 | Wilks $\lambda = 0.677$<br>P = 0.210                      | $F_{1,9} = 0.081$<br>P = 0.782 |
| Experience                     | Wilks $\lambda = 0.945$<br>P = 0.433 | Wilks $\lambda = 0.733$<br>P = 0.338                      | $F_{1,9} = 1.127$<br>P = 0.319 |

## REFERENCES

- Albert, M.S., & Moss, M.B. (1996). Neuropsychology of aging: Findings in humans and monkeys. In E.L. Schneider & J.W. Rowe (Eds.), *Handbook of the Biology of Aging*, 4<sup>th</sup> ed. (pp. 217-233). New York: Academic Press.
- Alexander, G.E., Crutcher, M.D., DeLong, M.R. (1990). Basal ganglia-thalamocortical circuits: parallel substrates for motor, oculomotor, 'prefrontal' and 'limbic' functions. *Progress in Brain Research* 85, 119-146.
- Alvarez, P., Zola-Morgan, S., Squire, L.R. (1995). Damage limited to the hippocampal region produces long-lasting memory impairments in monkeys. *Journal of Neuroscience*, 15, 3796-3807.
- Anderson, U. (2003). Aging, numerous judgments and summation in Western Lowland Gorillas (*Gorilla g. gorilla*). Unpublished master's thesis. Georgia Institute of Technology.
- Arias, E., Smith, B.S. (2003). Deaths: Preliminary data for 2001. National Vital Statistics Reports 51(5): 1-45.
- Bachevalier, J. (1993). Behavioral changes in aged rhesus monkeys. *Neurobiology of Aging*, 14, 619-621.
- Bachevalier, J., Landis, L.S., Walker, L.C., Brickson, M., Mishkin, M., Price, D.L., et al. (1991). Aged monkeys exhibit behavioral deficits indicative of widespread cerebral dysfunction. *Neurobiology of Aging*, 12, 99-111.
- Baddeley, A.D. (1986). *Working Memory*. Oxford, England: Oxford University Press.
- Baltes, P.B. (1987). Theoretical propositions of life-span development: On the dynamics between growth and decline. *Developmental Psychology*, 23, 611-626.
- Barnes, C.A., McNaughton, B.L., O'Keefe, L. (1983). Loss of place specificity in hippocampal complex-spike cells in the senescent rat. *Neurobiology of Aging*, 4, 113-119.
- Bartus, R.T., Dean, R.L., Fleming, D.L. (1979). Aging in the rhesus monkey: Effects on visual discrimination learning and reversal learning. *Journal of Gerontology* 34, 209-219.
- Bartus, R.T., Fleming, D., Johnson, H.R. (1978). Aging in the rhesus monkey: Debilitating effects on short-term memory. *Journal of Gerontology*, 33, 858-871.

- Bartus, R.T., Johnson, H.R. (1976). Short-term memory in the rhesus monkey: Disruption from the anti-cholinergic scopolamine. *Pharmacology, Biochemistry, and Behavior*, 5, 39-40.
- Bernstein, I.S. (1961). Response variability and rigidity in the adult chimpanzee. *Journal of Gerontology*, 16, 381-386.
- Bloomsmith, M.A., Anderson, U.S., Smith, A.D., Maple, T.L. In review. A longitudinal analysis of simple learning and memory tasks in two aged chimpanzees. *Experimental Gerontology*.
- Botwinick, J. (1984). *Aging and behavior*. New York: Spring Publishing Co.
- Cerella, L. (1985). Information processing rates in the elderly. *Psychological Bulletin*, 98, 67-83.
- Corkin, S. (1984). Lasting consequences of bilateral medial temporal lobectomy: Clinical course and experimental findings in H.M. *Journal of Neuroscience*, 2, 1214-1229.
- Craik, F.I.M. (1983). On the transfer of information from temporary to permanent memory. *Philosophical Transactions of the Royal Society of London*, B302, 341-359.
- Craik, F.I.M. (1986). A functional account of age differences in memory. In F. Klix & H. Hagendorf (Eds.), *Human memory and cognitive capabilities* (pp. 409-422). Amsterdam: Elsevier.
- Craik, F.I.M., Byrd, M. (1982). Aging and cognitive deficits: The role of attentional resources. In F.I.M. Craik & S. Trehub (Eds.), *Aging and cognitive processes* (pp. 191-211). New York: Plenum.
- Craik, F.I.M., Byrd, M., Swanson, J.M. (1987). Patterns of memory loss in three elderly samples. *Psychology and Aging*, 2, 79-86.
- Craik, F.I.M., Salthouse, T.A. (2000). *The Handbook of Aging and Cognition*, 2<sup>nd</sup> edition. Mahwah, N.J.: Lawrence Erlbaum Associates.
- Davis, R.T. (1978). Old monkey behavior. *Experimental Gerontology*, 13, 237-250.
- Derenne, A., Baron, A. (2002). Behavior analysis and the study of human aging. *The Behavior Analyst*, 25, 151-160.
- Dunnett, S.B., Evenden, J.L., Iversen, S.D. (1988). Delay-dependent short-term memory impairments in aged rats. *Psychopharmacology, Supplement 1*, 104-111.

- Elias, P.K., Elias, M.F. (1976). Effects of age on learning ability: Contributions from the animal literature. *Experimental Aging Research*, 2, 165-186.
- Engle, R.W., Cantor, J., Carullo, J.J. (1992). Individual differences in working memory and comprehension: A test of four hypotheses. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 18, 972-992.
- Erickson, C.A., Barnes, C.A. (2003). The neurobiology of memory changes in normal aging. *Experimental Gerontology*, 38, 61-69.
- Erwin, J.M., Hof, P.R., Ely, J.J., & Perl, D.P. (2002). One gerontology: Advancing understanding of aging through studies of great apes and other primates. In J.M. Erwin, & P.R. Hof (Eds.), *Aging in Nonhuman Primates. Interdisciplinary Topics in Gerontology* (pp. 1-21). Basel: Karger.
- Fletcher, H.J. (1965). The delayed response problem. In A.M. Schrier, H.F. Harlow, & F. Stollnitz (Eds.), *Behavior of Nonhuman Primates*, Vol. 1 (pp. 129-165). New York: Academic Press.
- Flicker, C., Bartus, R.T., Crook, T., Ferris, S.H. (1984). Effects of aging and dementia upon recent visuospatial memory. *Neurobiology of Aging*, 5, 75-83.
- Foldi, N.S., Helm-Estabrooks, N., Redfield, J., Nickel, D.G. (2003). Perseveration in normal aging: A comparison of perseveration rates on design fluency and verbal generative tasks. *Aging, Neuropsychology, and Cognition*, 10, 268-280.
- Frick, K.M., Stearns, N.A., Pan, J.Y., Berger-Sweeney, J. (2003). Effects of environmental enrichment on spatial memory and neurochemistry in middle aged mice. *Learning and Memory*, 10, 187-198.
- Gage, F.H., Dunnett, S.B., Bjorklund, A. (1984). Spatial learning and motor deficits in aged rats. *Neurobiology of Aging*, 5, 43-48.
- Gallagher, M., Rapp, P.R. (1997). The use of animal models to study the effects of aging on cognition. *Annual Review of Psychology*, 48, 339-370.
- Garner, J.P., Mason, G.J. (2002). Evidence for a relationship between cage stereotypies and behavioral disinhibition in laboratory rodents. *Behavioural Brain Research*, 136, 83-92.
- Garner, J.P., Meehan, C.L., Mench, J.A. (2003). Stereotypies in caged parrots, schizophrenia and autism: evidence for a common mechanism. *Behavioural Brain Research*, 145, 125-134.
- Glisky, E.L., Polster, M.R., Routhieux, B.C. (1995). Double dissociation between item and source memory. *Neuropsychology*, 9, 229-35.

- Goodrick, C.L. (1975). Behavioral rigidity as a mechanism for facilitation of problem solving for aged rats. *Journal of Gerontology*, *30*, 181-184.
- Graf, P., Schacter, D.L. (1985). Implicit and explicit memory for new associations in normal and amnesic subjects. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *11*, 501-518.
- Harlow, H.F., Harlow, M.K., Rueping, R.R., Mason, W.A. (1960). Performance of infant rhesus monkeys on discrimination learning, delayed response, and discrimination learning set. *Journal of Comparative and Physiological Psychology* *53*, 113-121.
- Hasher, L., & Zacks, R.T. (1979). Automatic and effortful processes in memory. *Journal of Experimental Psychology: General*, *108*, 356-388.
- Hasher, L., Zacks, R.T. (1988). Working memory, comprehension, and aging: A review and a new view. In G. Bower (Ed.), *The psychology of learning and motivation* (Vol. 22, pp. 193-225). New York: Academic Press.
- Herndon, J.G., & Lacreuse, A. (2002). The rhesus monkey as a heuristic resource in cognitive aging research. In J.M. Erwin, & P.R. Hof (Eds.), *Aging in Nonhuman Primates. Interdisciplinary Topics in Gerontology* (pp. 178-195). Basel: Karger.
- Herndon, J.G., Lacreuse, A., Ladinsky, E., Killiany, R.J., Rosene, D.L., Moss, M.B (1999a). Age-related decline in DHEAS is not related to cognitive impairment in aged monkeys. *NeuroReport*, *10*, 3507-3511.
- Herndon, J.G., Moss, M.B., Rosene, D.L., Killiany, R.J. (1997). Patterns of cognitive decline in aged rhesus monkeys. *Behavioral Brain Research*, *87*, 25-34.
- Herndon, J.G., Tigges, J., Anderson, D.C., Klump, S.A., McClure, H.M. (1999b). Brain weight throughout the lifespan of the chimpanzee. *Journal of Comparative Neurology*, *409*, 567-572.
- Howard, D.V., Howard, J.H., Jr. (1989). Age differences in learning serial patterns: Direct versus indirect measures. *Psychology and Aging*, *4*, 357-364.
- Killiany, R.J., Moss, M.B., Rosene, D.L., Herndon, J. (2000). Recognition memory function in early senescent rhesus monkeys. *Psychobiology*, *28*, 46-56.
- Lacreuse, A., Herndon, J.G., Killiany, R.J., Rosene, D.L., Moss, M.B. (1999). Spatial cognition in rhesus monkeys: Male superiority declines with age. *Hormones and Behavior*, *36*, 70-76.

- Lacreuse, A., Wilson, M.E., Herndon, J.G. (2002). Estradiol, but not raloxifene, improves aspects of spatial working memory in aged ovariectomized rhesus monkeys. *Neurobiology of Aging*, 23, 589-600.
- Lai, Z.C., Moss, M.B., Killiany, R.J., Rosene, D.L., Herndon, J.G. (1995). Executive system dysfunction in the aged rhesus monkey: Spatial and object reversal learning. *Neurobiology of Aging*, 16, 947-954.
- Lane, M.A. (2000). Nonhuman primate models in biogerontology. *Experimental Gerontology*, 35, 533-541.
- Lange, K.W., Robbins, T.W., Marsden, C.D., James, M., Owen, A.M., Paul, G.M. (1992). L-dopa withdrawal in Parkinson's disease selectively impairs cognitive performance in tests sensitive to frontal lobe function. *Psychopharmacology*, 107, 394-404.
- MacDonald, S.E. (1994). Gorillas' (*Gorilla gorilla gorilla*) spatial memory in a foraging task. *Journal of Comparative Psychology*, 108, 107-113.
- MacDonald, S.E., Agnes, M.M. (1999). Orangutan (*Pongo pygmaeus abelii*) spatial memory and behavior in a foraging task. *Journal of Comparative Psychology*, 113, 213-217.
- Medin, D.L. (1969). Form perception and pattern reproduction in monkeys. *Journal of Comparative and Physiological Psychology*, 68, 412-419.
- Menich, S.R., Baron, A. (1984). Social housing of rats: Life-span effects on reaction time, exploration, weight, and longevity. *Experimental Aging Research*, 10, 95-100.
- Meyer, D.R., Harlow, H.F. (1952). Effects of multiple variables on delayed response performance by monkeys. *Journal of Genetic Psychology*, 81, 53-61.
- Morris, R.K.M. (1981). Spatial localization does not require the presence of local cues. *Learning and Motivation*, 12, 239-260.
- Moscovitch, M., Ulmita, C. (1991). Conscious and unconscious aspects of memory: A neuropsychological framework of modules and central systems. In R.G. Lister, H.J. Weingartner (eds.) *Perspectives on Cognitive Neuroscience*, (pp. 229-266). New York: Oxford University Press.
- Moss, M.B., Albert, M.S., Butters, N., Payne, M. (1986). Differential patterns of memory loss among patients with Alzheimer's disease, Huntington's disease, and alcoholic Korsakoff's syndrome. *Archives of Neurology*, 43, 239-246.

- Moss, M.B., Rosene, D.L., Peters, A. (1988). Effects of aging on visual recognition memory in the rhesus monkey. *Neurobiology of Aging*, 9, 495-502.
- Muir, J.L., Fischer, W., Bjorklund, A. (1999). Decline in visual attention and spatial memory in aged rats. *Neurobiology of Aging*, 20, 605-615.
- O'Keefe, J., Nadel, L. (1978). *The Hippocampus as a Cognitive Map*. Oxford: Clarendon Press.
- Parkin, A.J., Walter, B.M., Hunkin, N.M. (1995). Relationships between normal aging, frontal lobe function and memory for temporal and spatial information. *Neuropsychology*, 9, 304-312.
- Peters, A., Rosene, D.L., Moss, M.B., Kemper, T.L., Abraham, C.R., Tigges, J., Albert, M.S. (1996). Neurobiological bases of age-related cognitive decline in the rhesus monkey. *Journal of Neuropathology and Experimental Neurology*, 55, 861-874.
- Poe, G.R., Teed, R.G.W., Insel, N., White, R., McNaughton, B.L., Barnes, C.A. (2000). Partial hippocampal inactivation: Effects on spatial memory performance in aged and young rats. *Behavioral Neuroscience*, 114, 940-949.
- Rapp, P.R. (1990). Visual discrimination and reversal learning in the aged monkey (*Macaca mulatta*). *Behavioral Neuroscience*, 104, 876-884.
- Rapp, P.R., Amaral, D.G. (1989). Evidence for task-dependent memory dysfunction in the aged monkey. *Journal of Neuroscience*, 9, 3568-3576.
- Rapp, P.R., Rosenberg, R.A., Gallagher, M. (1987). An evaluation of spatial information processing in aged rats. *Behavioral Neuroscience*, 101, 3-12.
- Rehbein, L. (1985). *Long-term effects of early hippocampectomy in the monkey*. Unpublished doctoral dissertation, Northeastern University.
- Riopelle, A.J., & Rogers, C.M. (1965). Age changes in chimpanzees. In A.M. Schrier, H.F. Harlow, F. Stollnitz (Eds.), *Behavior of Nonhuman Primates: Modern Research Trends* (pp. 449-462). New York: Academic Press.
- Roberts, J.A., Gilardi, V.K., Lasley, B., Rapp, P.R. (1997). Reproductive senescence predicts cognitive decline in aged female monkeys. *NeuroReport*, 8, 2047-2051.
- Roberts, J.A. (2002). The aged rhesus macaque in neuroscience research: Importance of the nonhuman primate model. In J.M. Erwin, P.R. Hof (Eds.), *Aging in Nonhuman Primates: Interdisciplinary Topics in Gerontology* (pp. 155-177). Basel: Karger.

- Rogers, J., Zornetzer, S.F., Bloom, F.E., Mervis, R.E. (1984). Senescent microstructural changes in rat cerebellum. *Behavioral Brain Research*, 292, 23-32.
- Rumbaugh, D.M. (1970). Learning skills of anthropoids. In L.A. Rosenblum (Ed.), *Primate Behavior, Vol. 1: Developments in Field and Laboratory Research* (pp. 2-70), New York: Academic Press, Inc.
- Salthouse, T.A. (1991). *Theoretical perspectives on cognitive aging*. Hillsdale, N.J.: Lawrence Erlbaum Associates.
- Salthouse, T.A. (1996). The processing speed theory of adult age differences in cognition. *Psychological Review*, 103, 403-428.
- Salthouse, T.A., Babcock, R.L. (1991). Decomposing adult age differences in working memory. *Developmental Psychology*, 27, 73-776.
- Schrier, A.M., Harlow, H.F., Stollnitz, F. (Eds.). (1965). *Behavior of Nonhuman Primates, Volume 1*. New York: Academic Press.
- Shimamura, A.P. (1993). Neuropsychological analyses of implicit memory: History, methodology, and theoretical interpretations. In P. Graf, M.E.J. Masson (Eds.), *Implicit memory: New Directions in Cognition, Development, and Neuropsychology* (pp. 265-285). Hillsdale, N.J.: Lawrence Erlbaum Associates.
- Spetch, M.L., Edwards, C.A. (1986). Spatial memory in pigeons (*Columba livia*) in an open-field feeding environment. *Journal of Comparative Psychology*, 3, 266-278.
- Squire, L.R. (1992). Memory and the hippocampus: A synthesis of findings with rats, monkeys, and humans. *Psychological Review*, 99, 195-231.
- van der Staay, F.J. (2002). Assessment of age-associated cognitive deficits in rats: A tricky business. *Neuroscience and Biobehavioral Reviews*, 26, 753-759.
- Stanley, W.C., Jaynes, J. (1949). The function of the frontal cortex. *Psychological Review*, 56, 18-32.
- Stevens, J.P. (2002). *Applied Multivariate Statistics for the Social Sciences, 4<sup>th</sup> edition*. Mahwah, N.J.: Lawrence Erlbaum Associates, Inc.
- Taylor Parker, S., Mitchell, R.W., Miles, H.L. (Eds.). (1999). *The Mentalities of Gorillas and Orangutans*. Cambridge: Cambridge University Press.
- Tarou, L.R., Bloomsmith, M.A., Hoff, M.P., Erwin, J.M., Maple, T.L. (2002). The behavior of aged great apes. In J.M. Erwin, P.R. Hof (Eds.), *Aging in Nonhuman Primates: Interdisciplinary Topics in Gerontology* (pp. 209-231). Basel: Karger.

- Verhaeghen, P., Marcoen, M., Goosens, L. (1993). Facts and fiction about memory aging: A quantitative integration of research findings. *Journal of Gerontology: Psychological Sciences*, 48, P157-P171.
- Voytko, M.L. (1999). Impairments in acquisition and reversals of two-choice discriminations by aged rhesus monkeys. *Neurobiology of Aging*, 20, 617-627.
- Whitbourne, S.K. (2001). *Adult Development and Aging: Biopsychosocial Perspectives*. New York: John Wiley and Sons, Inc.
- Whitley, B.E., Jr. (1996). *Principles of Research in Behavioral Science*. Mountain View, CA: Mayfield Publishing Co.
- Wilner, J., Otto, T., Gallagher, M., Eichenbaum, H. (1993). Hippocampal lesions that impair learning facilitate delayed nonmatching performance in rats. *Society for Neuroscience Abstract*, 19, 358.
- Wyss, J.M., Chambless, B.D., Kadish, I., van Groen, T. (2000). Age-related decline in water maze learning and memory in rats: Strain differences. *Neurobiology of Aging*, 21, 671-681.
- Zacks, R.T., Hasher, L. (1994). Directed ignoring: Inhibitory regulating of working memory. In D. Dagenbach & T.H. Carr (Eds.), *Inhibitory mechanisms in attention, memory, and language* (pp. 241-264). San Diego, CA: Academic Press.
- Zacks, R.T., Hasher, L. (1997). Cognitive gerontology and attentional inhibition: A reply to Burke and McDowd. *Journal of Gerontology: Psychological Sciences*, 52B, P274-P283.
- Zola-Morgan, S., Squire, L.R., Amaral, D.G. (1989). Lesions of the hippocampal formation but not lesions of the fornix or the mammillary nuclei produce long-lasting memory impairment in monkeys. *Journal of Neuroscience*, 9, 898-913.