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Cognitive control in rhesus monkeys (*Macaca mulatta*)

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M.A. Emory University, 2015
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An abstract of
a dissertation submitted to the Faculty of the
James T. Laney School of Graduate Studies of Emory University
in partial fulfillment of the requirements for the degree of
Doctor of Philosophy
in Psychology
2019

Abstract

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Cognitive control helps regulate behaviors and cognitions in circumstances where relying pre-potent habits might be inappropriate. In humans, cognitive control is critical for success in academic, occupational, and social domains. Cognitive control may also be important for nonhuman animals, however, we know little about the role of cognitive control in regulating nonhuman behavior. For study 1 of this thesis, I conducted two experiments that assessed attentional control in rhesus monkeys. In Experiment 1, I developed a nonhuman analog of the Eriksen flanker task to measure attentional control in rhesus monkeys. Monkeys were impaired by conflicting cues, paralleling findings from human subjects, and validating the test. In Experiment 2, I tested whether social dominance in group-housed rhesus monkeys was associated with chronic stress and impaired attentional control. Social subordination in the large social group I sampled was not associated with either impaired cognitive control or chronic stress, although there was substantial individual variation in cognitive control in the group. In study 2, I evaluated the extent to which mental imagery occurs in rhesus monkeys, focusing on another manifestation of cognition control: mental rotation. In Experiment 1, monkeys generalized from upright to rotated shapes and showed the hallmark relation between response latency and extent of rotation. In Experiment 2, monkeys transformed mental images in response to a rotational cue, allowing them to identify a shape that matched their mental image with a precision better than 30 degrees. In Experiment 3, monkeys used the same rotational cue in a new context, significantly flattening the rotation-latency function. Thus, monkeys have mental representations that contain fine perceptual details that remain isomorphic through mental transformation. Together, the work presented in this thesis provides new tools for the study of cognitive control in monkeys, and further clarifies the nature of cognitive control in nonhumans.

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Acknowledgments

I thank my advisor Rob Hampton for his guidance and encouragement, and for putting up with my habit of not reading emails for the past 6 years. I thank my committee members, Jocelyne Bachevalier, Harold Gouzoules, Stephan Hamann, and Mark Wilson for their support. I thank all the past and present members of the Hampton Labs for providing invaluable feedback, scientific discussion, and for dealing with my quirks. I thank my wonderful, hardworking undergraduates Celia Greenlaw and Victoria Lord, who made my job easy. I thank the monkeys—Byrd in particular—for their service. Finally, I thank my friends, dogs, and family, for without them I wouldn't be here.

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Chapter 1: General Introduction

Cognitive control is a collection of top-down processes that monitor and regulate our attention, memory, emotions, and behavior (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Diamond, 2013). The ability to exert control over ourselves is extremely important, particularly in circumstances where relying on impulse would be unwise. For instance, a store clerk uses cognitive control to remain calm when being yelled at by an unreasonable customer, and a student uses cognitive control to focus their attention when studying in a noisy room. Generally, researchers agree there are three processes that comprise cognitive control: inhibitory control, working memory, and cognitive flexibility (Friedman, et al., 2008; Miyake, et al., 2000). Inhibitory control allows us to regulate our behaviors and cognitions in circumstances where they may be contextually inappropriate (Diamond, 2013). Working memory is a system that allows us to actively maintain and manipulate information in mind (Baddeley & Hitch, 1974; Carruthers, 2013). Cognitive flexibility is a system that allows us to change mindsets or perspectives in the face of changing environmental demands (Diamond, 2013).

Cognitive control is one of the most important features of human cognition. Cognitive control is the foundation that allows us to engage in more complex behaviors like planning, problem solving, reasoning, and goal-directed behavior (Diamond, 2013). People who score higher on cognitive control tasks tend to be more successful in occupational, academic and social domains (Bailey 2007; Borella, Carretti, & Pelegrina, 2010; Diamond, 2005; Taylor-Tavares, et al., 2007). People with prefrontal cortical (PFC) brain trauma show no change in IQ, perceptual abilities, or general cognitive abilities; and yet, they struggle to maintain jobs, have difficulty completing daily activities, and show impaired performance on cognitive control tests (Shallice & Burgess, 1991). In many ways, cognitive control is what allows humans to be human-like: we need it to work, we need it to successfully navigate friendships and relationships, and without it we would be creatures of habit. However, cognitive control is far from a uniquely human process, and in fact, may play as central a role in nonhuman animal life as it does in human daily life.

Cognitive control in nonhuman primates is functionally homologous to human cognitive control. Rhesus monkeys with bilateral PFC lesions show pronounced social deficits, behave impulsively to the point of violating social dominance norms, and are eventually ostracized by their social group (Franzen & Myers, 1973; Myers, Swett, & Miller, 1973). Chimpanzees forage strategically, and it is believed that they use cognitive control when factoring in food quality, distance, and effort to obtain food (Genovesio, Wise, & Passingham, 2014; Sayers & Menzel, 2012). As is the case in humans, self-control ability in chimpanzees is correlated with problem solving (Beran, & Hopkins, 2018). Working memory is functionally and anatomically homologous across rhesus monkeys and humans, suggesting that nonhumans may have a need to actively hold information in mind in their natural environment (Basile & Hampton, 2013; Miller, 2000).

There is still a lot we do not know about nonhuman cognitive control. In humans, stress stemming from our social and economic environments impair cognitive control (Evans & Schamberg, 2009). We know comparatively less about whether stress stemming from social environments impair nonhuman cognitive control. We know very little about how frequently nonhuman animals use cognitive control, or whether they use cognitive control outside of experimental contexts (Carruthers, 2013). One reason for this is because we simply do not know the full capacities of nonhuman cognitive control. In fact, every major scientific development in nonhuman working memory has generated new hypotheses about how it functions to support nonhuman behavior (Carruthers, 2013). Thus, there is a need to continue studying cognitive control in nonhuman animals, as it is a scientifically rich field from which we can learn a lot about ourselves as well as nonhumans.

The primary focus of my graduate work has been to study the nature of cognitive control in rhesus monkeys. My masters research focused on defining the mechanisms that support cognitive flexibility in serial reversal learning (Hassett & Hampton, 2017). The two chapters included in this dissertation address the other two components of cognitive control: inhibitory control and working memory. My aims for this work were to develop new methodology for testing cognitive control in rhesus monkeys, to understand how social factors in nonhumans affect cognitive control, and to further our understanding of the capacities of nonhuman cognitive control. I will begin this dissertation providing a brief overview of two cognitive control processes: inhibitory control and working memory. I will then describe 5 experiments across two chapters which tested for cognitive control in rhesus monkeys. I will conclude this dissertation with a summary of my findings. My hope is that my work represents two small, but important steps in furthering our understanding of cognitive control in rhesus monkeys.

1.1 Inhibitory Control

Inhibitory control is a cognitive process that allows us to inhibit our attention, behaviors, and emotions when they are incompatible with current environmental demands (Diamond, 2013). Researchers generally agree that there are two forms of inhibition: an early developing *automatic* *inhibition* process, and a later developing *effortful inhibition* process (Howard, Johnson, & Pascual-Leone, 2014). Effortful inhibition is synonymous with the term 'inhibitory control' and allows us to suppress contextually inappropriate cognitions and behaviors (Howard, et al., 2014). Effortful inhibition is exemplified by performance on the Stroop task—a cognitive task where participants view colored words and are instructed to identify the color of the word. Participants are significantly slower to identify the color when there is incongruency (e.g., the word "blue" in yellow ink), than when there is congruency (e.g., the word "blue" with blue ink) because conflict requires effortful suppression of irrelevant information (Nigg, 2000). Effortful inhibition reaches mature levels around 16 years and appears dependent on prefrontal contributions (Andrés, Guerrini, Phillips, & Perfect, 2008; Pascual-Leone & Johnson, 2010). Automatic inhibition is a byproduct of effortful inhibition and acts to bias our attention away from previously inhibited information (Pascual-Leone, 1984). For example, in the stroop task, after participants complete a trial where they ignored the word "red" in order to identify the color yellow, they will take significantly longer to respond on the next trial if the color is red compared to any other color (Andrés, et al., 2008). Thus, whereas effortful inhibition is flexible, automatic inhibition is a comparatively inflexible system that biases attention away from historically irrelevant information. Automatic inhibition matures around 5 years and is comparatively less dependent on prefrontal contributions (Andrés, et al., 2008; Howard, et al., 2014; Pascual-Leone & Johnson, 2010).

Attentional control, a form of effortful inhibition that involves the top-down control of attention, plays an important role in cognition. Generally, the human attentional system can be controlled in one of two ways: by top-down effortful control or by bottom-up involuntary shifts in attention (but see Awh, Belopolsky, & Theeuwes, 2012). Top-down control, or attentional control, involves focusing our attention in order to selectively attend to relevant information and ignore irrelevant distractions (Braver, 2012, Lavie, 2005). We use attentional control regularly in our lives, such as when we need to focus our attention in a noisy room, or when we rapidly shift lanes in order to avoid a car accident. Without this control, our attention would be entirely under bottom-up control, or in other words, our attention would involuntarily shift to whatever shiny, noisy, or tantalizing stimulus within our perception (Awh, Belopolsky, & Theeuwes, 2012). People with relatively impaired attentional control are more likely to be distracted or will report being unable to hold their focus. Relatively new research even suggests that impaired attentional control may play a role in stress related mental disorders.

Deficits in attentional control, such as distractibility, are symptomatic of major depression, ADHD, schizophrenia, and generalized anxiety (American Psychiatric Association, 2013; Naim-Feil, et al., 2016). People high in trait anxiety exhibit pronounced impairments on attentional control tasks relative to those low in trait anxiety (Basanovic, et al., 2018). Anxious individuals are more prone to distractions than are controls, and distractibility is particularly pronounced for emotional and/or threatening stimuli (Eldar & Bar-Haim, 2010; Waszczuk, Brown, Eley, & Lester, 2015). Some evidence suggests that attentional control impairments may predispose individuals to depression later in life because they spend more time mentally occupied with stressful stimuli. One longitudinal study showed 6th grade girls with poorer attentional control were more likely to report being distracted by social stressors when reassessed in 7th grade, and were more likely to develop depression in 8th grade (Rudolph, Monti, & Flynn, 2018). Inability to resist distractions is also reported in those with substance abuse. In fact, relapse may be accounted for by a phenomenon called ‘attentional driven capture’ whereby cues once associated with drug use (e.g., paraphernalia, locations, people, etc..) overwhelm the attentional systems of drug addicts (Anderson, Laurent, & Yantis, 2011).

Researchers are now interested in the mechanisms that may impair attentional control in people. One likely factor is chronic psychosocial stress. In Chapter 2 I describe two experiments that tested for a relation between attentional control and chronic psychosocial stress in group-housed rhesus monkeys. In Experiment 1, I developed a nonhuman analog of the Eriksen Flanker Task to measure attentional control in rhesus monkeys. In Experiment 2, I tested whether stress stemming from low social dominance in group-housed rhesus monkeys was associated with impaired flanker performance. Group-housed rhesus monkeys have been previously established as an appropriate animal model to study the behavioral and physiological consequences of psychosocial stress in humans (Michopoulos, Higgins, Toufexis, & Wilson, 2012; Michopoulos, Reding, Wilson, & Toufexis, 2012). No study has yet determined whether there are cognitive deficits associated with social subordination in rhesus monkeys. Cognitive control is functionally and anatomically homologous across rhesus monkeys and humans, and thus, the implications of this research could be valuable for understanding how psychosocial stress affects attentional control across human and nonhuman species.

1.2 Working Memory

Working memory is a process that allows us to actively maintain and manipulate information in mind for relatively short durations (Baddeley & Hitch, 1974). Working memory is largely defined by being of short duration and vulnerable to distraction by competing cognitive loads

(Baddeley, 1996; Miller, 2000). However, working memory is also differentiated from long-term forms of memory (e.g., habit memory, familiarity) because it is vulnerable to distractors in a demand-dependent manner (Basile & Hampton, 2013). Thus, working memory is robust to, but not immune from, short delays and distractions. Early models of working memory proposed that it is comprised of three systems: the phonological loop, visuo-spatial sketchpad, and the central executive (Baddeley, 1996). The phonological loop stores acoustic or speech-based information, the visuo-spatial sketchpad stores visual and spatial information, and the central executive is posited to be the master system that controls and allocates attention (Baddeley, 1996). Though Baddeley and Hitch's (1974) model for working memory has been highly influential, recent work has challenged the scope of the model. Working memory for egocentric spatial information can be differentiated from working memory for allocentric spatial information (Postle & D'Esposito, 2003), working memory for pitch can be differentiated from loudness (Clément, Demany, & Semal, 1999), and humans even retain tactile information in working memory (Harris, Miniussi, Harris, & Diamond, 2002). The standard model of working memory does not account for all the ways in which we store information in mind. Newer models for working memory propose that it is an attentional system that allows us to actively store many types of sensory information (Postle, 2006).

Newer models of working memory invoke many properties of mental imagery. Mental imagery is a process that allows us to mentally represent sensory information in mind, in the absence of sustained sensory input (Kossyln, 1988). Humans represent a wide variety of sensory information using mental imagery, including those from visual, auditory, and tactile domains (Kosslyn, 1988; Marmor & Zaback, 1976). Despite their similarities, working memory and mental imagery are discussed in largely separate literatures and rarely, if ever, reference one another (Tong, 2013). More recent work has started to show that working memory and mental imagery are one in the same (Tong, 2013, Albers, Kok, Toni, Dijkerman, & de Lange, 2013). Decoding techniques show that visual information is encoded in early visual areas V1-V3 similarly in working memory and mental imagery (Albers, et al., 2013). Performance on visual mental imagery tasks correlates with performance on visual working memory tasks (Keogh & Pearson, 2011). Mental imagery and working memory are similarly affected by visual interference (Borst, Ganis, Thompson, & Kosslyn, 2012). In fact, the only major difference in mental imagery and working memory is in how we test the two phenomena. In working memory tasks, participants are shown a stimulus and told to remember it; in mental imagery tasks, participants are told to imagine a stimulus and remember it.

The potential overlap between mental imagery and working memory has important implications for the study of mental representations in nonhuman animals. One assumption held by some nonhuman cognitive researchers is that animal cognition relies heavily on mental imagery because animals lack ways of recoding information verbally (Griffin, 1976; Neiworth & Rilling, 1987; Premack, 1983). Indeed, there is evidence in favor of this assumption. Rhesus monkeys actively remember visual stimuli in the absence of sustained perceptual input (Basile & Hampton, 2013). Vocalizations and odors may produce mental images of familiar individuals and objects in dogs and rhesus monkeys (Adachi & Hampton, 2011; Adachi, Kuwahatam & Fujita, 2007; Bräuer & Belger, 2018). However, a defining characteristic of mental images is that they can be manipulated in a way that mirrors physical transformation, and there is little evidence of this in nonhumans (Neiworth & Rilling, 1987). In fact, there is very little evidence that nonhuman animals can actively manipulate information in mind (Carruthers, 2013). In Chapter 3 of this dissertation, I describe three experiments that use mental rotation paradigms to provide converging evidence that rhesus monkeys manipulate mental images

Chapter 2: An Investigation of Social Dominance, Psychosocial Stress, and Attentional Control in Rhesus Monkeys

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Cognitive control is a collection of top-down processes that allow us to control our behavior, attention, and emotions in circumstances where habits may be incompatible with environmental demands (Diamond, 2013). Cognitive control is comprised of three related yet functionally distinct processes: inhibitory control, working memory, and cognitive flexibility (Friedman, et al., 2008; Lehto, Juujärvi, Kooistra, & Pulkkinen, 2003; Miyake, et al., 2000; Miyake & Friedman, 2012). These processes play critical roles in daily behavior and support our ability to plan, problem solve, and reason. Individuals who score higher on tests of cognitive control tend to be more successful in occupational, academic, and social domains (Bailey 2007; Blair & Razza 2007; Borella, Carretti, & Pelegrina, 2010; Gathercole, Pickering, Knight, & Stegmann, 2004; Morrison, Ponitz, & McClelland, 2010). Individuals with impaired cognitive control struggle to maintain jobs, have difficulty completing daily tasks, and are more likely to exhibit a variety of mental disorders such as addiction, ADHD, depression, OCD, PTSD, and schizophrenia (Baler & Volkow, 2006; Barch, 2005; Diamond, 2005; Lui & Tannock, 2007; Penades, et al., 2007; Polak, Witteveen, Reitsma, & Olff, 2012; Shallice & Burgess, 1991; Tavares, et al., 2007).

Attentional control, the form of cognitive control that involves the top-down control of our attention, plays a central role cognition. Attentional control allows us to selectively attend to important information and ignore irrelevant distractions (Braver, 2012, Lavie, 2005). Attentional control plays a central role in cognitive control, supporting our ability to engage in both working memory, inhibitory control, and cognitive flexibility (Astle & Scerif, 2011). Participants that completed cognitive training programs that target attentional control show improvements in other aspects of cognitive control, such as working memory, cognitive flexibility, and multitasking (Green & Bavelier, 2012). Deficits in attentional control are symptomatic of numerous mental disorders including generalized anxiety and depression (Eldar & Bar-Haim, 2010; Naim-Feil, et al., 2016; Waszczuk, Brown, Eley, & Lester, 2015).

Tasks that measure attention control in humans assess how well an individual can selectively attend to relevant information and ignore irrelevant distractions. One exemplar of an attentional control task is the flanker task. The flanker task was originally developed in the 1970s to study the role of inhibition in visual search paradigms (Colegate, Hoffman, & Eriksen, 1973; Eriksen & Hoffman, 1972, 1973). The task is simple: participants view a horizontal array of arrows and are instructed to identify which direction the central-most arrow (i.e., the target) is facing. Participants are significantly faster to respond when the direction of the target and flanking arrows are facing the same (i.e., congruent) directions compared to when target and flanking arrows are facing opposite (i.e., incongruent) directions (Eriksen & Eriksen, 1974). This latency difference is not simply due to the fact that there is visual discordance on incongruent trials but not congruent trials, because when the target is flanked by non-directional stimuli (i.e., neutral) participants show an intermediate response latency (Eriksen & Eriksen, 1974). Incongruent and neutral trials tax attentional resources, and participants take longer to respond because they need to shift attention away from distracting flankers. This effect is particularly pronounced on incongruent trials because flankers are associated with an opposite response, and thus, are more salient (Verbruggen, et al., 2006). Neuroimaging studies report that the lateral prefrontal cortex (LPFC), an area associated with cognitive control, is activated on incongruent and neutral trials, but not congruent trials (Bunge, Hazeltine, Scanlon, Rosen, & Gabrieli, 2002; Van Veen, Cohen, Botvinick, Stenger, & Carter, 2001).

The brain areas supporting cognitive control are particularly vulnerable to chronic stress. The LPFC and, to a lesser degree, the hippocampus have been implicated in supporting cognitive control across development (Finn, et al., 2010). Lesions in the mid-dorsolateral frontal cortex (cytoarchitectonic areas 46 and 9) of the rhesus macaque produce impaired performance on tests of working memory, but not non-executive memory tasks involving recognition of recently seen objects (Bachevalier & Mishkin, 1986; Petrides, 1991; Petrides, 2005). The functional characteristics of LPFC neurons are uniquely suited to support active maintenance because they sustain activity in the presence of visual distractions (Desimone & Duncan, 1995; Miller & Cohen, 2001). The dorsolateral PFC has reliably been implicated in supporting working memory, inhibitory control, and cognitive flexibility in both humans and nonhuman primates (for a review see Aron, Robbins, & Poldrack, 2004). Early life stress impairs cell and network development within the PFC and hippocampus (Chetty, et al., 2014; Conrad, 2008; Pascual & Zamora-Leon, 2007). Developing rodents exposed to chronic stress show shorter prefrontal pyramidal dendritic projections, and effect that lasts throughout development (Arnsten, 2009; Pascual & Zamora-Leon, 2007). Early life stress slows the establishment of peripubertal hippocampal synapses, but does not change normal postpubertal pruning, resulting in lower overall synaptic density within subregions of the hippocampus (Teicher, et al., 2003). Stress also impairs cognitive control by modulating prefrontal dopamine transmission outside of normal bounds. Acute stress increases prefrontal dopamine whereas chronic stress reduces prefrontal dopamine, both of which have produced working memory impairments in rats, monkeys, and humans (Arnsten & Goldman-Rakic, 1998; Lange, et al., 1992; Mizoguchi, et al., 2000).

The effects of chronic stress on cognitive control are observable in the real world. Relatively new research suggests that chronic psychosocial stress stemming from poverty impairs cognitive control (Evans & Schamberg, 2009; Hackman & Farah, 2009; Hackman, et al., 2010; Lawson, et al., 2014). Children from low socioeconomic (SES) families show impaired attentional control relative to children from high SES families (D'angiulli, Herdman, Stapells, & Hertzman, 2008; Stevens, Lauinger, & Neville, 2009). The amount of time spent in poverty during childhood correlates with working memory impairments and poorer cardiovascular health in adulthood (Evans & Schamberg, 2009). Poverty appears to selectively impair cognitive control, as children from low SES show impaired working memory and inhibitory control, but normal performance on tasks measuring reward processing and perceptual ability (Farah, et al., 2006). Exposure to other forms of psychosocial stress have also been linked to impaired cognitive control. Adolescents exposed to either abuse or neglect forms of maltreatment perform worse on attentional control tasks than do control subjects (Mothes, et al, 2015). Some evidence suggests that stress stemming from discrimination leads to impairments in mental health (Hatzenbuehler, Keyes, & Hasin, 2009; Hatzenbuehler, McLaughlin, Keyes, & Hasin, 2010). Graduate students show impaired attentional control relative to controls while preparing for a major academic examination, but no difference 4-weeks after the examination (Liston, McEwen, & Casey, 2009).

Group-housed rhesus monkeys may be an appropriate animal model to study the effects of chronic psychosocial stress on cognitive control. Rhesus monkeys live in large social groups organized into linear dominance hierarchies (Vessey, 1984). Female rhesus monkeys stay within their natal group and will inherit their mother's rank upon reaching sexual maturity, while males will disperse from the group around puberty (Melnick, Pearl, & Richard, 1984; Missakian, 1972; Sade 1967, 1972). Dominance rank is maintained through agonistic interactions where socially dominant monkeys direct aggression or threats of aggression towards socially subordinate monkeys, and this directional aggression is believed to facilitate group stability (Bernstein, 1970; Bernstein & Gordon, 1974; Sapolsky, 2005). In captive settings, social dominance is a pronounced psychosocial stressor, where subordinate individuals exhibit a physiological profile that mirrors humans exposed to chronic psychosocial stress. Specifically, subordinate monkeys mount a blunted stress response to physiological and psychosocial stressors, impaired glucocorticoid negative feedback, and overall higher hair cortisol concentrations relative to dominant monkeys (Dong-Dong, et al., 2013; Michopoulos, Higgins, et al., 2012; Michopoulos, Reding, et al., 2012). It is believed that elevated cortisol in subordinate monkeys stems from a variety unpredictable stressors such as being more likely to receive aggression, having comparatively less social support, and receiving fewer affiliative interactions (Abbott, et al., 2013; Snyder-Mackler, et al., 2016).

No study has yet investigated whether social subordination in group-housed rhesus monkeys is associated with attentional control impairment. Rhesus monkeys are a highly appropriate animal model for studying cognitive control, and the implications of this research may be important for understanding how psychosocial stressors affect cognitive control in humans. Rhesus monkeys have been instrumental in developing our understanding of the neurobiological basis for cognitive control (Miller, 2000). The networks supporting cognitive control are functionally and anatomically homologous across humans and rhesus monkeys (Miller, 2000; Petrides, 1991; Petrides, Alivisatos, & Frey, 2002; Tanji, & Hoshi, 2008). Rhesus monkeys and humans show similar developmental trajectories with respect to both the prefrontal cortex, and corresponding cognitive control abilities (Bourgeois, Goldman-Rakic, & Rakic, 1994; Lewis, 1997; Diamond & Goldman-Rakic, 1989; Goldman-Rakic, 1987). The LPFC, and cognitive control, appear to be for maintaining social status in rhesus monkeys (Deutsch & Lee, 1991; Franzen & Myers, 1973).

We present two experiments that tested for attentional control in rhesus monkeys. In Experiment 1, we tested whether attentional control resources in monkeys are taxed by the presence of visual interference using a flanker task. The flanker task is an appropriate tool for measuring attentional control in humans but has not yet been adapted for nonhuman use. Thus, the motivations for Experiment 1 were to establish whether the flanker task is an appropriate method for testing inhibitory control in rhesus monkeys, and whether it is appropriate for use in a social group setting. In Experiment 2, we tested whether variation in flanker performance correlated with social rank.

2.1 Experiment 1

Attentional control, the ability to selectively focus one's attention on relevant information and ignore irrelevant distraction, is a central function of cognitive control (Botvinick, et al., 2001, Diamond, 2013). Established methodologies for testing attentional control in nonhumans overwhelmingly rely on measuring saccadic eye movements, and these methods are incompatible with testing cognition in social settings (Cole, Yeung, Freiwald, & Botvinick, 2009). The flanker task has been used extensively to measure attentional control in humans and may be appropriate for testing nonhuman cognition in social settings. The task is relatively simple to learn, does not require measurement of eye movements, but has not yet been adapted for nonhuman animal use.

The goal of Experiment 1 was to determine whether visual interference produced by flanking stimuli affects flanker performance in rhesus monkeys. In humans, response latencies are longer when the target and flanking stimuli are associated with incongruent responses compared to when target and flanking stimuli are associated with congruent responses (Eriksen & Eriksen, 1974). Slower latencies on incongruent trials are thought to reflect increased demands on attentional control because participants need to orient their attention away from flankers and selectively attend to the target (Verbruggen, et al., 2006). This effect cannot simply be explained by a difference in visual discordance between congruent and incongruent trials, because if the target is flanked by non-directional (i.e., neutral) stimuli, participants show an intermediate response latency (Eriksen & Eriksen, 1974).

We developed a nonhuman analog of the flanker task to test whether the valence of flanking stimuli (i.e., congruent and incongruent) differentially impaired attentional control in rhesus monkeys. We included neutral flanker trials in our task to determine whether the difference between congruent and incongruent performance could be explained by visual discordance. We hypothesized that if stimulus incongruency taxes attentional resources in rhesus monkeys, then monkeys will be significantly slower to respond on incongruent trials relative to congruent trials. Furthermore, we hypothesized that response latencies on neutral trials would be significantly faster than incongruent trials and significantly slower than neutral trials if this effect was due to attentional control differences and not simply visual discordance.

2.1.1 Procedure

Subjects

We tested seven adult male rhesus monkeys (*mean age: 7.8 years old*) that had extensive experience in cognitive testing. All monkeys were pair housed and had visual contact with conspecifics. Monkeys were tested in their home cages, and paired monkeys were separated only during testing hours. Monkeys tested for approximately 8 hours each day, six days a week. Monkeys had ad libitum access to water and received their daily caloric intake through a combination of nutritionally balanced reinforcement pellets earned in testing, and monkey biscuits fed at the end of the day.

Apparatus

Computerized testing systems consisted of a touch-sensitive LCD monitor (Elo TouchSystems, Menlo Park, Ca), two food dispensers (Med Associates Inc., St. Albans, VT), controlled by a custom program written in Visual Studio 2013 (Microsoft Corporation).

Flanker Training and Test Procedures

We developed an adaptation of the Eriken Flanker Task to parametrically measure inhibitory control in rhesus monkeys (Eriksen & Eriksen, 1974) (Figure 1). The flanker task consisted of 5 training phases and 1 test phase.

Training Phase 1: Trials were initiated by touching a green start square twice (Figure 1a). A centrally placed shape appeared with two choice stimuli in the lower left and right corners of the screen. The central shape was either a white diamond or tear-shaped stimulus, and these two stimuli were presented equally often, according to a pseudorandom schedule. If the central stimulus was a diamond, monkeys were reinforced for selecting the left choice stimulus, which was always an image of a cartoon school bus. If the central stimulus was the tear shape, monkeys were reinforced for selecting the right choice stimulus, which was always a cartoon image of a Reindeer. Correct choices resulted in positive audio feedback, a food pellet reward, and a 3000ms inter-trial interval. Incorrect choices resulted in negative audio feedback, a 6000ms time-out, and the trial was repeated. If the trial was repeated more than once, only the correct choice option would become visible, requiring monkeys to select that response. Each session consisted of 96 trials, and monkeys achieved 90% accuracy or better for 2 consecutive sessions in order to progress to Phase 2.

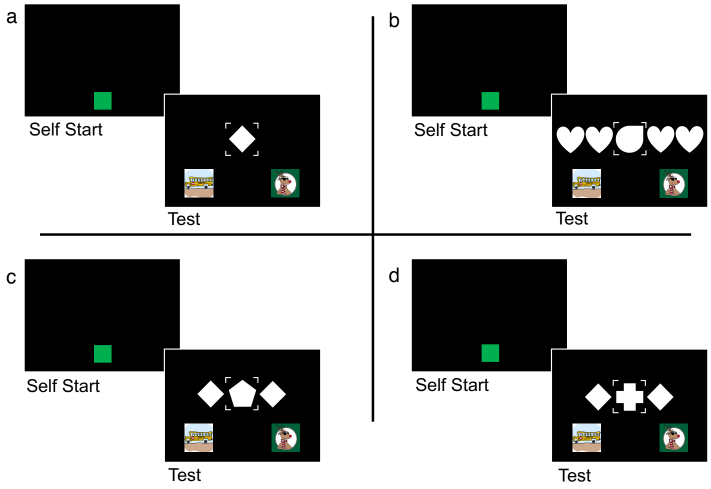

Figure 1. 4 different trial types encountered during training and test phases of the flanker task. (a) A training trial encountered during training phases 1-3. Monkeys self-started the trial by selecting the green start square. If a diamond or pentagon appeared at test, monkeys were reinforced for selecting the left response. If a cross or tear shape appeared, monkeys were reinforced for selecting the right response. (b) A neutral trial, encountered in training phases 4-5 as well as the test phase. (c) An example of a congruent trial. Monkeys encountered congruent trials in training phase 5 and the test phase. (d) An example of an incongruent trial. Monkeys encountered incongruent trials in training phase 5 as well as the test phase.

Training Phase 2: All aspects of training phase 2 were identical except that monkeys were trained to used two additional stimuli, a white pentagon and white cross. Monkeys were reinforced for selecting the left choice if the shape was a petagon, and right choice for cross.

Training Phase 3: All aspects of training phase 3 were identical to training phase 1 and 2, except, any of the 4 stimuli from the previous 2 phases could appear in the central location on a given trial.

Training Phase 4: Neutral flanking stimuli were introduced (Figure 1b). Each trial, 2 or 4 neutral stimuli flanked the target. There were a total of 8 neutral stimuli that were used according to a pseudorandom schedule. The number of left and right flanking stimuli were always equally distributed. The same performance criteria was used to move monkeys to the final training phase.

Training Phase 5: In the final training phase, flanking stimuli could be either neutral (Figure 1b), congruent (Figure 1c), or incongruent (Figure 1d) relative to the target. During a congruent trial, the central stimulus and flanking stimuli were associated with the same response. During an incongruent trial, the central stimulus and flanking stimuli were associated with opposite responses. Congruent, incongruent, and neutral trials were presented equally often within a given session. We lowered the performance criteria and monkeys needed to be 80% accurate or better for 2 consecutive sessions in order to progress to test.

Flanker Test Phase: The test phase was identical to training phase 5, however, no correction procedure was used. We analyzed the first 14 sessions of a monkey's test performance.

2.1.2 Results & Discussion

There was a significant main effect of flanker valence on latency (Figure 2: $F_{(2,12)} = 6.380$, $p = .013$). However, follow-up Bonferroni corrected pairwise comparisons indicated that there were no significant pairwise differences between any of the three conditions (Congruent vs Incongruent: $p = .101$, Congruent vs Neutral: $p = .091$, Incongruent vs Neutral: $p = .329$). It appears monkeys were generally slower to respond on incongruent trials relative to congruent trials, but this difference was quite small. It is not uncommon for monkeys to show small or no effects of response latency on cognitive tasks. Previous studies report that monkeys show an increase in errors rather than an increase in response latency when encountering incongruency in cognitive control tasks (*stroop*: Washburn, 1994; *stop signal*: Godlove, et al., 2011). Human participants will show an effect of accuracy but not latency when forced to respond rapidly on flanker trials (Rinkenauer, Osman, Ulrich, Müller-Gethmann, & Mattes, 2004). Thus, it may be that monkeys respond more rapidly, and thus, will show significant differences in accuracy between congruent and incongruent trials.

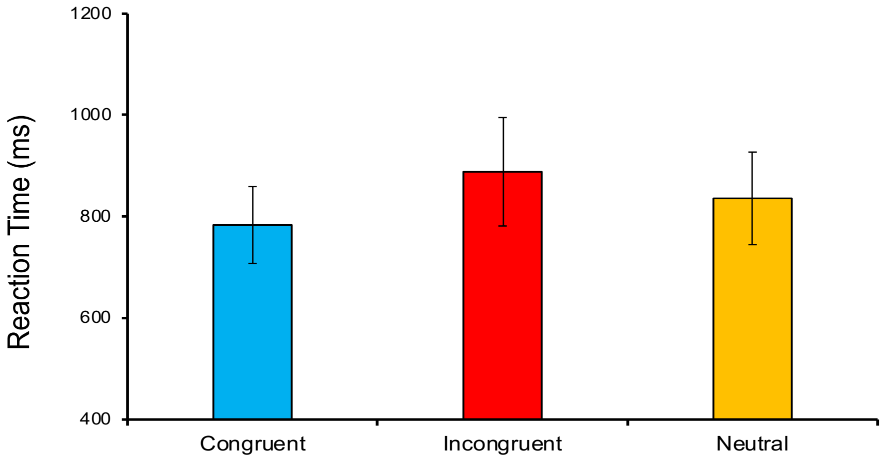

Figure 2. There was a main effect of flanker valence on response latency. Generally, monkeys were slower to respond on incongruent and neutral trials than on congruent trials, however, pairwise comparisons indicated that this difference was not significant.

We observed a significant main effect of flanker valence on accuracy (Figure 3: $F_{(2,12)} = 35.528$, $p < .001$). Follow-up Bonferroni corrected pairwise comparisons showed that all three conditions were significantly different (Congruent vs Incongruent: $p = .002$; Congruent vs Neutral: $p = .017$; Neutral vs Incongruent: $p = .002$). Monkeys were significantly more accurate on congruent trials relative to incongruent trials. The effect of incongruency was not simply due to a difference in visual discordance as monkeys were significantly more accurate on neutral relative to incongruent trials, and significantly less accurate on neutral relative to congruent trials. Our findings are consistent with those reported in human studies, albeit for accuracy rather than latency (Eriksen & Eriksen, 1974).

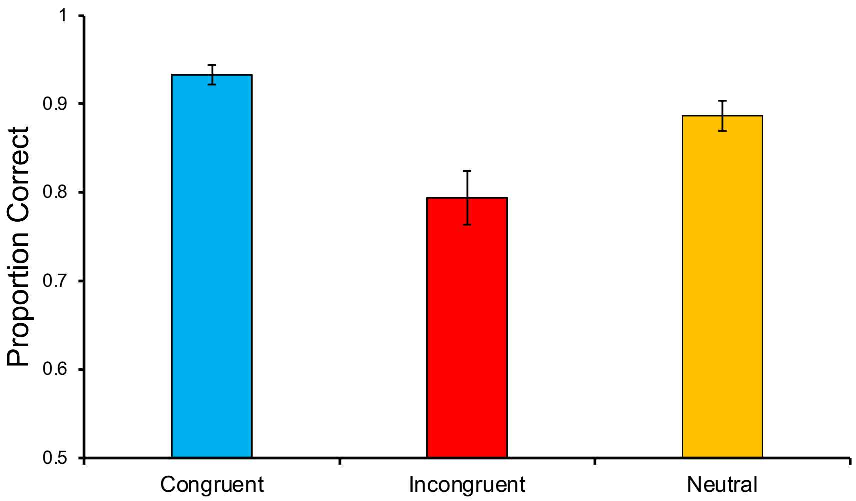

Figure 3. Accuracy differed significantly as a function of trial type. Compared to neutral trials, monkeys were significantly more accurate on congruent trials and significantly less accurate on incongruent trials.

The fact that monkeys show differences in accuracy where humans show differences in latency suggests that the species differ in how they resolve flanker conflict. In humans, incongruent flankers are highly distracting, and thus, interfere with a subject's ability to selectively attend to the target stimulus. Incongruent response latencies are longer because participants are more often needing to shift their attention away from distracting flankers (Kopp, Rist, & Mattler, 1996; Verbruggen, et al., 2006). In monkeys, incongruent flankers appear to similarly impair monkey's selectively attention, however, unlike humans who reliably shift attention away from distracting flankers, rhesus monkeys are more prone to impulsive responding.

The ability to selectively attend to relevant information and ignore irrelevant distractions is dependent on prefrontal contributions (Bunge, Hazeltine, Scanlon, Rosen, & Gabrieli, 2002). Patients with unilateral PFC lesions show a significantly greater difference in congruent and incongruent latency when trials are presented to the contralateral visual field compared to the ipsilateral visual field (Rafal, et al., 1996). Children at 6 years show a large accuracy difference between congruent and incongruent trials, and this difference progressively diminishes across development (Rueda, et al., 2004). Transcrainial direct current stimulation of the DLPFC has been shown to decrease reaction time on incongruent flanker trials (Brosnan & Wiegand, 2017; Gbadeyan, McMahon, Steinhauser, & Meinzer, 2016). Elderly participants show a smaller latency difference between congruent and incongruent trials compared to young participants, however, this is due to a floor effect because elderly are significantly slower for all trial types (Wright & Elias, 1979).

Chronic psychosocial stress has been shown to disproportionately impair prefrontal dependent cognitive processes, and thus, may be associated with impaired flanker performance in monkeys. In Experiment 2, we tested whether stress stemming from social subordination in group-housed rhesus monkeys was associated with impaired flanker performance.

2.2 Experiment 2

Prefrontal dependent cognitive processes, such as inhibitory control, appear vulnerable to chronic stress (Lange, et al., 1992; Lyons, et al., 2000; Mizoguchi, et al., 2000). In captive group-housed rhesus monkeys, social subordination is associated with chronic psychosocial stress as evidenced by blunted cortisol reactivity, impaired glucocorticoid negative feedback, and relatively higher hair cortisol levels (Dong-Dong, et al., 2013; Michopoulos, Higgins, et al., 2012; Michopoulos, Reding, et al., 2012). No study has yet tested whether social subordination in captive groups of rhesus monkeys is associated with inhibitory control impairments. In

Experiment 2 we addressed two related questions. First, we assessed whether social subordination was associated with chronic psychosocial stress in a large captive social group of rhesus monkeys. Second, we assessed whether social subordination was associated with impaired inhibitory control.

Hair cortisol can be used to non-invasively determine whether an animal—human or monkey—is experiencing chronic hypothalamic-pituitary-adrenal (HPA) activation. Hair cortisol differs from point estimates such as saliva and blood in that it reflects average circulating cortisol levels over the course of months (Meyer & Novak, 2012; Russell, Koren, Rieder, & Van Uum, 2012; Wright, et al., 2015). Cortisol accumulates within the hair shaft via blood, as well as on the surface of hair via sweat and sebaceous glands (Wright, Hickman, & Laudenslager, 2015). When hair samples are assayed, cortisol on the hair's surface is washed away, and only cortisol within the hair shaft is measured (Wright, et al., 2015). In both humans and rhesus monkeys, elevated hair cortisol concentrations are associated with greater exposure to psychosocial stressors (Davenport, Tiefenbacher, Lutz, Novak, & Meyer, 2006; Dettenborn, Tietze, Bruckner, & Kirschbaum, 2010). In small social groups of rhesus monkeys, social subordination is associated with elevated hair cortisol (Dong-Dong, et al., 2013). We collected hair samples from rhesus monkeys housed in a larger social group at the Yerkes National primate research center to determine if social subordination was associated with elevated hair cortisol.

In Experiment 1, we developed a nonhuman analog of the flanker task to parametrically test for inhibitory control in rhesus monkeys. Our findings from Experiment 1 suggested that variations in flanker performance are most clearly manifested in accuracy rather than latency. Thus, in the current experiment, we assessed whether accuracy varied as a function of social status among group-housed rhesus monkeys. Previous studies using the flanker task characterize relatively better or worse performance by looking at the difference between congruent and incongruent trials. Relatively better inhibitory control is operationalized as a smaller difference between congruent and incongruent performance; poorer inhibitory control is operationalized as a greater difference between congruent and incongruent performance (Rafal, et al., 1996; Rueda, et al., 2004). We hypothesized that if socially subordinate exhibit relatively higher levels of hair cortisol, then subordinates will show a relatively greater difference in accuracy between congruent and incongruent trials.

2.2.1 Procedure

Subjects

Subjects were group-housed in a large multi-male, multi-female group of approximately 144 individuals, varying in size year-to-year. The group was disproportionately female because juvenile males were removed from the group upon reaching sexual maturity. On average, there were approximately 26 juvenile males, 33 juvenile females, and 59 adult females within the group at any given time. There were 2 adult males that inhabited the group across the duration of testing. Monkeys were housed in a 30 x 30 meter outdoor enclosure and had access to temperature-moderated indoor housing. Monkeys were free to move about the outdoor and indoor enclosures unless weather permitted them to be temporarily housed inside. The outdoor enclosure was equipped with playground materials and various other forms of enrichment. Food and water were available ad libitum. Monkeys also received daily enrichment in the form of fruits and vegetables. All monkeys had small radio-frequency identification (RFID) microchips

(Biomark, Boise ID; Datamars, Temple TX) implanted in the wrists of each arm, which were used for identification at automated cognitive testing and feeding apparatuses.

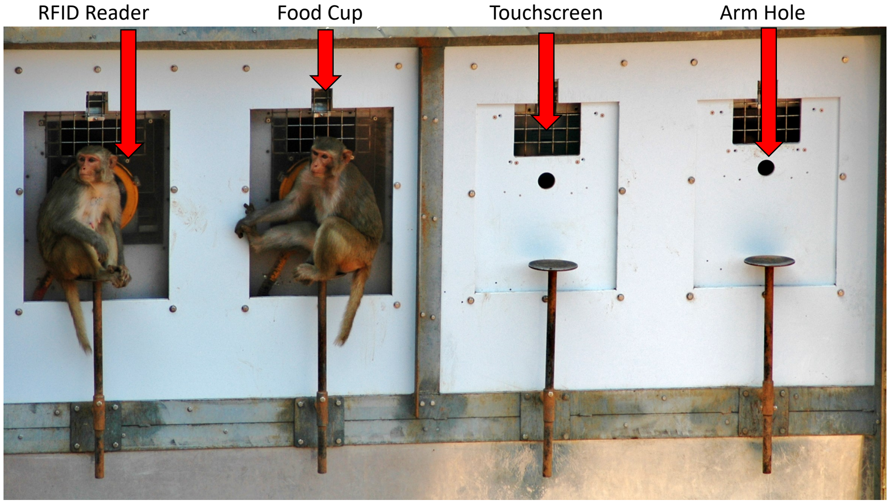

Figure 4. Equipment used to collect cognitive data from group-housed rhesus monkeys. Monkeys reached through an arm hole and were identified by an RFID reader. Cognitive tasks were presented on a touchscreen behind a viewing window (Gazes, et al., 2012).

Cognitive Testing Apparatus

Four touchscreen computer stations were built into the side of the group's enclosure (Figure 4). Touchscreens were placed 15cm behind a poly-panel, which was flush with the outer wall of the enclosure. Each station included a 15-inch LCD color monitor (3M, St. Paul, MN) running at a resolution of 1,024 x 768 pixels, an automated pellet dispenser (Med Associates Inc., St Albans, VT), an RFID chip reader (Biomark, Boise, ID), and a stool for monkeys to sit on while testing. Touchscreens were visible by looking through a 15 x 20 cm mesh window and could be reached by inserting one's arm through a 5-cm in diameter armhole. Surrounding the armhole was the antenna for the RFID reader, which allowed us to obtain information about the identity of the individual as they were reaching in to begin a trial. Monkeys were reinforced for successfully completing cognitive task trials with nutritionally balanced fruit-flavored pellets and audio reinforcement.

Cognitive tests were controlled by automated testing software written in Visual Studio 2013 (Microsoft Corporation). When a monkey reached through the armhole, the RFID chip in their wrist was read by the RFID reader antenna, and this information was sent to the computer associated with that testing station. RFID information was used to determine which individual was testing, what cognitive task they were assigned to, and how much progress they had made on the task since first being assigned to it. The software then presented the task assigned to that monkey, at the point in the task that they had left off since the last time they engaged with the testing apparatus.

Flanker Training and Test Procedures

The same training and test procedures described in Experiment 1 were used.

Hair Cortisol Collection & Assay

Hair cortisol was collected from 23 female rhesus monkeys on November 30th 2017. The 23 monkeys were chosen based on whether they had completed the flanker task or were currently participating in the training phases of the flanker task. The average age of monkeys selected for hair sample collection was 56.3 months, with a range of 28 months and 103 months. Hair samples were collected during an annual health survey in which all monkeys were under anesthesia. Hair samples were collected by shaving approximately 100mg of hair at the nape of each monkey's neck. Hair samples from each monkey were wrapped individually in aluminum foil and stored at -80° F until they were assayed. Samples were sent to the Yerkes National Primate Research Center Biomarker Core where cortisol concentrations within hair samples were determined using liquid chromatography-mass spectrometry (LC-MS). Samples from each monkey were divided in half and assayed separately. We assessed the reliability of assays by comparing samples assayed first to those assayed second and found the two were highly correlated ($r = .994$). We averaged the two assay values to create a mean cortisol concentration value for each monkey.

Behavioral Observation

We determined the dominance rank of monkeys in this study using a preexisting dataset of behavioral observations. The ranks of individuals had previously been determined using methods as described in Wilson et al. (2013). Researchers recorded the direction of dyadic agonistic interactions (aggressions, submissions) during 30-minute focal observation periods. Observations started in January 2014 and continued until December 2016, and dominance ranks of individuals remained stable across this timeframe. These observations were used to determine the relative ranking of the 9 matrilines within our social group. All monkeys belonging to the alpha matriline were given a rank of 1, all monkeys belonging to the beta matriline were given a rank of 2, and so on.

Statistical Analyses

We performed linear mixed effect analyses using used R (R Core Team, 2014) and the *lme4* package (Bates, Maechler, Bolker, & Walker, 2015). For all of our analyses, matriline rank was entered as a fixed effect. We also generated categorical values for each matriline and used those values as a random effect to account for genetic influences. The package *MuMIn* was used to determine our model's R^2 value (Barton, 2016). P-values were obtained by likelihood ratio tests comparing the full model against a model without rank included (i.e., the null model).

2.2.2 Results & Discussion

Participation

Data collection began on July 6th 2016 and finished on December 20th 2018. Over the course of the study, a total of 176 monkeys began flanker task training. Twenty-seven monkeys completed all phases of training and were included in our analysis. All twenty-seven monkeys completed at least 14 sessions of the test phase, and thus, we analyzed the first 14 sessions from each monkey.

Only seven of the twenty-seven monkeys that completed the flanker task were still living in the social group at the time in which we collected hair samples. Thus, we were unable to directly test whether hair cortisol predicted flanker performance because our sample was too small. Instead we analyzed the relationship between rank and flanker performance separately from rank and hair cortisol.

Flanker Performance Across Ranks

We calculated a flanker difference score for each monkey by subtracting the proportion of correct incongruent trials from the proportion of correct congruent trials. Previous work has shown that attentional control impairment is associated with a greater difference in performance between congruent and incongruent trials (Rafal, et al., 1996; Rueda, et al., 2004). A difference score also serves to control for between-subjects variation, because congruent and incongruent trials differ only by whether attentional control is necessary or not. Congruent performance reflects a monkey's aptitude for the task when not needing control their attention, whereas incongruent trials reflect both aptitude and attentional control ability. The difference score, therefore, best reflects variance explained by attention control. Prior to analyses, we checked to see if difference scores violated assumptions of normality. Visual inspection, a Shapiro test (*p* = .9535), and a qpplot confirmed that flanker difference scores were normally distributed.

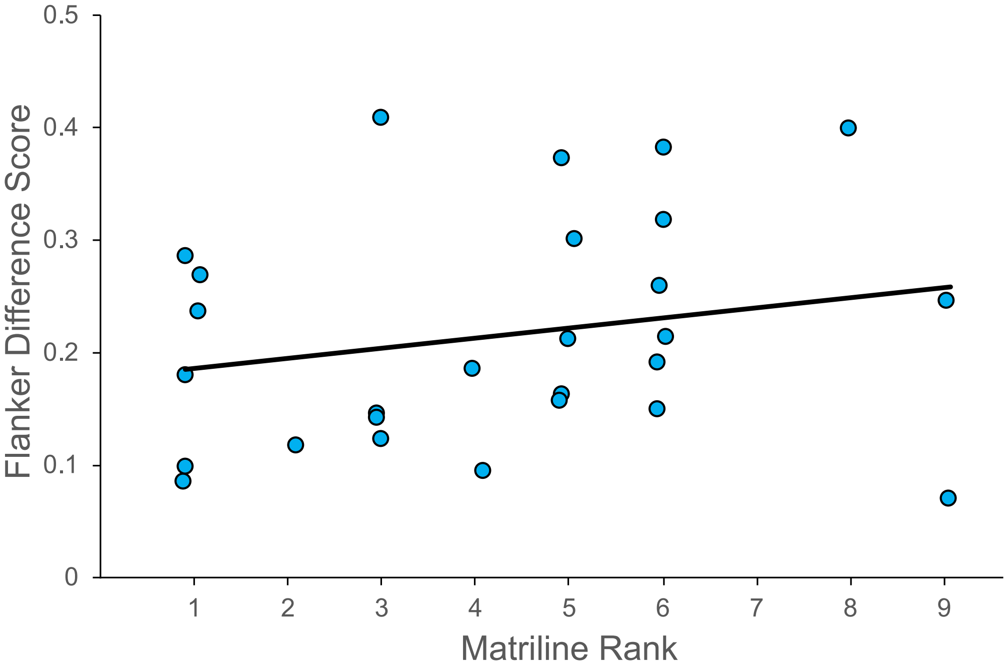

Figure 5: Flanker performance plotted as a function of matriline rank. Data here include both juvenile and adult rhesus monkeys. Rank and flanker performance were not significantly correlated.

We found no relationship between dominance rank and flanker performance (Figure 5: $R^2 = .047$, $p = .269$, 95% CI[.18,.25]). After visual inspection of the data, it became clear that the amount of variance across monkeys was quite high, and it was difficult to discern a clear trend in scores across rank. Fourteen monkeys in our analysis were younger than 3 years of age. The prefrontal cortex in juvenile monkeys is underdeveloped and deficits associated with prefrontal damage are not observed until approximately 3 years and after (Bourgeois, et al., 1994; Goldman-Rakic, 1987). Therefore, the effect of stress on flanker performance may only be observable in a population of adult monkeys and not in a population of juvenile monkeys. Thus, we analyzed juvenile (n=14) and adult (n=13) monkeys separately to see if dominance rank predicted flanker performance in adults but not juveniles. The adult-only model slightly improved on our original analysis, however, the relationship between dominance rank and flanker performance was still very weak (Figure 6: $R^2 = .123$, $p = .1895$, 95% CI[.19, .29]). The relationship between dominance rank and flanker performance was comparatively much weaker in juveniles (Figure 6: $R^2 = .000$, $p = .9676$, 95% CI[.10, .24]). All of these analyses compared monkeys rank based on which matriline they belonged to, but within matrilines monkeys differ in rank from one another. Thus, using matrilineal rank rather than absolute rank may be weakening our analysis by obfuscating the relative dominance rank between all individuals. Therefore, we performed one final analysis looking at flanker performance and absolute dominance rank. We found that no relationship between flanker performance and dominance rank regardless of whether we analyzed all monkeys, adults only, or juveniles only (Full Model: $R^2 = .044$, $p = .257$, 95% CI[.18, .25]; Adults only: $R^2 = .156$, $p = .296$, 95% CI[.19, .29]; Juveniles only: $R^2 = .004$, $p = .801$, 95% CI[.10, .24]).

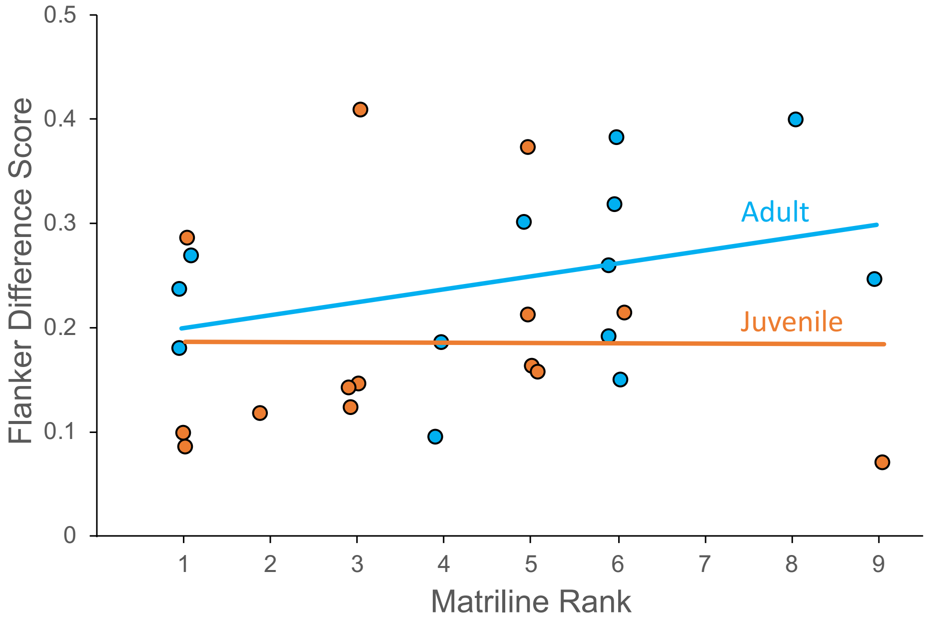

Figure 6: Flanker performance as a function of rank for adult (blue) and juvenile (orange) rhesus monkeys. Rank was not significantly associated with flanker performance in either adults or juveniles.

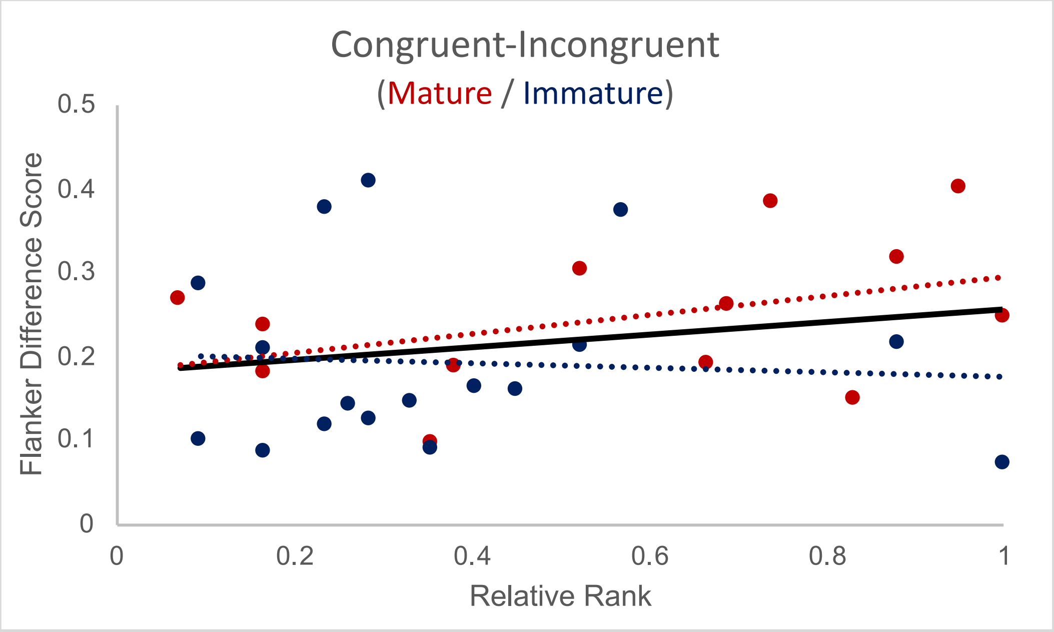

Figure 7: Flanker performance as a function of absolute rank for adult (red) and juvenile (dark blue) rhesus monkeys. Line of best fit for all monkeys is in black. We found that absolute rank did not significantly predict flanker performance when analyzing all animals, adults only, or juveniles only.

Hair Cortisol Across Ranks

One sample within our dataset was removed because it was greater than three standard deviations above the mean. We then checked to see if our data violated assumptions of normality. Through visual inspection, a Shapiro test (*p* = .0001), and a qpplot, we determined that cortisol concentrations were not normally distributed. We, thus, we log transformed cortisol values prior to statistical analysis.

There was no relationship between hair cortisol concentrations and matriline rank (Figure 7: R^2 = .05, *p* = .2837, 95% CI[270.99, 372.04]). We performed a follow-up analysis looking at hair cortisol and absolute dominance rank rather than matriline rank and, again, found no significant relationship (R^2 = .016, *p* = .556, 95% CI[270.99, 372.04]). Previous studies have shown that hair cortisol concentrations vary across development in rhesus monkeys (Dettmer, Novak, Suomi, & Meyer, 2012). Our sample included both pre and post-pubertal monkeys, and therefore our analysis may have been influenced by pubertal related changes in hair cortisol. We included age as an additional predictor variable in our model to determine whether there was an interaction between age, hair cortisol, and dominance rank in rhesus monkeys. We found that age significantly predicted hair cortisol (*p* = .049), dominance rank did not (*p* = .514), and there was no significant interaction between dominance rank and age (R^2=.18, *p* = .569, 95% CI[270.99, 372.04]). Hair cortisol is particularly useful for determining whether a monkey is experiencing chronic HPA activation as it reflects circulating cortisol over the course of months. Previous studies have shown that subordinate monkeys mount a comparatively blunted but prolonged stress response, which is associated with significantly elevated hair cortisol (Dong-Dong, et al., 2013; Michopoulos, Higgins, et al., 2012; Michopoulos, Reding, et al., 2012). Thus, our results deviate from previous findings, as we found that social subordination was not associated with chronic HPA activation.

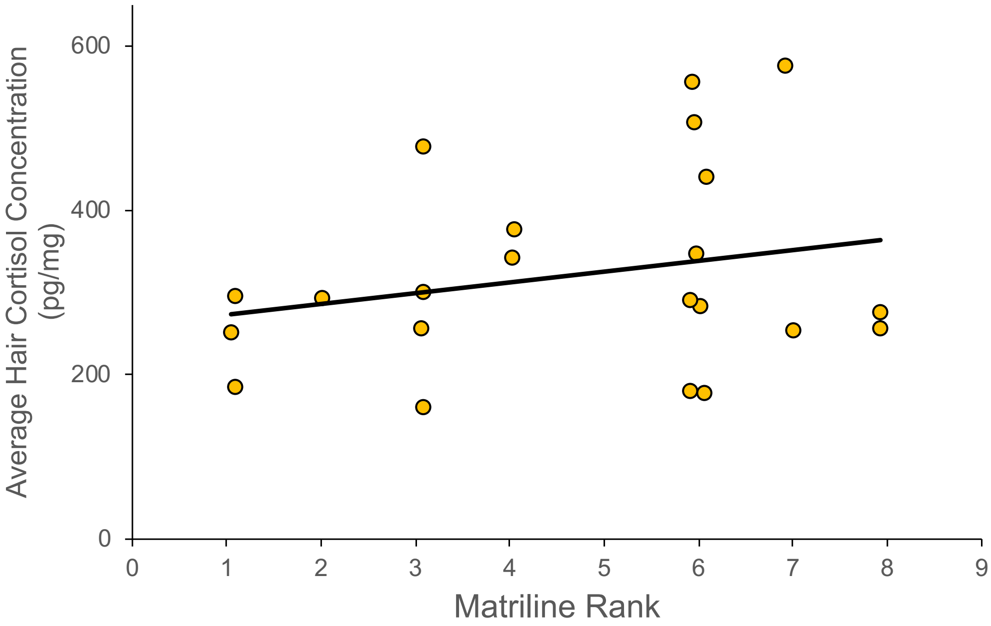

Figure 8: Hair cortisol concentrations as a function of matriline rank. Rank was a weak predictor of hair cortisol, and our results suggest that socially subordinate monkeys were not chronically stressed.

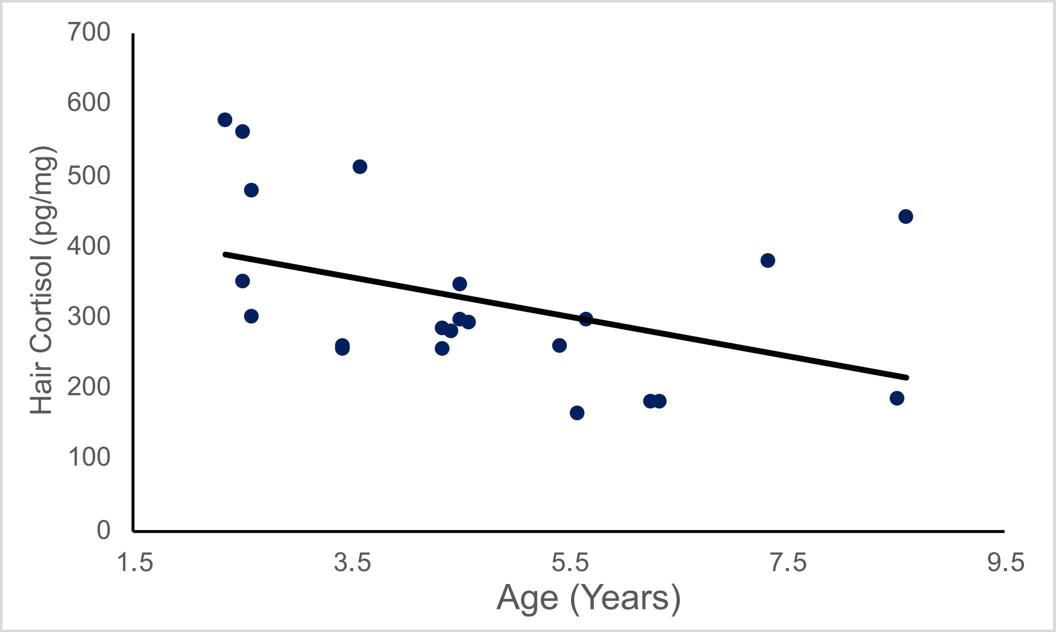

Figure 9: Hair cortisol concentrations as a function of age in rhesus monkeys. Age significantly predicted hair cortisol concentrations suggesting that our measure was sensitive to changes in development.

One reason why we may not have observed a relationship between cortisol and dominance rank is because we used suboptimal methods for collecting hair samples. The recommended procedure for collecting hair samples for a cortisol assay is to first shave the nape of the neck, re-shave the same spot 3 months later and use this second hair sample for analysis (Davenport, et al., 2006; Meyer & Novak, 2012). The process of shaving and re-shaving is important because it helps control for differences in the rate of hair growth across animals. We were only able to access the monkeys once for hair sample collection, and thus, our sample may reflect both differences in HPA activation as well as rate of hair growth across animals.

The results from these two analyses suggest that social subordination in large social groups is not associated with impaired attentional control or chronic HPA activation. Although this finding does not address our original hypothesis, it may nevertheless be important. Our results suggest that there is nothing inherent about subordination that predisposes a monkey to perform worse on cognitive control tasks. Previous research on group-housed rhesus monkeys show that subordinate animals attend to their social surroundings to a greater degree than dominant monkeys (Drea & Wallen, 1999). One concern we had was that subordinate monkeys could show relatively impaired attentional control because they divide their attention between their social surroundings and the cognitive task. Our results indicate that subordinate monkeys perform similarly to dominants, regardless of whether they are more likely to divide their attention or not.

The relatively large size of our social group may have contributed to why we did not see a relationship between social dominance and hair cortisol. Studies investigating dominance rank and HPA dysfunction in rhesus monkeys have often done so using group sizes of 5 or 6 individuals total (Dong-Dong, et al., 2013; Michopoulos, Higgins, et al., 2012; Michopoulos, Reding, et al., 2012; Sassenrath, 1970). The relationship between HPA dysfunction and dominance rank is not only observed in small groups, however, as there have been a few studies reporting this relationship in relatively larger social group sizes (Gust, et al., 1993; Wilson, et al., 2013; Abbott et al., 2013). It may be more common to observe a relationship between elevated cortisol and dominance rank in smaller groups of unrelated individuals because the frequency with which subordinates encounter unpredictable stressors may be higher. Elevated cortisol in rhesus monkeys is correlated with higher rates of received aggression, fewer affiliative interactions, and smaller family group size (Abbott, et al., 2013). In small rhesus social groups, aggression may be more focused on one or two animals, and subordinates receive little if any social support from other members of the group. Furthermore, small rhesus groups are often housed in relatively smaller spaces, which makes it more difficult for subordinate animals to avoid confrontation with dominants (Creel, 2001; Sapolsky, 2005). As group and housing size increases, the factors that contribute to elevated cortisol may become less severe. In larger social groups, aggression is likely to be more widely distributed among subordinate members; subordinates are housed with kin, and thus, are more likely to receive social support; and relatively larger housing makes it easier to avoid confrontation with dominant monkeys. Thus, future studies should test whether social subordination is associated with impaired cognitive control in relatively small social group sizes.

2.3 General Discussion

We tested for attentional control in rhesus monkeys across two experiments. In Experiment 1, we tested whether stimulus incongruency affected attentional control in rhesus monkeys using a nonhuman analog of the Eriksen flanker task. Monkeys were significantly less accurate on incongruent trials relative to congruent trials. The effect of incongruency was not simply due to a difference in visual discordance because monkeys were significantly more accurate on neutral relative to incongruent trials, and significantly less accurate on neutral relative to congruent trials. Our findings are consistent with those reported in human studies, albeit for accuracy rather than latency (Eriksen & Eriksen, 1974). In Experiment 2, we tested whether stress stemming from social subordination in rhesus monkeys was associated with impaired attentional control. We found that neither hair cortisol or flanker performance correlated significantly with social rank. The findings from Experiment 2 suggest that, impaired attentional control is not a consequence of social subordination in rhesus monkeys living in large naturalistic groups.

Future studies should continue to assess whether rhesus monkeys are an appropriate animal model for studying the effects of chronic stress on attentional control in humans. A rhesus monkey model of chronic psychosocial stress may be an important tool for understanding how chronic exposure to unpredictable stress impairs attentional control in humans. Twin studies, using groups of fraternal and identical twins with identical rearing environments show that cognitive control ability is a highly heritable trait (Friedman, et al., 2008). However, the degree to which genes account for variation in cognitive control is significantly lower for individuals of low socioeconomic status (SES) compared to individuals of high SES (Capron & Duyme, 1989; Turkheimer, Haley, Waldron, D'Onofrio, & Gottesman, 2003). It may be that stress stemming from poverty predisposes individuals to develop cognitive control impairments. Chronic exposure to psychosocial stress has been shown to temporarily impair attentional control in humans (Liston, McEwen, & Casey, 2009). These impairments may lead to more global impairments in both cognition and mental health. For instance, one longitudinal study showed 6th grade girls with poorer attentional control were more likely to report being distracted by social stressors when reassessed in 7th grade, and were more likely to develop depression in 8th grade (Rudolph, Monti, & Flynn, 2018).

It is important to note that a rhesus monkey model cannot account for all of the ways that unpredictable stressors impede with cognition. Factors unrelated to stress, such as the cognitive load associated with living in poverty, has been shown to account for cognitive impairments in the poor (Mani, Mullainathan, Shafir, & Zhao, 2013; Shah, Mullainathan, & Shafir, 2012). Being poor is often accompanied by an unstable income, having to juggle expenses, sacrificing wants for needs, and so forth; and it is thought that the unrelenting pressures of financial woes consumes cognitive resources to the same degree as losing a night of sleep (Mani, et al., 2013). Sugar cane farmers show relatively impaired cognitive control before harvest season when income is scarce, and relatively better cognitive control after harvest when income is plentiful (Mani, et al., 2013). The concept of subordination is also thought to affect cognitive control, as participants will show transient impairments in cognitive control being influenced to feel subordinate in a laboratory setting (Guinote, 2007a, 2007b, 2007c; Smith, Jostmann, Galinsky, & van Dijk, 2008; Smith & Trope, 2006). These studies highlight the limitations of a rhesus monkey model for chronic stress and cognitive control. Rhesus monkeys may be able to tell us much about how psychosocial stress affects the brain, but they cannot fully model the life experiences of those are living in poverty.

In the present study, social rank did not predict attention control ability as measured by the flanker task. This indicates that social rank, per se, does not associate with cognitive control in monkeys. The relatively large social group we sampled from may have buffered subordinates from the effects of stress. Future work on this topic should test whether subordinate animals in small groups of 5 or 6 individuals show impaired inhibitory control. Although, our findings cannot speak to whether stress from subordination affects cognitive control, they do suggest that impaired attentional control may not be inherent to subordinates in large social groups. If a future study were to show that rank correlates with both chronic stress and impaired cognitive control, we may be in better position to attribute the cognitive deficits to stress rather than to other factors such as divided attention. Our study leaves much room for further investigation and we believe more work investigating social dominance, chronic stress, and cognitive control is needed.

Chapter 3: Rhesus monkeys manipulate mental images

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Nonhuman animals cannot use words to mentally represent the world, but they may use mental images (Griffin, 1976; Premack, 1983). Human mental images are representations that partially recapitulate perception, occur in the absence of sustained perceptual input, and are associated with phenomenal visual experience (Ganis, Thompson, & Kosslyn, 2004; Kossyln, 1988). Mental images contain information about objects, such as shape, color, and orientation, and can be transformed in ways that are functionally isomorphic to physical transformations (Kosslyn, 1980; Neiworth & Rilling, 1987; Shepard & Cooper, 1986). Human mental imagery supports detailed memory and allows us to simulate states of the world, as when we mentally re-arrange furniture before physically moving it (Moulton & Kosslyn, 2009; Pearson & Kosslyn, 2015). Mental imagery may also be an important tool in the nonhuman cognitive tool kit.

Nonhuman mental representations have been found to have some, but not all, of the properties of human mental imagery. Nonhumans clearly represent distinguishing features of visual stimuli and can relate those to the external world (e.g., monkeys: Basile & Hampton, 2013; Miller, Erickson, & Desimone, 1996; dogs: Adachi, Kuwahata, & Fujita, 2007; Bräuer & Belger, 2018; pigeons: Neiworth & Rilling, 1987). Whether nonhumans experience phenomenal vision is difficult to determine, but there are at least two lines of evidence consistent with phenomenal vision in monkeys. First, studies of “blindsight” suggest the existence of both phenomenal and implicit vision in monkeys, in that the ability of monkeys to report the occurrence of visual stimuli can be dissociated from the ability to indicate the location in which stimuli were presented (monkeys with V1 lesions: Cowey & Stoerig, 1995; Moore, Rodman, & Gross, 2001; intact monkeys: Andersen, Basile, & Hampton, 2014). Second, nonhuman metamemory studies suggest that monkeys monitor the presence of representations in memory, which in humans is often accompanied by phenomenal visual experience (Basile, Schroeder, Brown, Templer, & Hampton, 2014; Hampton, 2001; Zakrzewski, Johnson, & Smith, 2017). Here we report our findings on a third feature of mental imagery in nonhuman animals - mental transformation. We report that rhesus monkeys transform mental representations in a way that is functionally isomorphic with physical rotation. Because monkeys mentally represent features of the physical world, appear to have phenomenal vision, and manipulate mental representations, they appear to meet the same criteria humans do for mental imagery. Such images may prove to be important components of cognitive accounts of nonhuman behavior.

Studies of mental rotation provide powerful insights into mental representation across species because such studies collect objective evidence about mental events without requiring explicitly introspective reports. Studies of mental rotation in humans played a major role in the “cognitive revolution,” which marked the resurgence of mental events as critical in the explanation of psychological phenomena. These studies found that people transform mental representations of objects in a way that is isomorphic to physical rotation (Pearson & Kosslyn, 2015; Shepard & Metzler, 1971). Much as it takes about twice as long to physically rotate a steering wheel 180 than 90 degrees, it takes about twice as long to visualize doing so. Participants in these studies decided whether a rotated test shape was identical to, or a mirror image of, a comparison shape. The farther the rotated shape was from upright, the longer it took to decide, establishing a functional isomorphism between mental representations and the physical world (Shepard & Cooper, 1986; Shepard & Metzler, 1971).

Findings on mental rotation in nonhumans are sparse and inconsistent. Two studies report that degree of rotation predicted response latency: one in a single California sea lion (Mauck & Dehnhardt, 1997), and one in baboons (Vauclair, Fagot, & Hopkins, 1993). The effect in baboons was reported to occur only with right visual field presentation (not left or bilateral presentation), and is contradicted by a second publication in the same year by the same group using almost identical methods (Hopkins, Fagot, & Vauclair, 1993). The majority of reported tests of mental rotation in nonhumans found no relation between degree of rotation and response latency (no evidence: baboons: Hopkins, et al., 1993; lion-tailed macaque: Burmann, Dehnhardt, & Mauck, 2005; rhesus macaque: Nekovarova, Nedvidek, Klement, Rokyta, & Bures, 2013; mixed evidence: rhesus macaque: Köhler, Hoffmann, Dehnhardt, & Mauck, 2005). Pigeons show rotational invariance, with good accuracy across rotations and flat reaction time functions (Hollard & Delius, 1982). Pigeons learned to anticipate the position of a rotating clock hand, but this is explained as readily by timing as by mental transformation (Neiworth & Rilling, 1987). To provide a more definitive assessment of mental rotation in monkeys, we tested a comparatively large group of animals, used three converging tests, and ensured that monkeys performed with reliable accuracy before assessing the evidence for mental rotation.

In Experiment 1 monkeys took longer to select shapes that matched a sample the further the shapes were rotated, demonstrating the hallmark of mental rotation. In Experiment 2, monkeys learned to use a rotational cue that informed them of how far to mentally rotate a shape in order to discriminate it from a distractor that differed by only 30 degrees. In Experiment 3 we found that the rotational cue flattened the function relating degree of rotation and response latency, suggesting that monkeys initiated mental rotation prior to seeing test stimuli. Converging evidence from these three experiments indicates mental rotation and mental imagery in rhesus monkeys.

3.1 Experiment 1

Monkeys discriminated between rotated and mirror images of shapes, closely paralleling methods used with humans (Figure 1A) (Cooper & Shepard, 1973; Köhler, et al., 2005). At study, monkeys saw a 2-dimensional shape that disappeared after they touched it. After 500-milliseconds the studied shape and its mirror image appeared together, both rotated up to 120 degrees. Monkeys were rewarded for selecting the previously seen shape, avoiding the mirror image. Mirror images contain identical geometric features, making it impossible to identify the rotated match on the basis of features alone (Cooper & Shepard, 1973; Shepard & Metzler, 1971). A signature of mental rotation in humans is a linear increase in response latency as a function of angular disparity between the studies sample and the target (Shepard & Cooper, 1986). We hypothesized that if monkeys mentally rotate images of shapes, they will show a linear increase in response latency.

3.1.1 Methods

Subjects

We tested six adult male rhesus monkeys (*mean age: 9.8 years old*) that had extensive experience in cognitive testing. Monkeys had ad libitum access to water and received their daily caloric intake through a combination of nutritionally balanced reinforcement pellets and monkey biscuits. They were individually housed due to social incompatibility but had visual and acoustic contact with conspecifics

Apparatus

Computerized testing systems mounted on monkeys' home cages and consisted of a touch-sensitive LCD monitor (Elo TouchSystems, Menlo Park, Ca), two food dispensers (Med Associates Inc., St. Albans, VT), and were controlled by a custom program written in Visual Studio 2013 (Microsoft Corporation).

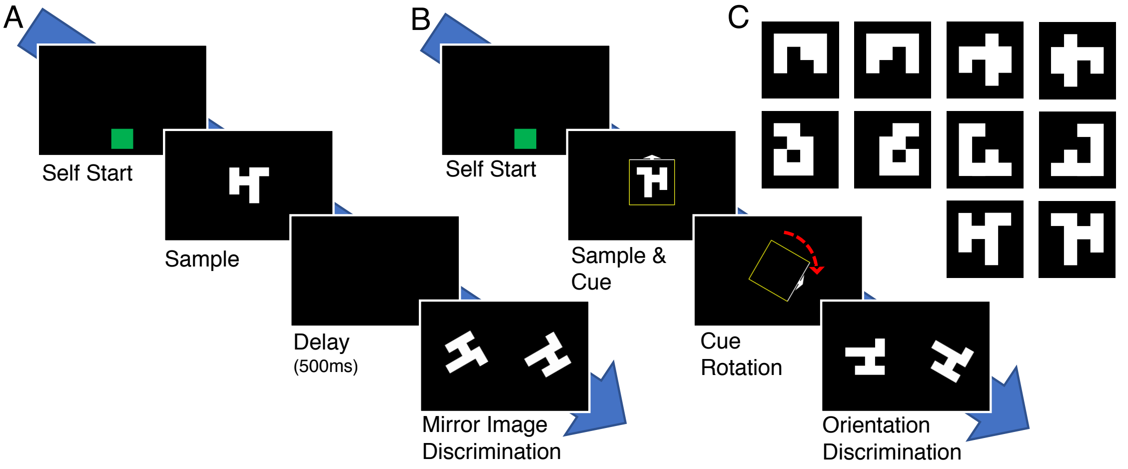

Figure 1: (A) Mirror image discrimination task used in Experiment 1. All trials started with two touches (FR 2) to the green square, followed by touching the sample shape (FR2), a 500-millisecond delay, and a mirror image discrimination test. Depicted here is a 60° test trial. (B) Cued angle discrimination task used in Experiment 2. After touches to the green square, the sample shape appeared inside a cue that would later indicate the angle of rotation to be selected at test. The cue began rotating after the sample was touched. In initial training the target image remained visible and rotated with the cue. As training progressed the target image disappeared progressively sooner until by the end of training the target image disappeared after it was touched, and only the cue rotated to the target angle. At test, monkeys were rewarded for selecting the image that was rotated to the extent indicated by the cue (here the right choice). In initial training, distractors were

+/- 60° from the target. In final testing, distractors were +/- 30° from the target (depicted here). (C) The pool of 10 stimuli used in Experiments 1, 2, and 3.

Procedure

Monkeys performed a match-to-sample task with a mirror image distractors (Figure 1A). Trials were initiated by touching a green start square twice (FR2). A sample shape then appeared centrally on screen. Samples were drawn from a pool of 10 stimuli: 5 shapes and their mirror images (Figure 1C). After touching the sample shape twice, the screen went blank for 500-milliseconds. At test, the sample shape and its mirror image were presented side by side, both rotated either 0°, 30°, 60°, 90°, or 120°. The position of the target and distractor were counterbalanced across trials. Selections of the rotated sample shape were followed by a reinforcing food pellet, positive audio feedback, and a 3-second inter-trial interval. Selections of the mirror image shape were followed by negative audio feedback and a 6-second time-out. All 10 stimuli appeared once as the correct response at each angle in each 50-trial session. Testing concluded for each monkey when it had completed at least 20 sessions and accuracy was significantly above chance at all orientations simultaneously over the last two blocks of five sessions (binomial test conducted for each orientation individually).

3.1.2 Results and Discussion

Monkeys were slower to respond on trials with larger angular disparity between sample and test shapes, showing the signature of mental rotation reported in humans (Figure 2, upper panel; median latency: $F_{(4, 20)} = 26.551$, $p < .001$) (Shepard & Cooper, 1986; Shepard & Metzler, 1971). Monkeys were also more likely to make errors as angular disparity increased (Figure 2, lower panel; arc-sine transformed proportion correct: $F_{(4, 20)} = 7.822$, $p = .001$). The increase in errors likely reflects forgetting and distortion of the mental image the longer monkeys had to retain and transform it in memory. However, correlated changes in accuracy may confound our latency finding because longer latencies often accompany guessing (Hampton, 2009). Thus, the increase in latency could reflect the fact that monkeys guessed more often at larger angular disparities, rather than reflecting the time-consuming process of mental rotation. We mitigated this possibility by analyzing latencies from correct trials only, but the proportion of trials containing correct guesses may nevertheless be greater with greater rotational disparity. We addressed this issue in Experiment 2 by designing a novel procedure that does not depend on latency as the source of evidence for mental rotation.

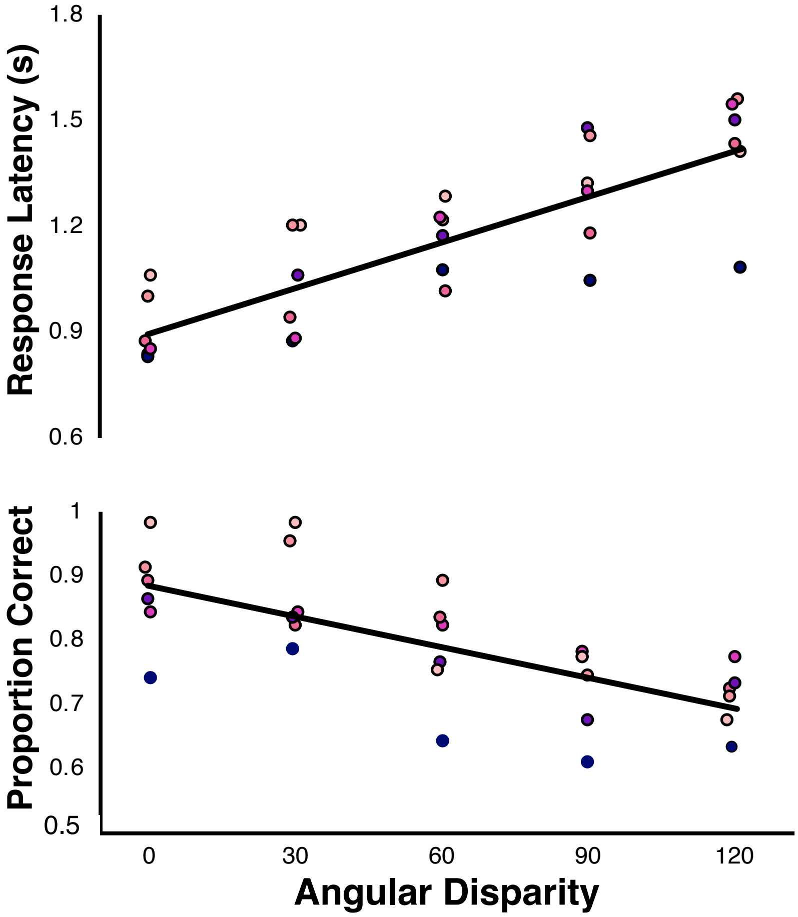

Figure 2. Monkeys responded more slowly and were less accurate with greater angular disparities in the mirror image discrimination task used in Experiment 1. *Top panel*, median response latency(s) on correct trials; *bottom panel* accuracy as a function of angular disparity.

We used mirror images as distractors because mirror images share symmetrical structural properties with the targets. Nonetheless, it is possible that monkeys generalized from the sample shape to the target shape by some means other than rotational transformation of the sample. Experiment 2 also addresses this issue by explicitly requiring monkeys to discriminate identical shapes that differ only in orientation.

3.2 Experiment 2

In contrast to Experiment 1, where monkeys discriminated rotated shapes from mirror-images, we required monkeys in Experiment 2 to discriminate identical shapes on the basis of orientation. At study monkeys were cued to mentally rotate a shape to a specific orientation. At test they saw two identical shapes, one rotated the cued amount, and the other rotated 30° more or less than the target (Figure 1B). The rotational cue only specified the amount of rotation and did not explicitly show how the sample would appear at test. Thus, monkeys had to transform the shape mentally, in the absence of concurrent perceptual input. If monkeys rotate mental images, then they should be able to use these images to identify the correct choice at test.

3.2.1 Methods

Subjects & Apparatus

Five of the 6 subjects used in Experiment 1 were used; the 6th monkey was unable to complete the training procedure. The same stimuli and apparatus were used.

Procedure

Monkeys learned in stages that a cue indicated the extent to which a target image would be rotated from the sample orientation.

<u>*Initial rotation discrimination training*</u>*:* After monkeys initiated a trial, a sample shape appeared surrounded by a rotational cue (Figure 1B). Monkeys touched the sample shape and the shape and the cue rotated clockwise 0°, 30°, 60°, 90°, or 120°. All rotations took the same amount of time, and involved the same number of animation frames, with each frame involving a larger

movement for larger rotations. For example, on a 30° trial, the cue was drawn and redrawn 30 times, rotating clockwise by 1° each time; and on a 120° trial, the cue was drawn and redrawn 30 times, rotating clockwise by 4° each time. The cue and sample remained onscreen for 500-milliseconds after rotation was complete. The test appeared after the screen was blank for 500ms. Both test choices were the previously seen shape. The target was rotated to the cued orientation, and the distractor was rotated +/- 60° relative it. The left-right position of the target on the screen, and whether the distractor was rotated more or less than the target was counterbalanced across trials. Each target orientation was used with each shape twice per session, once with a distractor at -60° and once with a distractor at +60°, yielding sessions of 100 trials. After monkeys were significantly above chance simultaneously at each orientation (binomial tests conducted every 5 sessions) the difference between the targets and distractors was reduced to 30°. After again meeting criterion, monkey progressed to the next stage of training.

Sample shape fading: Monkeys learned to follow the rotational cue in the absence of the target image rotating with it. We removed the sample shape before the cue had completed rotating. The point at which the target shape disappeared was pseudorandomly drawn from among 10 possible points between 67% and 100% of the total rotation achieved by the cue. Monkeys again had to reach criterion. This process was repeated with the sample shape disappearing between 33% and 67% and finally 0% and 33% of cue rotation.

Cue Only Tests: The sample was always removed immediately after being touched, and the cue then rotated to the to-be-tested orientation without the sample shape. Monkeys completed this test when they met the same accuracy criterion used in training.

3.2.2 Results and Discussion

All monkeys learned to discriminate the shape that appeared at the cue orientation from distractors that appeared rotated by +/- 30 degrees (binomial calculated individually for each monkey and each orientation over the last 5 sessions of testing; trials were the distractor appeared at an orientation that was never reinforced, e.g. -30 degrees from upright were excluded. See supplemental table for individual values). Monkeys succeeded at this task when the orientation of the target shape was indicated only by the cue, without the benefit of seeing the target shape itself rotate. Monkeys therefore mentally represented and transformed the orientation of the shapes with a fidelity better than 30 degrees. These results are indicative of mental imagery because they show that monkeys formed detailed shape representations with a high degree of fidelity to real world shapes, and that they transformed these representations in a way that preserved isomorphism.

One alternative interpretation of these findings is that monkeys learned a complex set of conditional associations of the sample shape and rotational cue combinations. This seems unlikely due to the large number, and the precision, of conditional associations that would be required. Furthermore, if monkeys learned a set of specific associations between sample shapes, cue positions, and targets, performance should not vary as a function of the extent of cue rotation. This is because the delay between study and test was constant and the difference in angular disparity between targets and distractors was a constant 30 degrees. Nothing about extent of rotation of the cue makes some trials more difficult than others. In contrast, if monkeys transformed images of the shapes through mental rotation, trials with more rotation should be more difficult because the precision of mental images should decline the more they are transformed. Monkeys were significantly less accurate on trials with greater cue rotation, consistent with mental imagery and rotation (main effect of cued angle: $F_{(4, 16)} = 11.509$, $p < .001$).

3.3 Experiment 3

When humans are informed about the orientation in which the target will appear in a mental rotation task, they show a flattened slope of the function relating latency and angular disparity. This shows that they use the cue to initiate mental rotation prior to the appearance of the test, and carry out the rotation in the absence of further perceptual input (Cooper, 1976; Cooper & Shepard, 1973; Suchan, Botko, Gizewski, Forsting, & Daum, 2006). We leveraged the fact that our monkeys learned to use a rotational cue in Experiment 2 to test whether monkeys show the same effect reported in humans. Monkeys repeated the mirror image discrimination task conducted in Experiment 1, but were either cued, or not cued, about the orientation in which the test stimuli would appear. If monkeys mentally rotate the mental image of the shape when cued, then the latency slope for cued mental rotation trials should be shallower than the slope for uncued trials.

3.3.1 Methods

Subjects & Apparatus

Monkeys and materials were the same as used previously.

Procedure

Monkeys first completed a block of trials using the same procedure in Experiment 2, except two types of tests were pseudorandomly intermixed. Half of trials were mirror image discrimination trials, the other half of trials were orientation discrimination trials. Intermixing the two types of trials ensured that monkeys used the rotational cue, because half of the time they needed to discriminate on the basis of orientation. Monkeys were required to perform at or above 64% across 2 consecutive 5-session blocks. Upon meeting this criterion, monkeys were moved onto the final block of mirror image discrimination trials without the rotational cue. Conducting these sessions last ensured that continued training could not account for any flattening of the curve observed in the cued trials. Monkeys completed the uncued block of trials after meeting the same performance criterion used in Experiment 1. We compared performance on the last 10 sessions of trials for both cued and uncued mirror image discrimination trials.

3.3.2 Results and Discussion

The response latency function was shallower for cued trials relative to uncued trials (Figure 3; rmANOVA, interaction: $F_{(4, 16)} = 3.441$, $p = .033$; cued vs uncued: $F_{(1, 4)} = .367$, $p = .577$; angle disparity: $F_{(4, 16)} = 3.441$, $p = .033$). These results provide a striking parallel to what is found when humans are allowed to mentally rotate a stimulus into congruence prior to test (Cooper, 1976; Cooper & Shepard, 1973; Suchan, et al., 2006). Monkeys were also more accurate on cued trials relative to uncued trials across all angular disparities (rmANVOA, cued vs uncued: $F_{(1, 4)} = 11.991$, $p = .026$; angular disparity: $F_{(4, 16)} = 7.389$, $p = .001$; interaction: $F_{(4, 16)} = .813$, $p = .535$). The rotational cue presumably reduced latency and improved accuracy because monkeys transformed their mental image to more closely match the target stimulus before it appeared. However, even with the cue, there was still a significant effect of angular disparity on latency and accuracy, suggesting that the rate of the rotational cue may have been faster than the rate of mental rotation in monkeys. Therefore, monkeys may not have completed rotation of their mental image before the test stimuli appeared, necessitating further rotation—albeit less than uncued trials. We tested this assumption by comparing performance in the concurrently administered orientation discrimination tests. If monkeys rotated mental images more slowly than the cue rotated, they should be more likely to make errors to distractors that are less rotated than the target, compared to distractors that are more rotated than the target. Monkeys were significantly more likely to err to underrotated distractors than to overrotated distractors (t_4 = 3.055, *p* = .038; 0° and 120° trials were not included in this analysis because -30° and +150° distractors were never reinforced).

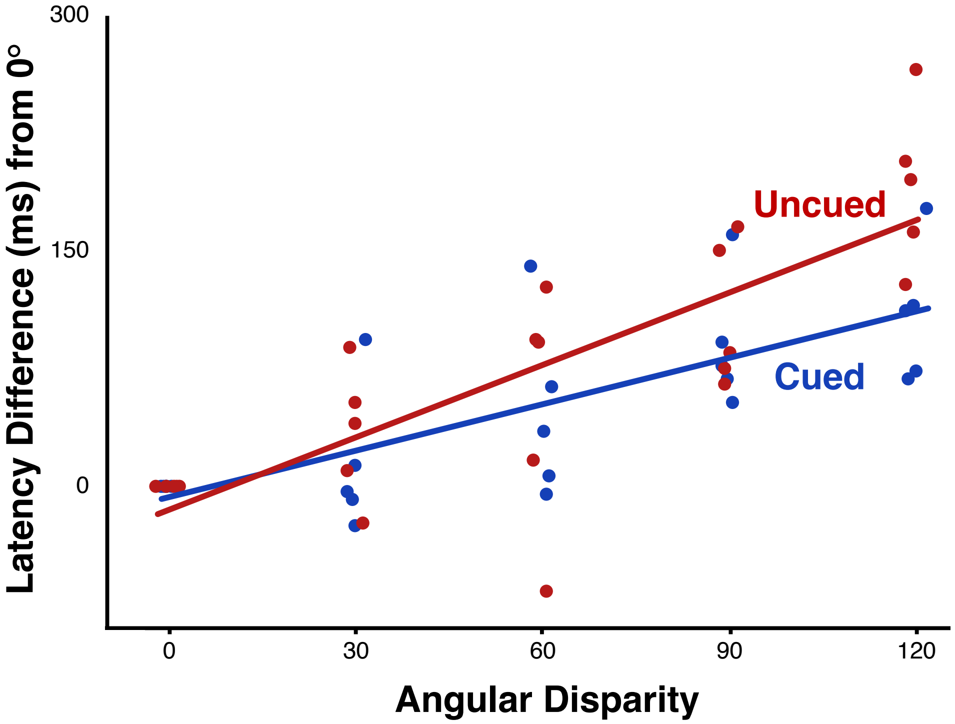

Figure 3. Monkeys produced a shallower latency function when cued (blue line) than when not cued (red line) in Experiment 3. To control for individual variation in response speed, we plotted the difference between

the latency at each angular disparity and the latency at 0° for each monkey. Trendlines indicate lines of best fit for cued (blue) and uncued (red) trials.

3.4 General Discussion

The results presented here indicate distinctive signatures of mental imagery in rhesus monkeys. In Experiment 1, monkeys generalized from upright to rotated shapes and showed the hallmark relation between response latency and extent of rotation. In Experiment 2, monkeys transformed mental images using a rotational cue, allowing them to identify a shape that matched their mental image with a precision of under 30 degrees. In Experiment 3, monkeys used the rotational cue to mentally rotate images prior to test, significantly flattening the rotation-latency function. Thus, the mental representations monkeys formed in this study included fine perceptual details about visual stimuli that remained isomorphic through extensive mental transformation in the absence of sustained perceptual input. The findings from these three experiments, combined with evidence from studies of blindsight that suggest phenomenal visual experience in monkeys, indicate that rhesus monkeys form and manipulate mental images (Andersen, et al., 2014; Cowey & Stoerig, 1995; Moore, et al., 2001).

Mental images could underlie a variety of nonhuman animal behaviors. Vervet monkeys make specific anti-predator responses when they hear particular alarm calls and may visualize the predator indicated by the call in support of this specificity (Cheney & Seyfarth, 1990). It is common for animals to form expectations of specific rewards, as shown by selective satiation experiments, and these expectations could involve visualizing the expected food (Baxter & Murray, 2002). While it may be considerably less common for nonhumans to have cause to transform mental images, tool-users might gain sophistication in their use of tools with the aid of isomorphic transformations of mental images, and navigation might be enhanced by visualization of mental maps (Hunt,1996; Tomasello, Davis-Dasilva, Camak, & Bard, 1987; Tolman, 1948).

Human mental representations often include propositional linguistic content in addition to, or instead of, recapitulating perceptual processes (Pearson & Kosslyn, 2015; Pylyshyn, 1973). Lacking language, nonhumans may be especially dependent on representations that are based in the processes that give rise to the initial perception of stimuli, rather than propositional representation. Our results suggest an evolutionary continuity, at least among primates, in the representation of stimuli with visual imagery. Evidence from other cognitive paradigms suggests that nonverbal animals rely on quasi-visual, rather than propositional, representations to solve a range of tasks (transitive inference: Gazes, Chee, & Hampton, 2012; Gazes, Hampton, & Lourenco, 2017; quantity discrimination: Gazes, et. al., 2017; Brannon & Merritt, 2011; Lourenco & Longo, 2010; memory for order: Templer & Hampton, 2013; Bunsey & Eichenbaum, 1996). Visual imagery may be an especially powerful form of representation for nonhumans. The evidence presented here showing that monkeys transform mental images may begin to transform our image of monkey mentality.

Chapter 4: General Discussion

Humans and nonhumans would be much less effective at navigating virtually every aspect their daily lives without cognitive control. In humans, cognitive control is needed to be successful at work, in school, and for maintaining relationships with other people (Diamond, 2013; Shallice & Burgess, 1991). Although we do not know the extent to which nonhuman animals use cognitive control in their daily lives, it nevertheless appears to be highly important feature of nonhuman cognition (Carruthers, 2013). Cognitive control is likely important for maintaining social relationships in rhesus monkeys. Rhesus monkeys with bilateral prefrontal lesions are ostracized from their social group because they act impulsively and are unable to adhere to social dominance norms (Franzen & Myers, 1973). Chimpanzees likely use cognitive control when foraging because they factor in effort, distance, and food quality when deciding where to collect food (Genovesio, Wise, & Passingham, 2014; Sayers & Menzel, 2012). Cognitive control is not limited to the primate order, as a wide variety of animal species have shown evidence of cognitive control in laboratory settings (Crows: Balakhonov & Rose, 2017; Dogs: Bräuer & Call, 2011; Rats: Bratch, et al., 2016). We are only just beginning to understand the role of cognitive control in nonhuman animals. Future laboratory studies will be important for studying the neurobiological basis of cognitive control in nonhuman animals. Future studies in natural or naturalistic settings will be important for identifying the functional role of cognitive control in nonhuman species. In this dissertation, I tested for cognitive control in rhesus monkeys across 5 experiments conducted in both a laboratory and a semi-naturalistic setting. The findings from this dissertation provide a small but meaningful advance in our understanding of cognitive control in rhesus monkeys.

In Chapter 2, I described two experiments that tested for attentional control in rhesus monkeys. In Experiment 1, we report that attentional control in rhesus monkeys is sensitive to stimulus incongruence as well as neutral visual noise, paralleling previous findings in humans (Eriksen & Eriksen, 1974). In Experiment 2, we tested whether stress stemming from social dominance in rhesus monkeys was associated with impaired attentional control. In humans, attentional control is sensitive to anxiety and stress, and impaired attentional control may predispose individuals to develop depression (Eldar & Bar-Haim, 2010; Rudolph, et al., 2018; Waszczuk, et al., 2015). Our motivation for Experiment 2 was to determine whether group-housed rhesus monkeys may be an appropriate animal model to study the effects of stress on attentional control in humans. We found that neither hair cortisol or attentional control correlated significantly with social rank. The findings from Experiment 2 suggest that matrilines in relatively large social groups do not inherently differ with respect to attentional control. Future work should address this question in smaller social groups where the relationship between social dominance rank and stress is more reliably found (Dong-Dong, et al., 2013; Michopoulos, Higgins, et al., 2012; Michopoulos, Reding, et al., 2012; Sassenrath, 1970).

Smaller social groups are better positioned to address whether stress stemming from social subordination impairs attentional control in rhesus monkeys. In smaller groups, it is possible to change the ranks of dominant and subordinate animals by reassigning them to new social groups (Kohn, et al., 2016). For example, if there are 5 social groups each containing 5 monkeys that fall along a social ranking of 1 (dominant) to 5 (subordinate), you can take all of the 1s from each group and reassign them to live together. This process can also be applied to the rest of the ranks within the social group. Reassigning monkeys cause all but one to change rank, thereby allowing us to see what happens to cognition when an alpha becomes the most subordinate monkey, and vice versa. This will allow us to isolate social status as a causal factor for impaired cognitive control.

Relatively new research in humans suggests that poor attentional control may be a risk factor for developing stress-related mental disorders such as clinical depression (Rudolph, et al., 2018). Future studies on social dominance may be able to clarify whether poorer attentional control predisposes an animal to develop stress-related pathology. When social groups of rhesus monkeys are formed in captive settings, monkeys are introduced incrementally rather than all at once. The order of introduction correlates with dominance status, whereby monkeys introduced earlier are more likely to occupy socially dominant positions within the hierarchy (Kohn, et al., 2016). We could use this feature of group formation to our advantage, and place monkeys with relatively greater and poorer attentional control in subordinate positions. As we observed in Chapter 2, monkeys within and across matrilines varied greatly with respect to flanker performance. Using the subject pool described in Chapter 2, we may be able to test whether monkeys with relatively poorer attentional control are more likely to exhibit chronic HPA activation compared to monkeys with relatively better attentional control.

In Chapter 3, I described three experiments that tested for mental rotation of mental images in rhesus monkeys. In Experiment 1, monkeys generalized from upright to rotated shapes and showed the hallmark relationship between response latency and extent of rotation. In Experiment 2, monkeys transformed mental images using a rotational cue, allowing them to identify a shape that matched their mental image with a precision of under 30 degrees. In Experiment 3, monkeys used the rotational cue to mentally rotate images prior to test, significantly flattening the rotation-latency function. Across these three experiments, rhesus monkeys formed and transformed mental representations containing fine perceptual details about visual stimuli. More generally, the findings from Chapter 3 suggest that rhesus monkeys form and manipulate mental images.

At present, we know very little about how or why mental imagery evolved. There are two reasons for this: 1) the field of mental imagery has primarily focused on proving the existence of mental images in humans, and 2) there has been very little research on nonhuman imagery (Moulton & Kosslyn, 2009; Pearson & Kossyln, 2015). Generally, there are two theories on why humans evolved to use mental images, and what their adaptive value is. First, researchers believe the primary function of mental imagery in humans is to simulate future events (Moulton & Kosslyn, 2009). For example, when moving into a new apartment, we may first imagine where furniture will go before moving in; or when we purchase a lottery ticket, we may imagine what our future would look like if we won. A second theory is that mental images are adaptive because they allow us to store information efficiently (Pearson & Kossyln, 2015). Much like the idiom “a picture is worth a thousand words”, mental images allow us to recall information that may not have been explicitly considered at encoding. For example, when giving directions you may recall details about landmarks or unique street features that you have only ever passively encountered, such as locations you pass by on your way to work. Indeed, mental images are instrumental for simulating future events and recalling information, but it seems unlikely that they evolved for this purpose. These theories are heavily biased in human behavior, and largely ignore the possibility that mental imagery may be a central process of nonhuman animal cognition.

It seems more likely that mental images are the product of cognitive control. First consider the definition of mental imagery: representations that mirror perception but occur in the absence of sustained perceptual input (Kossyln, 1988). The concept of mental imagery is highly similar to how we think about working memory. Working memory is a cognitive control process that allows us to actively maintain and manipulate sensory information in mind (Carruthers, 2013). Neuroimaging and behavioral research suggests that imagery and working memory may be the same process (Albers, et al., 2013; Borst, et al., 2012; Keogh & Pearson, 2011; Tong, 2013). Both visual imagery and visual working memory involve prefrontal top-down activation of visual sensory areas (Ganis, Thompson, & Kosslyn, 2004; Mechelli, Price, Friston, & Ishai, 2004). The only difference between mental imagery and working memory is in how representations are formed. In general, researchers classify the act of sustaining a perceived representation in mind as working memory, and the act of sustaining an imagined representation as mental imagery (Borst, Ganis, Thompson, & Kosslyn, 2012). At its core, mental imagery is a process that allows us to reactivate previous sensory experiences. This likely conferred an advantage over simply sustaining a recent sensory experience, particularly if the reactivated representation was associated with survival (Nairne, Pandeirada, & Thompson, 2008).

This view on the evolution of mental imagery is not without its own flaws. There is evidence to suggest that mental images form though associative learning (Paivio, 1969). Participants will report seeing or hearing an unconditioned stimulus after perceiving a conditioned stimulus (Dadds, Bovbjerg, Redd, & Cutmore, 1997). A similar phenomenon may occur in nonhuman animals. For instance, vervet monkeys (*Chlorocebus pygerythrus*) have three acoustically distinct predator alarm calls that cause nearby conspecifics to react as if there is a nearby snake, leopard, or eagle (Seyfarth & Cheney, 2003). One possibility is that vervet monkeys form a mental image of a predator in response to a specific call, causing monkeys to react appropriately to the call (but also see Owren & Rendall, 1997). There is also evidence to suggest that dogs and rhesus monkeys form mental images in response to olfactory and acoustic cues (Adachi & Hampton, 2011; Adachi, Kuwahatam & Fujita, 2007; Bräuer & Belger, 2018; Seyfarth & Cheney, 2003). Some evidence suggests that these involuntary experiences of mental imagery may be supported by the parahippocampal and retrosplenial cortices (Bar & Aminoff, 2003). Thus, mental images may be the product of any brain system that can reactivate a sensory experience, rather than just the product of the prefrontal cortex.

The field of mental imagery will benefit from studies using nonhuman animals. Much of the work on mental imagery has been performed with human subjects, and thus, theories on mental imagery tend to be overly anthropocentric. For instance, take the position by Moulton and Kosslyn (2009): the primary function of mental imagery is to simulate future events. Outside of chimpanzees and perhaps corvids, there is very limited evidence of future planning in nonhuman animals (Carruthers, 2013). For some animal species, imagery may primarily function to support memory. In other animal species, like humans, chimpanzees, and New Caledonian crows, mental imagery may contribute to a wider variety of processes such as memory, tool use, and future planning (Carruthers, 2013; Inoue-Nakamura & Matsuzawa, 1997; Weir, Chappell, & Kacelnik, 2002). To date, explicit tests on mental imagery have been confined to a small number of nonhuman species, and thus, we know very little about how widespread mental imagery really is. Future studies should aim to test imagery in a larger variety of both ape and non-primate species.

In this dissertation I describe 5 experiments that tested for cognitive control in rhesus monkeys. In Chapter 2, I investigated the nature of attentional control in rhesus monkeys, and found that the process appears to be functionally similar across human and rhesus monkeys. I also tested whether attentional control ability was predicted by social dominance rank in rhesus monkeys. The results showed that social dominance rank did not predict hair cortisol or attentional control performance. Future studies should aim to test whether stress stemming from subordination is associated with impaired attentional control in smaller rhesus social groups. In Chapter 3, I investigated whether rhesus monkeys manipulate mental images. We found that monkeys form and manipulate mental images in a functionally isomorphic manner. The results from Chapter 3 provide one of the first clear evidences of mental imagery in nonhuman animals. It is my hope that these two studies provide incremental, but important, advances in our understanding of cognitive control in rhesus monkeys.

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