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An abstract of
a thesis submitted to the Faculty of Emory College of Arts and Sciences
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Abstract

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Inhibitory control is a critical component of human cognition and behavior. According to the Strength Model, all inhibitory control behaviors rely on the same limited resource, and exerting inhibitory control depletes this resource. Support for this model comes from experiments showing that when humans experience consecutive tasks requiring inhibitory control, performance is impaired on the second task. In humans, this phenomenon is called ego depletion, but for nonhuman animals we will refer to it as inhibitory resource depletion. The Strength Model has been studied and debated extensively in humans, but little work has been done in nonhuman primates. The current study was designed to test whether rhesus macaques (*Macaca mulatta)* experience inhibitory resource depletion. Five monkeys were tested using touchscreen computer adaptations of the Flanker Task and the Wisconsin Card Sorting Test (WCST). The monkeys first completed 150 Flanker trials that were entirely incongruent, congruent, or absent. Incongruent flankers were designed to tax inhibitory control, whereas congruent and absent flankers do not. After the Flanker Task, the monkeys performed the WCST until they completed a WCST rule-switch. The WCST involves two rules, color or shape, and the monkeys respond based on the currently reinforced rule. Following a rule-switch, inhibitory control gets taxed because the subject must inhibit their learned response to the previously reinforced rule. We hypothesized that if inhibitory control behaviors in rhesus macaques rely on a limited resource, then monkeys will exhibit significantly impaired performance on the WCST rule-switch following incongruent flanker trials, compared to congruent or absent flanker trials. There was no apparent effect of inhibitory resource depletion in this experiment, as performance did not vary significantly following different Flanker types. Experimental design manipulations that may better assess inhibitory resource depletion are discussed.

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INTRODUCTION

Inhibitory control is a critical component of human behavior because it supports goal-directed actions through top-down control of behavior and cognitive processes (Diamond, 2013). Inhibitory control is one of three core executive functions, along with working memory, and cognitive flexibility (Diamond, 2013; Miyake *et al.,* 2000). Exerting inhibitory control is particularly important in situations where acting off of impulse would be inappropriate. Failures in inhibitory control are often linked to negative outcomes such as obesity, crime, or dishonest behaviors (Elfhag & Morey, 2008; Gottfredson & Hirschi, 2009; Mead *et al.,* 2009). Nonhuman animals also exert inhibitory control. For example, trained dogs will wait to consume food until given an explicit auditory or postural cue by their owner. The ability to control impulses, delay gratification, and regulate behavior is essential for engaging in social interactions and achieving future goals in both humans and other animals (Hagger *et al.,* 2010). It is easier to give into temptation than to resist it, and based on the Strength Model of self-control, exerting inhibitory control depletes a limited brain resource during times of overuse or mental exhaustion (Diamond, 2013; Baumeister, 2002; Muraven & Baumeister, 2000). In humans, this phenomenon is called ego depletion, but for nonhuman animals we will refer to it as inhibitory resource depletion.

The Strength Model and Inhibitory Resource Depletion in Humans

The Strength Model posits that all tasks requiring inhibitory control draw from the same limited resource, and just as a muscle gets tired from overexertion, repeated acts of inhibitory control exhaust this resource (Baumeister *et al.,* 2007). The analogy of inhibitory control as a muscle also works to explain the idea of a shared resource. While muscles derive their energy from the same source, the function of different muscles varies greatly, similar to how different acts of inhibitory control use the same resource, even on behaviors that are seemingly unrelated

(Baumeister *et al.*, 1998). In humans, inhibitory resource depletion is demonstrated by administering two inhibitory control tasks to participants consecutively and measuring performance on the second task. These experiments show that performing one task that requires inhibitory control will reduce performance on a subsequent inhibitory control task. A meta-analysis of current literature showed that ego depletion effects are moderated by multiple factors, such as task duration and intertask interim period (Hagger *et al.,* 2010). In general, inhibitory control strength is regained more slowly than it is used (Muraven & Baumeister, 2000). The exact mechanism for ego depletion is unknown, but Gailliot *et al.* (2007) found that exerting self-control, utilizes a large amount of blood glucose. In their study, replenishing blood glucose counteracted the effects of ego depletion. Some recent studies have corroborated this idea, but one study found that just tasting glucose is enough to reduce ego depletion (Sanders *et al.,* 2012). These data may suggest that the counteracting effect is not mediated by replenishing blood glucose, but rather that the glucose provides enough reinforcement and reward to reverse the depletion effects. Some alternative hypotheses for why ego depletion occurs include altered levels of motivation, self-efficacy, and affect (Inzlicht & Schmeichel, 2012; Hagger *et al.,* 2010).

Cognitive and Neurobiological Aspects of Inhibitory Control

In the current study, inhibitory resource depletion will be measured by administering variations of the Flanker Task and Wisconsin Card-Sorting Test (WCST) in rapid succession. The Flanker task requires subjects to respond selectively to centrally placed stimuli while ignoring information given by the flanking stimuli **(Figure 1;** Eriksen & Eriksen, 1974). Flankers can be congruent, incongruent, or absent. The Flanker task recruits selective attention, which is a component of inhibitory control that serves to focus cognitive resources on information relevant to goals, while ignoring extraneous information (Gazzaley & Nobre, 2012).

This kind of selective attention is called spatial suppression because you must suppress the processing of flanking stimuli (Zanto & Rissman, 2015).

In the WCST, subjects learn to discriminate different stimuli based on relevant dimensional "rules", such as color or shape **(Figure 2 & Figure 3)**. Across sessions of the task, dimensional rules change, thus requiring subjects to respond to one rule while simultaneously inhibiting the old rule. Subjects typically make two different types of perseverative errors. First, stuck-in-set errors occur when the subject continues choosing the answer that was correct previously, and second, recurrent perseverative errors are repetitions of a previous response after intervening correct responses (Nagahama *et al.,* 2005). The WCST uses different cognitive functions during each phase of the task, including working memory, cognitive inhibition, cognitive flexibility, and selective attention (for a review of executive functions see: Diamond, 2013). The type of selective attention used in the WCST is called feature-based suppression because the subject must suppress the dimensions of either color or shape (Zanto & Rissman, 2015).

There are many brain areas implicated in inhibitory control processes, but they are mostly contained within the prefrontal cortex (PFC), anterior cingulate cortex (ACC), and lateral parietal cortex. Reviews of studies in both humans and monkeys have demonstrated that spatial attention and feature-based attention use similar frontoparietal brain areas, indicating anatomical and functional homology within this domain of top-down control (Zanto & Rissman, 2015; Egner *et al.,* 2008; Maunsell & Treue, 2006). In a spatial suppression task similar to the Flanker task, the dorsolateral prefrontal cortex (DLPFC) was most important for inhibition of distracting stimuli in monkeys (Suzuki & Gottlieb, 2013). A fMRI study in humans found the largest amount of activation during the Flanker task incongruent trials in the right ventrolateral prefrontal cortex

(VLPFC), indicating its importance in response inhibition (Hazeltine *et al.*, 2000). A later fMRI study found activation of the left parietal cortex during both congruent and incongruent trials of the Flanker task, and the researchers suggested that this area is involved in the representation of possible response choices (Bunge *et al.,* 2002). The study additionally found activation in the lateral PFC and rostral ACC during incongruent trials only, indicating their selective importance in error inhibition. An investigation of subjects with neurodegenerative diseases found an association between left DLPFC and ACC atrophy and poorer accuracy on the Flanker task, as well as slower reaction times from DLPFC, VLPFC and temporal-parietal junction atrophy (Luks *et al.,* 2009). All of these studies taken together highlight the importance of the lateral PFC, left parietal cortex, and ACC for inhibitory control during the Flanker task.

Since the WCST has multiple phases, studies often find different brain areas implicated in each phase, but we will focus on the inhibition phase, which occurs following a rule-shift. Researchers and physicians utilize the WCST to screen for PFC damage, which can occur in neurodegenerative diseases such as Parkinson's disease. In a human functional magnetic resonance imaging (fMRI) study, researchers found that the mid-VLPFC, caudate nucleus, mediodorsal thalamus, and putamen showed increased activity after negative feedback, indicating a specific role in responding to a WCST rule-shift (Monchi *et al.,* 2001). One study in subjects with neurodegenerative dementia found that the rostrodorsal PFC crucially mediates the WCST rule shift (Nagahama *et al.,* 2005). In marmoset monkeys with selective PFC brain lesions, the lateral PFC was found to be most important for attending to the WCST rule-shift, and the orbitofrontal cortex was most involved in preventing stuck-in-set perseveration. An fMRI study in macaque monkeys and humans performing the WCST found activation in the posterior part of the ventrolateral PFC during rule-shifts, for both species (Nakahara *et al.,* 2002). The researchers postulated that these regions are functionally homologous in both species. A more recent study in adult male macaque monkeys found that the ACC was essential for the response slowing that occurs in the trials following a rule shift (Kuwabara *et al.,* 2014). The researchers postulated that the ACC was involved in monitoring the uncertainty of a WCST rule-shift, and that it might be useful for transitioning back into trial-and-error answering. While researchers have found many different brain areas involved in the WCST rule-shift, it is clear that in both humans and monkeys the PFC and ACC are essential for managing the inhibitory aspects of the task.

Inhibitory Resource Depletion in Nonhuman Animals

Numerous studies have demonstrated that nonhuman animals are capable of exerting inhibitory control, yet few nonhuman studies have investigated the Strength Model to determine the extent to which other animals experience inhibitory resource depletion. In a study on dogs, researchers found that when two consecutive tasks were given and the first task involved inhibitory control, the dogs persisted for a shorter time on the second task (Miller *et al.,* 2010). In the first task, dogs either needed to respond to a command of sit-stay for 10 minutes, or the dog was placed in a dog cage for 10 minutes. The sit-stay condition required active self-control and resulted in the dogs persisting for a shorter time on an unsolvable toy puzzle. The dogs in the cage condition did not need to exert active self-control, and they persisted for longer on the unsolvable puzzle. Interestingly, consuming glucose prior to testing eliminated this effect, paralleling the trend seen in humans. A very recent study by Petrillo *et al.* (2015) investigated the Strength Model in tufted capuchin monkeys, using a delayed gratification task to tax inhibitory control. The results of their study showed that monkey's performance on the delayed gratification task reduced as they experienced more iterations of the task, suggesting a short-term inhibitory resource depletion effect. However, preceding energy depletion or demanding cognitive tasks did not affect delayed gratification performance. The findings by Petrillo *et al.* (2015) imply the absence of inhibitory resource depletion for nonhumans, however this interpretation may be inappropriate because their study design appears unfit to tax inhibitory control resources. Specifically, the researchers attempted to induce inhibitory resource depletion using an Identity-Matching-to-Sample task, which is a working memory task, not an inhibitory control task. The Strength Model proposes a shared resource for inhibitory control processes, but it does not extend this resource to other executive functions. Thus, while inhibitory control, working memory, and cognitive flexibility all work together to support higher-level executive functions, they do not necessarily deplete the same limited resource. Non-inhibitory control tasks would not be expected to contribute to inhibitory resource depletion, which may be why Petrillo *et al.* (2015) did not see an effect of Identity-Matching-to-Sample on delaying gratification. With very few studies of the Strength Model in animals, there remains a need to test nonhuman animals using a dual inhibitory control task approach, similar to the method used in humans.

Current Study

The current study investigated whether rhesus monkeys experience similar inhibitory resource depletion as humans when performing two tasks that target inhibitory control, which could indicate a conserved evolutionary mechanism. We used the Flanker task for inhibitory resource depletion, and the WCST to measure the degree of inhibitory resource depletion **(Figure 4)**. Each test session began with 150 Flanker trials that were entirely incongruent, congruent, or absent **(Figure 1)**. Incongruent flankers strongly tax inhibitory control, and are likely to induce inhibitory resource depletion. Congruent flankers minimally tax inhibitory control, and thus are unlikely to induce inhibitory resource depletion. Absent flankers do not tax inhibitory control, and served as a control. Following the Flanker trials, subjects completed a WCST rule-acquisition phase, a WCST high conflict phase, and a WCST rule-shift. The number of errors the monkey made before reaching rule-shift criterion was measured as an indication of their inhibitory resource depletion. We hypothesized that if monkeys experience inhibitory resource depletion similar to humans, then they would make more errors before reaching WCST rule-switch criterion after experiencing incongruent flanker trials, relative to if they experienced congruent or absent flanker trials.

METHODS

Subjects & Materials

Six adult male rhesus macaques (*Macaca mulatta)* housed at Yerkes National Primate Research Center in Atlanta, GA, were tested. Monkeys were pair-housed and had access to their cage mate at all times of the day except during testing and feeding. Monkeys tested from 11am-5pm in their home cages, 6 days a week. Monkeys completed all phases of the present experiment using computerized touch-screen test systems. Touch-screen testing apparatuses were comprised of a 15-inch LCD color monitor, stereo speakers, two automated food dispensers and two food cups below the screen. Computer screens were locked to the front of each monkey's cage and the cage door was raised, giving subjects full visual and tactile access to the screen during testing. Monkeys were reinforced on an FR-2 schedule with auditory affirmation and a non-glucose food pellet. All training and testing tasks were programmed in Visual Basic.

Flanker Task Training

The Flanker task consisted of 2 training phases. During the first training phase, monkeys were trained to associate 4 distinct shapes with a response to a left or right image **(Figure 1)**. Each session of training phase one consisted of 100-trials, and all monkeys were required to complete 2 consecutive sessions at 90% or greater accuracy. In the second training phase, congruent, incongruent, or neutral flankers were added to all trials. Each session in the second training phase consisted of 100 trials, 40% of which were congruent trials, 40% incongruent, and 20% neutral. Monkeys were rewarded for responding to the information given by the centrally placed stimulus. Again, monkeys were required to complete 2 consecutive, 100-trial sessions at 90% or greater accuracy to progress out of the training phase. For both training phases, correction trials were administered following incorrect responses. One single incorrect response was followed by a 5-second time out, and then monkeys were given the exact same trial. A second incorrect response was followed by a 5-second time out, and then the exact same trial was presented, however, only the correct response was available. Once monkeys completed both training phases, they moved on to the test phase. The test phase was nearly identical to training phase two, with the only difference being that no correction trials were given following an incorrect response.

Wisconsin Card-Sorting Test Training

For all phases of the WCST, Monkeys were trained to select one of four corner targets by matching either the color or shape of the central sample, based on the currently relevant rule. Monkeys learned the relevant rule through trial and error, based on the selection that was previously reinforced. To make sure that monkeys attended to the central sample, trials began with the center stimulus surrounded by a small white square, and once the monkey touched the center, the white squares surrounded each of the corner targets **(Figure 2)**. No change occurred if a monkey touched the corner target prior to touching the center sample. No correction trials were used.

This version of the WCST included five colors, five shapes, and four corner target locations. For each trial, the corner targets were randomly assigned a color and shape, and no corner target had the same color and shape as the central sample. Monkeys experienced 3 phases per session: rule-acquisition phase, high conflict phase, and rule-switch phase. In the rule acquisition phase, monkeys were aided in learning either the color or shape rule. Specifically, in the rule-acquisition phase only one corner target matched the central sample in either shape or color, depending on the relevant rule **(Figure 2)**. All other corner targets had a different color and shape from the center sample. Monkeys were required to select the correct rule on at least 9 trials in a 10 trial window in order to progress to the high conflict phase. In the high conflict phase, one corner target matched the central shape, and one corner target matched the central color **(Figure 3)**. The other two corner stimuli did not match the center sample in either color or shape. Across the entire high conflict phase, the monkeys were reinforced for selecting the dimensional rule learned during the rule acquisition phase. Monkeys were required to select according to the correct rule on at least 9 trials in a 10 trial window in order to progress to the rule-switch phase. The rule-switch phase looked identical to the high-conflict phase, and monkeys received no signal that the phase changed. Throughout the rule-switch phase, monkeys were reinforced for the opposite dimensional rule as the high conflict and rule acquisition phases. To complete the session, monkeys needed to correctly select the new rule on 9 trials in a 10 trial window. We measured the number of errors monkeys made before reaching rule-switch criterion. Following a rule-switch there was a one-minute time out before returning to the rule-acquisition phase. Each monkey completed rule-switches until they were able to make an average of less than five errors before reaching rule switch criterion.

Test Design

Once monkeys reached criterion for learning both tasks, we implemented the test phase **(Figure 4)**. The test phase began with 150 Flanker trials that were either entirely congruent, incongruent, or absent. After completing the Flanker phase, monkeys immediately progressed onto the WCST. All phases of the WCST were identical to those described in the training section. Each monkey completed ten WCST rule-switches to the color rule and ten switches to the shape rule for each Flanker type, for a total of 60 sessions. Following each test session, there was a 30-minute replenishing time-out, before returning to the Flanker phase.

RESULTS

By the time of analysis, only four out of six monkeys completed enough test sessions to be included in the results. One of the four monkeys was later excluded after analysis showed that he made too many errors during the WCST rule-switch phase **(Figure 5)**. All results presented are based on preliminary analysis, and they will be expanded upon and finalized once all monkeys have completed testing. Prior to statistical analyses, all proportion correct scores were arcsine transformed (Aron & Aron, 1999). Statistical significance was set at $p \leq 0.05$.

We analyzed the Flanker Task data to ensure that we saw an inhibitory effect of the incongruent flankers **(Figure 6)**. We performed a repeated measures analysis of variance (ANOVA) to compare performance in the three flanker conditions. Monkeys performed significantly worse on the incongruent flanker trials compared to the congruent or absent flankers, $F(2, 4) = 17.748$, $p = 0.010$. This result indicates that the incongruent flanker trials are more challenging than the other conditions, and they are likely to require inhibitory control to complete. Next we looked at the trend of performance on the Flanker Task, comparing proportion correct scores on the first 50 trials to the scores from the last 50 trials, separated by flanker type **(Figure 7)**. A repeated measures ANOVA determined that there was a significant main effect of experience on Flanker Task performance, with monkeys performing better in the last 50 trials compared to the first 50 trials across all flanker types, *F* (1, 4) = 15.076, *p* = 0.018. There was no significant interaction between flanker type and experience, although the trend showed a more pronounced improvement in the incongruent flankers than the other conditions, *F* (2, 8) = 2.931, *p* = 0.065.

We performed a repeated measures ANOVA to compare the effect of incongruent, congruent, or absent flankers on WCST rule-switch performance. Our analysis included proportion correct scores from the first 10 trials following a WCST rule-switch. Mauchly's test indicated that the assumption of sphericity had been violated x^2 (2) = 7.382, *p* = .025, thus degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity (ε = 0.50). There was not a significant main effect of flanker type on WCST rule-switch accuracy, *F* (1, 2.001) = .766, *p* = 0.474 **(Figure 8)**. These results do not support the hypothesis that monkeys would make more rule-switch errors following incongruent flankers compared to congruent or absent flankers. Thus, our results suggest that rhesus monkeys do not exhibit inhibitory resource depletion. Lastly, we performed a repeated measures ANOVA to determine whether there was an effect of the incongruent, congruent, or absent flankers on WCST high conflict performance. There was no significant main effect of flanker type on performance during the high conflict phase, *F*(2, 4) =1.808, *p* = 0.276. These results indicate that the flankers did not have an effect on the working memory aspects of the WCST.

DISCUSSION

The goal of this study was to investigate whether inhibitory resource depletion is evolutionarily conserved in rhesus macaques. We administered two consecutive inhibitory control tasks to tax inhibitory control resources, based on the stipulation from the Strength

Model that repeated acts of self-control deplete the same limited resource (Baumeister *et al.,* 2007).

Our preliminary results suggest that monkeys do not exhibit inhibitory resource depletion when performing two consecutive inhibitory control tasks. Specifically, monkeys' performance during the WCST rule-switch did not differ as a function of flanker type. There are many possible explanations for why the results did not fit the predictions of the Strength Model. This experiment is only the second ever to try and find inhibitory resource depletion in nonhuman primates. Previous work by Petrillo *et al.* (2015) also failed to find inhibitory resource depletion in capuchin monkeys. Together, these results suggest that inhibitory resource depletion does not exist in nonhuman primates. However, our study design had some potential flaws that may have obscured any effect of inhibitory resource depletion. We propose two study manipulations to try before reaching a conclusion about the existence of inhibitory resource depletion and the Strength Model in nonhuman primates.

The high levels of reward during the Flanker phase may have decreased the inhibitory resource depletion effects of task. The experimental design of the current study used the Flanker Task for inhibitory resource depletion, and the WCST to measure the degree of resource depletion. While completing the Flanker trials, monkeys were reinforced for correct responses by auditory affirmation and a food pellet. The food pellet did not contain glucose, so it should not have replenished inhibitory resources (Gailliot *et al.*, 2007), but the continuous reward and affirmation could have dampened the resource depleting effects of the Flanker task. Studies in humans have shown that self-affirmation, positive mood, or even thinking about money is enough to counteract the effects of inhibitory resource depletion (Schmeichel & Vohs, 2009; Tice *et al.,* 2007; Boucher & Kofos, 2012). It is thought that these psychological interventions increase the motivation of participants, and as a result, decrease the subjective difficulty of the tasks. It is possible that the Flanker Task, which provides high levels of affirmation and reward for 150 trials, had very little effect on limited inhibitory resources. In a future study, it might be more appropriate to use a different inhibitory control task, such as a delayed gratification task, which provides less positive reinforcement.

The duration of the Flanker Task may have also acted to diminish inhibitory resource depletion effects. There is not an agreed upon timeframe for maximal inhibitory resource depletion. On average, monkeys in this study completed the Flanker phase in 19 minutes, and all WCST phases in 14 minutes. According to the Strength Model, the longer you engage in inhibitory control exercises, the more depleted your inhibitory control resources should be. By this logic, monkeys' performance on the incongruent trials of the Flanker Task should have decreased over time, since they were continuously exerting inhibitory control. The data from this study showed the opposite trend, and monkeys actually improved over more incongruent flanker trials **(Figure 7).** These results do not fit the predictions of the Strength Model, and therefore maybe there is a better alternate model that explains inhibitory control. In opposition to the Strength Model, the Cognitive Control Theory of inhibitory control does not view inhibitory control as a limited resource that can be depleted, but as a resource that can be selectively allocated. The cognitive control model says that when the cognitive system detects conflict, it recruits control processes to solve the conflict (Botvinick *et al.,* 2001). However, after many consecutive trials of the same task, the need to allocate cognitive control resources diminishes. One study found that when participants spent a longer time on an inhibitory control task, the resource depletion effect of the task was eliminated (Dang *et al.,* 2013). The researchers suggested that participants were able to adapt to the conflict of the inhibitory control task when they were given more time, which aligns with the cognitive control theory of resource depletion, and not the Strength Model. If the cognitive control theory is correct, it is possible that in the current study, our subjects spent so long completing the Flanker Task that they adapted to the conflict, and therefore did not exhibit impaired WCST performance. A future study should test which of these theories better explain inhibitory resource depletion by carefully manipulating the time spent on each phase of a dual-task paradigm.

Our preliminary findings indicate that performance during the WCST rule acquisition phase and the WCST high conflict phase did not differ as a function of incongruent, congruent, or absent flanker trials. Both the rule acquisition and high conflict phases require working memory to acquire and maintain the relevant dimensional rule. If the incongruent flankers selectively impaired performance on these WCST phases, it would suggest that inhibitory control and working memory rely on the same limited resources. There is thought to be a relationship between working memory capacity and the ability to exert inhibitory control, but the direction of the relationship is not clear (Redick *et al.,* 2007). One study found that training working memory reduced alcohol abuse in problem drinkers, suggesting a relationship between working memory capacity and inhibitory control (Houben *et al.,* 2011). A different study in dogs showed that self-control exertion impaired working memory performance on an invisible displacement rotation task (Miller, 2013). As previously mentioned, the Flanker Task is highly reinforcing and may not be an appropriate tool to exhaust inhibitory control resources, and therefore we cannot conclude that inhibitory resource depletion does not impair working memory. We propose combining the WCST with a different inhibitory control task, to investigate whether inhibitory resource depletion also has an effect on working memory.

In future studies on inhibitory resource depletion, we will use a dual-task paradigm where the initial task does not involve 150 trials of the Flanker Task. We could limit the Flanker Task to 50 trials, so that monkeys do not have time to adapt to the conflict, and they would receive less reward. Alternately, we could choose a task such as delayed gratification, which also involves less reward and less time. We will continue to use the WCST as the dependent measure, because it provides us the opportunity to measure the effects of inhibitory resource depletion on working memory, as well as inhibitory control. Investigating inhibitory resource depletion in rhesus macaques could provide evolutionary support for the limited resource model of inhibitory control in humans. The current study does not provide evidence for inhibitory resource depletion in rhesus macaques, but the investigation of this subject is ongoing.

FIGURES

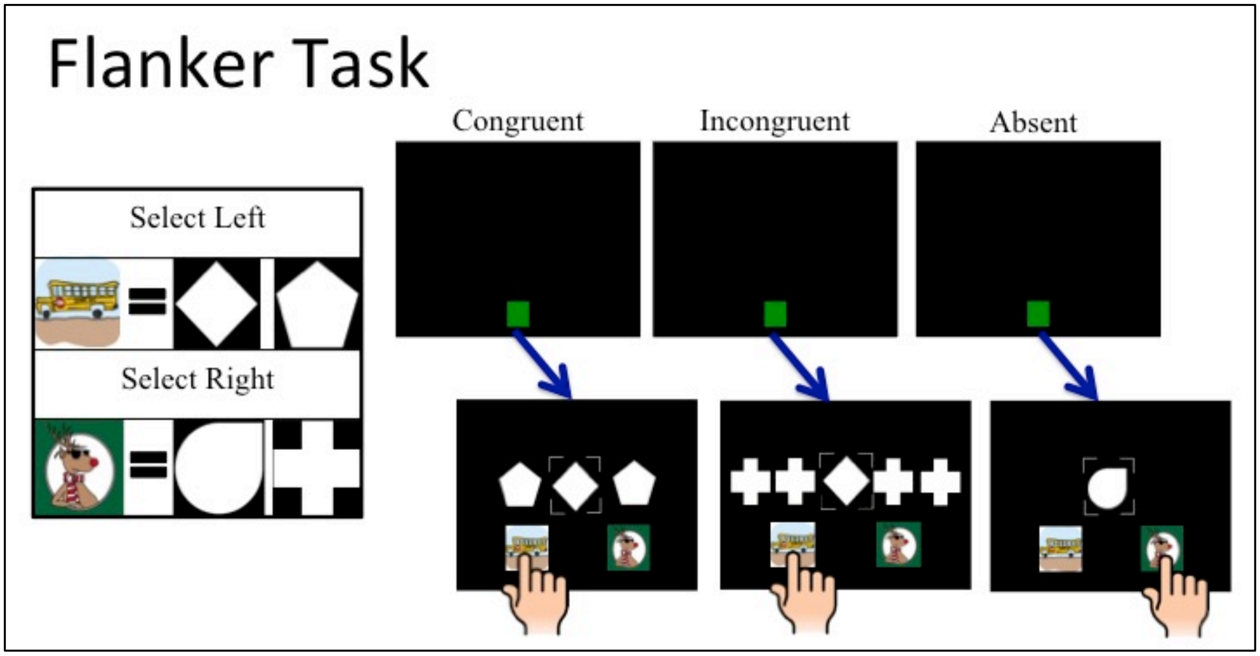

Figure 1: Flanker Task adapted for rhesus monkeys. Subjects initiate all trials by clicking the green start square. Monkeys are trained to associate 4 shape stimuli with a response to either a left or right image. Monkeys were reinforced for selecting the school bus image when the central stimulus was a diamond or a pentagon. Monkeys were reinforced for selecting the reindeer image when the central stimulus was a pointed-circle or a cross. The school bus was always on the left, and the reindeer was always on the right. Monkeys are reinforced for responding according to the central stimulus and ignoring the flanking stimuli. In congruent trials, the central shape indicates the same response as the flankers around it. In the incongruent trials, the flankers indicate the opposite response as the central shape. Absent trials do not have any flankers. Performance is assessed using accuracy and response latency data.

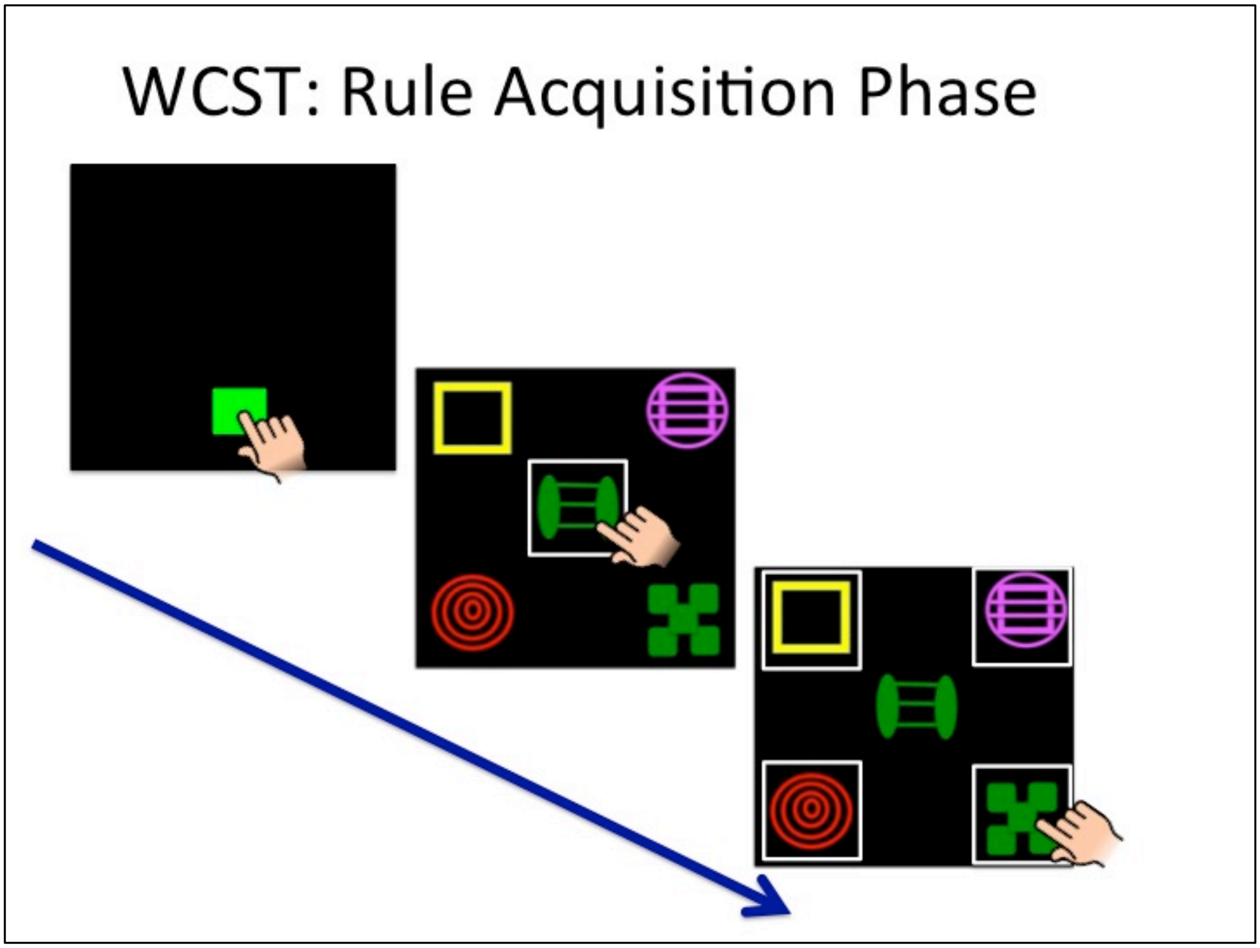

Figure 2: Wisconsin Card Sort Test rule acquisition phase. Subjects initiate the trial by clicking the green start square, and then they must click the center sample to make the corner targets available responses, as indicated by the white square outlines. Subjects are reinforced for matching the color or shape of the center sample to one of the corner targets. In this phase of the WCST, only one corner target matches the center sample on either color or shape, allowing the monkey to quickly learn the relevant rule for the test session. In this example, the subject is responding to the color rule.

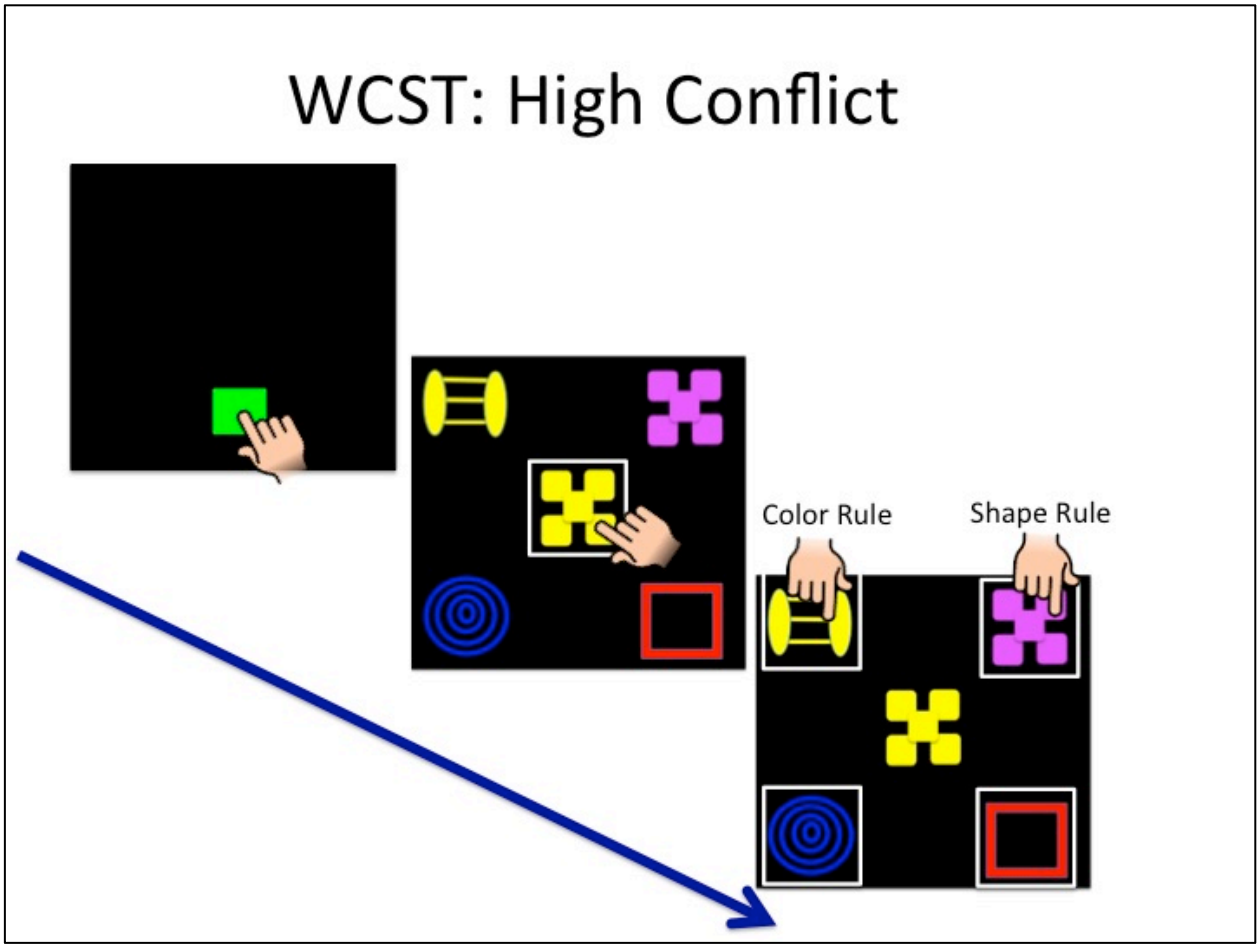

Figure 3: Wisconsin Card Sort Test high conflict. Subjects initiate the trial by clicking the green start square, and then they must click the center sample to make the corner targets available responses, as indicated by the white square outlines. In this phase of the WCST, subjects are reinforced for choosing the corner target that matches the center sample on either color or shape, based on the rule learned in the rule acquisition phase. One target will match the central color, and one target will match the center shape, so the subject must remember which dimension is currently relevant. For each session, once the subject reaches criterion for high conflict, the rule switches without warning, and the opposite rule will be reinforced.

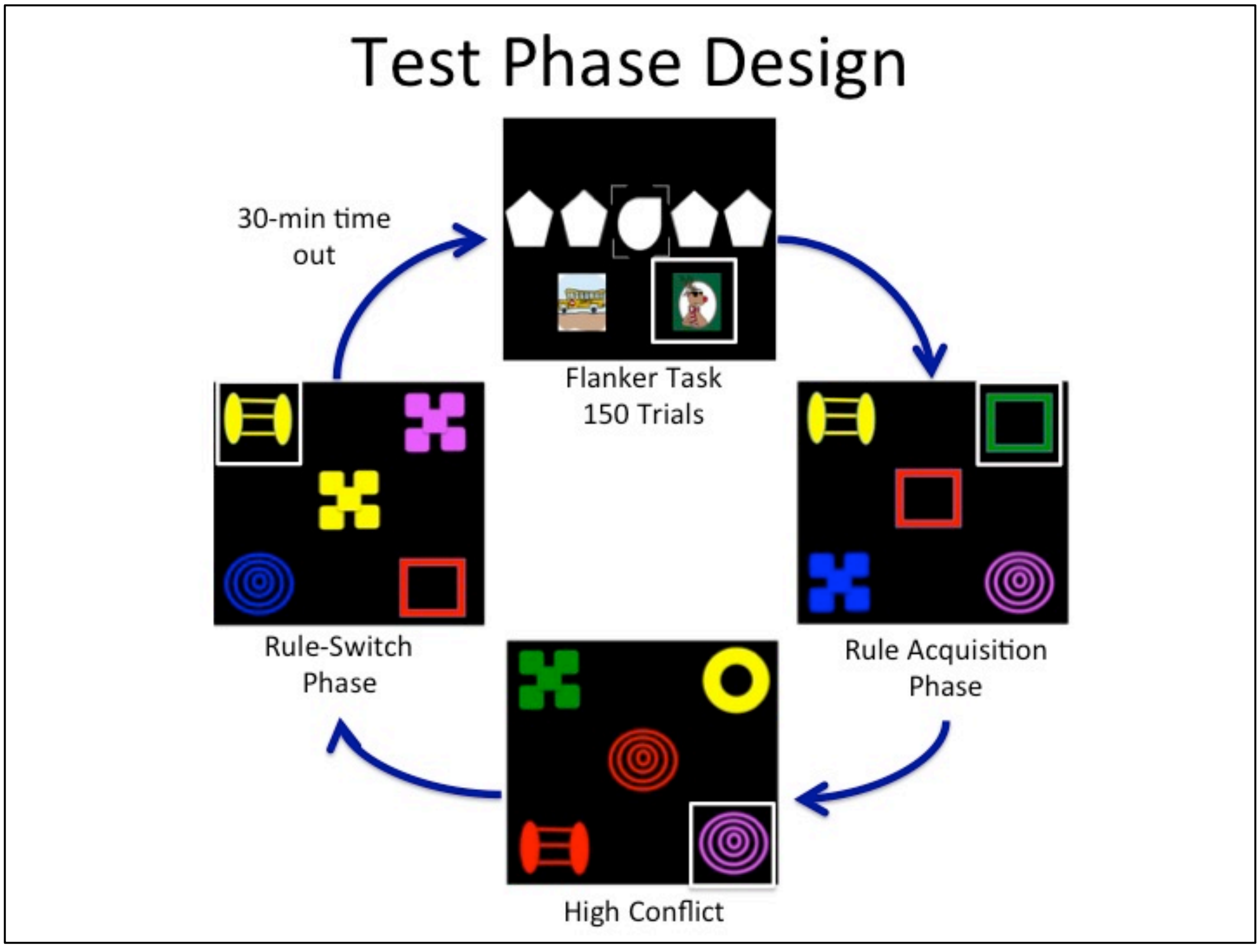

Figure 4: Test Phase Design. The test phase begins with 150 Flanker trials that are incongruent, congruent, or neutral. Immediately following the Flanker task, the subjects complete the WCST rule-acquisition phase, then the WCST high conflict phase, and finally a WCST rule-switch. We determined the proportion correct scores during the first 10 trials following a rule-switch for our analysis. After each test session, there is a 30-minute replenishing time out.

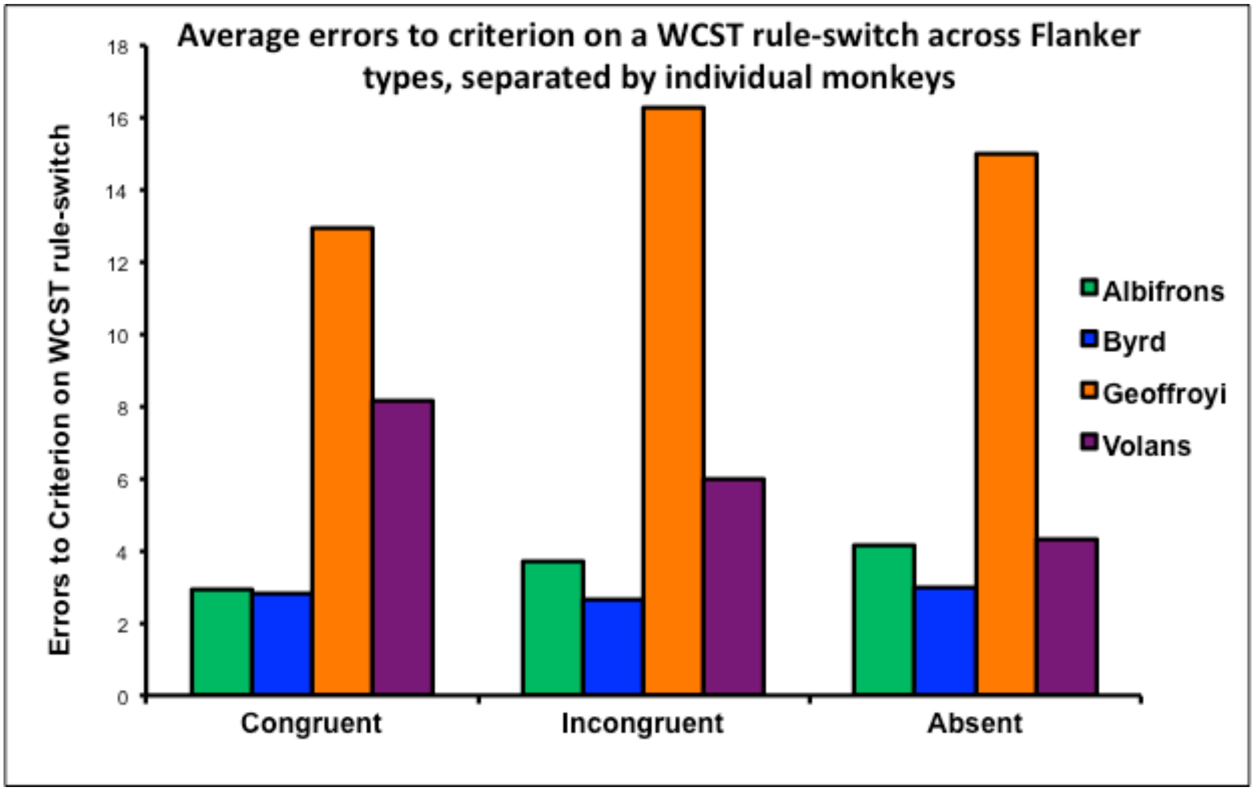

Figure 5: WCST rule-switch Errors to Criterion. The average errors made before reaching WCST rule-switch criterion are shown, separated by individual monkeys and by the preceding flanker type. Geoffroyi made an average of more than 10 errors before reaching WCST rule-switch criterion across all flanker types, and therefore he was excluded from analysis. He will complete the WCST training program improve his performance, before returning to the test phase.

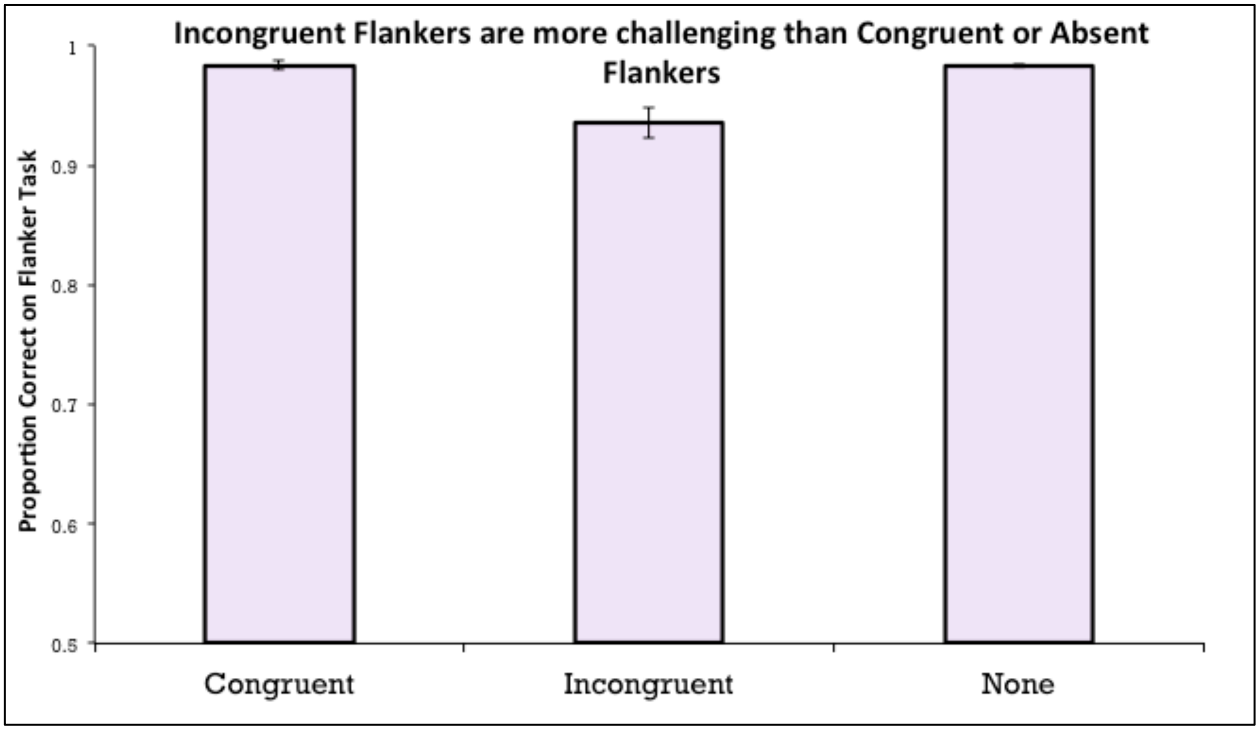

Figure 6: Flanker Task Proportion Correct Scores. The overall proportion correct scores were averaged for all subjects for each flanker type. Subjects performed significantly worse on the Incongruent Flanker trials compared to the Congruent or Absent Flankers (*p* = 0.010). Error bars are +/- SEM.

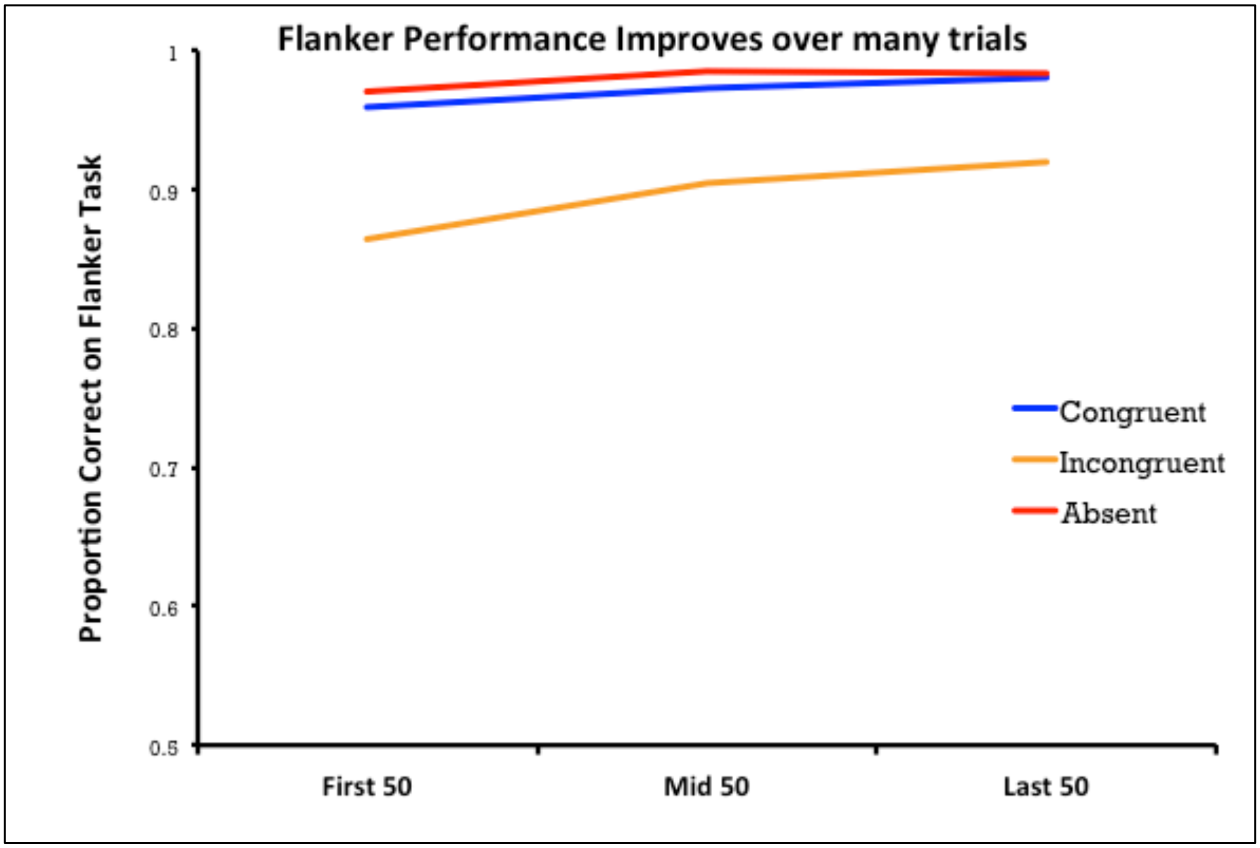

Figure 7: Flanker Task Proportion Correct Scores Across Trials. Proportion correct scores were averaged for the first 50 trials, middle 50 trials, and last 50 trials of the Flanker Task, separated by flanker type. There was a significant main effect of experience on Flanker Task performance, and monkeys performed better over more trials (*p* = 0.018).

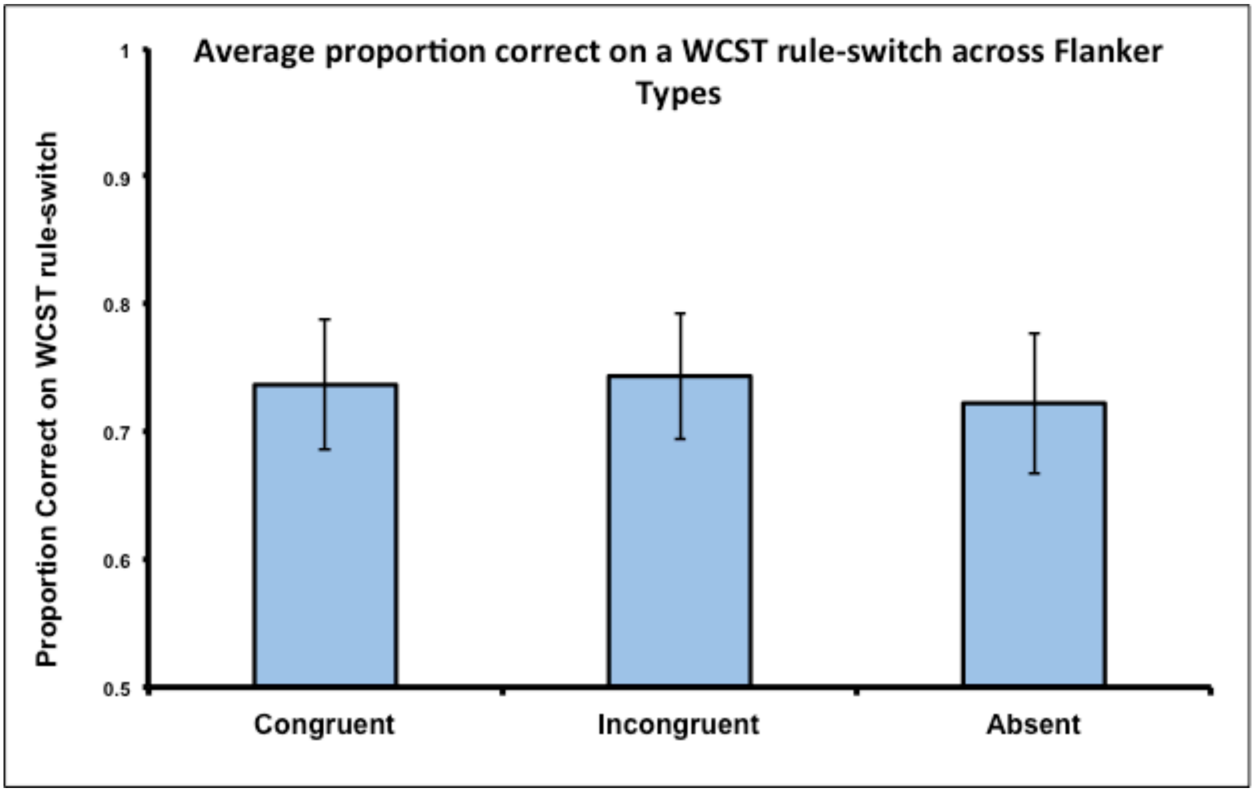

Figure 8: WCST rule-switch Average Proportion Correct Scores. The overall proportion correct scores are averaged for all subjects across preceding flanker types. Proportion correct averages were taken from the first 10 trials following a WCST rule-switch. There was no statistically significant difference in rule-switch performance between the different flanker manipulations (*p* = 0.474). Error bars are +/- SEM.

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