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The Effects of Positive and Negative Experiences on Subsequent Behavior and Cognition in Capuchin Monkeys (Cebus Apella)

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THE EFFECTS OF POSITIVE AND NEGATIVE EXPERIENCES ON SUBSEQUENT BEHAVIOR AND COGNITION IN CAPUCHIN MONKEYS (*CEBUS APELLA*)

by

MACKENZIE SMITH

Under the Direction of Sarah Brosnan, PhD

ABSTRACT

While it is known that acute and chronic stress can impact cognition, less is known about the immediate impacts of minor frustrations or positive experiences on subsequent behavior and cognition in primates. This study used a novel methodology to engineer both a positive and (slightly) frustrating experience, using the same apparatus, in 15 adult capuchin monkeys. Subjects were presented with a working memory task (DMTS) for 30 minutes after the experimental manipulations (or a control). As predicted, the frustrating task prior to testing resulted in a decrease in performance on the DMTS compared to performance after a positive experience or the control. Contrary to predictions, a positive experience did not facilitate performance to higher levels than the control condition. Manipulations also impacted several behaviors. Although there may be different results in different contexts, these results indicate that even mild negative experiences impact subsequent behavior and cognition in primates.

INDEX WORDS: Affect, Delayed match-to-sample, Working memory, Primate model, Behavioral indices, Affect manipulation

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1 INTRODUCTION

An interest in describing and explaining emotions dates back to the early philosophers. Actual scientific research on emotions however, has had a more recent and staggered history. In psychology, the scientific study of emotions has had three major stages (Gendron & Barrett, 2009). The first era, marked by prolific scientific study of emotions, is often attributed to Darwin's publication of *The Expression of the Emotions in Man and Animals* (1872). This lead to interesting debates in the scientific community over the manifestation of emotion (Cannon, 1927; James, 1884). Following this initial period of excitement and interest, the age of behaviorism swept in and left little room for the study of emotion (Gendron & Barrett, 2009; Lazarus, 1998). In the 1960's, with behaviorism's decreasing authority in American psychology, a renewed interest in the study of emotions appeared (Gendron & Barrett, 2009; Lazarus, 1991).

The history of the study of non-human animal (hereafter, animal) emotion follows a similar pattern. Darwin and James' discussions of human emotions included comparisons to the emotional lives of animals, but again interest diminished with the rising power of behaviorism (de Waal, 2011). Despite the decrease in the authority of behaviorism giving rise to increased psychological research on human emotions, the study of animal emotions did not follow the same trend.

There remains reluctance by some to attribute emotional states experienced by humans to any of our mammalian relatives (Bolhuis & Wynne, 2009). There are however many advocates in the scientific community for the position that animals do experience emotional lives akin to humans (de Waal, 2011; Panksepp, 2005). In the last few decades, there has been an increasing call for research on animal emotions from a functional and evolutionary standpoint to better understand human emotion (Lench, Darbor, & Berg, 2013; Trimmer, Paul, Mendl, McNamara,

& Houston, 2013; Weisfeld & Goetz, 2013), as well as for potentially important applications in neuroscience, psychopharmacology (Mendl, Burman, & Paul, 2010), and animal welfare (Boissy et al., 2007; Dawkins, 2000; Désiré, Boissy, & Veissier, 2002). De Waal effectively sums up the conundrum behind our relative lack of studies on animal emotions, asserting that while animal emotion is deemed of little importance, it is rarely denied existence, leaving us with "the curious situation that a widely recognized aspect of animal behavior is deliberately ignored or minimized" (de Waal, 2011).

Aside from leading to a failure to develop a broader understanding of animals, this may also hinder our ability to understand ourselves. Presumably, as with many other aspects of human psychology, basic human emotions have evolutionary roots exhibited in related taxa, particularly non-human primates (hereafter, primates), however little attention has been paid to this potentially highly illuminating connection, and comparative studies have been limited. Phylogenetic analyses could help determine whether there are similar interacting psychological processes in non-human mammalian brains, and further our understanding of the evolution and function of particular emotions in humans (Weisfeld & Goetz, 2013).

One of the barriers researchers of animal emotion have run into is a definitional one. Despite the increased interest in the study of emotion seen in recent decades, syntheses of research across disciplines are few and far between. The fundamental question of how to define 'emotion' lies at the heart of this issue. Emotions are something all humans are familiar with, but when asked, "what is an emotion?," many struggle to produce an explicit definition. Even when asking those who are sure of their definition, responses will vary quite drastically. This issue has not been fully resolved, and often definitions differ between psychologists, philosophers, neuroscientists, sociologists, and anthropologists (Barrett, 2006a) .

The matter of establishing definitional clarity across fields as to what constitutes an emotion is beyond the scope of this thesis. Nonetheless, it is important to define what I mean for the purposes of this study. The relevance of the debate for animal research lies in the factors included in some definitions of emotion, and their relation to studying emotions in animals. Oftentimes definitions will include a subjective experience component (Hockenbury & Hockenbury, 2010), which means that an emotional component necessitates consciousness. Whether or not non-human animals are conscious in the way we refer to human consciousness is an unresolved debate (Griffin & Speck, 2004; Mendl & Paul, 2004). Therefore, definitions of emotion that require consciousness pose a rather difficult hurdle for those who wish to study animal emotion. There are, however, many who define emotion without a subjective experience component (Boissy et al., 2007; de Waal, 2011), which is more tractable for empirical study. Additionally, regardless of whether scientists attribute 'emotion' in the human sense to animals' experiences, it is generally agreed upon that at minimum, animals experience changes in affect (Dawkins, 2000; Panksepp, 2005, 2011; Paul, Harding, & Mendl, 2005a).

It is then important to differentiate between the terms 'emotion' and 'affect'. For a time in psychology's past, and still to some extent today, affect and emotion were used almost interchangeably (Daniel, Shaw, & Oleson, 1992). In modern psychology there has been an effort to distinguish between the terms, but as with the challenge of defining emotion, there is not universal agreement. In general, affect refers to the mental aspect of the internal bodily states associated with our representations of emotion (Barrett & Bliss-Moreau, 2009; Spruijt, van den Bos, & Pijlman, 2001). Affect is the psychologically primitive state made up of an arousal level and hedonic valence (Duncan & Barrett, 2007; Russell, 2003). Affect can be a component of emotion, but also exists in pure forms alone. A person is constantly experiencing affect, just the nature and intensity of it are changing (Ekkekakis, 2013). Unlike emotions, affective states involve no judgment or assessment, and are not necessarily directed at anything (Russell, 2009). Affect has been a topic of psychological interest and research since the late 1800's, dating back to Wundt and Titchner, who argued that affect is a fundamental "psychological ingredient" that cannot be further reduced, and that affect combined with other cognitive components is what creates an emotion (Barrett & Bliss-Moreau, 2009). Therefore, emotion is the fusion of core affective feeling with conceptual knowledge and experience, integrated mentally to categorize the emotion (Barrett, 2006b).

For the purpose of the current study, I will typically use the term affect in reference to any potentially emotional experience in animals. With that being said, the relevant literature discussed will include studies referring to animal emotions, not just affect, and woven throughout the paper will be parallels drawn between research on animal 'affect' and human 'emotion'. Further, even animal research that generally refers to affect and not emotions often specifically utilizes emotional language such as 'stress', 'frustration' and 'anxiety' when referring to the affective experiences of their subjects (Gluck & Sackett, 1974; Maestripieri, Schino, Aureli, & Troisi, 1992; Troisi, 2002). The current study will also sometimes refer to a state of 'frustration' in the animal subjects, with the intention that this helps specify the type of affective state being experienced.

1.1 The Emotion-Cognition Interaction

Despite the fact that the emotion-cognition relationship has long been of interest to philosophers, in psychology, emotions and cognition have a history of being treated as separate entities and deemed of differential importance (Gendron & Barrett, 2009; Houwer & Hermans, 2013). Since the 1980's however, empirical research has started to address questions of the *interaction* between emotions and cognitive processing, such as attention, memory, learning, judgments and decisions, and it is now well known that emotions/affect and cognition are complex, interrelated components of psychological processing (Houwer & Hermans, 2013). Much of the research has focused on how emotional stimuli are treated different cognitively than neutral stimuli. Numerous studies have demonstrated that emotionally significant stimuli selectively receive more attention than non-emotional stimuli (Bradley, Mogg, & Lee, 1997; Compton, 2003; Öhman, Flykt, & Esteves, 2001). Further, emotional stimuli are better remembered than neutral stimuli (Cahill & McGaugh, 1998; Hamann, Ely, Grafton, & Kilts, 1999).

While some impacts of emotions are general and not emotion or even valence specific, such as the general enhancement of memory for positive *or* negative emotional stimuli (Hamann et al., 1999), other cognition-emotion interactions are more specific. Of particular interest to the current study, the impacts of emotion on working memory are asymmetric, such that positive emotions can have facilitating effects on some tasks and detrimental effects on others, while the opposite is true for negative emotions (Bartolic, Basso, Schefft, Glauser, & Titanic-Schefft, 1999). These results have been traced to differences in brain activation patterns when experiencing emotion.

Neurological research has demonstrated a different lateralization of activation in the frontal lobe when experiencing positive and negative emotions, such that positive emotions result in relatively higher levels of left frontal lobe activation, while negative emotions are associated with right frontal lobe activity (Ahern & Schwartz, 1985; Davidson, Ekman, Saron, Senulis, & Friesen, 1990). The interpretations one draws from these findings, however, have not been quite as straightforward. Some claim that brain activation in the area required by a task *facilitates* performance on that task, such that positive emotions (increasing left hemisphere activation) enhance performance on tasks reliant on left prefrontal cortex (PFC) activation, while negative emotions (increasing right hemisphere activation) facilitate performance on right PFC tasks (Gray, 2001; Heller & Nitscke, 1997). This stems from the idea that activation reflects a readiness to engage in certain tasks, such as those that require similar brain activation (Bartolic et al., 1999). Alternatively, dual processing models theorize that when two tasks or processes are utilizing the same brain region, performance on the task may be impaired if there is a depletion of cognitive resources or cross-talk interference (Kinsbourne & Hicks, 1978; Shackman et al., 2006).

Working memory poses a particularly good area of study in this regard, because different types of working memory, while all fairly reliant on PFC activity, differ in brain activation within different regions of the PFC. Numerous studies have demonstrated that verbal working memory is left lateralized while spatial working memory is right lateralized (d'Esposito et al., 1998; Davidson et al., 1990). Other studies have similarly found right lateralization for spatial working memory and compared it to object working memory tasks that are relatively left lateralized (Courtney, Petit, Haxby, & Ungerleider, 1998; d'Esposito et al., 1998; Smith et al., 1995). These findings inspired a series of studies looking at the asymmetric effects of emotion on cognition between different working memory tasks during positive or negative emotional states.

Bartolic and colleagues' (1999) study was one of the first to systematically induce positive and negative affect in participants and examine the effects on two tasks associated with different frontal lobe activation. Either positive or negative affect was induced in participants using the Velten Mood Induction Procedure (VMIP) in which subjects listened to, and then read silently and aloud, self-referent statements about their mood. Participants were then tested on either the Controlled Oral Word Association Task (associated with increased relative activation of the *left* frontal lobe), or the Ruff Figural Fluency Test (associated with increased activation of the *right* frontal lobe), to look at the effects of emotion on verbal and figural fluency, respectively. The results of the experiment were consistent with their predictions that emotionally induced brain activation would result in a 'readiness' that would facilitate subsequent tasks asymmetrically reliant on that brain region. Positive affect (left activating) enhanced verbal fluency (left activating) above figural fluency (right activating), while negative affect (right activating) coincided with the opposite effects.

In another pioneering study, Gray (2001) designed an experiment to contrast the effects of emotion on spatial and verbal working memory. An important distinction between Gray's study and those that preceded it was their ability to control for motivation and task difficulty by using a two-back task for both verbal and spatial working memory assessment. In the study, subjects had positive, negative (referred to in the paper as approach and withdrawal, respectively), and neutral emotional states induced by watching videos. Subjects were then tested on either a verbal or a spatial two-back task. In both tasks, a letter (a-f) appeared somewhere on the screen and subjects had to indicate whether it was the same or different than the item two items ago. For the verbal task subjects were told to ignore location and indicate whether the letter was the same or not, and for the spatial task they were told to ignore the letter and indicate whether it was in the same location on the screen or not. Overall, Gray found that positive emotional states increased performance on the verbal task while impairing performance on the spatial task, while the opposite was true of negative emotional states, increasing spatial performance while hindering verbal. The results also indicated that the effects were significantly stronger for those individuals who did the most poorly on the tasks (Gray, 2001). The importance of these studies was in demonstrating that emotional *valence,* and not just emotional arousal generally, had selective effects on cognitive functioning and may be a result of interacting brain activation patterns. Additionally, both of these studies supported the model predicting that prior activation of a brain region similarly activated in a subsequent task facilitated performance on that task.

Unfortunately the clear picture these studies painted has since been clouded. Lavric and colleagues (2003) and Shackman and colleagues (2006) both empirically tested the asymmetric effects of emotions on verbal and spatial working memory, and found the opposite effects of the previously discussed studies. Both of these later studies hypothesized that the cognitive demands of threat-evoked anxiety would deplete resources in the right PFC and impair spatial working memory (dependent on the right PFC) but not verbal working memory (dependent on the left PFC), and both of the studies found support for their hypotheses. They additionally both cited that a flaw of the previous studies (Bartolic et al., 1999 & Gray, 2001) was their lack of an objective measure of affect, like the inclusion of heart-rate measures or startle responses, as well as self-report. Shackman suggests that perhaps modest levels of anxiety do in fact produce an enhancing effect to right PFC tasks, however higher anxiety levels represent an increase in resource depletion that may lead to the deleterious effects found in these later studies.

This difference in the level of affect may explain both sets of data. If both Gray (2001) and Bartolic and colleagues' (1999) manipulations induced only mild negative affect, while the threat of a shock used in Lavric and colleagues' (2003) and Shackman and colleagues' (2006) studies induced much higher levels of anxiety, then this could explain the disparate results. Indeed, Shackman and colleagues note that in Gray's (2001) study, the level of anxiety reported by participants was half that reported by the later two studies. Regardless of a consensus on *how* brain activation is mediating asymmetric effects of emotion on cognition, which remains important, the research is clear that there is in fact an interaction between different valence emotions and subsequent working memory performance.

1.2 Research on Affect in Animals

Affective research with non-human animals had a later start than research with humans, and has also taken a different trajectory. While human research is also subject to a bias towards negative emotion, this is the predominant focus in animals (Moberg, 2013; Paul, Harding, & Mendl, 2005b; Rosen & Donley, 2006). Early emotional research with animals primarily stemmed from an interest in using animals as models of human emotion, and often exploited the less rigid ethical standards required for research with non-human animals compared to that with humans. This led to animals being used as models of pain exposure (Maier, Drugan, & Grau, 1982), drug use (Bodnoff, Suranyi-Cadotte, Quirion, & Meaney, 1989), early maternal separation (Higley, Hasert, Suomi, & Linnoila, 1991), and social isolation (Matsumoto, Pinna, Puia, Guidotti, & Costa, 2005), as well as the general effects of acute and chronic stress on cognition and behavior (Cazakoff, Johnson, & Howland, 2010; Moreira, Almeida, Leite-Almeida, Sousa, & Costa, 2016). Brain lesion research, used to look at the involvement of particular brain regions on emotional processing, was also only possible in animals (Bliss-Moreau, Bauman, & Amaral, 2011; Kalin & Sheltona, 2003).

While animal models of human emotional processing have been influential, the gap in knowledge on the behavioral, cognitive, and physiological responses to *positive* affect in non-human species is striking. Additionally, by focusing studies of animal affect on scenarios of such intensity that we cannot test human participants, or modeling animal research on clinical populations, we are neglecting the acquisition of knowledge on the key types of affective processing that we know much about in humans, specifically how normal fluctuations in positive and negative affect impact animal behavior and cognition in their day to day lives.

Recently though, and in line with the current study, researchers have begun to study animal affect in a way more comparable to what is seen in the literature on human affect and to discover the parallels and differences in the psychological processing of animal emotions. The most immediate challenge with this, however, is measurement, because of the difficulty in ascertaining *what* affective state is being experienced and *when*. The disproportionate representation of research on negative affect in animals continues in this area, at least in part due to the relative ease of observing and measuring negative affect as compared to positive affect (Boissy et al., 2007).

In humans, the most common measure of emotion is self-report. While self-report is obviously not possible when studying a non-human animal species, instead of being a shortcoming, it can be an opportunity to develop reliable objective measures of affect so that we can determine what an organism is feeling instead of what they *say* they are feeling. Indeed, in humans, self-report measures of emotions are not always reliable, particularly when reflecting on past emotional states as opposed to current states (Robinson & Clore, 2002). Mauss and Robinson (2009) purport that experiential, physiological and behavioral measures of emotion should not be treated interchangeably, but used in concert with one another for the most comprehensive understanding of emotional experiences.

As experiential measures are impossible with animals, physiological and behavioral measures have been the most utilized methodologies in determining affect in animals. Some commonly used physiological measures of animal affect are heart rate, skin conductance and temperature, blood pressure, and measures of hypothalamic-pituitary-adrenal (HPA) function

(Aureli, Preston, & de Waal, 1999; Blanchard et al., 1998; Elder & Menzel, 2001; Paul et al., 2005b; Süer, Dolu, Özesmi, Şahin, & Ülgen, 1998). These are not, however, the most ideal measures of affect alone, as many of them are invasive and require stress-inducing restraint of the animal, or have low temporal accuracy. Sampling methods that themselves cause stress and anxiety in the subjects cannot be used, and even those that do not do so, such as implanted heart monitors, may require an invasive surgery and/or expensive equipment to set up. Additionally, these physiological measures have a tendency to measure negative affect more reliably than positive affect, and they do not provide a high level of specificity for the affect being experienced, typically providing more information on arousal than valence. In general, these measures work best in conjunction with other measures, or to provide a very general measure of affective change.

As a result, researchers have turned to behavioral measures, which avoid many of these problems. Behavioral measures used to look at affect in animals include vocal expressions (*rats;* Knutson, Burgdorf, & Panksepp, 2002; *baboons;* Rendall, 2003; *cattle;* Watts & Stookey, 2000) approach/withdrawal behavior (*rhesus macaques;* Humphrey & Keeble, 1974; *rats;* Montgomery & Monkman, 1955) and spontaneous behaviors such as play (Fraser & Duncan, 1998; Paul et al., 2005b). Animals' startle responses have been a less widely used measure of affective state, but have promise as a simple indicator of affective valence, with negative affect increasing startle responses and positive affect attenuating them (Cook, Davis, Hawk, Spence, & Gautier, 1992; Lang, Bradley, & Cuthbert, 1990; Lang, Davis, & Öhman, 2000). Additionally, overt behaviors of organisms can often be used to measure affective state, and may be both the most easily recorded and reliable behavioral measure. In primates as well as other species, displacement behaviors such as scratching and other self-directed behaviors have been widely used as an indicator of negative affect (Maestripieri et al., 1992; Troisi, 2002), and stereotypic, repetitive behaviors have also been implicated as a sign of psychological distress (Garner, 2005; Garner, Meehan, & Mench, 2003; Novak, Bailoo, Melotti, Rommen, & Würbel, 2015; Pomerantz, Terkel, Suomi, & Paukner, 2012). Unfortunately, none of these behaviors are able to measure both negative *and* positive affect.

Recently, cognitive outputs, such as attention, memory, and judgment biases, have been proposed as a potential measure of affective states in animals (Paul et al., 2005). The idea behind this is that if different affective states are demonstrated to have predictable changes in cognitive outputs, then if you observe these changes in cognitive output, you may be able to trace the change back to the affective state being experienced. Attention biases in humans demonstrate that people experiencing negative affective states, particularly anxiety, bias their attention toward threatening stimuli more than when experiencing positive affect (Bar-Haim, Lamy, Pergamin, Bakermans-Kranenburg, & van IJzendoorn, 2007; Bradley et al., 1997). Similarly, memory bias studies with both humans and non-human animals have demonstrated that emotional states can impact memory retention and retrieval, such that negative affect can improve memory. This latter effect appears somewhat non-specific and more work has to be done before memory biases can be used as an effective tool for affect measurement in animals (Cahill & McGaugh, 1998; Kensinger & Schacter, 2008).

Judgment biases, such as interpretations of ambiguity, while arguably the most complex of the three cognitive biases mentioned, may also be the most promising area for animal affect research (Paul et al., 2005) and have already been utilized across a range of species (*rats*: Anderson, Munafò, & Robinson, 2012; Brydges, Leach, Nicol, Wright, & Bateson, 2011; Harding, Paul, & Mendl, 2004; *pigs*: Douglas, Bateson, Walsh, Bédué, & Edwards, 2012; *dogs*:

Michael Mendl, Brooks, et al., 2010; *sheep*: Doyle et al., 2010; *rhesus macaques*: Bethell et al., 2012; *capuchin monkeys*: Pomerantz et al., 2012; Schino et al., 2016). Generally speaking, judgment biases manifest with positive affect resulting in ‘optimistic’ interpretations of ambiguity, and negative affect resulting in ‘pessimistic’ interpretations. Research with humans demonstrates that subjects in positive moods assign higher probabilities to positive future outcomes than negative future outcomes, while the opposite is true for subjects experiencing negative affect (Hirsch & Mathews, 1997; Nygren, Isen, Taylor, & Dulin, 1996; Wright & Bower, 1992).

The initial methodology put forth by Harding, Paul, and Mendl (2004) utilized a go/no-go paradigm where rats were trained to press a lever after hearing a specific tone to receive a food reward, and refrain from pressing the lever after hearing a different tone in order to avoid a negative event. After this training, subjects were divided into two groups living in either ‘predictable housing’ or ‘unpredictable housing’. Unpredictable housing had been previously established as stress inducing for the rats. All subjects were then presented with an ambiguous tone, intermediate between the tones associated with positive and negative outcomes, and subsequent behavior was measured. Rats in the unpredictable housing condition were slower to respond, and significantly less likely to press the lever than were rats in the predictable housing condition, demonstrating that they tended to interpret the ambiguous stimuli as negative (expecting a shock) more often than the rats who lived in less stressful housing environments. Variations of this technique have been used, and regardless of methodology, these studies are finding significant judgment biases in the animal species tested, such that negative affective states correlate with a negative interpretation of ambiguous stimuli, while positive affective states correlate with a positive interpretation of ambiguity.

The issue with translating this measure to primates is that the original methodology put forth utilized positive and *negative* outcomes for the different stimuli. This poses an ethical dilemma for many species, since shocks or changes in housing are not always ethical or appropriate. To account for this, researchers have adapted the paradigm so that the only ‘negative’ outcome that subjects experience is a lack of reward (Bethell et al., 2012; Pomerantz et al., 2012; Schino et al., 2016). While this may solve the ethical dilemma, lack of reward is not especially salient as a negative outcome, particularly for subjects that are used to experimental tests in which they are unrewarded on some trials (i.e., following incorrect responses).

Despite this potential issue, recent studies with capuchins have successfully utilized the judgment bias measure to look at how normal positive social interactions such as grooming, as well as more long-term states such as rank or the expression of stereotypic behaviors, may be impacting affect (Pomerantz et al., 2012; Schino et al., 2016). In both of these studies, subjects interpreted an ambiguous length stimulus after learning that certain longer or shorter length stimuli corresponded to different value foods in specific locations. Subjects who looked in the location of the higher value reward in response to the ambiguous stimulus were deemed to be making an ‘optimistic’ judgment, while selection of the lower value reward location was marked a ‘pessimistic’ judgment.

The first study found that subjects who exhibited high levels of stereotypic behavior demonstrated negative judgment biases compared to monkeys who performed less stereotypic behavior, but the effect was only significant for stereotypic head-twirling and not pacing behavior (Pomerantz et al., 2012). The other study found that rank and high overall levels of received grooming correlated with positive judgments in the task, but there were no immediate effects of recently received grooming on the judgment bias (Schino et al., 2016). These results indicate that judgment biases may be most useful when looking at more long-term states than short-term, within-individual changes in affect, although it also could indicate that grooming does not impact subsequent affect.

While the purpose of these studies was to demonstrate that certain behaviors impacted the affective states of the monkeys, using judgment biases as merely a measure of affect, they also demonstrate that affective states affect cognition. While this was not a driving intention behind the studies themselves, the entire concept of this measurement relies upon the fact that different affective states are impacting cognition in specific ways. As the judgment bias is found in multiple species of animals as well as humans, this provides evidence that animal cognition is impacted by emotional processing in similar ways to humans (Brydges et al., 2011; Matheson, Asher, & Bateson, 2008; Michael Mendl, Burman, Parker, & Paul, 2009; Rygula, Pluta, & Popik, 2012).

Finally, research has now further demonstrated that animals, and specifically non-human primates, have similar psychological processing systems for emotions and affect as that of humans. Chimpanzees (*Pan troglodytes*) experience physiological arousal in response to emotionally charged videos, and are able to match conspecific emotional facial expressions to the valence of a video scene (Parr, 2001). Animals also apparently process emotional *stimuli* similarly to humans. Chimpanzees experience delayed reaction times in response to negative images in comparison to neutral stimuli in an emotional Stroop task, akin to the responses of humans (Allritz, Call, & Borkenau, 2015). Additionally, Blanchette et al. (2016) recently demonstrated that baboons (*Papio papio*) respond less accurately and with a greater response time to negative stimuli in comparison to neutral. This study was one of the first to demonstrate that the negative stimuli did not need to be visually present for the effect to occur, but still manifests when the stimulus is only mentally represented. These studies further demonstrate that the organization of emotional processing within primate brains may be similar to that in humans.

As in the human literature, animal researchers are interested in not just how task-related emotional stimuli can interfere with cognitive processing and attention, but how task-irrelevant affective states may be affecting behavior and cognition, and vice versa. We know that behavior can impact the affective states of animals (i.e., judgment biases), but how do those affective states impact subsequent behavior and cognition? This is the focus of my current work. Additionally, I will try to address a remaining issue facing animal researchers, the fact that the classification of positive affect remains elusive. While 'optimistic' judgment biases may allow for the identification of positive affect, there is uncertainly as to whether this bias would be effective in measuring small, short-term changes in affect. Specifically, my goal is to identify an observable behavioral indicator of positive affect.

1.3 Purpose of the Study

The primary purpose of the current study was to explore the inter-relationship between affect and cognition in a primate model. I wanted to make the research as comparable as possible to the human literature, so that I could consider the similarities between human and non-human animal psychological processing. With comparative research, however, it can be difficult to draw any definitive conclusions when procedures being compared are vastly different (Brosnan, Beran, Parrish, Price, & Wilson, 2013). Due to the prevalence of language-based inductions and measures in human emotion research, it is often impossible to use the exact same methodology with animals, and therefore keeping at least the nature of the experiments as similar as possible is vital. Previous research on animal affect has primarily focused on the effects of intense negative affect as the result of extreme stimuli (such as shocks), and while this is informative, in most human studies the affect inducer is relatively mild (and arguably more similar to naturally occurring context). Relatively little research has focused on animal affect as it plays out in a healthy organism's typical life (with a few notable exceptions described above), and past research has rarely generated affective states akin to those created within contexts in the subjects' natural lives.

I therefore attempted to present the capuchins with a manipulation reflecting their natural behavior, which I expected to induce both positive and negative affect in different contexts. Capuchin monkeys are extractive foragers (Fragaszy, Visalberghi, & Fedigan, 2004), meaning they routinely extricate food from difficult to obtain sources, such as inside hard-shelled nuts. This study's affect manipulation took advantage of this, artificially creating a negative experience where food was unobtainable from a previously reliable source, and generated a positive experience using the same task but allowing it to result in consistent high value reward acquisition.

Affect manipulation was immediately followed by a delayed match-to-sample task, to measure working memory performance in the monkeys. In line with the human literature on the effects of emotions and affective states on working memory, as well as some primate studies, I hypothesized there would be a decrease in cognitive performance after a negative experience and an enhancing effect of a positive experience (Ashby, Isen, & Turken, 1999; Oei, Everaerd, Elzinga, van Well, & Bermond, 2006; Schoofs, Preuss, & Wolf, 2008).

A second goal of the current study was to inform the sparse literature on the effects of positive affect in animals. My primary focus was to find behavioral indicators of positive affect, of which there are none in the current literature. In this study, I collected data on *all* behaviors exhibited by the subjects, not just behaviors known to be important in animal affective experience drawn from the literature, in the hopes of discovering a behavioral marker of positive affect. I did not have any direct predictions for what behaviors might increase after a positive experience, which presumably led to positive affect, and thus hoped to find behavioral measures that correlated with the condition. Consistent with the literature, I predicted that rates of displacement behaviors, such as scratching, self-touching and urine washing, as well as stereotypic behaviors, would increase after subjects had a negative experience that presumably led to negative affect (Garner, 2005; Maestripieri et al., 1992; Troisi, 2002).

2 METHODS

2.1 Subjects

Subjects used in the current study were 15 adult (7 male) tufted capuchin monkeys (*Cebus apella*), housed at Georgia State University's Language Research Center. Subjects were all socially housed in three separate multi-male, multi-female social groups composed of five, six and 10 individuals (Group 1, 2 and 3, respectively). Due to a husbandry issue, Group 2, with six monkeys, was separated into a group of four and a group of two prior to the beginning of data collection. The two males separated from their group were brothers, and remained within close proximity and constant visual and vocal contact with their original group. Subjects' housing enclosures included both indoor and outdoor areas with enrichment toys and climbing structures for natural movement and activity. Subjects received primate chow, as well as fruits and vegetables, daily, and additionally got supplemental enrichment foods most days. All subject participation in this study was completely voluntary, with no food deprivation, and water available *ad libitum*, including during testing.

Subjects expressed their willingness to participate by voluntarily separating into individual test boxes connected along the outside caging of their home enclosure on the morning of testing days. Subjects received either one peanut (Groups 1 and 2) or one pecan (Group 3) upon entering the individual test box. Out of the 21 monkeys housed at the Language Research Center, only 15 were used in the current study. Three of the monkeys were excluded because they do not readily separate into the individual test boxes. Another monkey was excluded from the study due to her impaired visual and motor abilities as a result of old age, and two monkeys failed to pass the training criterion for the delayed match-to-sample procedure (details below).

2.2 General Procedure

The current study investigated how different types of experiences (positive or negative) affect primate working memory, as measured by performance on a cognitive task. In order to explore this, we first needed to generate experiences that would be interpreted as either positive or negative by the subjects. In an attempt to keep methodology as similar as possible across conditions, and thus reduce the possibility of alternative explanations for my results, I used the same puzzle task for both the positive and negative experiences, adapted to be either rewarding or frustrating (see below). The apparatus used, shown in Figure 1, was an opaque tube that attached diagonally to the outside of the subjects' individual test boxes, hung at an angle that allowed food rewards placed in the top to roll down it. Three levers or slides, painted blue, were placed perpendicularly at equal lengths down the tube such that, when closed, they would stop the progression of rolling food. At the beginning of a trial, all three levers (located next to the arrows in Figure 1a) were closed. A small piece of colorful cereal (Cap'n Crunch OOPS! All Berries Cereal) was placed into the top of the tube, stopping when it hit the first lever. Subjects then had 30 seconds to retrieve the food reward, by lifting all three levers in successive order to drop the reward down the tube and into the retrieval tray (Figure 1b). If the subject was not successful within the 30 seconds, the trial timed out and there was a 15-second time out before the next trial began (this never occurred during testing sessions). If a trial was successful, subjects experienced a 10-second inter-trial interval (ITI) before the next trial began. Different manipulations were used to induce positive and negative affect (described below).

Subjects experienced the different conditions' manipulations immediately prior to 30 minutes on a computerized test of cognitive performance (a delayed match-to-sample task). While the human literature indicates that the temporal retention of some types of experimentally manipulated affect may be less than 30 minutes (Frost & Green, 1982; Gomez, Zimmermann, Guttormsen Schär, & Danuser, 2009), other research, specifically those relating to anxiety, indicate that the duration of an anxious mood may last much longer (Kuhlmann, Piel, & Wolf, 2005; Schoofs et al., 2008). The 30-minute testing session was therefore selected to simply ensure any record of potentially long lasting effects of the experimental manipulation was caught, as well as maintain consistency with typical testing procedures at the facility. Digital time stamps for each trial were recorded, which allowed us to go back and look at accuracy for shorter durations than the full 30-minute session. In particular, we analyzed the session in three 10-minute sections.

Each subject experienced 18 sessions, divided among six positive experience sessions, six negative experience sessions, and six control sessions (in which there was no manipulation), and subjects always immediately began the cognitive task after completing the affect manipulation (except in the control). All six sessions of each condition were presented to the subjects consecutively, with the order of condition presentation pseudo-randomized so that half the subjects (n=8) experienced the negative experience first, while the other half (n=7) experienced the positive experience first. All subjects were presented with the six control sessions in between the positive and negative sessions. All 18 sessions and the subsequent computerized testing were video recorded for behavioral analysis.

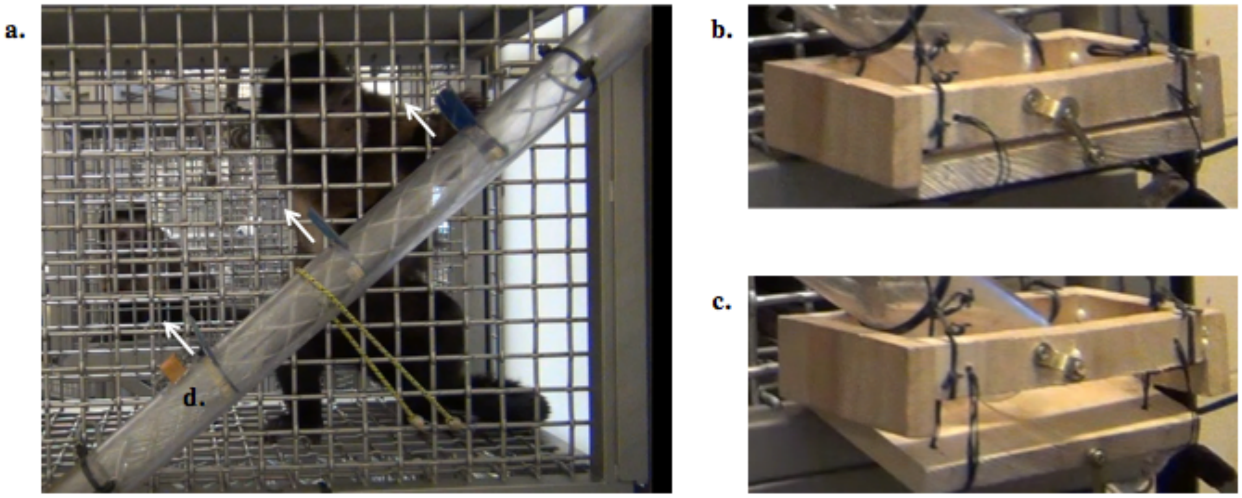


Figure 1. Puzzle apparatus used for manipulations. Arrows in (a) indicate the direction the three levers lifted in order for the food reward to pass down the tube, traveling from the top right in the picture to the bottom left, where the reward would fall into the retrieval tray (b) and be collected (see text for detail). (c) depicts how the tray opened in the "trap-door" sessions.

2.3 Positive/Negative Experience Manipulation

2.3.1 Training

Subjects were presented with the puzzle apparatus for training/familiarization sessions before testing. Each session consisted of 10 trials. Trials began when the tube was baited with the food reward, and the subjects had one minute to retrieve it. If the subject was unable to complete the trial within the allotted time, the experimenter lifted each lever herself, allowing the subject to watch the reward fall into the retrieval tray. Subjects were then allowed access to the reward, and incurred a 15 second time out before the next trial. Subjects passed the training phase when they successfully retrieved the reward (without the experimenter's assistance) on at least eight out of 10 trials on two consecutive sessions. All subjects successfully passed training within three sessions.

2.3.2 *Positive Experience*

To create an experience that I anticipated being pleasurable for the monkeys, subjects were presented with the familiar puzzle apparatus. Subjects completed six consecutive trials with positive reinforcement in the form of a food reward. Consistently receiving a desired food reward with minimal effort was assumed to be a positive experience. It has also been demonstrated that object manipulation tasks are mentally enriching to primates (Celli, Tomonaga, Udono, Teramoto, & Nagano, 2003), so this was predicted to further influence the positivity of the experience.

2.3.3 Negative Experience

To generate a negative experience, the subjects were presented with the same puzzle task, but successful completion of the task (and subsequent access to the food reward) was impossible on some trials. Subjects completed 10 consecutive trials during each negative experience session. During four of those trials however, the food reward was unobtainable, a presumably frustrating experience for the subjects. As subjects were unable to acquire the reward in 4/10 trials, the negative sessions resulted in a total of six actual food rewards, the same as in the positive condition, to control for satiation. The impossible trials occurred in a pseudo-randomized order within the 10-trial sessions, with no more than two impossible trials in a row.

There were two different types of impossible trials: jammed-lever trials and trap-door trials. During jammed-lever trials, the apparatus was experimentally manipulated by turning a screw (see Figure 1) so that the third and final lever was prevented from lifting high enough to allow the food reward to pass underneath. Trials lasted 30 seconds, after which the lever was un-jammed and the food reward was removed by the experimenter, which was followed by a 10 second ITI before the next trial. In trap-door trials, a latch in the bottom of the retrieval tray was unhooked, so that after successful lifting of the third lever, the food reward would fall through the retrieval tray to the floor, where it was unreachable (Figure 1c). During both types of negative affect sessions, before every trial the experimenter would manipulate the screw (jammed-lever) or the retrieval tray latch (trap-door) so that subjects were not cued to when an impossible trial was set to occur. I cannot be certain the subjects were completely unaware of which trials were the “bad” ones, however the fact that in every case all subjects attempted to solve each trial (impossible or not) indicates they likely were naïve to the condition. The two different types of negative experience (trap-door and jammed-lever) were included to ensure the generation of a negative experience in case one method may have been more effective than another, but there were no prior predictions on which would be more successful. Subsequent analysis revealed no differences between the two types of negative experiences on performance, so all further analyses grouped the two manipulations into a single negative experience condition.

2.4 Cognitive Task (Delayed Match-to-Sample)

The current study used a delayed match-to-sample (DMTS) task to assess working memory in the capuchin monkeys. The DMTS was presented to the subjects using the Language Research Center’s (LRC) Computerized Test System. The computerized testing occurred in the subject’s same individual test box as the experience manipulations occurred, immediately following the manipulation (except in the control condition, in which subjects began immediately after they separated into the individual box). Each subject had a personal computer with a 17-inch monitor, a joystick that moves a cursor on the screen, and a pellet dispenser that distributed small 45-mg banana flavored pellets to the subjects as rewards for a correct response. Personal computers were stationed approximately 30 cm in front of a Plexiglas window on the individual test box, with their personal joystick placed in the box with them. Subjects at the LRC have had years of experience testing, and are therefore extremely familiar with the computerized system. They also had extensive prior experience with the DMTS task (Beran et al., 2008; Beran, Evans, Klein, & Einstein, 2012; Beran & Smith, 2011; Evans, Beran, Chan, Klein, & Menzel, 2008).

Subjects were tested on a DMTS for 30 minutes, during which they could do as many or as few trials as they chose. At the onset of a trial, an image would appear centered near the top of the subject's screen, along with their cursor in the center. Subjects could move their cursor up towards the image, and upon contact with the border of the image, the picture would disappear. This would then be followed by a delay of 1, 2, 3 or 5 seconds (randomized order for five trials of each time delay presented within 20 trial blocks). After the delay, the target image and another picture would simultaneously appear, randomized between the right and left sides of the screen (Figure 2). If the subject moved the cursor to the image that matched the original sample, they would hear a familiar chime indicating a correct response and receive a small banana flavored pellet. This would be followed by a 2-second ITI before the next trial would begin. If the subjects moved their cursor over the incorrect image, they would hear a buzzer indicating an incorrect response and receive no reward and a 5-second timeout before the next trial. Regardless of accuracy, after every 20 trials there was a 1-minute time out to force brief periods throughout the task where behavior could be observed that was not specifically directed at the task.

My delay periods (1, 2, 3 and 5 seconds) were chosen based on a previous study with capuchin monkeys that indicated that 3-second delays affect both subject response time and accuracy as compared to shorter time delays (Truppa, De Simone, Piano Mortari, & De Lillo, 2014). The 5-second delay was also included to see if there were any effects of the experiences on a more challenging task, without increasing the duration so much so that performance sharply decreased (as is evidenced after 8-second delays; Tavares & Tomaz, 2002). Results indicated that performance on 1 and 2-second delay trials did not differ from one another, but performance was impaired by 3-second delays, and further compromised by 5-second delays. There was not an interaction between delay and condition on their impact on performance, so for all subsequent analyses data from all delays were combined to provide maximum power to the overall analysis.

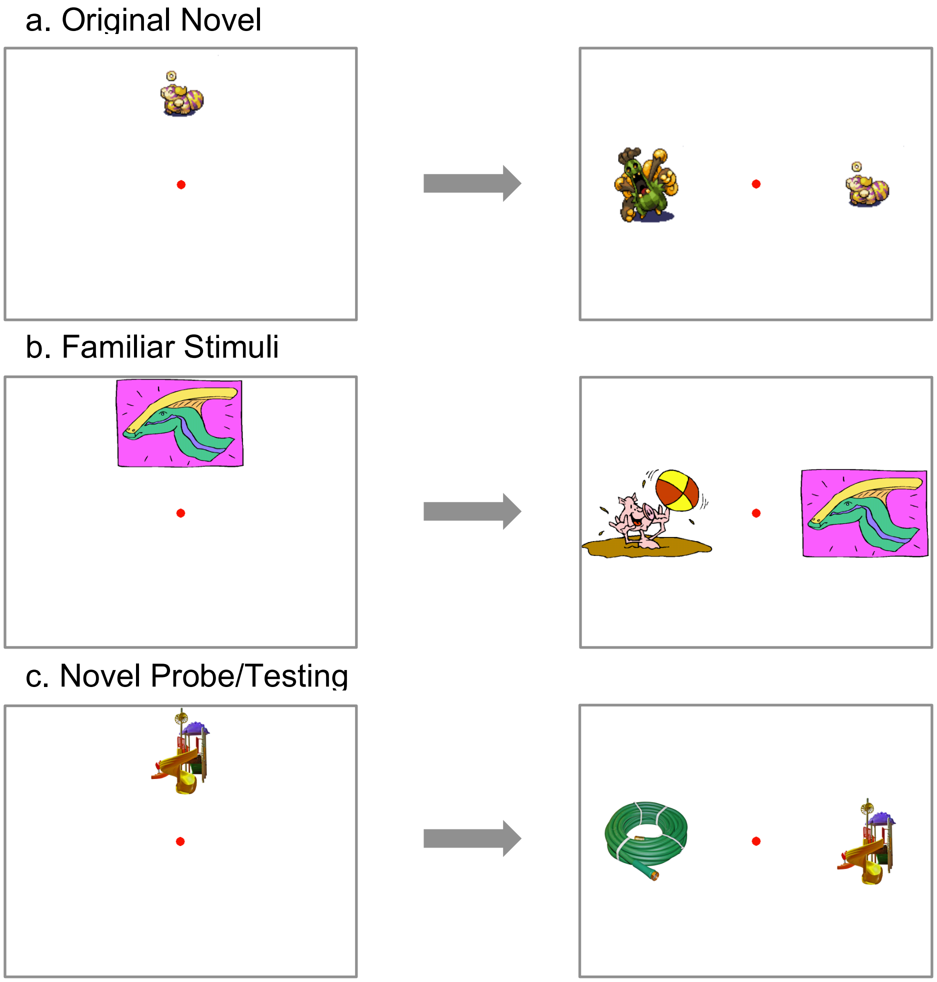


Figure 2. Example of the DMTS task screen with sample stimuli. Examples of the original novel stimuli used (a), familiar stimuli used in training (b), and the novel stimuli used for testing (c).

Subjects were not originally expected to require training, as all the monkeys had passed a computer training battery program that included a DMTS before the onset of the study. However, for some subjects, it had been some time since they had experienced a DMTS, so to verify that they all still met criterion, subjects were presented with the DMTS using novel stimuli. An analysis of the data from the subjects' first three sessions revealed that the subjects were performing below 80% accuracy (the criterion set for performance), so testing was immediately stopped and the subjects were placed on training.

2.4.1 Training

Training used the same computerized testing setup described above. The task was the exact same as described, with the four different time delays in 20 trial blocks, followed by a 1-minute timeout. The only difference in the task between training and the original testing attempt was the stimuli. In the original testing sessions, I introduced novel stimuli that were fairly complex, and may have been too difficult for the subjects to differentiate (Figure 2a). During training I used familiar clip-art stimuli that the subjects had seen before during their computer training (Figure 2b). Subjects also experienced 1-hour training sessions (no more than once daily) instead of 30-minute testing sessions. Subjects reached training criterion once they demonstrated 80% or better accuracy during two consecutive sessions. They were then placed on 1-2 Probe sessions, where subjects again experienced a 1-hour session, however the task used novel stimuli. Instead of the complicated novel stimuli used in the original testing, for Probe trials I used a bank of 238 images from the Bank of Standardized Stimuli (BOSS), a large normative photo database (Brodeur, Guérard, & Bouras, 2014). If subjects successfully maintained 80% or higher accuracy on the first or second Probe session (all subjects did), then they passed to the testing phase. Overall, it took the subjects an average of 11 sessions to reach the training criterion.

2.4.2 Testing

Testing followed the exact same procedure as training, but I used a bank of 450 *different* BOSS photos than were used during the Probe sessions.

2.5 Behavioral Analysis

Each session was video-recorded. Behavior was coded for the entire 30 minutes during which the subjects were on the DMTS task. All anticipated behaviors were compiled into an ethogram, and any novel behaviors observed during coding were added to the ethogram. No new behaviors were observed after one session of each subject was coded. The final ethogram included a total of 22 behaviors (see Appendix A). All behavior was recorded because, while there are some behaviors known to be associated with stress/anxiety, there are currently no behaviors in the literature that are behavioral indicators of a positive affective state, and so I was unable to make predictions about which behaviors would be relevant. Therefore, the purpose of this component was to identify relevant behavior(s) for use in future work.

Of the 22 behaviors recorded, I eliminated four that were observed in fewer than 10 of the subjects. One behavior, water drinking, was also eliminated because it was deemed irrelevant to the manipulation, as thirst is a state behavior unlikely to be affected by experiential changes. Joystick touching was eliminated because it was presumably correlated with trial number, and was additionally difficult to reliably code. Likewise, vocalizations could not be reliably coded or differentiated without specialized recording equipment. Finally, in two cases several behaviors were combined because there were strong theoretical grounds to do so (this also increased power). ‘Licking the cage’, ‘picking at the cage’, and ‘wiping the cage’ were all grouped together into ‘cage-directed behaviors’. ‘Pacing’, ‘head-twirling’, and ‘rub hands’ behaviors were grouped together into a ‘stereotypic behavior’ category, as these are all stereotypical, functionless and repetitive behaviors often manifest in captive primate populations (Garner, 2005; Garner et al., 2003; Pomerantz et al., 2012). The stereotypic behaviors alone would have each been eliminated from analysis based on the criterion that at least 10 subjects display the behavior, but as a category this involved 10 or more individuals. Therefore, for the ultimate analysis I looked at nine individual behaviors and two behavioral categories.

2.6 Data Analysis

All statistical analyses were run in R version 3.23 (R Core Team, 2015). Model analyses were conducted using the *lme4* package (Bates, Maechler, Bolker, & Walker, 2015). All model comparisons were compared using the Akaike information criterion (AIC) to determine the best-fit models. P-values were determined via likelihood ratio tests comparing the full model with the fixed effects against a null model with just the random effects. Behaviors were measured as counts of every occurrence of the behavior (or behavioral category) of interest within a session. Sessions were divided up by time into three sections; 0-10 minutes, 10-20 minutes and 20-30 minutes to examine any possible effects of time within a session. Accuracy was measured as the proportion of correct responses to the total number of trials completed. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality.

First, to initially determine if condition influenced overall levels of participation in the DMTS task, I ran a Generalized Linear Mixed Model (GLMM) with trial number as the dependent variable (DV). I included condition (control, positive and negative) and time as fixed effects, and Subject ID as a random effect. I compared the full model to the null model (which included only the random effect) using a likelihood ratio test.

Second, to assess whether behaviors differed across the conditions, I ran a series of GLMMs with Poisson distributions for each behavior. I constructed separate models with counts of each behavior (or behavioral category) as the DVs, condition as a fixed effect, and Subject ID entered as a random effect. Analysis excluded 3 cases with missing data.

Third, I examined the effects of both condition and behavior on accuracy. To assess whether condition and time influenced accuracy, I constructed a model comparison analysis comparing 4 Linear Mixed Models (LMM) with accuracy as the DV; two models with each condition or time as fixed effects alone, a combined model with both factors, and a model with an interaction effect. All controlled for Subject ID as a random effect.

To determine whether the behaviors influenced by condition were also influencing DMTS task performance, I ran a series of LMMs with accuracy as the DV, each behavior as a fixed effect, and Subject ID as a random effect. The behaviors that significantly predicted accuracy were then further analyzed with another series of LMMs, comparing three models for each behavior's effects on accuracy (DV); a model that included just the behavior, one with both the behavior and condition as fixed effects, and one model with an interaction effect (all with Subject ID as a random effect).

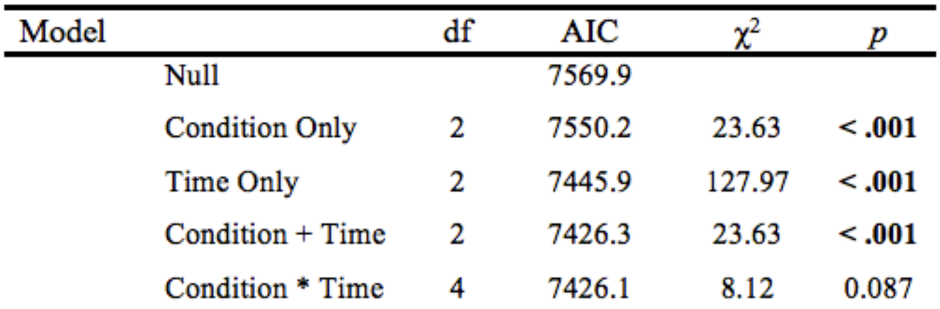
Finally, to determine the overall best model for predicting cognitive performance, a model comparison was conducted comparing models including each of the fixed effects (condition, time and the behaviors that significantly influenced performance) with and without each other, as well as models with any significant interactions.

3 RESULTS

3.1 Behavior

The best-fit model for predicting trial number included both condition and time as fixed effects. Model comparisons revealed that a model including both factors better-explained trial number than models with either factor alone or a null model, but there was no interaction effect between condition and time (Table 1). On average, subjects performed 32.8 (± 0.70) trials in the positive condition, significantly less than the number of trials performed in the negative condition (34.1 ± 0.73 trials; $b = -0.05$, $z = -3.38$, $p = .002$) or in the control (34.5 ± 0.69 trials; $\beta = -0.07$, $z = -4.72$, $p < .001$; Figure 3). Regardless of condition, subjects completed the most trials during the first 10 minutes of sessions (36.9 ± 0.54), significantly fewer during the middle third of the session (34.2 ± 0.72 trials; $\beta = -0.08$, $z = -5.33$, $p < .001$), and the fewest number of trials during the last 10 minutes (31.3 ± 0.80 trials; $\beta = -0.09$, $z = -5.98$, $p < .001$).

Table 1. Comparison of the models used to predict Trial Number



Model	df	AIC	χ^2	p
Null		7569.9		
Condition Only	2	7550.2	23.63	**< .001**
Time Only	2	7445.9	127.97	**< .001**
Condition + Time	2	7426.3	23.63	**< .001**
Condition * Time	4	7426.1	8.12	0.087

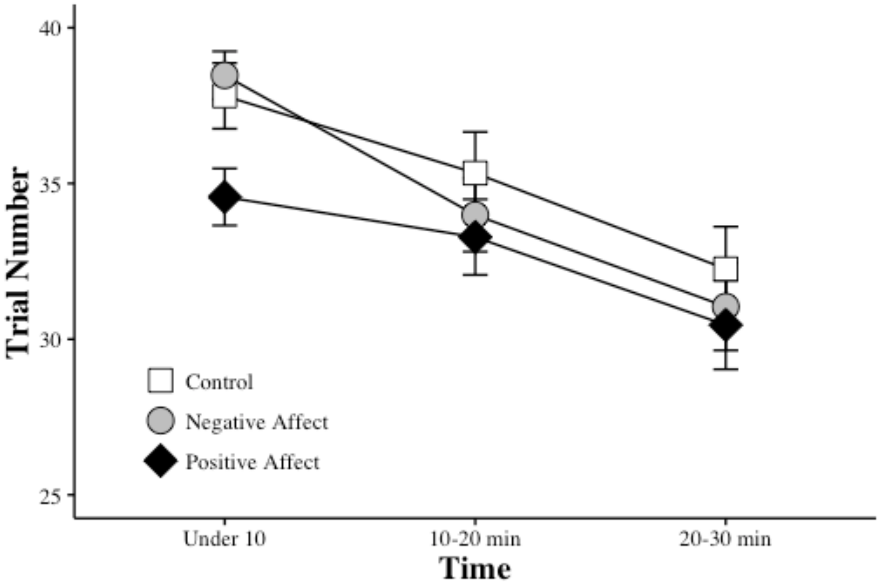


Figure 3. The effects of Condition and Time on the number of trials subjects completed. Error bars reflect 1 ± SE.

I found that of the 11 behaviors analyzed, 7 significantly differed between conditions (see Figure 4; Scratching; $\chi^2(2)= 12.63$, $p = .002$, Self-licking; $\chi^2(2)= 15.17$, $p < .001$, Threatening; $\chi^2(2)= 18.98$, $p < .001$, Self-touching; $\chi^2(2)= 12.90$, $p = .002$, Playing with pellet; $\chi^2(2)= 23.83$, $p < .001$, Cage-directed behavior; $\chi^2(2)= 82.62$, $p < .001$, Stereotypic behavior; $\chi^2(2)= 161.95$, $p < .001$).

Specifically, I found that compared to the control condition, in both the positive and negative conditions there was significantly *more* stereotypic behavior (Figure 4a; negative: $\beta = 0.26$, $z = 8.66$, $p < .001$; positive: $\beta = 0.36$, $z = 12.37$, $p < .001$), and self-touching (Figure 4e.; negative: $\beta = 0.26$, $z = 3.50$, $p = .001$; positive: $\beta = 0.18$, $z = 2.49$, $p = .034$), and significantly *less* cage-directed behaviors (Figure 4c.; negative: $\beta = -0.19$, $z = -6.51$, $p < .001$; positive: $\beta = -0.26$, $z = -8.65$, $p < .001$) and playing with the pellet (Figure 4d.; negative: $\beta = -0.14$, $z = -3.32$, $p < .001$; positive: $\beta = -0.20$, $z = -4.73$, $p < .001$).

Compared to the negative condition, in both the positive and control conditions there was significantly less scratching (Figure 4b.; positive: β = -0.08, z = -3.04, *p* = .007; control: β = -0.09, z = -3.10, *p* = .005) and threatening behavior (Figure 4f.; positive: β = -0.51, z = -2.55, *p* = .028; control: β = -0.97, z = -4.14, *p* < .001). There was also *more* stereotypic behavior in the positive condition than the negative (Figure 4a.; β = 0.10, z = 3.69, *p* < .001), and *less* in the control (β = -0.26, z = -8.66, *p* < .001)

The only behavior significantly different in just the positive condition was self-licking behavior (Figure 4g.), of which there was significantly more in the positive condition than either the negative condition (β = 0.17, z = 3.28, *p* = .003) or the control (β = 0.18, z = 3.42, *p* = .002).

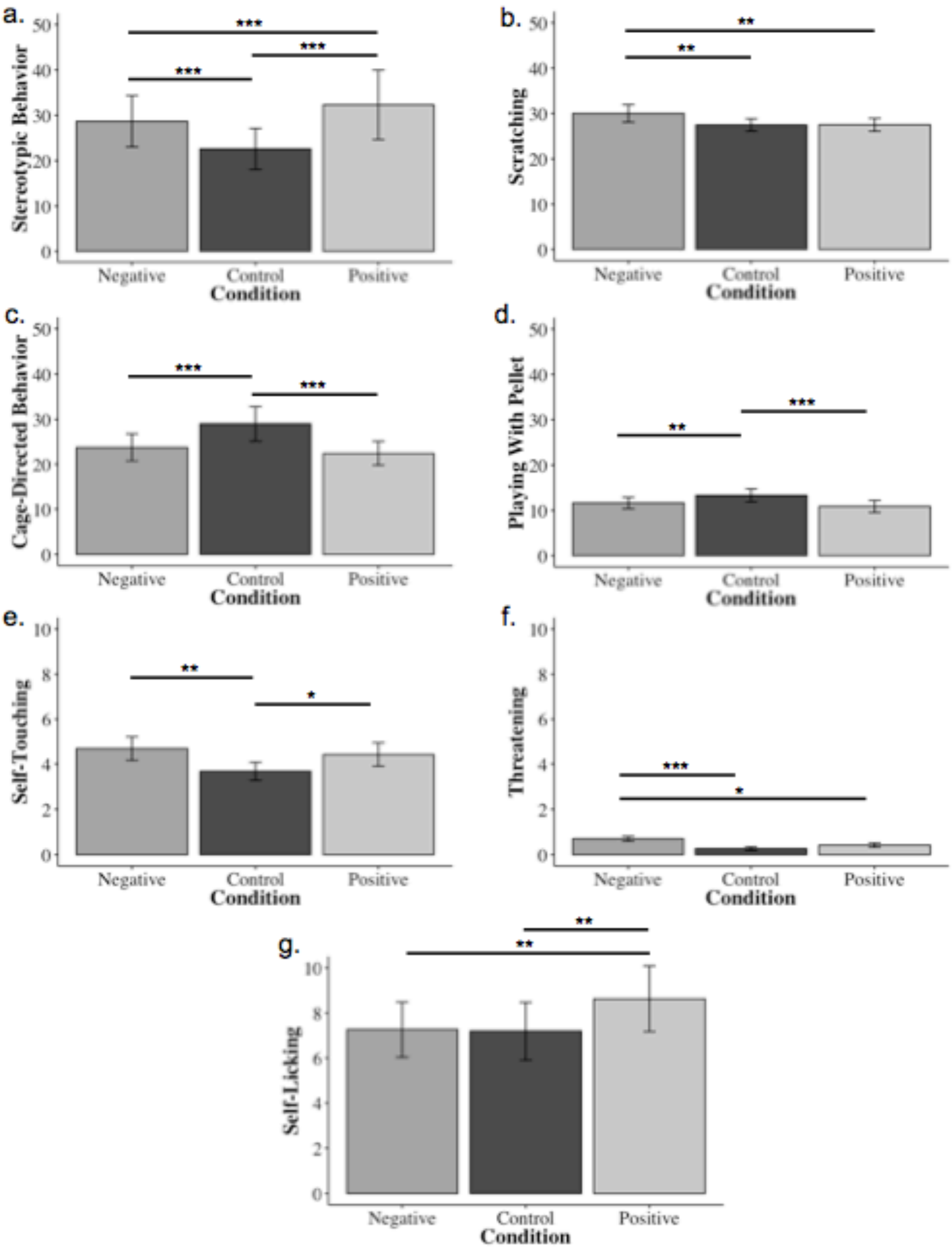


Figure 4. Results for the average occurrences of stereotypic behavior (a), scratching (b), cage-directed behavior (c), playing with the pellet (d), self-touching (e), threatening (f) and self-licking (g) between conditions. Error bars reflect ± 1 SE. '*' $p < .05$, '**' $p < .01$, '***' $p < .001$. *Note*: Graphs depict mean aggregated summary results and do not control for subject differences, while the *p* values come from GLMM's that control for Subject ID as a random effect. *Note:* Y-axis change between graphs a-d (ymax = 50) and e-g (ymax = 10).

3.2 Cognitive Performance

Overall, subjects performed quite well on the DMTS task, with a composite average of 83.4% (± 0.40) correct. This was as expected, since the criterion to participate in the study was 80% or greater accuracy. There was a significant effect of condition on DMTS task performance ($\chi^2(2) = 12.43$, $p = .002$), with higher performance in the positive condition (84.1 ± 0.64%, $\beta = 0.02$, $t = 2.96$, $p = .003$) and control (84.5 ± 0.67%, $\beta = 0.03$, $t = 3.09$, $p = .004$) compared to the negative condition (81.5 ± 0.75%). There was no significant difference in performance between the positive condition and the control, and there was no significant effect of time on accuracy or an interaction between time and condition (Figure 5).

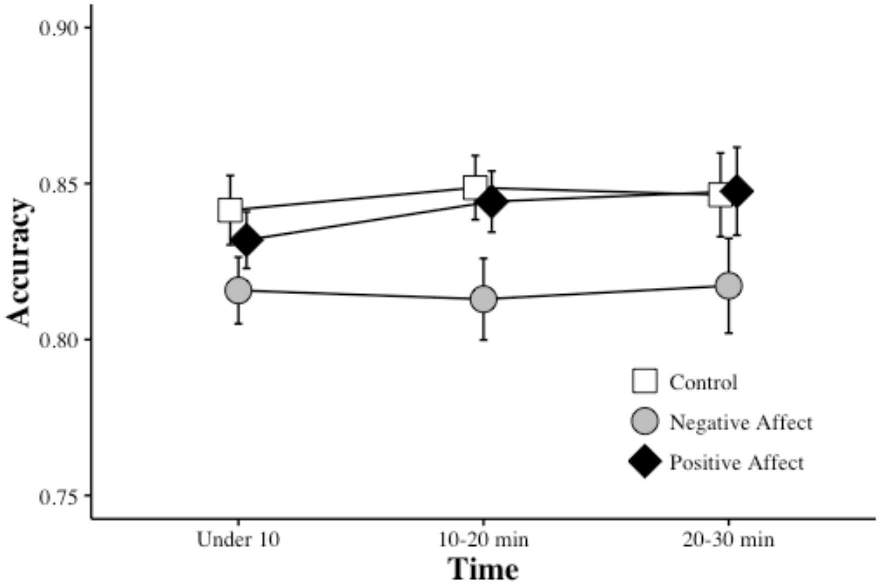


Figure 5. The effects of Condition and Time on subject Accuracy (as measured by the proportion of correct trials to the total number of trials completed). Error bars reflect ± 1 SE.

Of the seven behaviors significantly affected by the experimental manipulation, three also significantly affected performance on the DMTS task. Higher rates of playing with the pellet ($\beta = .001$, $t = 3.66$, $p = .003$, see Figure 6b) and self-licking behavior ($\beta = 0.002$, $t = 3.84$, $p < .001$, see Figure 6c) related to higher levels of accuracy on the task. Contrasting this, increased rates of scratching correlated with decreased performance on the DMTS task (β = -0.001, t = -2.60, *p* = .010, see Figure 6a). Increased rates of stereotypic behavior also related to decreased performance, however the effect was not statistically significant (*p* = .055).

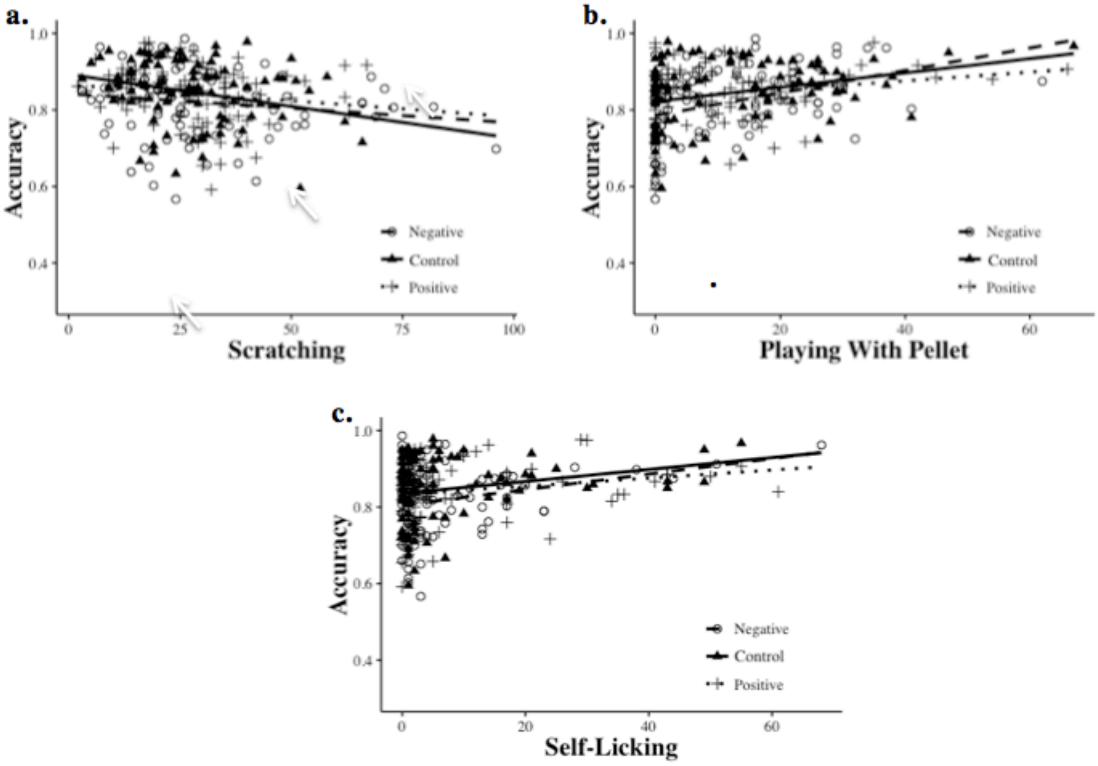
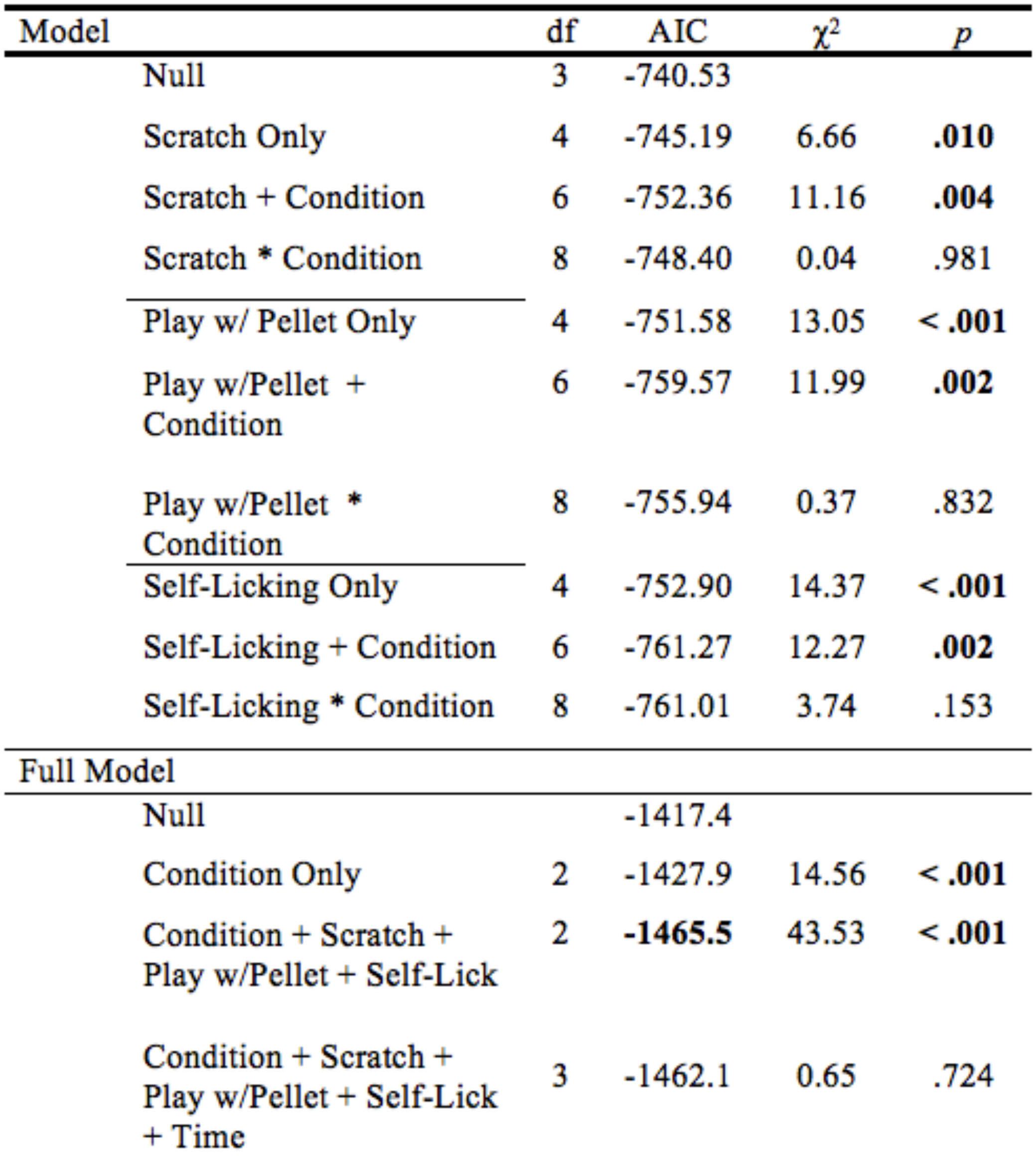


Figure 6. The effects of scratching (a), playing with pellets (b) and self-licking (c) on Accuracy (as measured by the proportion of correct trials to the total number of trials completed)

Since both behavior and condition significantly affected cognitive performance, model comparisons were run to determine whether condition and the behavior were independently impacting performance, or whether there was an interaction. While each model predicting accuracy with behavior alone as a factor was significantly better than a null model, and every model was improved by the addition of condition as a fixed effect, none of the models showed a significant interaction (Table 2).

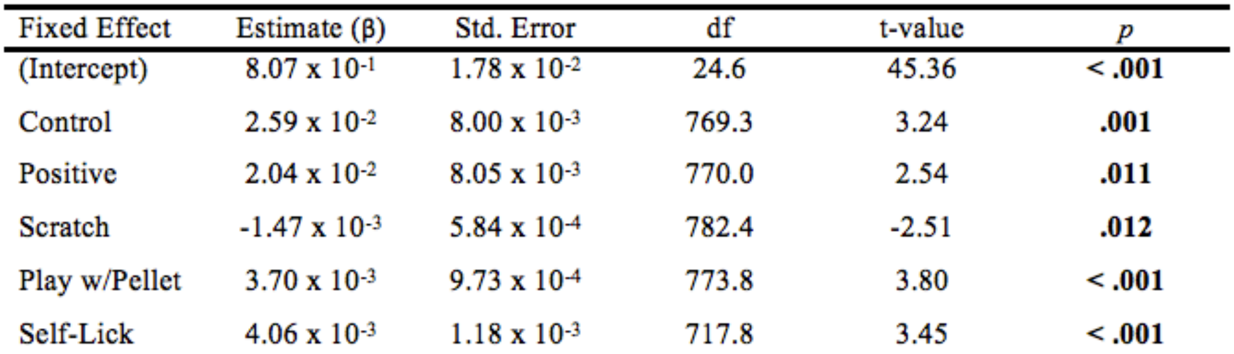
Table 2. Comparison of the models predicting Accuracy on the DMTS task



Model	df	AIC	χ^2	*p*
Null	3	-740.53		
Scratch Only	4	-745.19	6.66	**.010**
Scratch + Condition	6	-752.36	11.16	**.004**
Scratch * Condition	8	-748.40	0.04	.981
Play w/ Pellet Only	4	-751.58	13.05	**< .001**
Play w/Pellet + Condition	6	-759.57	11.99	**.002**
Play w/Pellet * Condition	8	-755.94	0.37	.832
Self-Licking Only	4	-752.90	14.37	**< .001**
Self-Licking + Condition	6	-761.27	12.27	**.002**
Self-Licking * Condition	8	-761.01	3.74	.153
Full Model				
Null		-1417.4		
Condition Only	2	-1427.9	14.56	**< .001**
Condition + Scratch + Play w/Pellet + Self-Lick	2	**-1465.5**	43.53	**< .001**
Condition + Scratch + Play w/Pellet + Self-Lick + Time	3	-1462.1	0.65	.724

The overall best-fit model for predicting accuracy on the DMTS task included scratching, self-licking, playing with the pellet, and condition as fixed effects, with Subject ID as a random effect. Adding time to the model did not improve the fit. In this final model, performance was significantly higher in both the positive and the control conditions compared to the negative condition, increased rates of playing with the pellet and self-licking behavior related to better performance, and increased scratching was related to a decrease in performance. Estimates (β) and *p*-values for all of the fixed effects in the final model can be found in Table 3. Overall, the final model reveals that while condition alone significantly predicts accuracy better than the null model, adding behaviors into the model as predictive factors provides a significantly better model for predicting accuracy than condition alone. Therefore, behavior can help explain variance in accuracy beyond what just the conditions explain.

Table 3. Fixed effects values for the full model predicting Accuracy on the DMTS (including scratching, self-licking, play with pellet behavior, and condition with subject ID and session as random effects)



Fixed Effect	Estimate (β)	Std. Error	df	t-value	*p*
(Intercept)	8.07 x 10^{-1}	1.78 x 10^{-2}	24.6	45.36	**< .001**
Control	2.59 x 10^{-2}	8.00 x 10^{-3}	769.3	3.24	**.001**
Positive	2.04 x 10^{-2}	8.05 x 10^{-3}	770.0	2.54	**.011**
Scratch	-1.47 x 10^{-3}	5.84 x 10^{-4}	782.4	-2.51	**.012**
Play w/Pellet	3.70 x 10^{-3}	9.73 x 10^{-4}	773.8	3.80	**< .001**
Self-Lick	4.06 x 10^{-3}	1.18 x 10^{-3}	717.8	3.45	**< .001**

4 DISCUSSION

Experiences immediately prior to cognitive testing affected both the subsequent performance on the cognitive test and the behavior of the capuchin monkeys. In line with predictions, a negative, frustrating experience impaired working memory performance compared to a previous positive experience or a control. This is consistent with previous studies in humans and primates that find impairments to working memory after stress (Arnsten & Goldman-Rakic, 1998; Oei et al., 2006; Schoofs et al., 2008). Increases in dopamine release as the result of the experience of positive affect is theorized to enhance working memory (Ashby et al., 1999), however contrary to my predictions, a positive experience prior to the working memory test did not have an augmenting effect on task performance.

While it is possible that positive affect may not have a facilitative effect on primate working memory in the task, it is also possible that the manipulation did not generate a sufficient increase in positive affect. For example, despite the fact that all subjects were ultimately successful with the task, some subjects never learned the most effective way to lift the lever (lifting straight up allowed for a very smooth and easy movement), and instead fought with the lever, trying to pull it towards them. This made the task somewhat more difficult. Additionally, and perhaps more importantly, several of the subjects responded quite aggressively to the *removal* of the apparatus. Anecdotally, these subjects would vocalize and threaten the experimenter as the tube was being unclipped from their cage, and they would often grab on to the apparatus and tightly hold it to prevent removal, to the point of nearly (and occasionally actually) breaking it. This may have mitigated any possible *positive* effects of the apparatus. Finally, my control may not have been appropriate. In the control, subjects were placed on a relatively easy task (the DMTS) after receiving a food reward for a behavior and protocol they are extremely familiar with (entering their individual testing box). I therefore may be seeing some level of positive affect in the animals even during the control. Thus, the lack of a facilitative effect of positive affect on working memory above and beyond the control should be interpreted cautiously, and future work should focus on developing procedures that ensure the generation of positive affect.

In line with my predictions, after the negative experience, subjects displayed increased rates of scratching and threatening behavior compared to both the positive condition and the control, as well as increased levels of stereotypic behavior, although this was only significantly greater than the control. Increases in these types of behaviors are strongly indicative of negative affective states (Lutz, 2014; Maestripieri et al., 1992; Troisi, 2002), signifying the effectiveness of the study's negative manipulation in inducing a negative affect in the subjects.

As there were no a priori predictions for what behaviors might increase when experiencing positive affect, I recorded all behaviors to see what I could find. The only behavior that occurred at significantly different rates in the positive condition than both the negative condition and control was self-licking behavior, which occurred at the highest rate after the positive experience. I do not have any explanations for why this may have been the case. While this behavior may be something important to look into in future research, the fact that I could not independently verify that I induced positive affect suggests caution. In fact, for all of the other behaviors for which I see a significant difference between the positive condition and the control, the difference for the positive condition is in the same direction as that of changes in behavior in the negative condition. Since I can more confidently conclude that the negative experience did result in negative affect, these findings imply that the positive condition created an affective state more akin to the negative condition than the control.

This conclusion is not, however, consistent with the results of scratching behavior, arguably the most reliable indicator of negative affect, or threatening behavior, both of which were significantly higher in the negative condition than either the positive or the control condition (which did not significantly differ from one another). Thus, an alternate possibility for the pattern of similar increases and decreases in some behaviors between the positive and negative conditions compared to the control is that some of these behaviors are more linked to arousal than affective valence. Both the positive and negative experiences involved interactions with a manipulated puzzle task, while the control did not. This may have caused arousal levels in both of these conditions that surpassed that of the control, and resulted in increased self-touching and stereotypic behavior and reduced cage-directed behaviors and playing with the pellet. This is further supported by the fact that cognitive performance was only affected by the negative condition (and not the control or positive) indicating this impact may be the result of negative affect and not an increase in arousal generally.

Finally, in the control, the subjects received no additional food prior to testing, as in the other conditions. Therefore, another possible explanation for this pattern of behavior is that subjects were less satiated in the control, changing their behavior. On the other hand, there is no reason to predict that satiation would have directly affected any of the observed behaviors. In fact, the one behavior that there is theoretical grounds to expect would differ based on satiation levels was trial number, because less satiated subjects may be more motivated to get food rewards and therefore do more trials, but there was not a significant difference in the number of trials done in the control versus the negative condition.

Ultimately I was unable to find a behavior reliably indicative of positive affect, in part because the experimental manipulation did not appear to effectively generate positive affect.

Although some of these behaviors (i.e., cage-directed behavior, self-licking and playing with food) may be related, this can only be demonstrated with further testing. I was, nevertheless, able to further validate the use of scratching behavior as an indicator of negative affect. The correlation between scratching and the negative condition compared to *both* of the other conditions, in conjunction with the significant finding that beyond condition, scratching itself can be predictive of decreased working memory performance, indicates that scratching may be the most reliable behavioral indicator of negative affect.

It is important to note that my final, best-fit, model for predicting accuracy on the task included both condition and behavior as predictive factors. In other words, including the behaviors as factors significantly improved predictions of accuracy *beyond* what condition alone predicted. The most likely explanation for this is that despite my best attempts, the subjects' affect was not entirely within my control. The subjects of the study live in complex social groups, and were subject to outside influences both before and during testing. It is possible that what behavior was measuring was the additional influence from non-testing factors on affect. This is a hypothesis that deserves further testing, but in the meantime, it is important to remember such outside influences when designing studies on affect.

One final comment regards the relation of these studies to previous neuroscience work. Although I did not measure brain activation, our knowledge of which areas are activated for these tasks allows us to speculate. Unfortunately, these data do nothing to break the impasse between the two competing hypotheses of whether activation prepares organisms for subsequent responding and improves performance, or depletes necessary resources and impairs it. Research on prefrontal cortex (PFC) activation during different types of working memory tasks shows a lateralization of brain activation, with object working memory tasks (as used in the current study) demonstrating relatively high left PFC activation (Courtney et al., 1998; Smith et al., 1995). Similarly, as discussed in the Introduction, neurological studies have clearly demonstrated asymmetric effects of positive and negative emotions on brain activation, with negative affect activating the right hemisphere and positive affect activating the left (Ahern & Schwartz, 1985; Davidson et al., 1990).

Interestingly, following the assumptions of this research, the current study found a damaging effect of negative affect (right hemisphere activating) on a task relying predominately on the left PFC. These results are clearly in contrast to the resource depletion hypothesis, which predicts that we would only see deficits in tasks reliant upon the activated area (right PFC). Due to the fact that I was unable to verify the experience of positive affect, further interpretation of the results is challenging. Indeed, it is not clear whether there was no positive affect, or whether both the positive experience and the control generated positive affect in the subjects, in which case the finding of an *increase* in performance in the positive and control conditions compared to the negative condition may be interpreted as supporting the facilitating activation hypothesis.

There is also another possible explanation for the current results. As I did not take any measures of brain activation in the current study, and am only assuming left PFC dominance in the DMTS task because research has shown that object working memory is left lateralized. These studies, however, utilized non-meaningful shapes as visual stimuli, while the current study used distinct pictures. Some research has shown that working memory for images under short delays may actually be *right* lateralized in the PFC (Courtney, Ungerleider, Keil, & Haxby, 1996). Courtney and colleagues (1998) argue that working memory involving short-term, icon-like maintenance of an image relies more on the right prefrontal cortex, while learning rules for non-meaningful shape memory may be more akin to verbal working memory, previously demonstrated to be left lateralized (d'Esposito et al., 1998; Davidson et al., 1990), and thus explains the results of the other studies. This has since received additional empirical support (Wager & Smith, 2003), and would then imply that the current task relied predominately on *right* PFC activation, and results are consistent with the resource depletion hypothesis. This would also be congruent with my finding that negative experiences seemingly *reduced* working memory performance from the positive experience and a control baseline. Future research on how frustration such as experienced in this experiment may differentially, or not, impact object and spatial working memory is needed.

In summary, the current study found a significant decrease in cognitive performance on a working memory task following a mild, negative experience. Previous studies have demonstrated deleterious effects of acute and chronic stress on working memory (Cazakoff et al., 2010; Mika et al., 2012), and some have even shown impairments after "mild" stress (Arnsten & Goldman-Rakic, 1998), although I would argue that their stressor, a continuous loud noise for 30 minute prior to testing, is slightly more than mildly stressful. To my knowledge, however, this is the first study to look at the cognitive effects of a mild, negative experience that induces negative affect through a relatively natural behavior of the species. These results further inform the literature on the effects of mild stressors on cognition, as well as have implications for animal welfare and animal research (i.e. the order of the presentation of tasks/tests of varying difficulty levels, and therefore possibly frustrating, may affect subsequent performance).

To improve future studies, researchers are badly in need of alternative measures of affect. One possibility is judgment bias tasks used in conjunction with the experimental manipulations of the current study, which may help to indicate whether positive affect was actually generated above and beyond the control, and I simply did not see working memory effects, or whether modifications of the experience are needed (as is suspected) to actually generate positive affect. Further, multiple measures of affect would help improve the confidence of behavioral indicators of positive affect, once correlations between behaviors and positive affect are found. Additionally, in future work it will be important to control for non-test related activities that generate affect on their own (i.e., the frustration engendered by removing the apparatus or the positive affect engendered by the reward upon coming into the test area). This would help to better pinpoint which actions are changing affect, and thereby better predict the subject's affect. Future work should also look at the effects of positive and negative affect on a variety of cognitive tasks as well as the effects of positive and negative experiences on subsequent social behavior.

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APPENDICES

Appendix A. Behavioral ethogram for all recorded behaviors

Behavior	Description
Joystick Touch[a,b]	*Subject meaningfully touches the joystick with a hand or foot (does not count if subject leans against joystick or accidental touches it)*
Water Drink	*Subject consumes water from their water spout or bottle*
Scratch	*Rapid, repeated touching of the body with either a foot or hand. If a different part of the body is scratched it's counted as a new occurrence, or if the same body part is scratched but with a different limb*
Shake	*Subjects full body vibrates, typically starts in the tail and runs up the body*
Auto-groom	*Subject touches, picks at or combs through their fur with one or both hands. Characterized by a pinching behavior, often accompanied with pushing their fur around and biting the area*
Self-touch	*Brief contact from the subjects hand or foot to another part of their body that is not better categorized by scratch or auto-groom*
Pace[a,b]	*Subject travels back and forth the full length of their test box. The same pace/tempo must be maintained in both directions, with no pause or hesitation at either end*
Manipulate object	*Subject holds or moves an object around, such as a tray or carabineer attached to the cage or a food item remaining*
Head twirl[a,b]	*Subject's head rapidly jerks back and arcs around. All occurrences of behavior counted, does not require 3-second interval, and an exception to the rule for interrupting a behavior*
Urine wash	*Subject's hand is urinated on while being held between their legs, followed by a rubbing/scratching behavior elsewhere on the body*
Lick caging	*Subject licks or pushes teeth or mouth against caging or faceplate*
Bounce	*Subject crouches over onto all fours and jumps with all four limbs off of the caging*
Threaten	*Subject bares teeth and assumes a rigid posture; or slams both hands into front/back of box quickly and aggressively*
Wipe caging	*Subject uses entire hand and palm and rubs it across a section of the caging or faceplate*
Pick at caging	*Subject pokes, scratches or touches the caging or faceplate with a finger or fingers*
Lip-smack	*Subject rapidly chatters their teeth or touches their lips together, often accompanied by grunts or squeaks and a headshake*
Push on faceplate	*Subject uses both hands to move the front or back faceplate. Hands are either both flat against the faceplate, or one is pushing against the faceplate with the other in the pellet dispenser hole to move the faceplate right or left*
Play with pellet	*Subject removes pellet from their mouth. This behavior may*

	include simply spitting out the pellet and then eating it again, removing the pellet and tapping it against some part of the cage or themselves, or rubbing it back and forth between their hands
Lick self	*Subject uses their tongue to contact or pushes their mouth against another part of their body*
Rub hands	*Subject places palms together and rapidly moves hands back and forth*
Reach	*Subject extends hand or arm out past caging (must have limb extended to wrist or further)*
Play with water	*Subject touches or hits the water source, causing water to run but does not drink*

Note: Every occurrence of behavior was recorded. Behavior was counted as a new occurrence instead of a continuation of the last if there was a 3-second period between the end of the first occurrence and the start of the second. If another behavior occurred between two occurrences of a different behavior (regardless of time) the interrupted behavior is counted again.

[a] Every occurrence of this behavior is counted regardless of the amount of time between occurrences

[b] Occurrences of this behavior do not interrupt the 3-second count on another behavior being a new occurrence or not