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THE ASSESSMENT OF COGNITIVE BIAS IN CAPUCHIN MONKEYS USING A COMPUTERIZED TASK

by

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Under the Direction of Michael J. Beran, PhD

ABSTRACT

Cognitive bias refers to the influence of affective state on the interpretation of ambiguous stimuli and has been used to assess emotional state in nonhuman animals. The current study assessed cognitive bias in 12 brown-tufted capuchin monkeys using three distinct computerized psychophysical tasks and a novel manipulation to affect that involved giving moneys gelatin foods that tasted either pleasant or unpleasant. In addition, monkeys were trained on several positive and negative training cues. Results showed that food type was not a factor in monkeys' responses to ambiguous stimuli. Behavioral observation during test sessions revealed the unpleasant food may have acted as a form of enrichment, thereby providing the monkeys with two pleasant activities prior to assessments of their emotional states. Further, results indicated that monkeys displayed a preference for the positive response class when classifying the ambiguous probe, but that this preference was subject to both task and individual differences.

INDEX WORDS: Emotion, Cognition, Nonhuman primates, Decision-making, Psychophysical judgement, Cognitive bias

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DEDICATION

The following manuscript is dedicated to my mother, Jennifer Spangler, my husband, Jensen Brock, and to my advisor and mentor, Michael J. Beran. The completion of this document would not have been possible without the immense support, guidance, and encouragement received from each of these individuals.

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1 INTRODUCTION

The study of emotion in humans and nonhuman animals has a long and checkered past. Despite questions regarding emotion dating back centuries, researchers still debate how to best study emotions and also *what* emotion truly is and whether it can be defined for scientific study. Distinguishing between terminology such as “affect,” “mood,” and “emotion” has been the source of much struggle in the field, with little agreement between and within the scientific and non-scientific communities (Alpert & Rosen, 1990; de Vere & Kuczaj, 2016; Izard, 2010; Kleinginna & Kleinginna, 1981). What is agreed upon, however, is that emotion is highly complex and multifaceted, meaning it is composed of multiple components (Izard, 2010; Kleinginna & Kleinginna, 1981; Russell, 2003). These components typically draw on neurological, cognitive, behavioral, and biological processes and include attributes such as duration, experience, cause, quality, intentionality, and intensity that serve to distinguish emotion from other processes as well as the terms used within emotion from one another (Alpert & Rosen, 1990; Beedie, Terry, & Lane, 2005; Cabanac, 2002; de Vere & Kuczaj, 2016; Izard, 2010; Kleinginna & Kleinginna, 1981; Mulligan & Scherer, 2012). No one definition has entirely placated the field, but many definitions incorporate the above components of emotion. For current purposes, the following working definition of emotion is this: Emotion is an intense episode of either short- or long-term duration accompanied by changes to physiology, cognition, and behavior that is typically directed at either an internal or external stimulus and that functions to aid in the seeking out of rewards and the avoidance of harm (Kleinginna & Kleinginna, 1981; Mulligan & Scherer, 2012; de Vere & Kuczaj, 2016). With regard to terminology within the study of emotion and general agreement that “moods” are more sustained and internally focused, I will use “affect” and “affective state” to refer to short-term, externally focused (i.e., directed at an object, person, or situation) emotion states as well as operate under the assumption that it is acceptable to use the terms “affect” and “emotion” synonymously (Alpert & Rosen, 1990; Beedie, Terry, & Lane, 2005; de Vere & Kuczaj, 2016; Mulligan & Scherer, 2012).

Due to its multi-aspect nature, researchers have been forced to study emotion in a piecemeal fashion. As such, it is important to keep in mind the context of findings in emotion research, because they may not generalize to all animals, human or nonhuman, or to all situations. The complexity of emotion has made it a difficult area of study for many psychologists. For decades, emotions were considered the direct opposite of reason and logic, and emotion and cognitive researchers operated on competing sides, or at least rarely worked together (e.g., Peters, Västfjäll, Gärling, & Slovic, 2006). As a result, a problematic division between cognitive and emotion research arose, with arguments supporting the independence of emotional and cognitive processing (Baddeley, 2007; Storbeck & Clore, 2007). Eventually, after evidence accumulated of the inter-relatedness of cognition and emotion and the bi-directional relationship between emotions and the mind, researchers studying the emotions of human and nonhuman animals began to advocate for the inclusion of affect and emotion in other fields of psychology. Specifically, there was a great emphasis to understand the impact emotions can have on cognitive processes and vice versa (Bower, 1981; Bower, Gilligan, & Monteiro, 1981; Brosch, Scherer, Grandjean, & Sander, 2013; Clore, Schwarz, & Conway, 1994; Clore, Gasper, & Garvin, 2001; Forgas, 1995; Liu, Fu, & Fu, 2009; Loewenstein, Weber, Hsee, & Welch, 2001; Schwarz & Clore, 1996).

Research on emotion has to designate measurable and observable indicators. There are several indicators of emotions, including verbal, physiological, and behavioral, and these indicators are often studied in combination with one another. However, evidence has shown that different measures do not always correlate with one another. For example, verbal reports do not always match physiological measures of affective states (Patrick, Bradley, & Lang, 1993; Stone & Nielson, 2001). Issues with correlations between the measures of emotion are especially problematic when attempting to measure emotional states in speech-impaired humans, pre-verbal children, and nonhuman animals. Whereas using multiple measures of affective state to combat these challenges is ideal, it is not always possible or practical. Along with several possible emotional indicators, emotion is generally assessed and measured along three dimensions: pleasure, arousal, and dominance (Liu et al., 2009). Pleasure, also known as valence, and arousal are most commonly used to assess affective states. However, many studies with animals tend to focus on negative valence or ignore valence in favor of arousal altogether (de Vere & Kuczaj, 2016). Despite the challenges of measuring emotion, by using behavioral, physiological, and cognitive measures of emotion and pulling from areas of psychology, biology, and neuroscience, evidence has suggested that cognition can be influenced by emotional states. Further, this influence spans many cognitive processes, including attention, memory, information-processing, perception, and decision-making (Baddeley, 2007; Kensinger, 2004; Lerner, Li, Valdesolo, & Kassam, 2015; Schwarz & Clore, 1996). Finding that emotion can influence cognitive processes was only the beginning as further research was needed to determine just *how* emotion impacts cognition as well as its role and function in humans and nonhumans.

With regards to how emotion operates on cognition and what function it serves, evidence has suggested that although emotions generally function to guide behavior toward survival goals such as attainment of resources and avoidance of harm (de Vere & Kuczaj, 2016; Mendl, Burman, Parker, & Paul, 2009) and to enable flexible responding to the environment (Brosch et al., 2013), they can both enhance and hinder cognition, and cognition can also positively or negatively impact emotional states (Clore & Huntsinger, 2007; Liu et al., 2009). Emotion can guide our decision-making, attention, perception, and memory in ways that may result in either improved or impaired cognition depending on the situation (Blanchette & Richards, 2010). Emotional disorders, specifically, have generally harmful effects on cognition, such as biasing memory recollection of negative events in depressed individuals (Dalgleish & Watts, 1990) or biasing attention toward threatening stimuli in those with anxiety disorders (Bar-Haim, Lamy, Pergamin, Bakermans-Kranenburg, & Van Ijzendoorn, 2007; MacLeod, Matthews, & Tata, 1986). However, it is generally accepted that emotional influences on cognition have adaptive benefits, such as directing attention to potentially dangerous situations, individuals, or objects, enhancing memory for emotional events to quicken action at a later time, or guiding decisions to enable efficient reaction to social or individual events (Clore & Huntsinger, 2007; de Vere & Kuczaj, 2016). This is evident not just through use of cognitive assessments but also through findings in neuroscience, which indicate that similar areas in the brain show corresponding patterns of activation during periods of cognitive processes and emotional behavior (Ghashghaei & Barbas, 2002; Liu et al., 2009; Storbeck & Clore, 2007). In some cases, brain damage to specific areas impaired the ability to use affective information and reduced performance in judgment and decision-making tasks (Damasio, 1994). The differential impact of emotional states on cognition is the center of much research in the field, as it can inform on the interaction between emotion and cognition in healthy and unhealthy individuals and in a variety of contexts (Baddeley, 2007; Bechara, H. Damasio, Tranel, & A. Damasio, 1997; Brosch et al., 2013; Damasio, 1994; Storbeck & Clore, 2007).

1.1 Emotional Influences on Memory

Effects on memory have been found at various stages, including during encoding, consolidation, and recall (Brosch et al., 2013; Liu et al., 2009). The specific effect that emotion has on memory depends on the affective state at the time of recollection and encoding as well as the emotional charge of the memory itself. According to the *mood congruency hypothesis*, people are more likely to recall memories that are congruent with their current mood (Bower, 1981; Buchanan, 2007; Schwarz, 2000). This differs from *state-dependent learning* in that the affective state at recall resembles the emotion of the recalled material itself rather than the emotion at the time of encoding.

The influence of emotion on memory can be both beneficial and harmful. Eysenck, Mogg, May, Richards, and Mathews (1991) demonstrated that anxious individuals were more likely to interpret ambiguous sentences as threatening during a memory recognition test. Specifically, participants rated whether sentences at testing were similar in meaning to sentences presented at an earlier time, and anxious individuals rated remembered ambiguous sentences as similar in meaning to threatening sentences presented at testing. Along with interpretations and memory of ambiguous stimuli, extreme, intense emotions, such as fear, anxiety, and craving, can act to disrupt working memory by biasing attention away from the task at hand and occupying limited working memory capacities (Baddeley, 2007). For example, patients with emotional disorders, such as anxiety and depression, experience reduced memory performance when compared to healthy participants (Dalgleish & Cox, 2002). While threat does impair working memory in healthy individuals, individuals who struggle with anxiety disorders are even more susceptible to threat-related distractions and exhibit more pronounced working memory deficits as a result (Baddeley, 2007). In contrast, individuals with depression-related disorders do not show the same attentional impairments as those with anxiety disorders, instead exhibiting impairments in learning, long-term memory, and prospective memory (Cronholm & Ottosson, 1961; Rude, Hertel, Jarrold, Covich, & Hedlund, 1999). Although emotion can certainly bias memory recollections and confidence, some data suggest that there may be an adaptive benefit, such that increased confidence in memories resulting from emotional stimuli may enhance attention and improve reaction to potentially harmful stimuli or events (Phelps & Sharot, 2008). As described above, affective influences on memory are often tied to attention, which is also impacted by emotional state and stimuli.

1.2 Emotional Influences on Attention

Because attention impacts many other aspects of cognition, emotional influences on attention not only affect attention itself but also any further processing, and these interactions can operate in both directions (Kensinger, 2004). The emotional relevance of a stimulus can work to direct attention and selection, such as when emotional targets are detected more quickly than neutral targets among distractors (Brosch et al., 2013; Öhman, Flykt, & Esteves, 2001). Specifically, both adults and young children were found to detect fear-relevant images of spiders and snakes more quickly among fear-irrelevant distractor images such as flowers and caterpillars (LoBue & DeLoache, 2008; Öhman et al., 2001). The capture of attention by fear-relevant stimuli was suggested to stem from evolutionary survival adaptations in which potentially life-threatening stimuli took attentional precedence over all other stimuli to facilitate enhanced detection, memory, and action.

Enhanced attention to threatening stimuli is evident in both humans and nonhuman animals and is also further enhanced by negative affective states and emotional disorders. For example, anxious emotional states greatly influence the direction of attentional resources

(Öhman & Soares, 1994). MacLeod et al. (1986) suggested that this effect is indicative of differences in attention between anxious and non-anxious individuals when dealing with emotional material, such that anxious individuals tend to shift attention toward threats while non-anxious individuals shift their attention away from such material.

Regardless of the seemingly negative impacts of the bias in attention that emotional stimuli and states can create, this relation may also have its origins in adaptive benefits (Baddeley, 2007; Paul, Harding, & Mendl, 2005). For example, Nairne, Pandeirada, and Thompson (2008) found that memory recall and recognition were best both for survival-related words and when participants engaged in survival-related processing when compared to other proven forms of retention enhancing processing strategies. This would seem to indicate that there are adaptive benefits for directing attention toward threatening stimuli. The interaction between emotion, attention, and memory can serve to increase defensive or offensive responses to threats, which surely is an invaluable process for self-preservation in many animals (Oatley & Johnson-Laird, 1987).

Along with enhancing attention to an emotional stimulus or when in an emotional state, affect can also influence how stimuli and situations are perceived. This is a particularly important relation, because perception of stimuli is largely outside of conscious cognitive control, unlike some of the earlier described cognitive processes that also are affected by emotion. This means that emotional influences on perception can “kick-start” the entire processing mechanism in a given ultimate memory recall or decision-making scenario. How one perceives the world sets the stage for how one remembers or acts on the world, and if such perception is influenced by emotion, this helps account for the relation of emotion and cognition more broadly.

1.3 Emotional Influences on Perception

Perception involves the sensory modalities and the interpretation of sensed stimuli. Emotion influences these interpretations in interesting ways, depending on the arousal and/or valence of either the individual or the stimuli. For example, the arousal and valence of both auditory and visual stimuli can differentially influence the perception of time by lengthening the perceived passage of time when stimuli are highly arousing and negatively valenced or by shortening the perceived passage of time when stimuli are highly arousing and positively valanced (e.g., Angrilli, Cherubini, Pavese, & Manfredini, 1997; Droit-Volet & Meck, 2007; Noulhiane, Mella, Samson, Ragot, & Pouthas, 2007). Alternatively, low arousal stimuli have an opposite effect on time perception, such that negatively valenced stimuli result in reports of shorter durations while positively valenced stimuli result in longer reported durations (Angrilli et al., 1997). Affective states can also have an impact on estimations of likelihoods and probabilities. For example, Johnson and Tversky (1983) found that positive affective states resulted in overestimations of the likelihood of positive events while negative affective states resulted in the overestimation of negative event likelihoods. In addition, participants who listened to sad music versus happy music tended to overestimate the incline of a hill (Riener, Stefanucci, & Proffitt, 2003). The exact mechanisms behind the general improvement in perception seen for emotional stimuli were investigated by Zeelenberg, Wagenmakers, and Rotteveel (2006), who sought to determine whether the impact of emotional stimuli on perceptual processing was due to enhanced encoding or to a bias toward emotional rather than neutral stimuli. Through a study constructed to parse these two explanations by differentially manipulating the valence of distractor and target stimuli during a perceptual task, Zeelenberg et al. (2006) determined that the enhancement in performance when perceiving emotional stimuli is due to enhanced processing and not to bias. These and other findings suggest enhanced perceptual processing of emotional stimuli is likely an adaptation evolutionarily designed to improve detection of potentially threatening or rewarding environmental stimuli that must take precedence over neutral stimuli not related to survival or fitness (Stefanucci, Gagnon, & Lessard, 2011; Zeelenberg et al., 2006). Differences in perceptual experiences resulting from emotional states can have a large influence on the decisions made and the resulting actions taken, such as not attempting to climb a perceptually inflated incline or to flee from a perceived predator. Indeed, differences in perception can lead to differences in interpretation, judgment, and eventual action.

1.4 Emotional Influences on Decision-Making

Lerner et al. (2015) stated that "Decisions can be viewed as a conduit through which emotions guide everyday attempts at avoiding negative feelings (e.g., guilt and regret) and increasing positive feelings (e.g., pride and happiness)" (p. 801). However, the way in which emotions influence decision-making depends on the specific emotions at play. Whether the emotions involved are related or unrelated to the decision itself can influence the eventual outcome in very different ways (Blanchette & Richards, 2010; Västfjäll et al., 2016)

Emotions that result from the decision itself can have a positive or negative impact on cognition. For example, brain damage in the ventromedial prefrontal cortex impairs the ability to feel emotion and to optimize decision-making when compared to healthy individuals (Bechara, Damasio, Damasio, & Lee, 1999; Damasio, 1994). A gambling task described by Bechara et al. (1997) was presented to brain-damaged and healthy participants to observe both their physiological and behavioral responses to decks of cards that varied in reward value and probability. Healthy participants exhibited skin conductance responses (SCRs) when choosing between the two disadvantageous decks and, after several losses, began to avoid these decks. Further, after experiencing a number of losses, healthy participants verbalized awareness that the disadvantageous decks were, in fact, the sub-optimal choice, and their SCRs and behavior reflected this realization. However, participants with damage to their ventromedial prefrontal cortex exhibited no SCRs in response to the disadvantageous decks, expressed little awareness of the nature of the decks, and chose sub-optimally. Even in the rare cases where participants with brain damage verbalized some knowledge of the disadvantageous decks, they still continued to choose sub-optimally. These results suggested that emotional states driven by the decisions themselves can impact both behavioral responses and the efficiency of decision-making processes.

Emotions resulting from unrelated events that are then carried over into the current decision can also greatly influence decision-making, including both verbal reports and probability estimations (Blanchette & Richards, 2010; Clore & Huntsinger, 2007; DeSteno, Petty, Wegener, & Rucker, 2000; Johnson & Tversky, 1983; Lerner & Keltner, 2000; Schwarz & Clore, 1983; Wright & Bower, 1992). Emotions can have a great impact on decision-making, but the degree of influence exerted by emotions can be even more pronounced when the outcome of a decision is ambiguous or uncertain.

1.4.1 Emotional Influences on Ambiguous Decision-Making

Expected Utility theory holds that ambiguous decisions should be made according to expected value, which is defined as the positive or negative evaluation of potential outcomes, and to the probability of those outcomes occurring (Loewenstein, 2000; Mendl et al., 2009). In this model, emotion influences choice behavior by acting on the evaluations of outcomes in terms of their utility. Negative affective states, such as depression and anxiety, result in more pessimistic judgments of ambiguous stimuli (MacLeod & Byrne, 1996), which impacts objective value determination due to the tendency for individuals in negative affective states to minimize the likelihood for disappointment or harm (Rolls, 2005; Schwarz, 2000). However, specific negative affect can influence the evaluation of value and outcome probability in different ways. For example, depressed individuals may experience a decrease in the perceived value of an outcome as well as in the probability of positive events, while anxious individuals may experience a perceived increase in the probability of negative events, suggesting that probability and value estimations may be encoded separately in the brain and may be independently subject to emotional influences (e.g., Mendl et al., 2009).

Negative affective states clearly influence judgments of ambiguous stimuli by making those judgments more negative. This hold true not only for object and location stimuli but also for faces. Brown, Raio, and Neta (2017) found that individuals experiencing high levels of stress were more likely to rate ambiguous facial expressions (e.g., surprise) as negative when compared to individuals with lower stress levels, demonstrating the impact negative affective states such as stress can have on the interpretation of and potential response to social situations. However, the influence of emotion on the judgment of ambiguous stimuli is not entirely negative. In fact, the reverse is true of positive affective states which tend to result in more positive judgments (Nygren, Isen, Taylor, & Dulin, 1996). Further, ambiguity is not the only factor that may enhance the effects of emotion on decision-making. The influences of affective state can also have an impact on other cognitive biases, such as risk and loss aversion. Ambiguous decisions involve a certain amount of risk and potential for loss, and aversions to risk and loss can impact how value and probability are evaluated. People are, in general, risk and loss averse when dealing with ambiguous situations (Ellsberg, 1961; Kahneman & Tversky, 1979; Tversky &

Kahneman, 1981). However, affective state may influence these aversions by either enhancing or diminishing them (Hsu, Bhatt, Adolphs, Tranel, & Camerer, 2005; Kliger & Levy, 2003; Maner et al., 2007; Mendl et al., 2009; Platt & Huettel, 2008; Rangel, Camerer, & Montague, 2008). Shiv, Loewenstein, Bechara, Damasio, and Damasio (2005) provided evidence of the impact emotion can have on risk aversion and decision-making. Participants with lesions in emotion-related brain areas were less risk-averse than controls and responded more advantageously when making investment decisions. Anxiety disorders can serve to decrease the tolerance for uncertainty, resulting in an enhanced aversion to ambiguity (Dugas, Gagnon, Ladouceur, & Freeston, 1998). These influences interact with other processes involved in decision-making and further elucidate the multifaceted and highly complex relationship between decision-making and emotions.

1.5 Relation of Emotion and Cognition for the Present Study

Emotion acts on the perception, interpretation, processing, and memory of information. As stated above, negative emotions can alter emotional influences on cognition in ways that hinder or distract from efficient responding. Tasks that require discrimination at the perceptual level are of particular interest in studies of emotion and cognition, due to the potential for emotional influences on perception to go largely unnoticed by the individual. Perception is generally an automatic process, and emotion states can alter perceptive experiences without the conscious awareness of the individual. This allows for research in this area to filter out the potential impact of emotional awareness and other “higher order” emotional processes on cognition. In light of this advantage, studies involving perception and emotion in nonhuman animals present an opportunity to study the effects of emotion on cognition at a more basic level, such as in the absence of language, social influence, and complex emotional awareness. Other cognitive processes such as memory and decision-making are highly complex and can be influenced by numerous factors, while perception is generally agreed to be a more basic process and less vulnerable to interpretive errors. Assessing the impact of emotion at this level of processing is a necessary foundation for further research, in that it sets the stage for further cognitive processing, and emotional influences on perception can often account for influences at “higher levels” of cognition.

Nonhuman animal perception is often similar to that of humans, so employing perceptual tasks with nonhuman animals allows for a more direct comparison of performance and error. The potential for emotion to alter the perception of nonhuman animals suggests that emotions can act on nonhuman animal cognition in much the same way as it does in humans, and that may begin at the perceptual level. Further, changes to nonhuman animal perception as a function of their affective state can inform on their psychological welfare, as enacting positive changes to their environment may be perceived differently depending on their current emotional states.

1.6 Emotion and Cognition in Nonhuman Animals

As detailed above, cognition and emotion are highly intertwined and the impact of emotion on cognitive processes has been well-studied in humans. However, much of this research has either sprung from or led to research on emotions and nonhuman animal cognition. Many similarities exist in the cognitive and emotional processes of humans and nonhuman animals, and because animals do seem to experience suffering and pleasure, it stands to reason they may also exhibit emotional influences on their cognition (Roitblat, Bever, & Terrace, 1984; Shettleworth, 2009; Zentall & Wasserman, 2012). Indeed, animals have been found to show similar emotion and cognition interactions in their behavior and psychology (Phelps, 2006). Although assessment of emotion in animals can be challenging, research has revealed that emotional states influence memory, attention, perception, and decision-making in nonhuman animals in much the same way as they do in humans (Berridge & Robinson, 2003; Paul et al., 2005).

Research on nonhuman animal emotion and cognition serves to expand upon findings in the human literature, but also allows for unique methods and questions that research with humans does not permit. Because emotional expression and recognition have been observed as universal across human cultures as well as in some nonhuman species, questions regarding the evolutionary origins of emotions and their impact on cognitive processes are often studied in nonhuman animals (Darwin, 1872; Evans & Cruse, 2004; Shariff & Tracy, 2011). Studying the cognitive processes of animals when under various affective states and with a variety of emotional stimuli can elucidate the adaptive value of emotions (Shariff & Tracy, 2011). For example, mood states in animals can inform on their response to their environment and how persistent threat and the potential for reward impacts cognition and coping efficiency (Mendl, Burman, & Paul, 2010). Further, emotion-cognition research in nonhuman animals works to address what the function of emotion is, such as guiding behavior and decisions, directing attention, and engaging in social communication (Paul & Mendl, 2018). Lastly, studying cognition and emotion across species serves to provide a better account of the breadth of emotion in phylogeny, including how widespread it is and how it has evolved over time into the complex process that exists in humans.

We know that animals demonstrate emotion, and emotions influence their cognition and behavior in ways similar to humans (e.g., Darwin, 1872; Hess & Thibault, 2009). However, the breadth and complexity of emotion in animals is highly variable and still under much debate (Izard, 1992). Basic emotions that are generally described as primitive, innate, automatic, and universal, such as fear and pleasure, have been demonstrated widely across the animal kingdom, while more complex emotions that are assumed to require a degree of self- awareness and higher order cognition, such as shame and pride, are generally reserved for the human emotional spectrum, with some exceptions in nonhuman primate species (Clark, 2013; Izard, 1992). In some nonhuman animal species, the absence of complex emotions provides a unique opportunity for researchers by allowing for the study of the relationship between basic emotions and cognition without the potential for more complex emotions to cloud results and interpretations. Indeed, when studying the influence of fear on cognition, researchers tend to study nonhuman animal participants due to the complexity of the human fear system and the potential for other emotions to influence humans' behaviors and cognition (Mendl et al., 2009; Storbeck & Clore, 2007).

Animal cognition and emotion research also has directly applicable benefits. Animal models have been used in pharmacology for studying the effectiveness of medications used to treat emotional disorders in humans and in neurology for studying the neural underpinnings of emotion and associated disorders (LeDoux, 2012; Panksepp, 2004; Paul & Mendl, 2018; Takamatsu et al., 2003; Willner, 1997). In addition to pharmacological and neurological research, cognitive and behavioral research on emotions in nonhuman animals requires a unique perspective on methodology. Nonhuman animals cannot voice their emotional states as humans can, so researchers must search for ways to study emotion in nonhuman animals using nonverbal assessments. These assessments are useful for nonhuman animal research and for research with humans who are either pre-verbal or speech impaired, as well as providing an additional measure of emotion in humans to assess the validity of verbal reports.

Apart from what research on emotion in nonhuman animals can achieve for humans, it is imperative for the welfare of the animals themselves. de Vere and Kuczaj (2016) addressed this point by stating that human and animal emotions need not align perfectly for the study of animal emotion to be a valuable endeavor in its own right. Animals kept in captivity in laboratories, zoos, and farms for use in research, husbandry, or entertainment are a large part of society, and it has become apparent that enhancing the quality of life of these animals is necessary to reduce unnecessary suffering as well as to improve the research or businesses these animals contribute to. Assessing the welfare of captive animals must first begin with the determination of their current emotional states and what factors either improve or diminish their well-being. Assessing the neural underpinnings, behavioral expression, and function of emotion in animals works to inform on their overall psychological health. In turn, these assessments work to provide the necessary information to enact positive changes in animal care policy, regulation, and maintenance (Baciadonna & McElligott, 2015; Boissy & Lee, 2014; Mendl et al., 2009).

When approached with care and caution, research with nonhuman animals allows for manipulations to cognition or emotion that would be considered unethical to perform with humans, such as lesion studies or the impact of negative environmental situations on welfare. Further, research involving the nonverbal aspects of emotion and cognition is a necessary consideration with animals and would be difficult to approach from a purely human perspective, such as with the speech-impaired or pre-verbal children. Human emotion is a vastly complex area of study that often overlaps with other factors, including socialization, education, and language, and while the emotional lives of animals may be subject to other factors as well, they are likely less complex, allowing for more basic assessment of the influences of emotion on cognition and vice versa. Work with nonhuman animals requires researchers to study basic mechanisms which can improve current research with humans by returning to the foundation of the questions involving emotion. Indeed, researchers had to begin their study of emotion in nonhuman animals by first describing what they meant by emotion so as to define a starting point for further investigation.

Paul et al. (2005) described a componential view of emotion, suggesting that many components of emotion can be studied either simultaneously or independently. Because the aspects of emotion are so complex and varied, prescriptive definitions of terms used in emotion research with animals are a necessity. The key components of emotion discussed in relation to animals mirror those discussed above, including valence, scalability/ intensity, persistence, and generalization, and all four of these components of emotion have been found in animals (Anderson & Adolphs, 2014). Although much debate still exists over the nuances of animal emotion, such as whether conscious awareness is necessary, the general agreement is that animals do in fact possess emotions and that, at least in some species, they reflect emotions seen in humans (de Vere & Kuczaj, 2016). Further, studies with animals show similar effects on their cognition from their affective states to those seen in humans, such as emotional influences on memory acquisition, recall, and consolidation (McGaugh, 2004; Sandi, Loscertales, & Guaza, 1997), on attention (Kawai & Koda, 2016; Treves, Drescher, & Ingrisano, 2001; van Rooijen, Ploeger, & Kret, 2017), and on decision-making and judgments (Davidson, 1994; Mendl et al., 2010; Paul et al., 2005). For example, animals in negative affective states are more likely to direct their attention toward threatening stimuli (Kawai & Koda, 2016). In addition, nonhuman animals show amygdala activation patterns in response to emotional stimuli as well as connections between amygdala activation and memory consolidation that closely resemble those seen in humans (McGaugh, 2004). Emotion-cognition studies with nonhuman animals are an increasingly larger part of the literature on animal mental lives, providing evidence that animals resemble humans in the areas of stress (Koolhaas, B. De, A. De, Meerlo, & Sgoifo, 1997), fear and learning (Davidson, 1992; Forkman, Boissy, Meunier-Salaün, Canali, & Jones, 2007; Maren, 2001), risk-taking (Blanchard, Blanchard, & Rodgers, 1991) and facial expressions (Steiner, Glaser, Hawilo, & Berridge, 2001). Many tasks have been constructed to study emotion using innate and learned responses as well as responses resulting from induced emotional states in nonhuman animals (Paul et al., 2005). Because animals cannot verbalize their emotional states, these tasks relied on indirect measures as a hallmark of emotion in nonhuman animals.

Measures in animals are commonly behavioral or physiological and primarily focus on mammals and negative affective states (de Vere & Kuczaj, 2016; Paul et al., 2005). Physiological measures include changes in heart rate, skin conductance, hormone and neurotransmitter levels, blood pressure, and facial expressions and are often taken as indicators of affective state changes in nonhuman animals. Emotion researchers use changes in stress physiology as indicators of anxious affective states (Paul et al., 2005). However, several issues exist with measures of physiology, namely timing issues and a lack of valence and positive affect information (Boissy et al., 2007; Mendl et al., 2009). Specifically, physiological measures such as heart rate and blood pressure can occur in response to any number of environmental inputs and may not be directly related to the manipulation or object of study. Further, using physiological measures in studying the effects of long-term emotional states is not particularly efficient, considering they can be short-lived and impacted by a variety of factors. With regards to information on emotional valence, physiological measures are indicative of the occurrence of an emotion but are not informative about the nature of that emotional state. For example, increases in heart rate can result from both positive and negative affective states.

In contrast with physiological measures, behavioral measures do provide information on valence, frequently observed as approach and withdrawal responses. Further, vocal and facial expressions in nonhuman animals have been found to be homologous with those of humans and have been used as an indirect measure of affect (Steiner et al., 2001). However, observer bias and misunderstanding as well as underlying motivations for the behavior create a challenge for interpreting the emotional state of the subject (Mendl et al., 2009). Even if researchers are cautious in their interpretations of observed behavior, there is still a measure of subjectivity. Behavioral expression can be indicative of a variety of underlying emotional states, and especially when it comes to animals, emotional state, intention, and motivation may not map on perfectly to overt behavior.

Verbal report is considered the ideal measure in human emotion research. However, these reports have been found to sometimes differ from the physiological and behavioral measures described above (Mendl et al., 2009). Due to this discrepancy, animal researchers expressed concerns with applying these physiological measures in animals, who cannot confirm or deny their accuracy as proxies for affect (Barnett & Hemsworth, 1990; Boissy et al., 2007; Mendl et al., 2009; Paul et al., 2005). These limitations can be partially addressed by using multiple measures simultaneously. However, interpretation accuracy remains a concern. Thus, cognitive measures were investigated as an alternative indicator of emotional state.

1.7 Cognitive Bias

Due to the fact that emotion and cognition are highly interconnected and that emotion can have a profound impact on cognitive processes, cognitive measures of emotional states in animals can be an alternative or supplemental assessment to behavioral and physiological measures. Cognitive bias is one such phenomena that has emerged from investigations into animals' emotion and decision-making. Stemming from the finding that humans in a negative emotional state interpret ambiguous stimuli more negatively (Eysenck et al., 1991; Gotlib &

Krasnoperova, 1998; MacLeod & Byrne, 1996; Mayer, Gaschke, Braverman, & Evans, 1992; Nygren et al., 1996; Wright & Bower, 1992), research with nonhuman animals has shown that they too exhibit this cognitive bias in judgment when presented with ambiguous stimuli (Bateson, Desire, Gartside, & Wright, 2011; Bateson & Matheson, 2007, Brilot, Asher, & Bateson, 2010; Burman, Parker, Paul, & Mendl, 2008a; Burman, Parker, Paul, & Mendl, 2009; Douglas, Bateson, Walsh, Bédué, & Edwards, 2012; Doyle, Fisher, Hinch, Boissy, & Lee, 2010; Hales, Stuart, Anderson, & Robinson, 2014; Harding, Paul, & Mendl, 2004; Löckener, Reese, Erhard, & Wöhr, 2016; Matheson, Asher, & Bateson, 2008; Mendl et al., 2010; for review see Mendl et al., 2009).

The judgment bias paradigm (first used by Harding et al., 2004) has been used to assess cognitive bias in animals by employing both short- and long-term manipulations to emotional states (Mendl et al., 2009). This paradigm involves a manipulation to affective state and two distinct responses (or one response and one non-response) that are reinforced either positively or negatively. The general method used in the judgment bias paradigm first involves training animals to make a response following one cue (i.e., the “positive” cue) and to either make a different response or withhold a response following another cue (i.e., the “negative” cue). Depending on the specific study and the cue given, animals will receive a reward for a correct response to the positive cue, avoid an unpleasant stimulus for a correct response to the negative cue, experience an unpleasant stimulus for incorrect responses to a negative cue, and have reward withheld for incorrect responses to a positive cue. By the end of training, animals have one cue that is associated with a positive event and one that is associated with a negative event. Taking place between the training phase and the testing phase is a manipulation to emotional state, which can include changes to housing, veterinarian procedures, or access to enrichment, and there is usually one group that acts as a control and undergoes no such manipulation. Following training is a testing phase in which animals are presented with ambiguous cues that are intermediaries of the positive and negative cues to see whether the subjects classify these cues using the positive response or the negative response. Many species have shown that negative affect manipulations often result in either a slowing response to ambiguous stimuli or an active classification of those stimuli as negative (see below for more details).

The judgment bias paradigm has been demonstrated to assess the impact of emotional states on nonhuman animals' judgments of ambiguous stimuli in general, but it also has the potential to inform on specific types of bias that relate to human emotional disorders. For example, in cases where there are multiple ambiguous probes presented, a tendency to classify probes as negative that more closely resemble the positive training cue or the negative training cue (i.e., location bias) can be telling as to whether animals are experiencing a bias that more closely resembles anxiety or depression (Mendl et al., 2009). Biases that occur to probes closer to the positive training cue may be indicative of a reduced anticipation for positive events, similar to depressed humans, while biases occurring to probes closer to the negative training cue may predict an increased anticipation for negative events, similar to anxious humans (Mendl et al., 2009). For example, if an animal is presented with an ambiguous probe tone that is objectively more similar to the positive cue but the animal instead classifies the probe as negative, it could be indicative of a reduced expectation of positive events. However, an animal that classifies an ambiguous probe tone that more closely resembles the negative cue as negative is likely showing an increased expectation of negative events. Studies of cognitive bias in animals can serve to inform on the mechanisms underlying emotional disorders in humans as well as on the welfare of the animals themselves (Hales et al., 2014; Roelofs, Boleij, Nordquist, & van der Staay, 2016).

Cognitive bias has been demonstrated in a multitude of species beginning with rats and moving to birds, livestock, and nonhuman primates. Harding et al. (2004) used a go/no-go task to assess cognitive bias, which involved training rats to press a lever upon hearing a specific tone to receive food and to avoid pressing the lever upon hearing a different tone to avoid exposure to aversive white noise. An affect manipulation of unpredictable versus predictable housing was also used, in which half of the rats were left in their standard housing environments while the remaining rats were subjected to unpredictable experiences (e.g., cage shaking) within their housing environments. The results indicated that rats placed in unpredictable housing responded less frequently and more slowly to ambiguous tones close to the positive training tone as well as to the training tone itself when compared with rats in predictable housing. Further assessments concluded that these results were not due to differences between treatments in feeding motivation, general activity, or response accuracy. Because the observed bias was at the tone closer to the positive training cue, Harding et al. (2004) concluded that the rats exhibited a reduced anticipation of positive events and suggested this demonstrated depressive-like effects.

Further studies on cognitive bias in rats sought to expand on this finding by introducing variants to the judgment bias paradigm. The use of visual or spatial cues, different manipulations to affect, and different positive and negative reinforcers are just a few examples of changes made to the methodology to assess various aspects of cognitive bias in rats. Burman et al. (2008a) employed a variety of these alterations including use of a spatial task and a different affect manipulation. Rats were given enrichment for seven weeks, which was then removed for half of the rats prior to training on the judgment bias task. Training involved running to one location for food and avoiding another location without food. Following testing with ambiguous probe locations, Burman et al. (2008a) found that for the probe located closest to the unrewarded location, rats with removed enrichment were slower to reach it than rats with continued enrichment. In contrast to the Harding et al. (2004) findings, the rats were likely experiencing an increased expectation of negative events, which more closely mirrors anxiety than depression. In another variant on the judgment bias paradigm, Saito, Yuki, Seki, Kagawa, and Okanoya (2016) employed the use of positively or negatively associated conspecific vocalizations to manipulate affect in rats following training on an auditory cognitive bias task. They reported that rats responded positively to ambiguous tones when previously played positive conspecific vocalizations but responded negatively to ambiguous tones when played negative vocalizations. It was suggested this was evidence of emotional contagion brought about by attributions of valence to the vocalizations of conspecifics.

Other studies with rats have investigated contrast effects in cognitive bias. Burman et al. (2009) manipulated light intensity during training on a spatial location task that employed aversive punishers and pleasant reinforcers for different locations with rats, with half of them trained in high-intensity light and half of them trained in low intensity light. Following successful training and prior to testing with ambiguous probes, half of the rats in each group were switched to the other light intensity. Results indicated that rats who were switched from high to low intensity light ran faster to ambiguous probe locations than rats who were switched from low to high intensity. Further, rats who were in the high intensity group at outset and were not switched to the other light intensity prior to testing showed no differences in their responses to ambiguous locations, though overall rats tested in high intensity light were slower than rats tested in low intensity light. These findings suggested that rats who were switched from high to low intensity experienced a reduction in anxiety rather than rats who were switched from low to high intensity experiencing an increase in anxiety.

While not the judgment bias paradigm specifically, Burman, Parker, Paul, and Mendl (2008b) used affect manipulations to test rats' sensitivity to rewards and losses. Half of the rats were trained on a spatial location task with one pellet as a reward while the other half were trained with 12 pellets. Rats who were trained with 12 pellets ran faster to the reward than those trained with one pellet. When testing provided only one pellet for all the animals, rats who had originally received 12 pellets were slower to reach their goal than rats who had received one pellet from the outset. However, rats who had their enrichment removed and who also experienced the drop from 12 pellets to one pellet were more sensitive to the loss for a longer period of time when compared to rats who continued receiving enrichment but also experienced the reduction in pellet amount. This suggests that changes in affect, brought about by the removal of environmental enrichment, can influence the sensitivity of rats' responses to loss, such that inducing a negative affective state resulted in an increase of sensitivity and the longevity of that sensitivity to reward loss.

The literature on cognitive bias in rats is by far the largest for all nonhuman species, and the findings are robust (also see Brydges, Leach, Nicol, Wright, & Bateson, 2011; Papciak, Popik, Fuchs, & Rygula, 2013; Richter et al., 2012). However, cognitive bias is not limited to rats or even to mammals. Several studies with starlings have provided evidence that birds also exhibit positive cognitive bias following enrichment as well as negative cognitive bias following removal of enrichment using both discrimination and go/ no-go tasks and a variety of reinforcers such as instant or delayed food and palatable or unpalatable food (Bateson & Matheson, 2007; Matheson et al., 2008). In addition, choosing the pessimistic response in a cognitive bias assessment was found to correlate with stereotypic behavior in starlings, a behavioral measure of anxiety or stress (Brilot et al., 2010). Along with rats and birds, cognitive bias has also been demonstrated in many other species.

Cognitive bias tasks have been used to assess affective states in dogs (e.g., Burman et al., 2011; Starling, Branson, Cody, Starling, & McGreevy, 2014). Mendl et al. (2010) sought to understand the underlying affective states of dogs exhibiting problematic behaviors when isolated from their owners, known as separation-related behaviors (SRBs). In a spatial location task, dogs were trained to discriminate between one side of a room containing a food reward and the other side of a room with no food reward. Once discrimination was deemed satisfactory, ambiguous probe locations were set up. Mendl et al. (2010) found that dogs who exhibited higher levels of SRBs, determined by a previous test, were slower to approach probes closest to the negative location and to the middle location. Dogs who displayed high levels of SRBs responded more pessimistically to the cognitive bias task, suggesting that SRBs may reflect an underlying anxious affective state in dogs.

Following from these results, Karagiannis, Burman, and Mills (2015) employed cognitive bias testing as a method to verify potential treatments for SRBs in dogs. Dogs with SRBs, who had previously exhibited negative biases on a judgment bias task, were found to respond more similarly to control animals with no separation-related problems after receiving behavioral and pharmacological treatments. Further studies found that dogs treated with oxytocin were more optimistic in their expectations when compared to placebo-treated dogs (Kis, Hernádi, Kanizsár, Gácsi, & Topál, 2015). Another common household pet also exhibits cognitive bias. Hamsters that were provided with caging enrichment were found to be more likely to approach ambiguous stimuli in a spatial location task than hamsters who received no enrichment (Bethell & Koyama, 2015). Cognitive bias has also been used as a complementary assessment of affective state in dolphins, such that positive biases were found to correlate with higher frequencies of synchronous swimming (Clegg, Rödel, & Delfour, 2017) while pessimistic biases were found to correlate with higher frequencies of anticipatory behaviors prior to positive training sessions (Clegg & Delfour, 2018).

Evidence of cognitive bias extends also to insects. Honeybees exhibit cognitive bias in response to simulated predatory attacks. Bateson et al. (2011) trained honeybees to discriminate between pleasant and aversive olfactory cues and then subjected them to shaking to simulate an attack from a predator. Bees who were shaken were more likely to classify ambiguous stimuli as negative. In addition, links between exploratory behaviors and cognitive biases in carpenter ants were found by d'Ettorre et al. (2017), such that fast-exploring ants tended toward negative biases while slow-exploring ants tended toward positive biases.

Cognitive bias assessments also have received much attention in research on the welfare of farm animals. Researchers recognized that to begin improving conditions for these animals, they must first assess their overall affective state and how that affective state may be influenced by their environment and human-induced procedures (Baciadonna & McElligott, 2015; Boissy & Lee, 2014). When horses were presented with a spatial location judgment bias task, those with access to an open field and conspecifics displayed a stronger positive cognitive bias when compared to horses who were housed alone with no open field access (Löckener et al. 2016). Further, horses living under naturalistic conditions showed optimistic cognitive biases while horses living under poorer riding conditions exhibited pessimism as well as correlated behavioral and health-related problems (Henry, Fureix, Rowberry, Bateson, & Hausberger, 2017). While results have been mixed, cognitive bias has also been assessed in goats. Female goats that were recently rescued from neglectful conditions and moved to a sanctuary showed an optimistic bias compared to control females and to males in the same rescue group (Briefer & McElligott, 2013). These authors suggested that the assessment may have revealed affective states of relief in the rescued females rather than lingering negative effects from their previous living situation. Other findings suggested that grooming sessions with human caretakers had no impact on cognitive bias assessments in goats, which were optimistic overall, potentially due to the healthy welfare environment that often included positive human interactions (Baciadonna, Nawroth, & McElligott, 2016).

The importance of improving living conditions for captive animals has resulted in an increased interest in cognitive bias assessments that can provide effective measures of animals' affective states along with what aspects of their environment can influence those states positively or negatively. For instance, Douglas et al. (2012) looked at the impact of enrichment on pigs using a go/ no-go task, finding that enriched pigs were faster to respond to ambiguous auditory probes while pigs that were moved from an enriched to a barren environment were slower and less likely to respond to the same probes. Negative judgment bias in pigs has also been found to correlate with fearful responses to novel objects (Carreras et al., 2016). Work with dairy calves has shown that pessimistic cognitive biases are suggestive of negative affect states following separation from maternal care (Daros, Costa, von Keyserlingk, Hötzel, & Weary, 2014) as well as dehorning procedures (Neave, Daros, Costa, von Keyserlingk, & Weary, 2013). Cognitive bias assessments have also been performed with laying hens (Hernandez, Hinch, Lea, Ferguson, & Lee, 2015; Wichman, Keeling, & Forkman, 2012) and chicks (Salmeto et al., 2011). The study involving chicks sought to provide comparisons for both anxious- and depressive-like states by isolating chicks for either a short time to induce anxious affect or for a long time to induce depressive affect. Salmeto et al. (2011) found that chicks in an anxious state were slower to approach ambiguous cues in a spatial location task that were close to the negative cue while chicks in a depressive state were slower to approach ambiguous cues that were either close to the negative cue or to the positive cue. These findings further demonstrated that anxious states may reflect an increased expectation of negative events while depressive states may reflect a decrease in expectation of positive events.

There has been much work done on cognitive bias in sheep, generally finding that affective states and responses on cognitive bias assessments reflect changes to the environment, such as access to enrichment or restraint, in similar ways to other animals as noted above. For example, sheep under chronic stress, induced by subjecting the sheep to unpredictable and aversive events, took significantly longer to approach ambiguous probe locations in a spatial location task when compared to unstressed sheep (Destrez et al., 2013). Further, sheep under stress resulting from production systems were also less likely to approach ambiguous stimuli (Doyle et al., 2011).

Pharmacological approaches to judgment bias in sheep have revealed the impact of various drugs on the cognitive biases of sheep. Lambs who were not treated with diazepam, a drug commonly used to reduce negative affect states, were slower to approach one of the ambiguous locations in a spatial location task when compared to treated lambs, suggesting that treated lambs were less fearful of ambiguous stimuli than untreated lambs (Destrez, Deiss, Belzung, Lee, & Boissy, 2012). In contrast, when administered a serotonin-depleting drug, which could increase depressive symptoms, sheep displayed a negative cognitive bias (Doyle et al., 2011). While unpredictable environments and chronic stress negatively impact affective states in sheep, other studies have found evidence of positive biases in a variety of situations, including following release from restraints (Doyle et al. 2010), release from shearing (Sanger, Doyle, Hinch, & Lee, 2011), and access to enrichment after previous stress (Destrez, Deiss, Leterrier, Calandreau, & Boissy, 2014).

As the studies above illustrate, the scope of cognitive bias extends throughout the animal kingdom and researchers have understood that using cognitive bias in animals as a model for emotional disorders in humans and as a measure of laboratory, zoo, and farm animal welfare is a valid and lucrative endeavor (Baciadonna & McElligott, 2015; Boissy & Lee, 2014; Mendl et al., 2009). Given the potential value of animal models of emotional disorders in humans, nonhuman primates are of particular interest to researchers of emotion. Nonhuman primates share many cognitive similarities to humans, including their systems for memory, perception, and decision-making (Maestripieri, 2003; Roitblat, Bever, & Terrace, 1984; Shettleworth, 2009; Tomasello & Call, 1997; Zentall & Wasserman, 2012). In addition, nonhuman primates present an opportunity to test cognitive bias effects in a nonhuman species that also has complex cognition, offering an additional perspective that other nonhuman animals with less advanced cognitive processes cannot provide. Further, nonhuman primate welfare in laboratories and zoos is of great concern to those charged with the ethical care of those animals and researching new ways to assess their psychological and emotional states aids not only the well-being of the animals themselves but also offers possible models for human mental health and wellbeing assessments. Finally, assurances of nonhuman primate well-being in research environments enables investigations in all fields to continue working respectfully and humanely with these animals in pursuit of other important scientific goals.

Behavioral and physiological indicators of emotional states in nonhuman primates are common, including displacement activities such as self-grooming and scratching (e.g., Maestripieri, Schino, Aureli, & Troisi, 1992). Behavioral indicators of emotion have been used in assessing responses to differing levels of enrichment in squirrel monkeys (Izzo, Bashaw, & Campbell, 2011) as well as risky decision-making in capuchin monkeys (De Petrillo, Tonachella, & Addessi, 2017). However, such measures still suffer from the same issues of interpretation and lack of information on positive affective states and valence that plague emotion research on the rest of the animal kingdom (Boissy et al., 2007; Mendl et al., 2009; Pomerantz, Terkel, Suomi, & Paukner, 2012; Schino, Massimei, Pinzaglia, & Addessi, 2016). As a result, focus turned to the use of cognitive measures of emotion and to the influences of emotion on cognition and vice versa in nonhuman primates. Indeed, work on the link between emotion and cognition has been done with many species of primates, including chimpanzees (Allritz, Call, & Borkenau, 2016), Japanese macaques (Kawai & Koda, 2016), rhesus macaques (Bethell, Holmes, MacLarnon, & Semple, 2012a; Cronin et al., 2018), marmosets (Gordon & Rogers, 2015), and baboons (Blanchette, Marzouki, Claidière, Gullstrand, & Fagot, 2017). Research on attentional bias in nonhuman primates has revealed that negative affective states do influence where attention is directed and how quickly threatening stimuli are attended to. For example, Allritz et al. (2016) found that chimpanzees' responses on an adapted emotional Stroop task were similar to those found in humans, such that chimpanzees were slower to respond to emotional stimuli than to neutral stimuli. Further, Kawai and Koda (2016) found attentional biases in rhesus macaques toward snakes such as those also found in humans, suggesting an evolutionary basis of enhanced attention to fearful stimuli. Cronin et al. (2018) demonstrated that when under stress from loud noises, macaques displayed a slowing of response times to threatening face stimuli. Rhesus macaques were also found to respond differently to threatening faces depending on whether they received a visit from the veterinarian or enrichment prior to seeing those faces. Veterinarian visits resulted in increased avoidance of the threatening faces while enrichment resulted in attendance to the faces (Bethell et al., 2012a). Further evidence for avoidance of negative stimuli was demonstrated in baboons when they were presented with a memory task with negatively valenced targets and distractors, such that accuracy increased when the distractors were negatively valenced (Blanchette, et al., 2017). In addition, Bethell, Holmes, MacLarnon, and Semple (2016) found that a macaque who was recently stressed by a veterinary visit was significantly slower to respond on an attention task when emotional distractors were present.

Due to the similarities in nonhuman primate responses to emotional stimuli, cognitive bias assessments in nonhuman primates have been used to further the understanding of interactions between cognition and emotion and of the emotional welfare of these animals. In the first study of judgment bias in nonhuman primates, Bethell, Holmes, MacLarnon, and Semple, (2012b) presented a rhesus macaque with a go/no-go task in which the monkey was trained to discriminate the lengths of two lines where different responses were associated with either a food reward or white noise and a time out. After training was successful, testing sessions occurred following either a visit from a veterinarian or enrichment and involved presentation of ambiguous lines of intermediate length. Bethell et al. (2012b) found that the macaque was less likely to respond to ambiguous stimuli following a veterinary visit but was more likely to touch the ambiguous probe closest to the positive cue and the middle probe following enrichment. These results suggested that the macaque’s emotional state was more optimistic when having had access to enrichment while the macaque’s response following a stressful veterinary visit reflected a more pessimistic emotional state. Further, this study provided evidence that judgment bias tasks can pick up changes to affect within one individual rather than only between groups who experienced different manipulations to their affective states.

Tests of cognitive bias in common marmosets revealed that there may be connections to handedness and aggression, such that left-handed marmosets were more pessimistic in their responses and experienced higher levels of aggression from conspecifics, while right-handed marmosets were more optimistic (Gordon & Rogers, 2015). The authors suggested that this relation between handedness, aggression from conspecifics, and pessimistic cognitive bias may stem from behavioral predispositions based in right hemispheric dominance. Further, Gordon and Rogers (2015) propose that cognitive bias testing and handedness may be a worthwhile technique for differentiating animals that may require additional welfare monitoring. Capuchin monkeys have also showed cognitive biases that correlated with stereotypic behaviors that are generally assumed to indicate negative affective states. Specifically, Pomerantz et al. (2012) found that capuchin monkeys who performed higher levels of head twirling were prone to pessimistic biases and also possessed higher levels of corticosteroids in their fecal matter. The correlation between pessimistic judgment bias and stereotypic behavior was further supported in another study that also found that dominant monkeys and monkeys who received more overall grooming displayed optimistic biases (Schino et al., 2016).

While cognitive bias has been demonstrated in a variety of monkey species, results from the great apes have been mixed. Chimpanzees displayed individual differences in biases on a judgment test, and such tasks were deemed good potential measures for affective states in chimpanzees (Bateson & Nettle, 2015). However, gorillas have proven to have difficulty during training. When gorillas were successfully trained on a cognitive bias task, they displayed optimistic biases, but the results remained unclear as to whether this was truly indicative of affective state (McGuire & Vonk, 2018; McGuire, Vonk, Fuller, & Allard, 2017).

Despite the mixed results with great apes, cognitive bias has been demonstrated widely across the animal kingdom. However, several issues have been raised regarding both the execution and interpretation of cognitive bias studies. Firstly, the ambiguous cues presented at test objectively have no correct answer and so it remains unclear as to how the animals are approaching these stimuli (Bateson, 2016). Further, responses to ambiguous stimuli at baseline (i.e., prior to affect manipulations) are not recorded, making it impossible to determine exactly how emotion may be influencing the judgment of these stimuli. Secondly, the majority of cognitive bias studies that employ manipulations to affect rely on between-subjects designs that require comparison between separate groups of subjects following changes to affective state. As a result, the potential for extraneous factors to influence responses to ambiguous stimuli is high, especially when using pre-existing changes to affect, as well as potential individual differences in how certain animals respond to those changes (Bateson, 2016; de Vere & Kuczaj, 2016). The use of control groups also introduces an issue of relative versus absolute biases, creating difficulty in determining whether subjects are experiencing objective changes to their affect and in measuring both long-term and short-term emotion states (Bateson, 2016; Bethell, 2015). Lastly, a large concern with the judgment bias paradigm involves the reward system of ambiguous stimuli or, more specifically, the lack thereof. Ambiguous cues are not rewarded which creates the possibility of subjects learning that these cues never result in positive reinforcement, leading to reduced responding irrespective of emotional state (Bateson, 2016; Perdue, 2017).

To address some of these issues, Perdue (2017) presented rhesus macaques and capuchin monkeys with a continuum of elliptical stimuli consisting of 40 sizes. Monkeys were trained to respond “SMALL” or “LARGE” and received either one or four pellets for correct responses to the smallest (e.g., level one) and the largest (e.g., level 40) stimuli. Specifically, for some monkeys, responding correctly on small ellipse trials resulted in a one pellet reward while large ellipse trials would result in four pellet rewards, and for other monkeys those contingencies were reversed. Following training on the two anchor stimuli, monkeys were shown intermediate stimuli ranging from level 2 to level 39. These intermediate stimuli were not reinforced, meaning no pellets or time outs were received for either correct or incorrect answers. After initial testing, the reward amounts were switched, such that monkeys who originally received one pellet for small trials now received four pellets and vice versa. This study involved no manipulation to affective state, but found that despite initial responses being unbiased, repeated exposure to ambiguous probes resulted in a shift toward negative responding (e.g., the lowest reward payout). Further, reversing the reward payouts resulted in a shift of response class preference to favor the lowest reward payout, suggesting that with repeated exposure to the cognitive bias task, monkeys tended to choose the response class associated with negative events regardless of previous training and in lieu of any manipulations to affective state. It was suggested that negative cognitive bias may be a result of learning that the ambiguous intermediate stimuli do not provide reinforcement and therefore a negative cognitive bias is observed not due to a negative affective state but to reward payout contrasts and learning effects.

Given the results of her study, Perdue (2017) suggested caution when interpreting cognitive bias tasks. She suggested that negative biases may be due to learning or other factors outside of affect manipulations. Along with the prevalence of contradictory findings, studies on cognitive bias in nonhuman primates are relatively few in number when compared to studies with rats and livestock species. Further, the tasks used with capuchin monkeys have been solely manual tests and affect manipulations among nonhuman primates are centered either around husbandry procedures or are not used at all, with researchers opting instead to use cognitive bias as a potential correlate of stereotypic behaviors generally accepted to indicate negative affect. Due to the complexity of nonhuman primate cognition, they present a greater challenge when studying emotional state and potential connections to cognitive processes. Indeed, the literature on cognitive bias in nonhuman primates is greatly lacking when compared to other species. Continued study of cognitive bias in nonhuman primates is necessary to determine whether these animals might be resistant to cognitive bias effects, why that might be the case, and how we might be able to adapt an assessment of emotional state through cognitive tasks for successful use with nonhuman primates.

1.8 Purpose of the Current Study

To address the shortcomings described above, the current study assessed cognitive bias in brown-tufted capuchin monkeys using a computerized program with a novel discrimination task and an affect manipulation that can be controlled among subjects as a within-subjects factor. Very few studies with nonhuman primates, and with nonhuman animals more generally, have assessed the impact of affect manipulations on a large number of responses to trained stimuli. Research has focused on training only one positive and one negative cue. The drawback of this is that responses to intermediate stimuli are only observed following the manipulation to affect, and it is possible that responses to these stimuli are driven by something other than affect, such as novelty, uncertainty, or surprise at the introduction of such stimuli. Due to this, the current study included training of both endpoint and intermediate stimuli prior to testing, allowing for assessment of the impact of affect manipulations on previously learned as well as previously unseen intermediate stimuli. In response to concerns raised by Perdue (2017), the current study also employed the use of non-differential reinforcement for the true intermediate stimulus to prevent learning of reward outcomes as well as the testing of multiple intermediate stimuli to assess responses to previously unseen and ambiguous stimuli that still objectively fall in either the positive or negative cue categories.

1.9 The Current Study

The current study involved training capuchin monkeys to classify a stimulus on a computer screen as one of two possible discriminations. For Experiment 1, monkeys saw either a speed discrimination task, which required classifying a moving circle stimulus as either slow or fast, or an orientation discrimination task, which required classification of rectangles as either tall or wide. Movement speed or orientation ranged across 15 stimulus levels, with Level 1 being the slowest speed (or widest rectangle) and Level 15 being the fastest speed (or tallest rectangle). Training occurred in three phases: (1) Monkeys were trained only on levels 1 and 15 with standard reward contingencies, (2) Monkeys were trained on levels 1 through 5 and 11 through 15 with standard reward contingencies, and (3) Monkeys were trained on levels 1 through 5 and 11 through 15, but with reward contingencies that created a positive association with one response class and a negative association with the other response class. Following training, monkeys moved onto a test phase consisting of ten sessions. Test sessions began with the presentation of either a pleasant tasting or unpleasant tasting gelatin food, alternated every test session. Monkeys were then set up on the computer program identical to phase three of training, except with the addition of stimulus levels 6 through 10 that were oversampled so as to provide a large corpus of data on the objectively more ambiguous stimuli.

1.10 Expected Results

It was hypothesized that when monkeys were given the pleasant food prior to testing, they would be more likely to classify test stimuli (levels 6 through 10) using the positive response, while they would be more likely to respond negatively to test stimuli when given the unpleasant food prior to testing.

If the monkeys showed a positive bias when given access to a pleasant food and a negative bias when given an unpleasant food, there are several conclusions that may be drawn. Monkeys’ perception and interpretation of ambiguous stimuli was influenced by environmental, short-term manipulations to their emotional states. Leading from this, access to mood-improving foods or treats may improve animal welfare and emotional well-being in captive environments. On the contrary, a negative emotional state can result from unpleasant food sources. Overall, the emotional state of nonhuman primates can alter whether they interpret ambiguous events as positive or negative, and this can inform on better practices for housing and enrichment for captive animals.

2 EXPERIMENTS

2.1 Experiment 1

There were two potential tasks used for Experiment 1: a speed judgment task and an orientation judgment task. All monkeys received training on the speed judgment task, and if they could not meet criterion after 1,000 trials or five training sessions, they were given an increased time out (from 20 s to 60 s) for another 1,000 trials. If criterion was still not reached, monkeys were moved onto the orientation judgment task.

2.1.1 Subjects

Testing occurred at the Language Research Center (LRC). I tested 12 brown-tufted capuchin monkeys, 3 males and 12 females, aged 11 to 23 years. Capuchin monkeys were housed in four different social groups with frequent access to outdoor enclosures as well as other forms of enrichment and were fed a daily diet of chow, fruit, and vegetables. All testing conducted with these monkeys was voluntary and at no time were they food or water deprived.

2.1.2 Apparatus

All monkeys were previously trained to use a joystick connected to a computer that delivers pellets though an attached dispenser (Richardson et al., 1990; Rumbaugh, Richardson, Washburn, Hopkins & Savage-Rumbaugh, 1989). Rewards were 45mg banana flavored pellets. Capuchin monkeys gained access to their testing stations by voluntarily entering testing boxes attached to their indoor enclosures. On the front of test boxes was a transparent plexi-glass faceplate with openings for the joystick and the pellet dispensing tube. In the test boxes, monkeys were able to access the computer system which was placed in front of the faceplate, allowing monkeys to see a computer screen, manipulate a joystick, and receive pellet rewards. Monkeys remained in their testing boxes for the duration of testing, usually lasting around four hours. While in the testing box, monkeys had visual and auditory access to their groupmates. Following testing, capuchin monkeys were released from their boxes and were provided with access to their outdoor enclosures and their group mates. Programs were written using Visual Basic 6.0.

2.1.3 Phase 1 Training

To begin a trial, monkeys used their joystick to move a cursor on the screen to a centered "Start Trial" button. Initiation of the trial replaced the cursor at the bottom center of the screen. For the speed judgment task, a black circular stimulus then appeared at the top center of the screen and began to move horizontally back and forth in the middle third region of the screen, starting randomly on either the left or right side and moving either very quickly or very slowly. More speed levels were introduced in subsequent training sessions, but for phase 1 of training, monkeys only saw the slowest speed (Level 1) and the fastest speed (Level 15). At the bottom left of the screen was the word "FAST" and at the bottom right of the screen was the word "SLOW." The monkeys moved the cursor to either word depending on the speed of the stimulus. If the cursor was moving quickly (Level 15), the monkey should have moved the cursor to the left option to choose "FAST," but if it was moving slowly (Level 1), the monkey should have moved the cursor to the right option to choose "SLOW." The orientation judgment task looked similar to the speed judgment task, except that the stimulus was a stationary black box that was either tall or wide. The response classes were in the same placement as the previous task but instead said "TALL" on the left and "WIDE" on the right. This task also used multiple levels of orientation in further training, but only included the widest (Level 1) and the tallest (Level 15) stimuli during phase 1 of training. Monkeys received one 45mg banana-flavored pellet for correct responses but received a 20 s or 60 s time out for incorrect responses. All monkeys began with a 20 s time out. However, following a monkey’s failure to reach criterion after 1,000 or more trials, the time out was increased to 60 seconds (see Table 1). Monkeys had to reach a criterion of 80 percent correct overall and 50 percent correct on each stimulus level to move onto the next training phase.

2.1.4 Phase 2 Training

Training continued as described above with the addition of eight intermediate levels of speed or orientation (Levels 2, 3, 4, 5, and 11, 12, 13, 14), excepting five of the very middle levels (Levels 6, 7, 8, 9, 10). Depending on the assigned task, monkeys were required to classify levels 2, 3, 4, and 5 as “SLOW” or “WIDE” and levels 11, 12, 13, and 14 as “FAST” or “TALL,” receiving rewards and time outs as detailed above for Phase 1. Trial stimulus level was randomly selected on each trial. Once the monkeys reached the criterion of 80% correct overall and 50% correct per level on the most recent 100 trials, they were moved onto the third and final phase of training.

2.1.5 Phase 3 Training

The final phase of training presented monkeys with the same 10 stimulus levels as in phase 2. However, the reward system was changed to reflect the standard cognitive bias reward contingencies in order to induce an association of one response class with a positive event (e.g. the “positive” cue) and the other response class with a negative event (e.g. the “negative” cue). Half of the monkeys were assigned to associate “SLOW” or “WIDE” with positive events and “FAST” or “TALL” with negative events, depending on the task received during training, while the other half were assigned to the opposite associations (e.g. “SLOW” or ”WIDE” with negative events and “FAST” or “TALL” with positive events). This association was trained by introducing varying reward and time out contingencies depending on the assigned valence of the monkey. Responding correctly to the positive cue (fast or slow/ tall or wide, counterbalanced across monkeys) resulted in the delivery of a food pellet while responding incorrectly resulted in no food reward and a 1 s inter-trial interval (ITI) before the next start box appears to begin the next trial. Correct responses to the negative cue (the opposite cue from whatever the monkey was assigned for the positive cue) resulted in avoidance of a 20 s (or 60 s) time out and a 1 s ITI, while incorrect responses resulted in experience of a 20 s (or 60 s) time out before the 1 s ITI and the next trial appears. For example, a monkey assigned to associate slow-moving stimuli with positive events received a food pellet when correct on slow trials but moved on to the next trial with no time out when incorrect. The same monkey received a 20 second time out when incorrect on fast trials but moved on to the next trial with no time out and no pellet when correct. At the end of the ITI, the "Start Trial" button appeared again to initiate the next trial. Monkeys were again required to reach 80% correct overall and 50% correct per stimulus level in order to be moved to the testing phase.

2.1.6 Testing Phase

As stated above, some monkeys were not able to complete training on the speed judgment task and so were moved to the orientation judgment task. This resulted in a total of five monkeys trained and tested on the speed judgment task and a total of seven monkeys trained and tested on the orientation task. Prior to starting the computerized testing portion of the session, a researcher entered the room surrounding the indoor enclosure and set up a camera for filming test sessions. The researcher then left the room and re-entered carrying either a pleasant-tasting or unpleasant-tasting gelatin treat. Both versions of the food were made with gelatin powder and water in small ice cube trays as the base. Previous to any task training, pilot tests were conducted to determine a flavor that the monkeys liked and a flavor they disliked. If monkeys ate the food, it was concluded they liked it, but if they did not eat it and/or threw the food on the ground, then it was concluded they did not like it. As a result, a stevia-sweetened, fruit-flavored liquid water enhancer was used for the pleasant gelatin food while turmeric powder was used for the unpleasant gelatin food. Throughout testing sessions, monkeys did not eat the unpleasant gelatin food, while they did eat the pleasant gelatin food.

Monkeys were given a piece of gelatin food weighing between 2.5 and 3 grams before each test session. Whether the pleasant or unpleasant food type was encountered first was counterbalanced between monkeys, and then was alternated over ten testing sessions, generating a total of five sessions with the unpleasant food and five with the pleasant food. Following presentation of the food, the researcher observed and coded the monkey’s behavior for five minutes. Then, the computer system was affixed to the front of the test box faceplate and the relevant judgment task as seen during training was begun.

The computerized portion of the test sessions continued until one hour had elapsed. The task otherwise resembled Phase 3 of training, but with the addition of the five remaining stimulus levels (Levels 6, 7, 8, 9, 10). Responses to levels 6, 7, 9, and 10 resulted in a reward or time out as described in Phase 3 of training, while the true intermediate ambiguous probe (Level 8) was non-differentially reinforced in the following way. Trials lead to a pellet reward with probability 0.33, to the ITI with 0.33 probability, or to the timeout with 0.33 probability. Responses to all fifteen stimulus levels were recorded by the computer program, as well as response time data.

2.2 Experiment 2

This experiment was conducted to demonstrate the generalization of any cognitive bias effects seen in Experiment 1 to various stimulus classifications and to determine whether any evidence of cognitive bias in Experiment 1 was replicated with a new type of discrimination task.

2.2.1 Training Phases

The procedure was identical to Experiment 1, with the only exception being the replacement of classification of stimulus speed or orientation with classification of various shades of gray boxes. The response “LIGHT” was located on the bottom left of the screen while “DARK” was located on the bottom right of the screen. Counterbalanced across monkeys, light (or dark) gray boxes were trained as the positive cue, while dark (or light) gray boxes were trained as the negative cue. Rewards and time outs were identical to Experiment 1, with some monkeys receiving a 20 s time out while others were given a 60 s time out (Table 2). Following successful classification of the darkest gray box (Level 1) and the lightest gray box (Level 15) in Phase 1, eight more shades of gray (Levels 2, 3, 4, 5, and 11, 12, 13, 14) were trained to criterion in Phase 2, and then again with the introduction of the cognitive bias response contingencies as described in Phase 3. The criteria for progression were the same as in Experiment 1. One monkey (Gambit) was given the orientation task as her secondary task due to an inability to learn the shade task.

2.2.2 Testing Phase

The testing sessions were identical to Experiment 1 and again consisted of the presentation of either a pleasant or unpleasant gelatin food, followed by continued training with the previously seen stimuli as well as the addition of the remaining intermediate stimulus levels (Levels 6, 7, 8, 9, 10). Responses to the ambiguous probe (Level 8) were non-differentially reinforced as in Experiment 1. The classifications of the stimuli as light or dark and the response times were recorded by the program.

2.3 Data Analyses

Performance (e.g., percent correct) was graphed for stimulus levels 1-5 and 11-15 during the training phases in which the criterion was reached. Each stimulus level had a proportion correct for that level, which is averaged across all subjects and sessions, as well as a distance value which reflects how far from the central level of the continuum it is located. For example, stimulus level 2 had the proportion correct (e.g., 80/100) and a distance value of 6 because it is 6 stimulus levels away from level 8. It was predicted that performance would increase with increasing distance level from the center level.

All statistical analyses were run using SPSS (IBM Corp, 2017). For the test phase, a repeated-measures ANOVA was run to compare responses to the ambiguous probe (Level 8) across the condition of receiving the pleasant or unpleasant gelatin food as well as across block number. The percentage of times the monkeys chose the positively reinforced response class for this level was calculated for each block and food type. Specifically, Block Number One included the percentage of positive response class choices made during the first time the monkey received the unpleasant food and the first time the monkey received the pleasant food, and so on until Block Five to include all ten test sessions. The percentage of positive choices made over Block Number and Food Type were compared in order to determine whether food type influenced the frequency of positive responses to the probe stimulus. It was predicted that monkeys who received the pleasant food would be more likely to classify the ambiguous level 8 stimulus using the positive response class, while monkeys who received the unpleasant food would tend toward a negative classification. If the ambiguous probe was more often classified as negative, then this would indicate a negative, or “pessimistic,” bias. A higher frequency of positive classifications would indicate a positive, or “optimistic,” bias. If there was no difference in classification of the ambiguous probe, then that would indicate food type had no effect on the monkeys’ affective state.

Responses to the remaining stimulus levels (1-7 and 9-15) in the pleasant food condition and the unpleasant food condition were also analyzed. Using a repeated measures ANOVA, the percentage of positive classifications collapsed across stimulus level was analyzed by food type and by block number, as described above. It was predicted that positive responses would be higher across the full stimulus range when monkeys received a pleasant food than when they received an unpleasant food. Further, this effect was expected to drop off over block number, such that monkeys were more equal in their positive classifications when having received a pleasant or an unpleasant food. This would reflect that manipulations to affective state using differing food types are relatively short-lived and do not exhibit influence over repeated exposures to the food and to the discrimination task.

Percent correct was also analyzed by food type and block number to assess whether task performance was impacted by the food type received as well as over time. A repeated measures ANOVA was used to compare the average percent correct for each block and food type, as described above, to determine whether food type influenced performance on previously learned ambiguous stimuli and novel ambiguous stimuli. It was hypothesized that monkeys’ performance would not be impacted by food type, but that performance should increase over block number.

3 RESULTS

3.1 Experiment 1 and 2 Training Phases

All monkeys reached the criterion level of 80% correct overall and 50% correct per stimulus level on each of the three training phases before moving on to the test phase in both Experiment 1 and Experiment 2. Trial counts varied across monkeys and across training phases. For Experiment 1, Table 1 displays the total trial counts for each of the three phases for each monkey, their percent correct for the session in which criterion was reached, the length of their time outs, their age, their sex, and the positive valence assignment. For example, Gretel was assigned to associate “FAST” with positive events (i.e., a pellet), and so in Table 1, her positive valence is listed as “Fast.” Means and standard deviations for Experiment 1 trial counts and for performance in the criterion session are also displayed in Table 1. The same descriptive statistics, means, and standard deviations are listed for Experiment 2 in Table 2.

Training Phase 2 included stimulus levels 1 through 5 and 11 through 15 but maintained standard reward contingences from the first training phase, meaning monkeys received a pellet for correct answers and either a 20 s or 60 s time out for incorrect answers. Stimuli closer to the center of the presented range are more ambiguous and therefore more difficult to assess, while stimuli on the ends, or anchors, of the stimulus range are easier to classify. Due to this, Train 2 and Train 3 performances from the session in which criterion was reached are graphed in Figure 1 for Experiment 1 and Figure 2 for Experiment 2 as a function of distance from the central trial level. Distance was calculated as follows: (3) levels 5 and 11 , (4) levels 4 and 12, (5) levels 3 and 13, (6) levels 2 and 14, and (7) levels 1 and 15. Graphically, performance in the Train Phase 2 criterion session was above criterion and increased as distance from the probe increased for both Experiment 1 and Experiment 2.

Training Phase 3 introduced nonstandard reward contingencies in order to train monkeys to associate one response class with positive events and the other response class with negative events (i.e., a pellet or a time out respectively). Stimulus levels were the same as in Phase 2 of training. As with Phase 2, monkeys reached the criterion of 80% overall and performance increased as distance from the ambiguous probe (level 8) increased for phase 3 of training in both Experiment 1 and Experiment 2 (see Figure 1 and Figure 2). However, the introduction of the cognitive bias reward contingencies created a large bias to whichever response class was assigned as positive, as explained in further detail in the discussion.

3.2 Experiment 1 Test Phase

Data were analyzed using repeated measures ANOVAs and One Sample t-tests. There were two dependent variables analyzed: percent positive and percent correct. Percent positive denoted the percentage of times monkeys chose their assigned positive response class while percent correct was their objective performance rates. Trial Block and Food Type were the independent variables included in the analyses. Block referred to the session number and ranged from one to five. Block 1 included the first session the monkeys received the pleasant food and the first session they received the unpleasant food, and so on. Food Type referred to whether the monkeys received the pleasant or unpleasant food. Three separate ANOVAs were run. The first included percent positive for Block and Food Type for stimulus level 8 *only,* as this was the true ambiguous probe. The second analysis included percent positive for Block and Food Type for all remaining stimulus levels that were grouped together excluding level 8. The third analysis included percent correct for Block and Food Type for the full range of stimulus levels excluding level 8 which had no correct classification. The aim of these three analyses was to assess whether monkeys were more likely to choose the positive response class or respond more correctly on sessions in which they received a pleasant food. In addition, Block was included to assess if any effects changed over time and with more exposure to the psychophysical task. The One-Sample T-Test was also performed on the percentage of positive choices for the level 8 data set in order to assess whether the percentage of positive choices was significantly different from chance and leaned more toward positive or negative responses for the ambiguous probe overall.

3.2.1 Ambiguous Probe (Level 8)

Monkeys' positive response class choices were not impacted by block number, $F(1.554, 12.436) = 1.24$, $p = 0.31$, $\eta_p^2 = 0.13$. Note that sphericity was violated in this analysis, and so Greenhouse-Geisser values were used. The percentage of positive response class choices was also not affected by food type, $F(1, 8) = 1.06$, $p = 0.33$, $\eta_p^2 = 0.12$. There was no interaction between block number and food type, $F(4, 32) = 0.83$, $p = 0.52$, $\eta_p^2 = 0.09$. For the ambiguous probe, monkeys showed no bias to choose the positively or negatively reinforced response class as a function of session number or as a function of having had a pleasant food or unpleasant food (Figure 3).

To determine whether monkeys chose the positive response class significantly more than chance when presented with the ambiguous level 8 probe, a One-Sample t-test comparing percent positive to a test value of 50 was performed. It was found that monkeys chose the positively reinforced response class for stimulus level 8 significantly above chance, but only for certain test sessions and food types (see Table 3). Positive response class choices were not significantly above chance for the second unpleasant session, for the third unpleasant session, or for the fifth pleasant and unpleasant sessions. This indicates that monkeys chose the positive response class more often overall, but this effect diminished as testing progressed (Figure 4).

While monkeys were overall more likely to classify the level 8 ambiguous probe stimulus as their positive response class, a task difference in this effect was observed (Figure 7). Monkeys chose their assigned positive response class at or above 80% of the time when they were tested using the speed discrimination task. However, monkeys who were tested on the orientation task, which was evidently an easier task for them, chose their assigned positive response class at close to chance levels. This indicates that monkeys on the orientation task did not discriminate the level 8 stimulus as resembling either the positive or negative response class, while monkeys on the speed task were more likely to classify the level 8 ambiguous probe as their positive response class. The task differences in positive responses to the level 8 ambiguous probe are examined further by individual monkey and task in Figures 13, 14, and 15.

To determine whether individual monkeys were significantly above chance in choosing their positive response class when presented with the level 8 ambiguous probe, binomial tests were run on the percentage of positive choices each monkey made in the pleasant sessions and the unpleasant sessions. Further, data was separated by task type (e.g., speed, orientation, or shade discrimination) for graphical representation to examine both individual and task differences in the percentage of positive response class choices to the level 8 ambiguous probe (see Figures 13, 14, and 15).

Figure 13 depicts the percentage of positive response class choices made to the level 8 ambiguous probe by each of the five monkeys presented with the speed discrimination task for both food types given during testing. All five monkeys chose their positive response class significantly above chance levels for both food types, indicating they were more likely to classify the level 8 ambiguous probe as their positive response class regardless of whether they received a pleasant or unpleasant food.

The percentage of positive response class choices made to the level 8 ambiguous probe by each monkey tested using the orientation discrimination task is depicted in Figure 14. Note that the orientation discrimination task was the first task (e.g., Experiment 1) for all of the monkeys except for Gambit, who received this task as her second task (e.g., Experiment 2). Unlike the speed discrimination task, the preference for the positive response class when presented with the level 8 stimulus was not universal across all monkeys. Bailey, Gonzo, Griffin, Lily, and Gambit were significantly above chance when classifying the level 8 ambiguous probe, suggesting they were more likely to choose their positive response class for the level 8 stimulus. However, Logan, Nala, and Widget were significantly below chance when classifying the level 8 stimulus as their positive response class, indicating these three monkeys were actually more likely to choose their negative response class when presented with the level 8 ambiguous probe. This explains why there were such large task differences observed in positive responses to the level 8 stimuli in Figure 7. It seems individual differences in the classification of the level 8 stimulus as the positive response class underlie the task differences in this measure, and, more particularly, three monkeys were driving this difference in level 8 classifications between tasks. Despite these individual differences in overall percentages of positive classifications, food type had no impact of the classification of the level 8 stimulus as the positive response class. In other words, monkeys who responded significantly above chance were as likely to do so for both food types and monkeys who responded significantly below chance were as likely to do so for both food types.

3.2.2 Remaining Stimulus Levels (Levels 1-7 and 9-15)

For the remaining stimulus levels that were all combined, monkeys were not more likely to choose the positive response class over block number, $F(4, 40) = 0.92$, $p = 0.46$, $\eta_p^2 = 0.085$.

Further, food type had no impact on the percentage of positive response class choices made, F(1, 10) < .01, p = 0.99, $\eta_p^2 < .01$. There was no interaction between block number and food type, F(4, 40) = 0.78, p = 0.54, $\eta_p^2 = 0.07$. Monkeys were no more likely to choose the positively reinforced response class over sessions or when they had a pleasant food or unpleasant food (Figure 5).

When assessing whether objective performance changed according to food type or block number, it was found that monkeys' performance was not affected by block number, F(4, 40) = 1.37, p = 0.26, $\eta_p^2 = 0.12$. Food type also had no impact on performance, F(1, 10) = 0.007, p = 0.93, $\eta_p^2 = 0.001$. There was no interaction between food type and block number, F(4, 40) = 1.17, p = 0.34, $\eta_p^2 = 0.10$. Monkeys' performance on non-probe trials was not impacted by unpleasant or pleasant foods or over session number (Figure 6).

Figure 7 depicts the percentage of positive responses as a function of the stimulus level. Monkeys are graphed according to their assigned positive response class. Monkeys chose their assigned positive response class close to 100% of the time when the stimulus was itself of the positive class. When the stimulus was of the negative class, monkeys chose the positive response class at much lower rates. This indicates that when the stimulus was of the positive class, monkeys chose the positive response at ceiling rates. Overall, performance was very high, such that monkeys chose correctly most of the time and especially if the stimulus was of the assigned positive class.

3.3 Experiment 2 Test Phase

All data gathered in Experiment 2 were analyzed using the same methods as in Experiment 1. The independent and dependent variables were the same as in Experiment 1. ANOVAs and One-Sample T-Tests were used to analyze all Experiment 2 data.

3.3.1 Ambiguous Probe (Level 8)

As in Experiment 1, classifying the ambiguous probe as the positively reinforced response class was not affected by block number, $F(4, 24) = 0.96$, $p = 0.45$, $\eta_p^2 = 0.14$, or food type, $F(1, 6) = 4.55$, $p = 0.08$, $\eta_p^2 = 0.43$. In addition, there was no interaction between block number and food type, $F(1.813, 10.880) = 1.23$, $p = 0.33$, $\eta_p^2 = 0.17$. Note that sphericity was violated in the previous analysis, and so Greenhouse-Geisser values were used. Monkeys' tendency to choose the positive response class was not impacted by the session number or whether they received a pleasant or unpleasant food (Figure 8).

Unlike in Experiment 1, classifying ambiguous probe stimuli into the positively reinforced response class occurred at levels significantly above chance for all blocks and both food types (Table 4). Overall, monkeys chose the positive response class more often than the negative response class across all blocks and for both pleasant and unpleasant food types for their second task (Figure 9).

In the second experiment, all monkeys were tested using the same shade discrimination task except one monkey who was tested with the orientation discrimination task. As such, no task differences in responses to the positive response class were observed. Monkeys responded to the level 8 ambiguous probe using their positive response class around 80% of the time, indicating that they were more likely to classify the level 8 stimulus as resembling their positive response class rather than their negative response class (Figure 12). This was true for monkeys on the shade discrimination task and the sole monkey on the orientation discrimination task.

For the final task, monkeys discriminated between shades of gray boxes. This was the second task (e.g., Experiment 2) presented to the monkeys who participated in Experiment 2, except for Gambit who was given the orientation discrimination task as her second task. The percentage of positive responses to the level 8 stimulus for both food types and for each monkey is shown in Figure 15. Similar to the speed discrimination task, all seven monkeys were significantly above chance when choosing their positive response class for the level 8 ambiguous probe. This indicates that monkeys were more likely to classify the level 8 ambiguous probe as their positive response class regardless of whether they received the pleasant or the unpleasant food type.

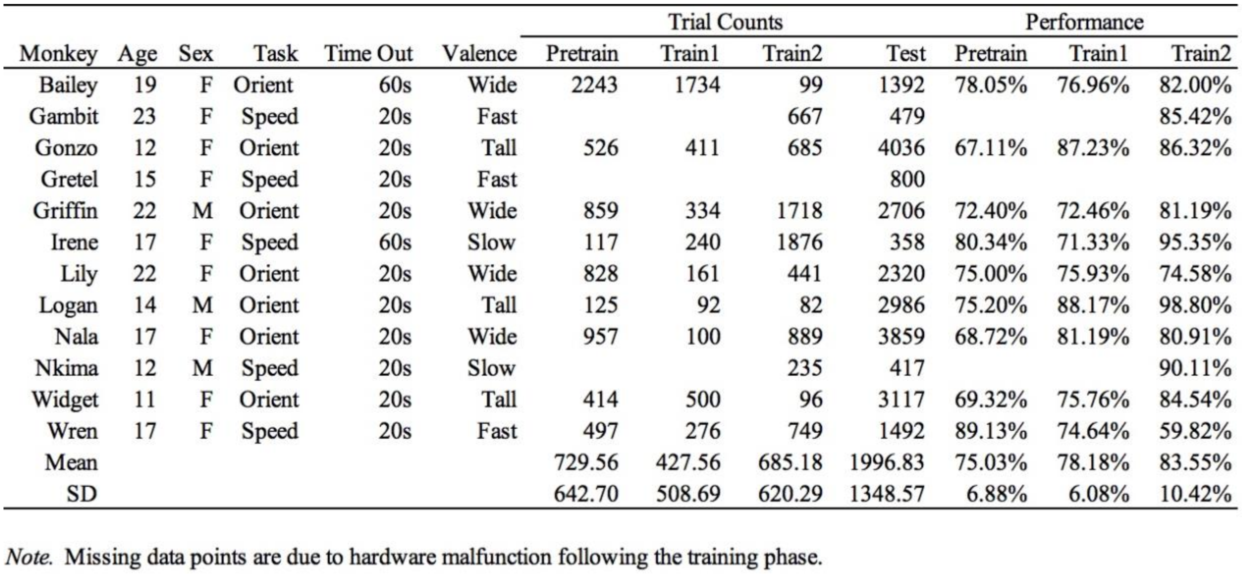
3.3.2 Remaining Stimulus Levels (Levels 1-7 and 9-15)

The percentage of positive responses was not influenced by block number, $F(4, 24) = 2.52$, $p = 0.07$, $\eta_p^2 = 0.30$, or food type, $F(1, 6) = 0.68$, $p = 0.44$, $\eta_p^2 = 0.10$. No interaction between block number and food type was found, $F(4, 24) = 1.83$, $p = 0.16$, $\eta_p^2 = 0.23$. For non-probe (level 8) trials, monkeys were equally likely to choose the positive response class regardless of block number and whether they received a pleasant or unpleasant food (Figure 10).

Similar to Experiment 1, no effect of food type on performance was found, $F(1, 6) = 1.58$, $p = 0.26$, $\eta_p^2 = 0.21$. However, a significant effect was found for block number, $F(4, 24) = 2.90$, $p = 0.043$, $\eta_p^2 = 0.33$. Monkeys' performance increased over sessions. Further, an interaction between block number and food type was also significant, $F(4, 24) = 4.57$, $p = 0.007$, $\eta_p^2 = 0.43$. The interaction between block and food type is graphed in Figure 11. Post-hoc analyses, using a repeated-measures ANOVA assessing block number and sessions in which only a pleasant food was received, showed that performance improved over blocks only for pleasant food test sessions, $F(4, 24) = 7.50$, $p < 0.001$, $\eta_p^2 = 0.56$. Further post-hoc analyses, using a paired-sample t-test comparing each block to every other block for the pleasant food test sessions, revealed that this effect was driven by blocks two, four, and five in the pleasant food sessions. Specifically, performance significantly improved from block two to block four, $t(6) = 2.56$, $p = 0.043$, and from block two to block five, $t(6) = 2.940$, $p = 0.026$.

As in Experiment 1, monkeys chose their assigned positive response class at exceptionally high rates when the stimulus was of the positive class. Their performance overall was high, especially when responding to stimuli that was of their assigned positive response class (Figure 12).

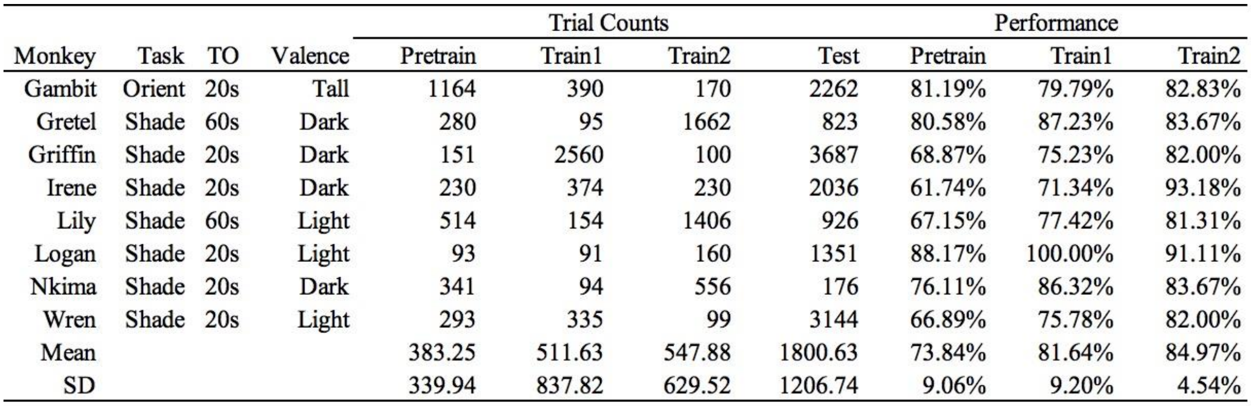
Table 3.1 Experiment 1 Descriptive Statistics



						Trial Counts				Performance		
Monkey	Age	Sex	Task	Time Out	Valence	Pretrain	Train1	Train2	Test	Pretrain	Train1	Train2
Bailey	19	F	Orient	60s	Wide	2243	1734	99	1392	78.05%	76.96%	82.00%
Gambit	23	F	Speed	20s	Fast			667	479			85.42%
Gonzo	12	F	Orient	20s	Tall	526	411	685	4036	67.11%	87.23%	86.32%
Gretel	15	F	Speed	20s	Fast				800			
Griffin	22	M	Orient	20s	Wide	859	334	1718	2706	72.40%	72.46%	81.19%
Irene	17	F	Speed	60s	Slow	117	240	1876	358	80.34%	71.33%	95.35%
Lily	22	F	Orient	20s	Wide	828	161	441	2320	75.00%	75.93%	74.58%
Logan	14	M	Orient	20s	Tall	125	92	82	2986	75.20%	88.17%	98.80%
Nala	17	F	Orient	20s	Wide	957	100	889	3859	68.72%	81.19%	80.91%
Nkima	12	M	Speed	20s	Slow			235	417			90.11%
Widget	11	F	Orient	20s	Tall	414	500	96	3117	69.32%	75.76%	84.54%
Wren	17	F	Speed	20s	Fast	497	276	749	1492	89.13%	74.64%	59.82%
Mean						729.56	427.56	685.18	1996.83	75.03%	78.18%	83.55%
SD						642.70	508.69	620.29	1348.57	6.88%	6.08%	10.42%

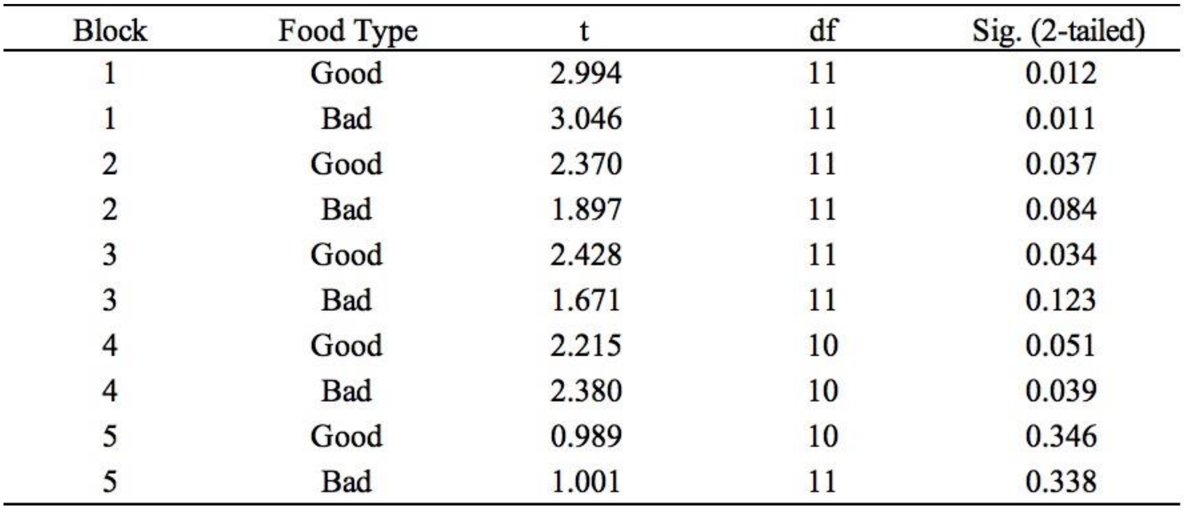
Note. Missing data points are due to hardware malfunction following the training phase.

Table 3.2 Experiment 2 Descriptive Statistics



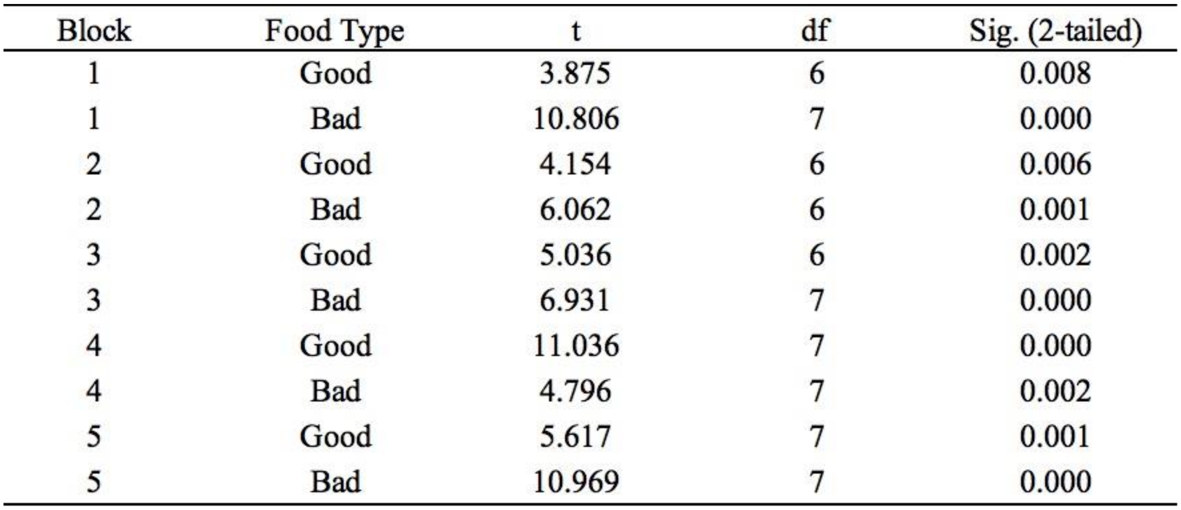
				Trial Counts				Performance		
Monkey	Task	TO	Valence	Pretrain	Train1	Train2	Test	Pretrain	Train1	Train2
Gambit	Orient	20s	Tall	1164	390	170	2262	81.19%	79.79%	82.83%
Gretel	Shade	60s	Dark	280	95	1662	823	80.58%	87.23%	83.67%
Griffin	Shade	20s	Dark	151	2560	100	3687	68.87%	75.23%	82.00%
Irene	Shade	20s	Dark	230	374	230	2036	61.74%	71.34%	93.18%
Lily	Shade	60s	Light	514	154	1406	926	67.15%	77.42%	81.31%
Logan	Shade	20s	Light	93	91	160	1351	88.17%	100.00%	91.11%
Nkima	Shade	20s	Dark	341	94	556	176	76.11%	86.32%	83.67%
Wren	Shade	20s	Light	293	335	99	3144	66.89%	75.78%	82.00%
Mean				383.25	511.63	547.88	1800.63	73.84%	81.64%	84.97%
SD				339.94	837.82	629.52	1206.74	9.06%	9.20%	4.54%

Table 3.3 Experiment 1 One-Sample t-test Level 8 Percent Positive vs Chance (50%)



Block	Food Type	t	df	Sig. (2-tailed)
1	Good	2.994	11	0.012
1	Bad	3.046	11	0.011
2	Good	2.370	11	0.037
2	Bad	1.897	11	0.084
3	Good	2.428	11	0.034
3	Bad	1.671	11	0.123
4	Good	2.215	10	0.051
4	Bad	2.380	10	0.039
5	Good	0.989	10	0.346
5	Bad	1.001	11	0.338

Table 3.4 Experiment 2 One-Sample t-test Level 8 Percent Positive vs Chance (50%)



Block	Food Type	t	df	Sig. (2-tailed)
1	Good	3.875	6	0.008
1	Bad	10.806	7	0.000
2	Good	4.154	6	0.006
2	Bad	6.062	6	0.001
3	Good	5.036	6	0.002
3	Bad	6.931	7	0.000
4	Good	11.036	7	0.000
4	Bad	4.796	7	0.002
5	Good	5.617	7	0.001
5	Bad	10.969	7	0.000

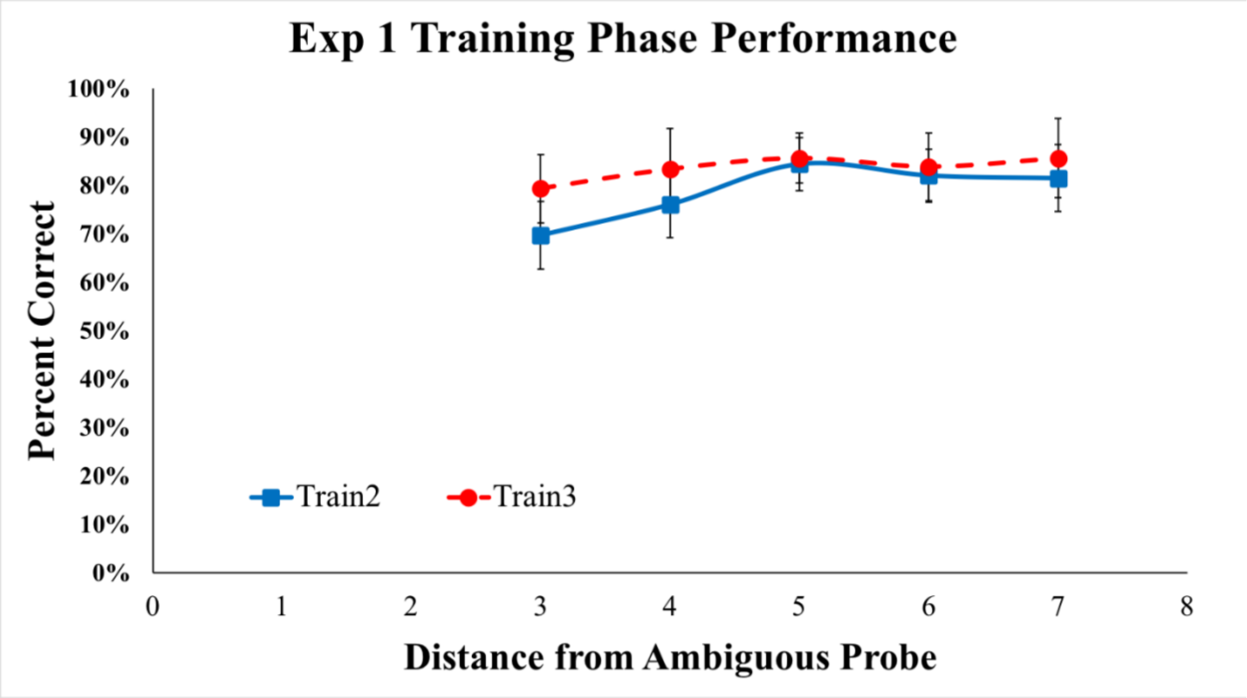


Figure 3.1 Experiment 1 Training Phase Performance.

Performance, measured by percentage correct, for the second and third training phases in Experiment 1. Performance shown was for the training session in which criterion was reached, averaged across all monkeys. Error bars represent 95% confidence intervals.

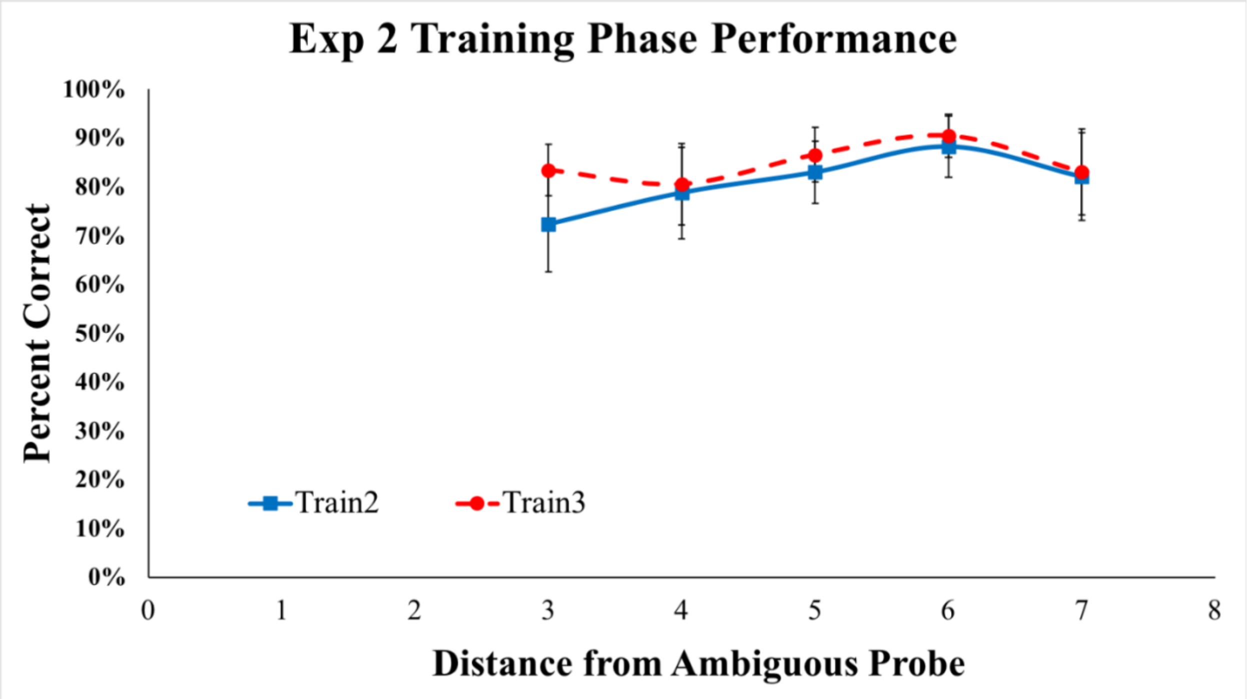


Figure 3.2 Experiment 2 Training Phase Performance

Performance, measured by percentage correct, for the second and third training phases in Experiment 2. Performance shown was for the training session in which criterion was reached, averaged across all monkeys. Error bars represent 95% confidence intervals.

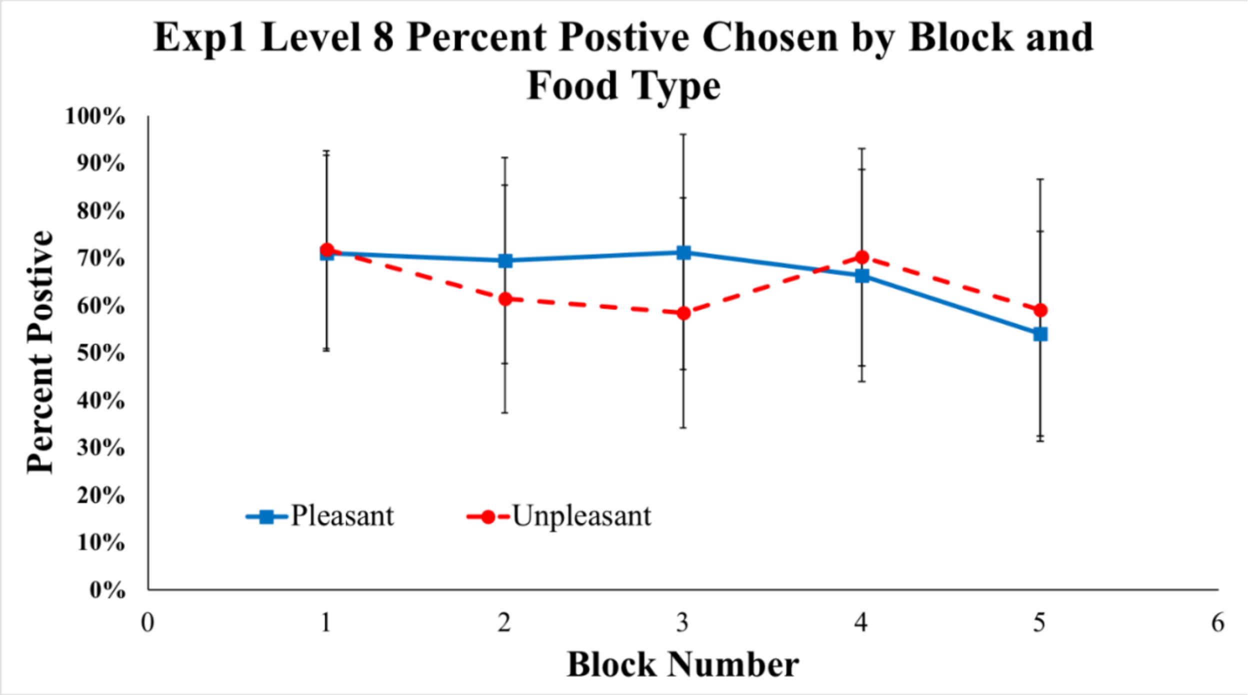


Figure 3.3 Experiment 1 Level 8 Percent Positive Chosen by Block and Food Type

The percentage of positive response class choices made in Experiment 1 compared between block number and food type for only the Level 8 ambiguous probe. Error bars represent 95% confidence intervals.

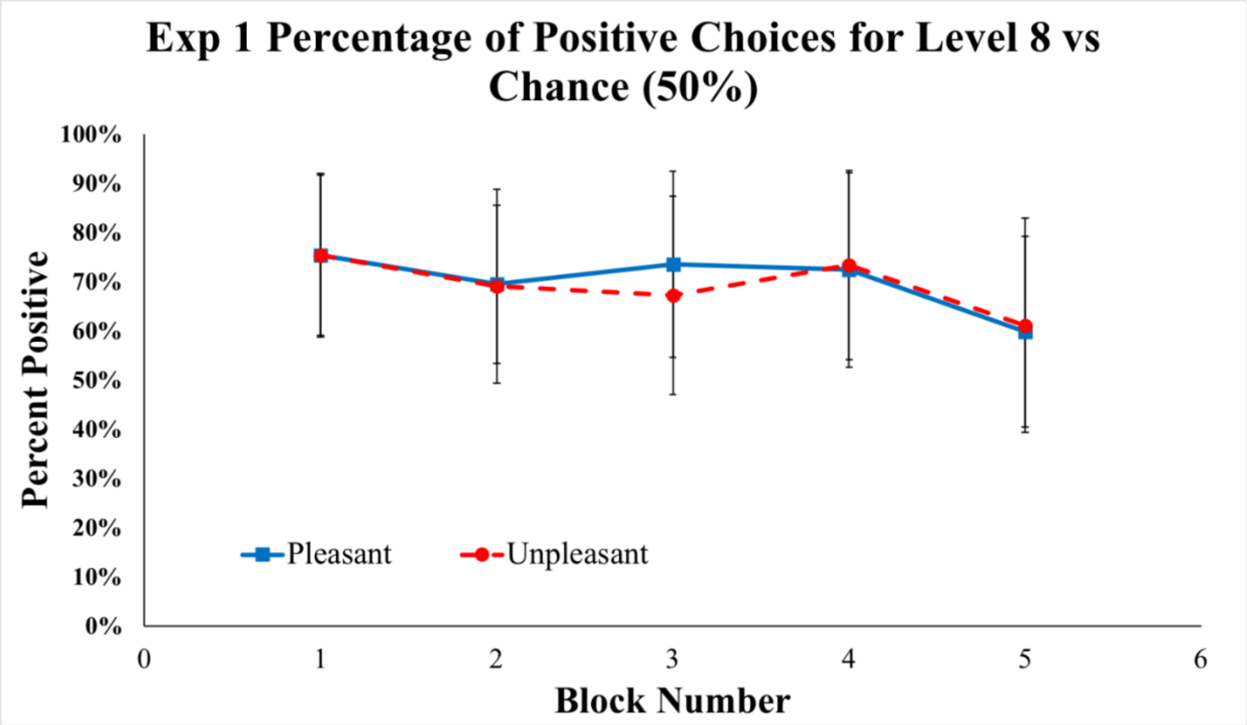


Figure 3.4 Experiment 1 Percentage of Positive Choices for Level 8 vs Chance (50%)

The percentage of positive response class choices made in Experiment 1 compared across block number and food type against chance level (50%) for the Level 8 ambiguous probe. Error bars represent 95% confidence intervals.

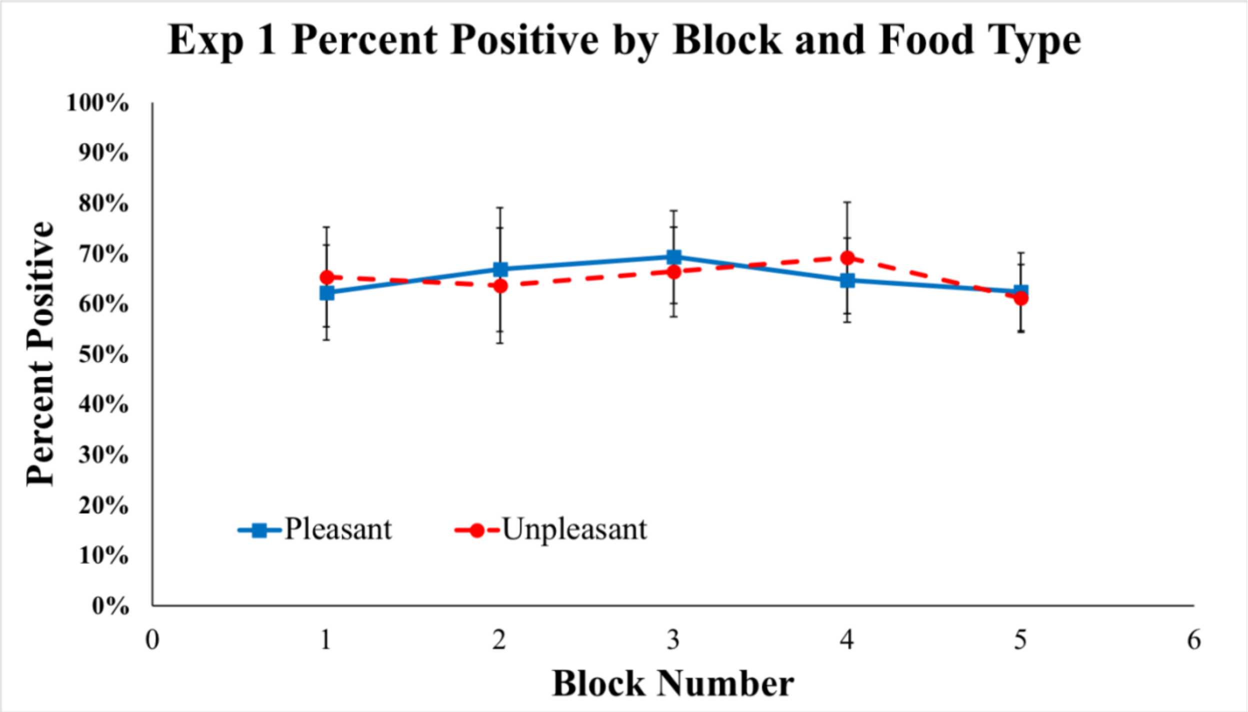


Figure 3.5 Experiment 1 Percent Positive by Block and Food Type

The percentage of positive response class choices made in Experiment 1 compared between block number and food type for stimulus levels 1-7 and 9-15. Error bars represent 95% confidence intervals.

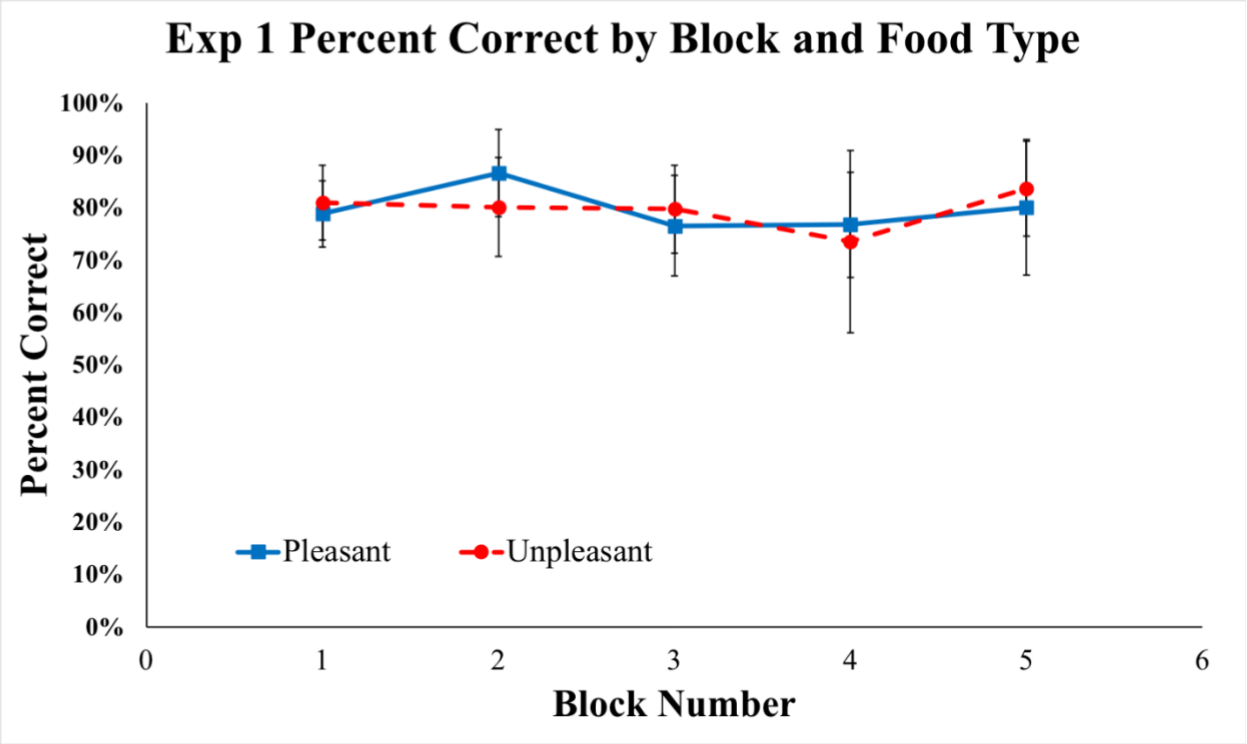


Figure 3.6 Experiment 1 Percent Correct by Block and Food Type

The percentage of correct choices made in Experiment 1 compared between block number and food type for stimulus levels 1-7 and 9-15. Error bars represent 95% confidence intervals.

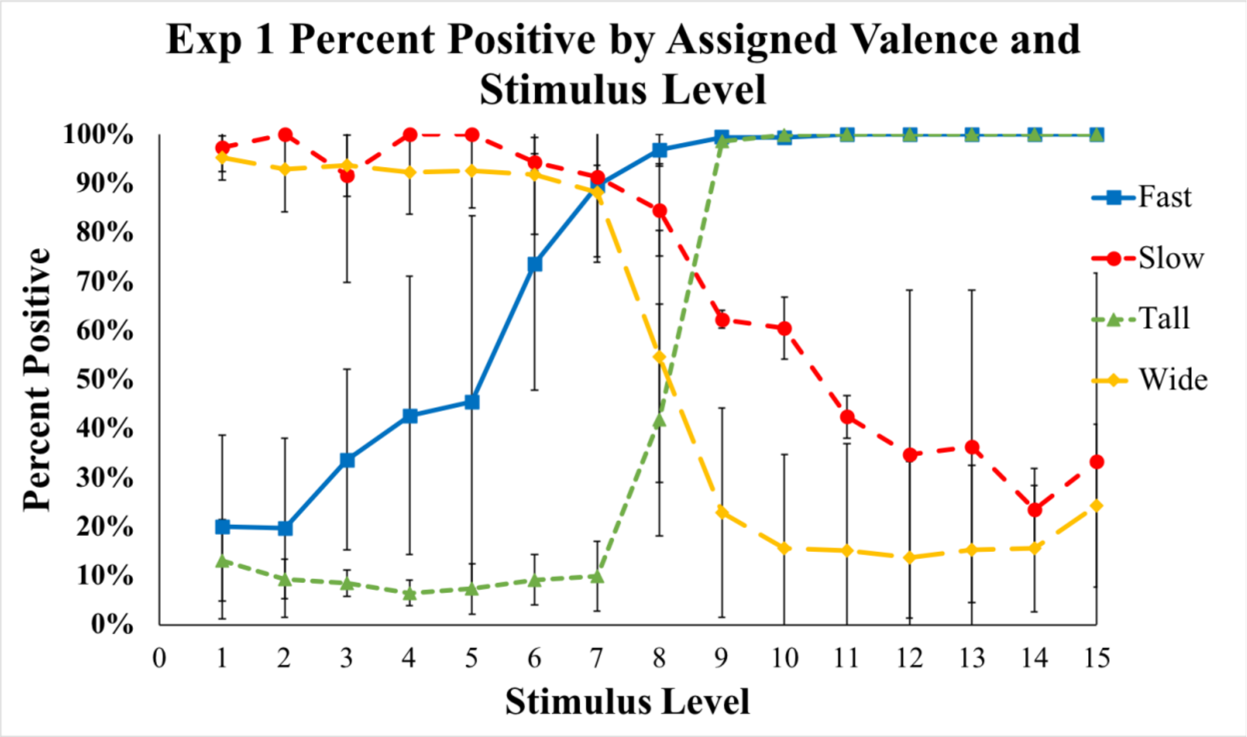


Figure 3.7 Experiment 1 Percent Positive by Assigned Valence and Stimulus Level

The percentage of positive response class choices made in Experiment 1 compared between stimulus level and according to assigned positive valence response class. Stimulus levels 1-7 were objectively slow or wide, depending on the task, while stimulus levels 9-15 were objectively fast or tall, depending on the task. Error bars represent 95% confidence intervals.

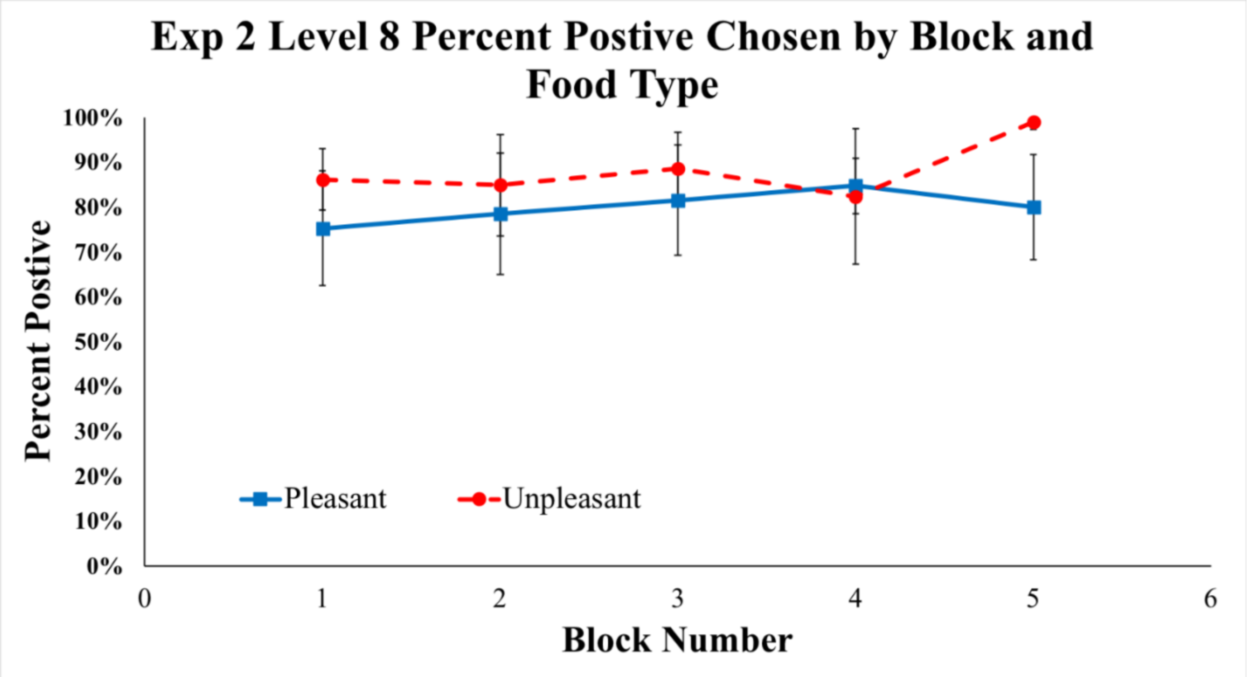


Figure 3.8 Experiment 2 Level 8 Percent Positive Chosen by Block and Food Type

The percentage of positive response class choices made in Experiment 2 compared between block number and food type for only the Level 8 ambiguous probe. Error bars represent 95% confidence intervals.

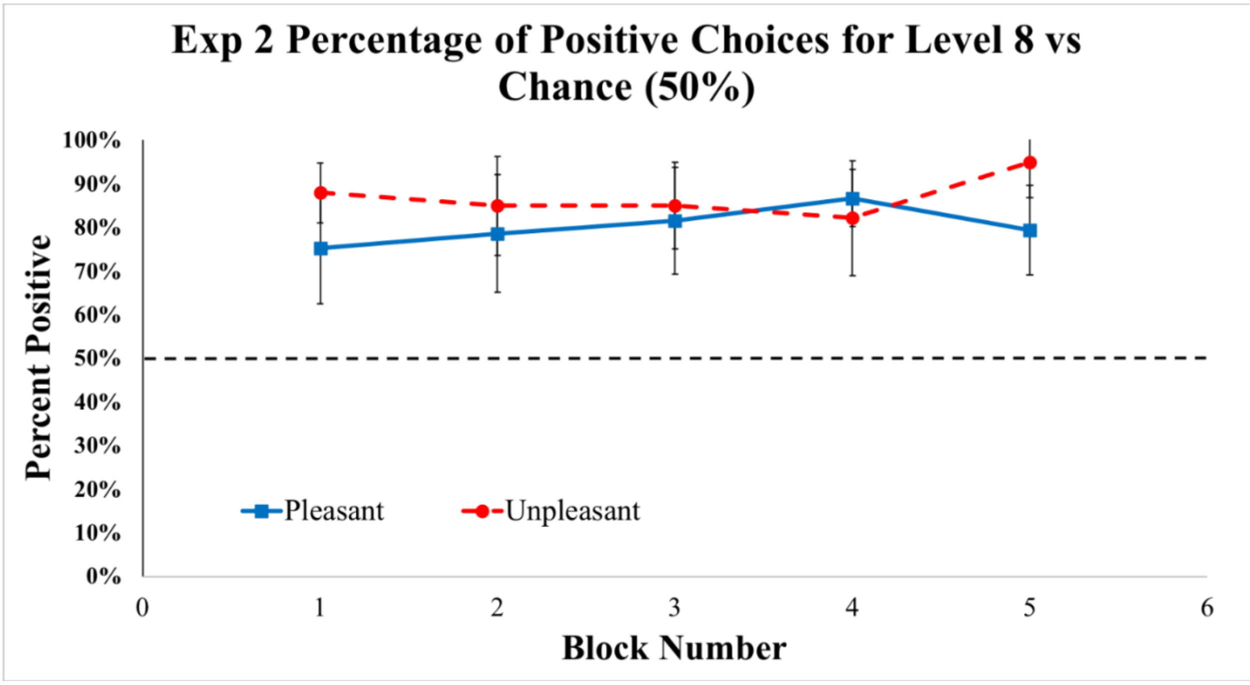


Figure 3.9 Experiment 2 Percentage of Positive Choices for Level 8 vs Chance (50%)

The percentage of positive response class choices made in Experiment 2 compared across block number and food type against chance level (50%) for the Level 8 ambiguous probe. Error bars represent 95% confidence intervals.

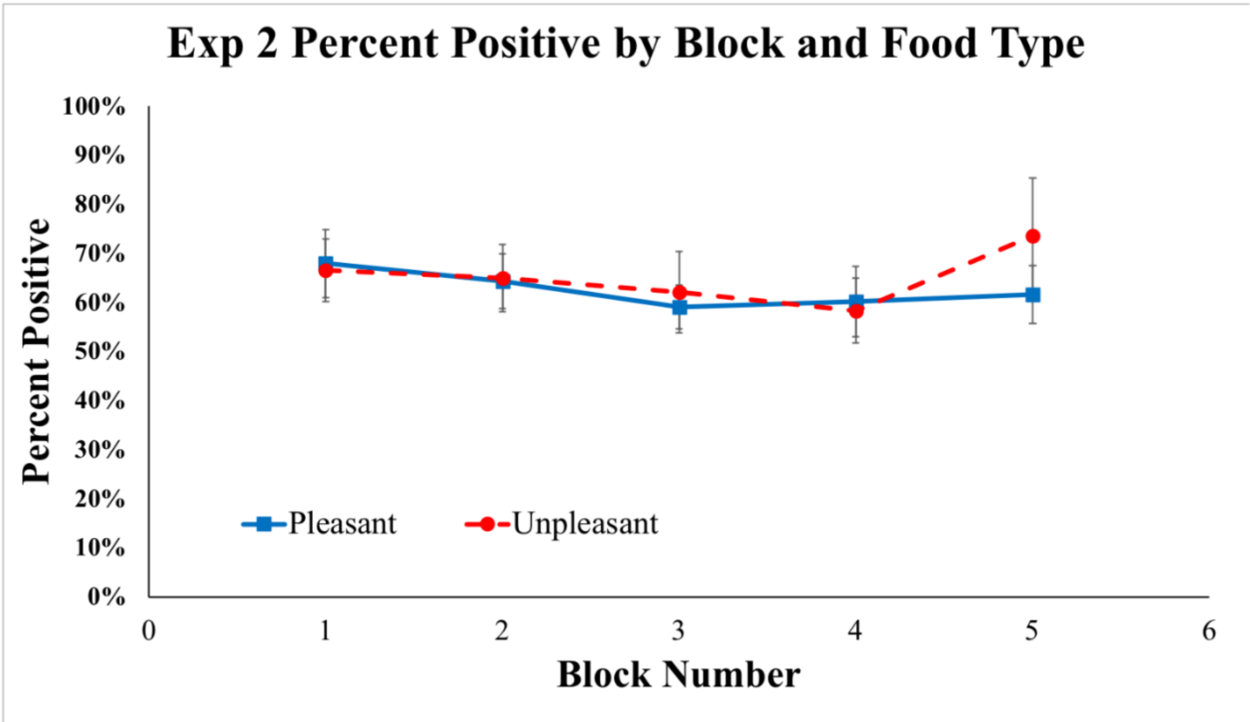


Figure 3.10 Experiment 2 Percent Positive by Block and Food Type

The percentage of positive response class choices made in Experiment 2 compared between block number and food type for stimulus levels 1-7 and 9-15. Error bars represent 95% confidence intervals.

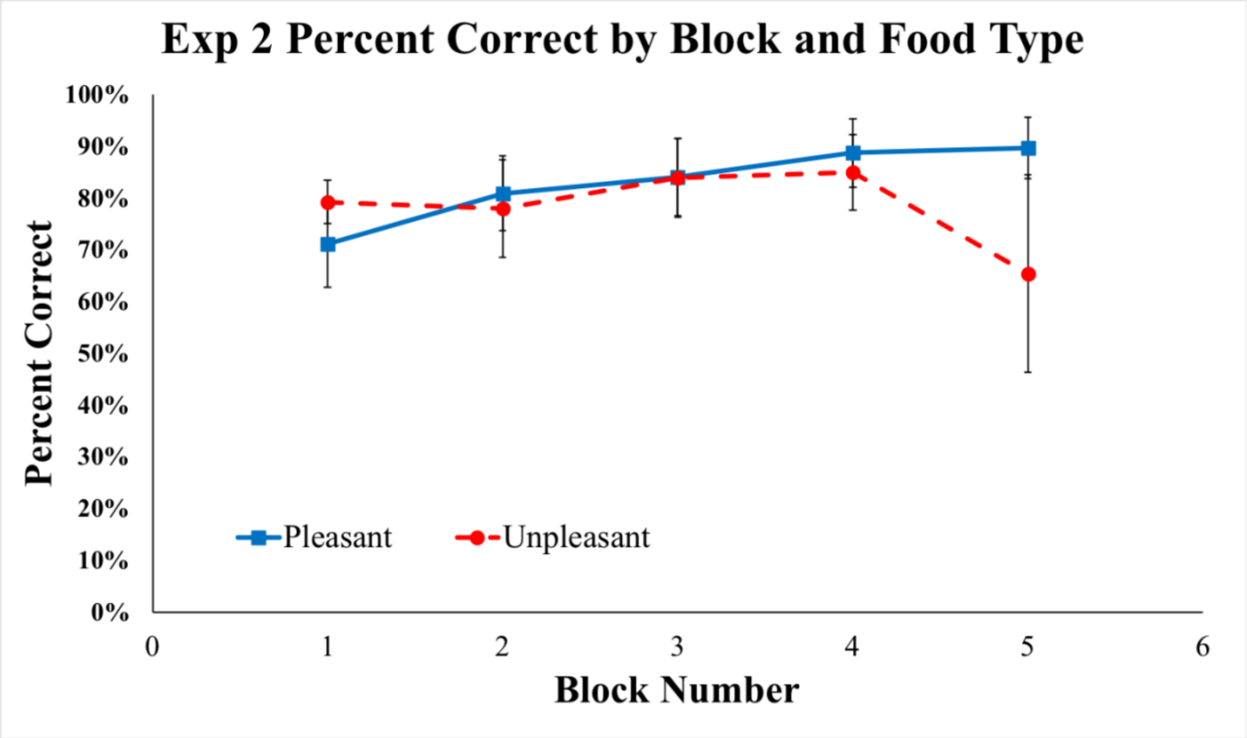


Figure 3.11 Experiment 2 Percent Correct by Block and Food Type

The percentage of correct choices made in Experiment 2 compared between block number and food type for stimulus levels 1-7 and 9-15. Error bars represent 95% confidence intervals.

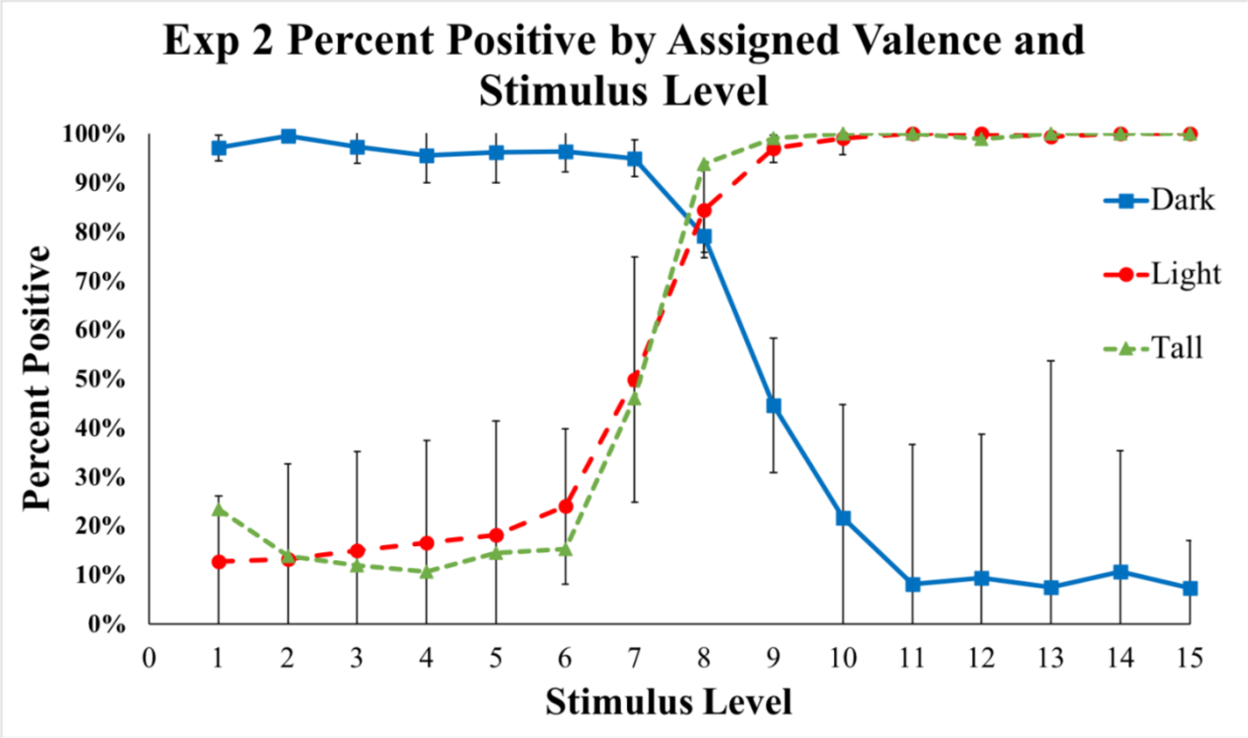


Figure 3.12 Experiment 2 Percent Positive by Assigned Valence and Stimulus Level

The percentage of positive response class choices made in Experiment 2 compared between stimulus level and according to assigned positive valence response class. Stimulus levels 1-7 were objectively dark, while stimulus levels 9-15 were objectively light or tall, depending on the task. Error bars represent 95% confidence intervals.

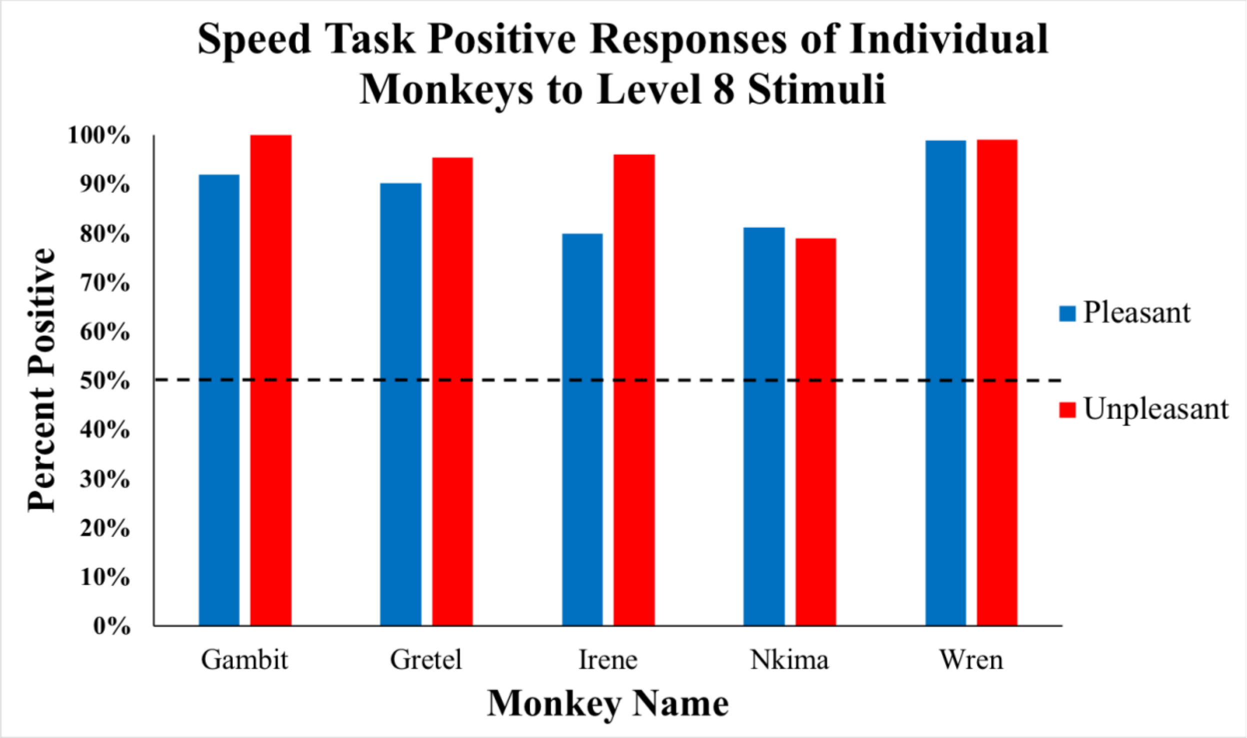


Figure 3.13 Speed Task Positive Responses of Individual Monkeys to Level 8 Stimuli

The percentage of positive response class choices made in the speed discrimination task compared across individual monkeys and food type against chance level (50%) for the Level 8 ambiguous probe.

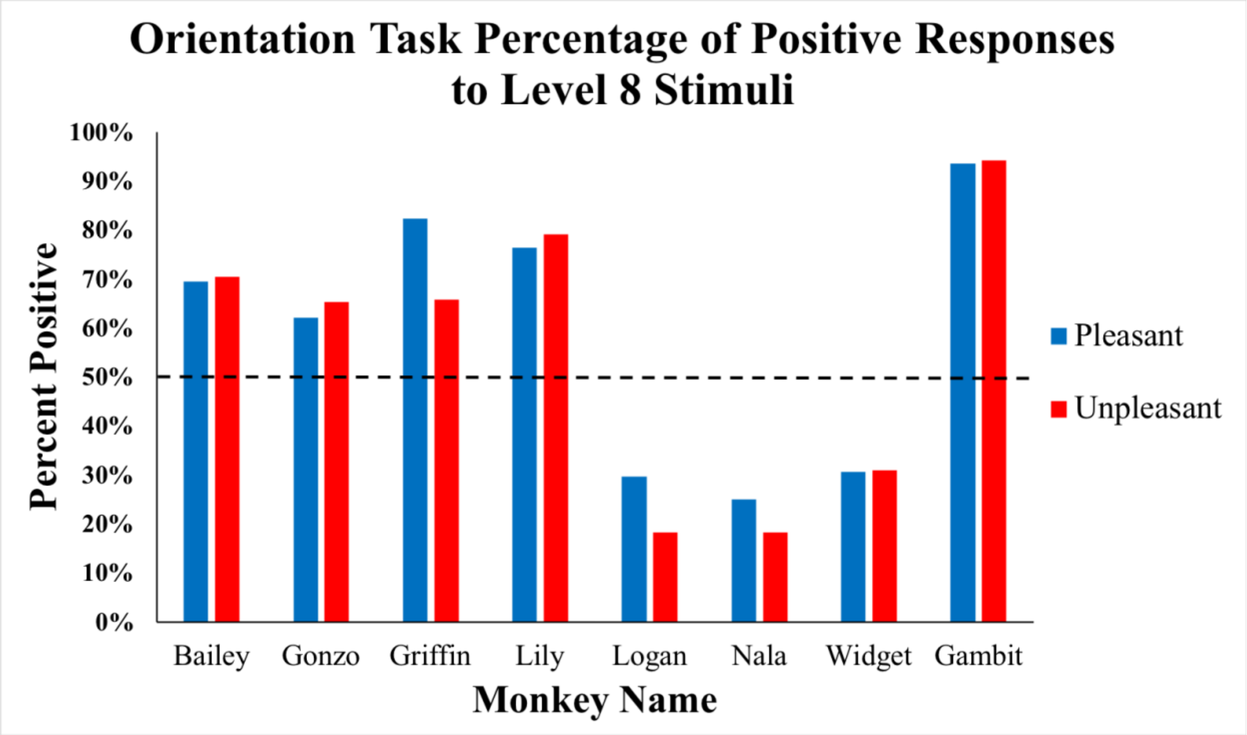


Figure 3.14 Orientation Task Positive Responses of Individual Monkeys to Level 8 Stimuli

The percentage of positive response class choices made in the orientation discrimination task compared across individual monkeys and food type against chance level (50%) for the Level 8 ambiguous probe.

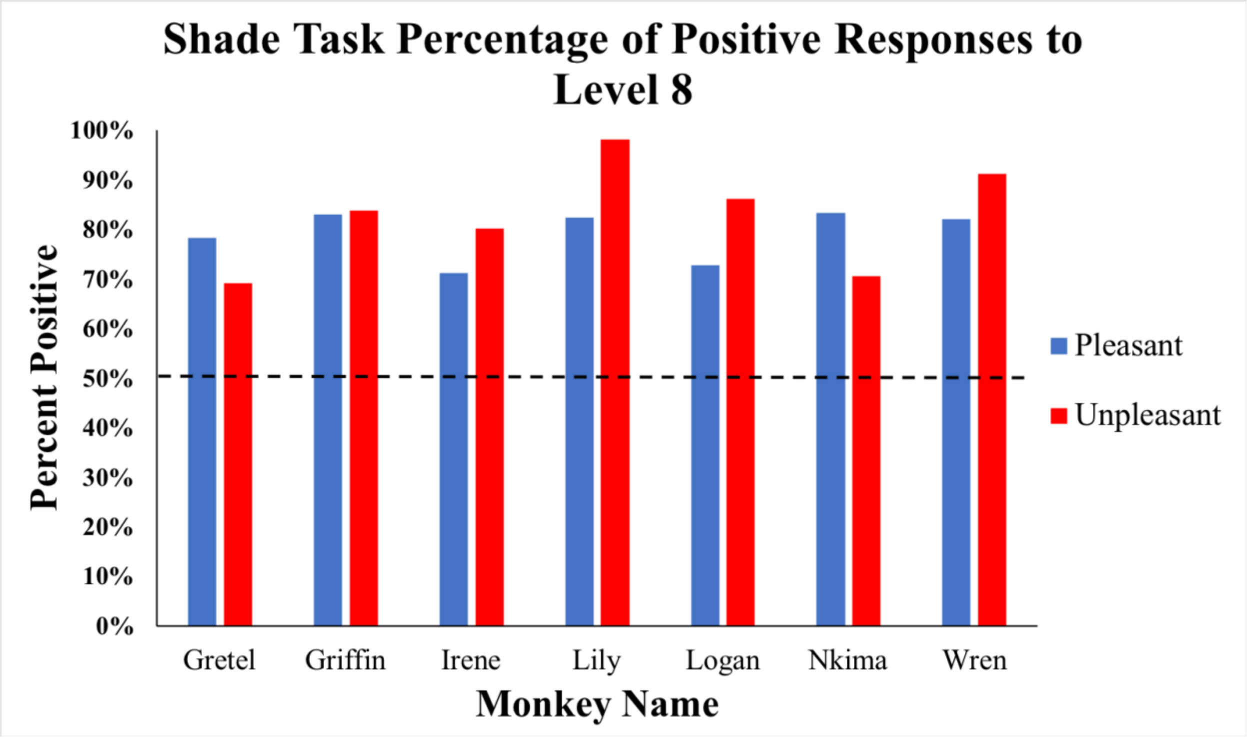


Figure 3.15 Shade Task Percentage of Positive Responses to Level 8

The percentage of positive response class choices made in the shade discrimination task compared across individual monkeys and food type against chance level (50%) for the Level 8 ambiguous probe.

4 DISCUSSION

Prior to any manipulation to affect during the testing phase, monkeys were trained to classify stimuli into one of two response classes. Criterion was reached on all training phases and decreases in performance reflected increasing difficulty as the central stimulus level was approached (i.e., as the task became objectively more difficult). This indicates that the speed, orientation, and shade tasks used were appropriate psychophysical tasks that became more difficult and ambiguous to classify as the center of the stimulus range was approached. Because cognitive bias tasks rely on ambiguous stimuli to elicit a cognitive bias effect, the differences in ambiguity and difficulty were important to maintain. For the current study, both Experiment 1 and 2 employed the use of psychophysical tasks that the monkeys were able to learn but that also included sufficiently ambiguous stimuli for testing purposes.

Not all monkeys were successful with the discrimination of stimulus speed and were moved therefore to a task requiring discrimination of orientation. The difficulty of some monkeys to learn the discrimination of slow or fast moving stimuli is interesting and could be a subject of future study. However, for the purposes of the current study, any psychophysical task the monkeys could successfully complete was sufficient for assessment of cognitive bias effects. There were also notable individual differences in the number of trials needed to reach criterion across monkeys. This is not abnormal for cognitive testing with nonhuman primates as the monkeys differ on how quickly they may learn a task. More notably, average trial counts to reach criterion were much lower for the second task monkeys completed. It is possible monkeys were more familiar with the general aim of the task, even though they were now discriminating shade rather than speed or orientation.

Some monkeys also experienced difficulty in learning the final phase of training in which the nonstandard reward contingencies for cognitive bias assessment were implemented. For many monkeys, a large bias emerged in favor of the response class that gave a reward, such that performance was still above 50% for all stimulus levels but was at ceiling for levels that were of the assigned positive response class. The inclusion of multiple training stimuli allowed for the revelation of this bias toward the positive response class even before the presentation of ambiguous stimuli or affect manipulations. The majority of cognitive bias assessments train only the anchor points of stimuli, such as only the fastest moving (level 15) and slowest moving (level 1) stimuli. Training several points in between allowed for further assessment of how monkeys may respond to intermediate stimuli prior to manipulations to affect and with non-standard reinforcement contingencies in place.

The bias toward the positive response class during training in the current study carried into the testing phase. For previously trained stimuli presented during the test phase, monkeys classified correctly stimuli that were of the positive response class at very high rates, such that their performance and positive responses were at ceiling with these stimuli. Further, monkeys' positive classifications were significantly above chance when presented with the ambiguous probe (level 8). This indicates that monkeys were classifying the ambiguous probe as being from the positively reinforced stimulus class regardless of the food they were given. Although this may be evidence of overall positive affect in the current subjects, the presence of a positive bias during training is suggestive that there may be more at play than affective state in positive cognitive biases. Indeed, when presented with ambiguous stimuli, monkeys may be gravitating toward positive response classes due simply to the fact they receive food only for that response regardless of their inner mood states. The pattern of responding may be a strategy to maximize the rewards gained during a given session and may have had little or nothing to do with general affective state. The addition of multiple training stimuli and probe stimuli assisted in revealing the responses of monkeys to ambiguous stimuli when under the cognitive bias reward contingencies, and potentially suggests that these reward contingencies may bias this species toward positive responding irrespective of emotional state. This could account for the bias toward positive responding such that the potential to receive a reward was more beneficial than the cost of a potential time out.

Overall, monkeys were more likely to classify the level 8 ambiguous probe using their positive response class. However, this was not universal across the tasks used in Experiment 1. When discriminating the speed of the ambiguous probe, monkeys more frequently chose their positive response class. In contrast, monkeys who were discriminating the orientation of the ambiguous probe did not show a preference for either their negative or positive response class. Based on accuracy data, monkeys had higher performance on the orientation task, suggesting it was less difficult than the speed task, but why this might make their perception of the ambiguous probe less positive than a more difficult task is unclear. One possible explanation is that the difficulty of the speed discrimination task allowed for more uncertainty when presented with the ambiguous probe, and this uncertainty resulted in monkeys choosing their positive response class due to the inherent biases toward responses that give rewards. Because they displayed very high performance on the orientation discrimination task, responding at chance levels reflects their enhanced understanding of the task itself, due to the ambiguous probe truly being neither wide or tall. In other words, rather than defaulting to the response class that resulted in rewards, monkeys on the orientation discrimination task instead responded to the ambiguous probe equally as both the negative and positive response class. Further investigation into how monkeys approached these two tasks would be required to provide a full explanation of these differences.

All monkeys assigned to the speed discrimination task showed similar preferences for their positive response class when responding to the ambiguous probe. However, monkeys assigned to the orientation discrimination task differed in their positive classifications of the ambiguous probe. Specifically, three of the seven monkeys were significantly below chance in their level 8 responses, indicating they classified the ambiguous probe more often using their negative response class. The remaining four monkeys showed results that were similar to the monkeys assigned to the speed discrimination task. When considering these three monkeys' performance and previous experience, no patterns emerge as explanation for these individual differences. Further investigation would be required to determine why some of the monkeys seemed to differ in their perceptions of the ambiguous probe and whether these differences resulted from the task itself or from individual differences in the monkeys. With regards to the second task, one of the three monkeys from Experiment 1 showed an increase in his classification of the ambiguous probe using the positive response class. This could result from prolonged exposure and experience with the cognitive bias reward contingencies, but because the remaining two monkeys did not progress to the second experiment, it is difficult to draw conclusions based on the data of one monkey.

Unlike Experiment 1, the second task experienced by the monkeys showed no task differences in classifications of the ambiguous level 8 probe, with monkeys all preferring their positive response class. Again, further investigation into the tasks used in Experiment 1 would shed light on these differences. It is possible that monkeys gravitated toward their positive response class over time and experience with the cognitive bias tasks and reward contingencies, or that the monkeys who participated in Experiment 2 have a stronger preference for the positive response class than those monkeys who only participated in Experiment 1. This possibility is discussed further with regard to individual monkeys' classifications of the ambiguous probe.

The positive bias of monkeys for the ambiguous probe (level 8) was present for most blocks and food type in the first experiment. However, it was present across all blocks and both food types in Experiment 2 (i.e., the second task). The universal preference for the positive response class in the second task may be due to several factors. The second task may have been easier for the monkeys. Shade may be an easier psychophysical discrimination when compared to speed or orientation, and the trial counts are reflective of faster acquisition. An easier task may account for the increase in positive responses either because it improved the mood of the monkeys or because time outs were less of a deterrent when the monkeys were correct on a majority of trials. While further testing would be needed to determine if task difficulty is a factor in affective state, it is more probable that monkeys chose the response that would reward them with food and were unconcerned with the possibility of a time out due to the easier nature of the task.

Another explanation for the positive bias in the second task is that monkeys who progressed to Experiment 2 may be more positive (i.e., "optimistic") than the monkeys who did not progress to the second task. In general, the monkeys who participated in Experiment 1 but not Experiment 2 took longer to complete the training phases for Experiment 1. It may be that the monkeys who had more difficulty are less positive either due to personality differences or to effects of task difficulty on frequency of positive response class choices as described above. In order to address this question fully, one would need to assess the data for Experiment 2 when all monkeys from Experiment 1 have completed testing on their second task.

Another potential explanation for the increase in positive class responses for the ambiguous probe in the second task is that over time and experience, monkeys' responses may skew toward the positive response class regardless of affective state. This relates to the study performed by Perdue (2017) in which monkeys' responses to ambiguous stimuli skewed toward negative responding over time and in the absence of any manipulation to their affective states. While the direction of the bias is in opposition to the current study, the presence of a pre-existing bias during training with cognitive bias reward contingencies prior to any food-related manipulations in the current study and of a negative bias in lieu of any affect manipulation in the Perdue (2017) study suggests that positive or negative biases observed during test phases may not necessarily be indicative of emotional state and may be due to other factors. Indeed, Perdue (2017) demonstrated that reward payouts shifted the bias from one response class to another (i.e., whichever class was the lowest paying class). In the current study, the inclusion of multiple stimulus levels during training may have skewed the monkeys toward positive responding because they were rewarded only when they chose that response class. It is possible that the results observed in both the current study and Perdue (2017) are indicative of a strategy derived from the potential for reward and not from affective state. For example, monkeys in the Perdue (2017) study were not rewarded or punished for responses to any of the ambiguous stimuli, while the monkeys in the current study were trained and reinforced on several levels of ambiguous stimuli. It may be that training resulted in a preference for the positive response class while unreinforced response classes beget negative response preferences. This is an interesting and important question to consider when moving forward with cognitive bias assessments, especially when dealing with nonhuman primates.

A final explanation of the current results lies in the design of time outs and rewards for responses to “negative” and “positive” stimuli. In Perdue (2017), rather than implementing rewards for positively valenced stimuli and a deterrent (e.g. a timeout) for negatively valenced stimuli during training, monkeys were trained to associate one response class with a low quantity of pellets and the other response class with a high quantity of pellets. The current study demonstrated that overall, monkeys were more likely to choose their positive response class when presented with ambiguous stimuli, while the monkeys in the Perdue (2017) study favored their negative response class when discriminating ambiguous stimuli. The use of rewards and time outs in the current study may have contributed to the findings of increased preferences for positive response classes.

Specifically, the monkeys in the current study have extensive experience with time outs as indications of errors throughout any given task. In the current study, when monkeys correctly identified a stimulus that was of their negative response class, they avoided either a 20 s or 60 s timeout. The avoidance of a time out allowed for quicker access to the next trial and therefore to more potential rewards. The less time monkeys spent sitting through a time out, the more able they were to maximize the number of rewards they received, providing motivation to correctly identify those stimuli that were of the assigned negative response class. Further, time outs are typically used to indicate a monkey has made an error in responding to a stimulus, and the avoidance of a time out provides, albeit indirectly, feedback that the monkeys were not in error when responding to the stimulus in question. However, the use of time outs as an association with negative consequences may not have had the intended impact, such that time outs are perceived as a teaching mechanism rather than as a punishment or deterrent. This could have resulted in a reduced perception of the negative response class as a negative experience and merely as a class of responses that were less desirable than those of the positive response class, thereby producing an overall preference for the positive response class.

The evident bias of monkeys toward the reward-giving response may be a product of the design or an inherent preference, and which of these underlies the current results would benefit from further study. Indeed, Perdue (2017) implemented differing quantities of pellets for the positive and negative response classes, which may work toward combatting either a design-induced or inherent bias toward reward-giving responses by providing rewards regardless of response class and using differing quantities to create associations with response classes such as “positive” and “less positive” or “more positive” depending on the amount of pellets rewarded. The current study may have benefitted from this method of reward quantities rather than rewards and time outs in order to balance the response classes more fully.

While no effect of food type was found to impact the judgment of ambiguous stimuli as either belonging to the positive or negative response class, it was found that in the second task only the pleasant food influenced an increase in performance across sessions whereas the unpleasant food did not. This finding was unexpected, especially considering that this effect is only true when comparing block two to block four and block two to block five. While it is possible that receiving a pleasant food before testing may have improved motivation and thereby performance, further investigation is required before making such statements. Further, that this increase in performance over time and for only pleasant sessions occurred in the second task but not in the first task indicates that there may be fundamental differences in the tasks used or that prolonged exposure to cognitive bias assessments may influence the potential for pleasant foods to improve motivation. Due to the large effect size associated with this finding, it is likely worth investigating the potential impact of pleasant foods and emotional state on task performance over time.

The manipulation to affect using pleasant and unpleasant foods had no impact on the judgment of ambiguous stimuli as either positive or negative in both tasks presented to the monkeys. There are several explanations for these null results and some originate in the training phase while others regard the test phase. During the training phase, monkeys completed as many trials as necessary to reach criterion, and as a result, performance on testing sessions was high overall, especially with regards to positive response classes. In previous studies on the cognitive bias effect, subjects were given little training in comparison, only enough to ensure an association of one response with positive events and one with negative events and a basic understanding of the task. The monkeys in the current study are well-versed in and highly experienced with psychophysical discriminations and also received extensive training on the particular tasks used in the study. Due to this, the monkeys may have been *too* well-trained on the psychophysical tasks in that their understanding of stimulus discriminations eclipsed any impact pleasant or unpleasant foods may have had on their judgment of ambiguous stimuli. Whether this may be due to the current monkeys' previous experience with similar tasks or to the experience gained during training of the current tasks is uncertain, and further study could illuminate how experience with the judgment task itself may influence cognitive bias assessments. Nevertheless, over-training could explain why the current results failed to support an effect of emotional state on the judgment of psychophysical stimuli, though there are many more reasons that may explain the null results either apart from or in tandem with the issue of over-training.

Another possible reason no effect of food type was discovered also related to the training phases in the current study. As discussed above, monkeys developed a strong bias toward their positive response class during the final phase of training, when the reward contingencies were shifted to reflect cognitive bias assessments. A pre-existing bias toward the positive response class could have impacted the results by masking any negative effects of the affect manipulation. That is, the tendency to favor the positive response class brought about by the preference for the response class that provided rewards was stronger than any potential negative affects brought on by the unpleasant food. However, this explanation assumes that pleasant and unpleasant foods have an impact on affective states in nonhuman primates and also that the unpleasant food used in the current study was truly a negative experience for the monkeys. Regarding the issue of affect manipulation effectiveness, two limitations of the current study regarding experiences during the testing phase are possibly responsible for the null results.

First, it may be that pleasant and unpleasant foods were not sufficient to bring about short-term changes in affective state in the subjects, at least not enough to impact judgments of psychophysical stimuli. The monkeys in the current study are well-cared for and receive fresh fruits and vegetables daily as well as a variety of high preference foods from other researchers and care staff. A brief experience with a pleasant food is not out of the ordinary for these animals nor is it a special occurrence. Therefore, any increase in mood brought about by pleasant foods may not be salient enough to alter perception judgments on a cognitive task, especially considering the monkeys’ expert-level experience with a variety of cognitive tasks over years of research. Further, any negative emotion evinced by the unpleasant food would likely have had little effect on their ability to judge ambiguous stimuli when taking into account their overall state of well-being and task proficiency. Due to this, the monkeys in the current study offered some unique challenges to assessing emotional state that were difficult to overcome. Future studies would need to take these into account when designing cognitive bias assessments to mitigate the monkeys' experience level with cognitive tasks.

Second, the unpleasant food used in the current study was a gelatin-food mixed with turmeric. While pilot studies indicated monkeys did not eat the unpleasant food, and monkeys did not eat it during the formal tests, it was repeatedly observed during test phases that monkeys would manipulate the unpleasant food for several minutes before discarding it. Manipulation of the unpleasant food included behaviors such as pulling it apart into pieces, rolling it in their hands or around their test boxes, pushing it into various areas around the test box, and running drinking water over it. As such, it is possible that manipulating the unpleasant-tasting gelatin food was indeed an enrichment-like experience for them, meaning a pleasant experience. If this was the case, the current study employed the use of two pleasant affect manipulations, one a primary reinforcer and one a secondary reinforcer, rather than a pleasant and an unpleasant manipulation. In this light, the failure to find a difference in the frequency of positive responses depending on food type as well as the overall positive classifications of the ambiguous probe may insinuate that a primary reinforcer, such as a pleasant food, may improve affective state as much as a secondary reinforcer, such as enrichment, improves affective state. An interesting question regarding the importance of access to pleasant foods as well as enrichment for animals in captivity arises and may be answered in future studies. The current study could address this question by providing monkeys with enrichment similar to that provided by the unpleasant food and comparing this against sessions with no enrichment at all in order to determine whether the presence or absence of enrichment may impact affective state sufficiently.

Apart from the explanations concerning the training and testing phases in the current study, a more general explanation of the failure to find cognitive bias effects lies in the nature of the species participating in the study. Nonhuman primates are highly intelligent creatures, which is a potential explanation of the scarcity and difficulty experienced when assessing cognitive bias effects with these animals. Specifically, nonhuman primates, especially the cognitive task experts in the current study, may be too intelligent or well-trained for small changes to their environment to alter the practiced and experienced subjects' responses to psychophysical tasks. Cognitive bias assessments have been successful with a large number of species, but the current study presents some issues that may be addressed with other species not subject to the challenges of nonhuman primates. For example, the inclusion of multiple intermediate stimuli with other species may provide insight into how the cognitive bias reward contingencies impact judgment of ambiguous stimuli apart from affect manipulations (see also Perdue, 2017). In addition, further investigation of how repeated exposure to cognitive bias assessments may impact results should be pursued. Other species may respond differently to repeated exposure and multiple training stimuli and this may lead to further explanations of why cognitive bias assessments with nonhuman primates are uniquely challenging.

Despite the failure to find a cognitive bias effect in the current study, there is much evidence that emotion and cognition in monkeys are linked as they are in humans, but the cognitive abilities of nonhuman primates may be too advanced for simple perceptual discriminations to be influenced by short-term manipulations to affective state. In other words, the cognitive bias assessment may not be suited for detecting influences of emotional state on responses to cognitive tasks in monkeys. Indeed, it can be difficult to determine just how emotion and cognition are linked in nonhuman primates based on the challenges of studying emotional state objectively in nonhuman primates. Tasks that assess attention in nonhuman primates have determined that threatening stimuli does impact attention under stressful circumstances. However, it may be that the cognitive bias technique does not tap into the need for emotion to be involved when discriminating between simple stimuli. There may be no evolutionary imperative for emotional state to be a part of judgments in cognitive tasks in nonhuman primates whereas attention may be more sensitive to emotionally salient situations and stimuli. Future studies could attempt to assess whether emotional influences on cognition is more situation specific in nonhuman primates than in other species or even in humans.

In sum, nonhuman primates are an understudied group of species in the cognitive bias literature, but they offer a unique and challenging perspective that should continue to be investigated. It may be discovered that cognitive bias assessment methodology must be altered significantly in order to accurately assess nonhuman primate emotional states, and this could only improve methods of welfare assessment in the future.

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