The Effects of Perceived Controllability on Decision Making and Affective Processing

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A Dissertation submitted to the

Graduate School-Newark

Rutgers, The State University of New Jersey

For the degree of

Doctor of Philosophy

Graduate Program in Psychology

written under the direction of

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Newark, New Jersey

May 2017

ABSTRACT OF THE DISSERTATION

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By CATHERINE CHO

We often face challenging events that require regulating our emotions to guide appropriate decision making. For instance, the negative feeling associated with being stuck in traffic that will make you late for work can cause undue stress and have maladaptive consequences on our behavior and health. One way to cope with negative emotions is to exert control over the situation, for instance, by taking another route and avoiding the traffic. Both scenarios may get you to your destination at the same time, but an individual may be more satisfied by finding an alternative path as it involved perceiving control over one's environment. Here, perceiving control and exerting choice may serve as a way to regulate one's emotions. The vast literature on perception of control suggests that it can be a powerful motivator by allowing one to assert their preference. Indeed, people feel more satisfied, competent, and engaged when they have an opportunity to exercise choice. The act of choosing itself, or exercising choice has also been found to be inherently rewarding, motivating the idea that perceiving control may be a means for regulation emotions during exposure to aversive stimuli. Although research has examined the influence of perceived controllability on specific domains such as pain,

medical conditions, and fear conditioning, its effect on general negative emotions is yet to be explored.

This dissertation research examines the influence of perceiving control on decision making and affective processing. The first four studies explore how exercising choice modulates emotional responses elicited by negative outcomes such as pictures that depict negative scenarios from the International Affective Picture System (IAPS). Experiments 1—4 explored how exercising choice modulates emotional responses elicited by negative outcomes. Across the experiments, participants showed a preference for choice, but emotional influences based on perceived controllability were only observed during specific categories of pictures (e.g., grief). In Experiment 5, we investigated how reward sensitivity contributes to neural responses associated with free and forced choices and found that individuals with high reward sensitivity recruit regions involved in attentional control and response selection given the opportunity for choice. Finally, Experiment 6 examined the dynamic interplay between brain regions involved in affective processes underlying choice anticipation. Here, we found distinct neural patterns involving cortical-striatal pathways during the anticipation of choice. Taken together, the studies have the potential to inform how individuals can employ a stance that involves perceiving control in negative contexts to effectively regulate one's emotions and for adaptive decision making.

Acknowledgements

I would like to thank many important people who have made this journey possible. First of all, I am grateful for my advisor, Mauricio Delgado for his boundless support and generous guidance throughout my graduate career. From Mauricio, I have learned the power of endurance and endless faith in me. Without support from him, this journey would have been impossible.

I am grateful for my committee members, Elizabeth Bonawitz, Catherine Hartley, and Elizabeth Tricomi, who have provided insightful feedback and suggestions that enormously helped improve my work. I am thankful to postdocs that have been in the lab, David Smith, Jamil Bhanji, Lauren Leotti, and Noriya Watanabe, for their intellectual input and assistance that triggered my motivation to improve and develop my work. I would like to thank all members and friends in the Delgado lab, Jeff Dennison, Dominic Fareri, Stephanie Kim, Andrea Lewis, Heena Manglani, Anastasia Rigney, Meg Speer, and Sally Wang, who have been truly wonderful, humorous, and supportive, throughout my five years in the lab. I am grateful to them for sharing wonderful memories and times we spent together during times of joy and intellectual struggles. I thank members of the Tricomi Lab, Christina Bejjani, Ahmet Cecili, Brynn DiMenichi, Dina Mattern, and Holly Sullivan-Toole, for their boundless friendship and support as fellow cognitive neuroscientists. I am grateful to the people I started and completed this work with, Jessica Benson, Meagan Docherty, Alexandra Margevich, and Shahram Peyvandi, who have shared their enduring journey towards earning our PhD degree in Psychology. I thank faculty members in the Psychology Department, especially Harold Siegel, who made sure I was happy while living away from family in Korea. I feel enormously lucky to have had

Harold as my second advisor, who has been caring and supportive during my graduate life at Rutgers University. I thank my previous advisors and mentors at Korea University, Mimi Bong, Sung-il Kim, and Hackjin Kim, for their support during my masters that motivated me to further pursue doctoral work in cognitive neuroscience. I would like to thank my friends, Sunha Ro, Jennifer Huh, Shelly Lim, Juhye Lim, Moonsub Yun, Hyeonyeong Lee, Gumyee Lim, and Hyunji Byun for their kind suggestions and encouragement during my study.

Finally, I would like to thank my beloved parents and my one-and-only brother. I am forever grateful to my mother and father for bringing me out to the world and allowing me the freedom to explore the world in all dimensions and to satiate my curiosities in search of my passion and to better understand the world.

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Chapter 1: Introduction

We make choices everyday and act on our decisions to meet our desired goals. Making choice allows us to act as causal agents, which helps develop beliefs in our ability to exercise control over our environment. These beliefs in control are known to be adaptive and can have profound consequences on our affect and behavior. For instance, unpleasant experiences can feel worse if they result from circumstances that we believe are outside of our control. On the contrary, same experiences can seem less aversive when we have a means of modifying the experience. For example, a job applicant may be less troubled by an interview if given a choice about where and when to undergo the interview. Research supports the adaptiveness of control beliefs in various domains of psychosocial functioning, such as well-being and motivation (Bandura, 1997; Ryan & Deci, 2000). To date, a number of findings suggest that choice is an important tool for shaping behavioral and affective responses to both positive and negative events. Such studies indicate perceiving control via choice can increase rewarding feelings (Leotti & Delgado, 2011, 2014; Sharot et al., 2009, 2010) and buffer against stressful events (Hartley et al., 2014; Salomons et al., 2004; Sharot et al., 2010). These findings suggest that control beliefs may influence behavioral and affective processes important for emotion regulation.

Emotions signal important information that direct our attention and help shape our behavior. For instance, emotional responses may serve an important role by guiding approach and avoidance behaviors (Panksepp, 1998). Although some levels of arousal can help direct attentional resources to goal-directed behavior, extreme arousal can damage performance and memory. Negative emotions in particular, can hinder

performance and memory (Dolcos, Kragel, Wang, & McCarthy, 2006; MacNamara, Ferri, & Hajcak, 2011) and impair goal-directed attentional systems (Eysenck, Derakshan, Santos, & Calvo, 2007), suggesting a need to regulate negative emotions to promote adaptive behavior. Although recent work has begun exploring the effects of perceived control in response to negative events such as pain, its role in regulating general negative emotions has not been directly studied. Given the significance of the effects of controllability over pain, one potential hypothesis is that perceiving controllability over a stressor can diminish negative emotional responses, which can promote adaptive behavior. The current research explored whether enhancing levels of perceived control via exercising choice can dampen emotions towards aversive stimuli.

Further, investigating how choice influences decisions during positively arousing contexts, such as receiving a reward, could help understand the general mechanism through which choice impacts affective processing. The opportunity for choice can be rewarding (Leotti et al., 2015), hence we could expect individuals to expend greater effort and attention for decisions involving free choice as opposed to externally forced choices. Despite research demonstrating reward-related brain regions responsible for opportunity for choice, the precise neural mechanisms underlying the affective experiences of control remain unclear. Beliefs in control have important implications for various psychiatric disorders including anxiety, depression, and reward sensitivity. Hence, it is important to understand the psychological and neural mechanisms underlying the influence of control beliefs on decision making and affective processing.

Effects of Perceived Control on Affective Processing

Perceived controllability research indicate a robust relationship between control beliefs and emotional outcomes, implicating the significance of control beliefs on affective processing. For example, studies have shown beliefs of control to influence tolerance for pain, motivation, and the ability to cope with chronic pain (Mineka & Henderson, 1985; Maier & Watkins, 1998; Jensen & Karoly, 1991; Jensen et al., 2001), revealing detrimental consequences of uncontrollability over painful or stressful conditions (Maier & Watkins, 1998; Salomons et al., 2004; Amat et al., 2005). Typical experiments investigating effects of controllability have contrasted groups that do or do not have behavioral control over a stressor such as shock. In these studies, groups that did not have control over a stressor exhibited heightened fear responses, greater negative affect, and increased stress levels (Amat et al., 2005; Maier & Watkins, 2005; Mohr et al., 2012). Collectively, these studies suggest that a lack of control may produce deleterious effects on mood and anxiety, and even lead to the development of psychiatric disorders (Weiss & Simson, 1986).

Perceiving a lack of control is at the core of various psychiatric disorders (Beck, 1976; Ryan, Deci, & Grolnick, 1995; Shapiro, et al., 1996; Taylor & Brown, 1988, 1994) such as alcohol and drug addictions (Bandura, 1999; Shapiro Jr & Zifferblatt, 1976), eating disorders (Fairburn, Shafran, & Cooper, 1999; Shapiro Jr, Blinder, Hagman, & Pituck, 1993), anxiety (Abramson, Garber, & Seligman, 1980; Bandura, 1988), and depression (Schwartz, et al., 2002; Seligman, 1975). In some emotional disorders, a lack of control over negative events such as emotional and bodily reactions are at the root of these illnesses. For instance, a lack of control is considered vital for the experience of

both anxiety and depression (Barlow, 1988, 1991). Bursts of unexpected acute emotions may trigger anxiety or affective disorders particularly in vulnerable individuals because these individuals view their own emotions or physical responses as being out of control. Patients who suffer from panic disorders experience an unanticipated and intense bursts of discrete emotions (i.e., fear) (Rapee, Craske, Brown, & Barlow, 1996). This leads to a development of anxiety due to a potential reoccurrence of this phenomenon in an uncontrollable manner. Such findings highlight the significance of the ability to perceive control on the development of psychiatric disorders and its role in the regulation of negative emotions.

In contrast to negative consequences resulting from uncontrollability over events, control over stressors has been shown to block against the adverse effects of stress (Amat et al., 2006; Christianson et al., 2008). In a review evaluating effects of control over stressful events, Lefcourt (1973) concluded that a sense of control provides an individual the illusion that one is able to exercise choice, and has a definite and positive role in sustaining life. When patients were able to use patient-controlled analgesia, they reported lower pain levels, use less pain-alleviating medication, and have greater functional capacity (Ballantyne et al., 1993). Other positive outcomes of perceiving control are associated with maintaining psychological and physical well-being, ability to cope with chronic pain, and buffering against negative consequences occurring as much as a week later (Maier & Watkins, 1998; Jenson & Karoly, 1991; Jensen et al., 2001). Additionally, when individuals believed that they had selected the task such that they perceived control over their behavior, people tend to perceive their environment as less intimidating, estimating the distance to be traveled as shorter, and a hill to be climbed as less steep

(Balcetis & Dunning, 2007). Moreover, having individuals choose between positive events such as vacation destinations modulated expected hedonic outcomes of these events (Sharot et al., 2009). Sharot and colleagues (2010) further tested whether choosing an aversive event lowers its expected aversive outcome. Results indicated that participants rated medical conditions as less aversive after choosing to go through them compared to their initial responses before choosing to go through the disease. Therefore, people's expectations of negative events were rated as less aversive if they had made a choice to encounter them in the future. Altogether, these findings suggest having choice reduces the aversiveness of an event, highlighting an important function of choice on modulating affective processing. In Aim 1, we investigated whether exercising choice may serve as an emotion regulation strategy while viewing negative stimuli. We predicted responses to negative stimuli would decrease as a function of exercising choice.

Impact of Behavioral Controllability (Instrumental Control) on Affective Processes

When examining the impact of perceived control on affective and decision-making processes, it is important to consider the different types of control. The current section describes the role of behavioral control, which was first studied in animals. Controllability research was initially motivated in the 1960's when a series of experiments found rats exposed to behaviorally uncontrollable shocks produced adverse behavioral and emotional consequences. These studies found that rats exposed to sequences of uncontrollable (inescapable) shocks later failed to learn to escape in a new environment (Seligman & Maier, 1967; Weiss, 1968). In these laboratory experiments, each rat was placed in a shuttle box in which its tail was connected by electrodes to exert

shock. Rats in the controllable group received a series of tail shocks but were able to turn the wheel to terminate shock, whereas rats in the uncontrollable condition were exposed to identical shocks and responses but had no behavioral control over the termination of the shock. Rats in the uncontrollable condition later failed to learn to escape from shock and were more likely to develop negative health consequences such as ulcers and exaggerated fear conditioning (i.e., struggling behaviors) to subsequent novel stressors (Amat, Paul, Zarza, Watkins, & Maier, 2006; Grissom, Kerr, & Bhatnagar, 2008). However, rats exposed to identical shocks but were in the controllable (escapable) condition produced neither consequence. To date, similar effects have been reported across studies in both humans and animals, indicating that a lack of control under stressful or painful events is associated with negative consequences (Amat et al., 2005; Maier & Watkin, 1998; Salomons et al., 2004; Salomons, Johnstone, Backonja, Shackman, & Davidson, 2007) and perceived control is critical for regulating emotional responses (Jensen & Karoly, 1985; Jensen et al., 2001).

The influence of behavioral control on affective processing has been also well-established in humans. Behavioral control refers to the ability to modify an event outcome through behavioral response (Maier & Seligman, 1976). For instance, individuals are able to avoid negative stimuli via performance on a task, terminate an aversive stimulus, or limit the intensity of a negative stimulus or shock (Averill & Rosenn, 1972; Hokanson et al., 1971; Geer & Maisel, 1972). The reinforcement learning theory (Skinner, 1953; Thorndike, 1933) on instrumental learning posits that when a specific behavior results in a desirable outcome, that behavior is reinforced and is more likely to be repeated in the future. Thus, when an action is successful at producing

desired results, the individual is also successful at choosing the appropriate action. Behavioral control has been shown to diminish arousal during anticipation of noxious noise (Glass, Singer, & Friedman, 1969) or photographs (Geer & Maisel, 1972), and to increase tolerance to electric shock (Staub, Tursky, & Schwartz, 1971), and pain (Kanfer & Seider, 1973). When patients are able to self-administer analgesic medication, they report consuming less analgesic medicine, report less pain, and experience greater satisfaction in treatment (Ballantyne, et al., 1993; Shiloh, et al., 2003). Therefore, exercising control over a stressor through direct manipulations on termination, intensity, or avoidance of the negative event dampens emotional responses to a subsequent stressor.

Effect of Subjective Perceived Control (Decisional Control) on Affective Processes

Individuals may perceive control by having direct influences on outcome, but perceptions of control can be enhanced even when there is no immediate contingency between one's behavior and outcome. To examine the phenomena of subjective controllability, motivational theories have investigated the processes underlying perceived controllability by examining psychological variables such as locus of control (Rotter, 1966), self-determination theory (Ryan & Deci, 2000), illusion of control (Langer, 1975), and self-efficacy (Bandura, 1997). For instance, self-efficacy refers to a belief in one's ability to execute control over the environment to achieve one's goals (Bandura, 1997). According to Bandura's social cognitive theory, convictions about one's capacity to exert control over the environment can impact one's thoughts, emotions and behaviors which in turn can affect their beliefs (Bandura, 1977). Thus, exercising

control over a stimulus may change the way an individual feels, which can alter responses to a stimulus in subsequent trials.

Even if one's behavior does not directly impact the outcome, exerting choice that emanates from the self can increase subjective experiences of control. Decisional control is the capacity to select a single course of action from potential alternatives (Averill, 1973). Thus, the opportunity for choice facilitates motivation to engage in behavior by allowing an individual to act as a causal agent to accomplish a desired goal. A way in which choice facilitates behavior is expectancy for desirable results, that may be related to previous experiences of success. According to the self-determination theory, autonomy is one of the three fundamental needs that underlie people's motivation to engage in behavior (Ryan & Deci, 2000). Feelings of satisfaction and competence are enhanced when people feel that their actions are freely determined by the self as opposed to others. When the environment is perceived as controlling or forced, motivation to engage in behavior is diminished. Positive outcomes from perceiving control have been found in varying domains of psychosocial functioning, including work-related performances (Stajkovic & Luthans, 1998), child development (Bandura, Caprar, Barbaranelli, Gerbino, & Pastorelli, 2003), academic achievement and persistence (Multon, Brown, & Lent, 1991), and health functioning (Holden, 1992). Consequently, controllability is a critical determinant of physical and psychological well-being (Jensen, Turner, & Romano, 2001; Maier & Watkin, 1998), which suggests subjective perceptions of control (decisional control) can induce meaningful cognitive changes that affect emotional processing.

Altogether, theories pertaining to perceptions of control converge on the idea that both decisional control and behavioral control have significant impact on subsequent decision making and affective processes. However, the precise mechanisms in which the two types of control impact affective processing are yet unclear. The current research investigated the ways in which behavioral control and subjective experiences of control influence affective processing (Aim 1) and examined the neural circuitry underlying perceptions of control via exercising choice (Aim 2 & 3).

Choice as an Impetus for Perceiving Control

Control beliefs are critical to individuals' well-being (Bandura, 2006; Ryan & Deci, 2006), and individuals seek to exercise control over their environment by means of having choice. The opportunity for choice can be a powerful motivator (DeCharms, 2013; Lewin, 1951), and enhance motivation and performance on tasks by allowing one to assert their preference (Patall, 2013; Patall, Cooper, & Robinson, 2008). When people are able to express their will through choice, people feel more satisfied, competent, and engaged (Cordova & Lepper, 1996; Grolnick & Ryan, 1987; Langer & Rodin, 1976; Patall, et al., 2008; Patall, Cooper, & Wynn, 2010; Ryan & Deci, 2000). Having an opportunity to choose over something inconsequential can even influence quality and duration of life (Langer & Rodin, 1976), providing evidence that choice opportunity may be critical for maintaining healthy affect and well-being.

Opportunities for choice can be motivating and desirable to an extent that they create an illusion of control (Langer, 1975). For instance, healthy individuals tend to overestimate their personal control and ability to achieve success even when true control

does not exist (Lewinsohn, Mischel, Chaplin, & Barton, 1980). Studies have shown that people have a preference for choice even when there is no explicit incentive associated with choice (Bown, Read, & Summers, 2003; Suzuki, 1997, 1999), indicating that choice itself confers an inherent value. People report greater preference for options that lead to bonus choice (Bown, Read, & Summers, 2003; Leotti & Delgado, 2011a; Suzuki, 1997, 2011), even when the secondary choice involves greater effort without additional incentive. According to the free-choice paradigm (Brehm, 1956), individuals show greater preference for items after they have selected them whereas those that are rejected are rated as lower in value. These shifts in post-choice preference cannot be explained merely by desire for cognitive dissonance (i.e., increasing value of an item because one has chosen it to minimize a gap between one's thoughts and actions). These changes in choice-induced preference can last for years after initial decision (Sharot, Fleming, Yu, Koster, & Dolan, 2012). These studies suggest opportunity for choice is valuable and can impact motivational and affective processes.

Perceiving choice over events has been linked with affective experience of events, implicating that choice has significant consequences on emotional processing. When people believed that they had selected tasks themselves, individuals were more likely to perceive their environment as less intimidating, estimating distance to be traveled as shorter, and a hill to be climbed as less steep (Balcetis & Dunning, 2007). Another study by Sharot and colleagues (2009) found that having participants choose between positive events (vacation destinations) modulated expected hedonic outcome of those events, such that after making a choice between two equally rated vacation destinations, individuals rated the chosen option as more positive and the unchosen

option as more negative. Therefore, simply choosing an item increased its subjective rating and recruited reward-related circuitry in the brain (Sharot et al., 2009). Hence, the motivation for choice suggests that choice itself has an inherent positive value that increases the desire for choice.

In order to better characterize the affective experience of choice, Leotti & Delgado (2011) tested whether individuals prefer to have an opportunity for choice even when there is no other additional incentive for choice. Participants performed a choice-task in an fMRI scanner, where equal number of choice and no-choice conditions were randomly presented. In the choice condition, participants had an option of choosing a key, whereas in the no-choice condition, had to choose the key chosen by computer. The results showed that participants preferred to choose choice cues over no-choice cues, and rated the choice cues significantly higher than no-choice cues, suggesting that individuals preferred the choice cue far more than the no-choice cue. Participants selected the option that led to future choice significantly more often than the option that led to no-choice, even though they both led to equal reward amounts. These results suggest that the need for control – or the need for choice – is biologically motivated (Leotti, Iyengar, & Ochsner, 2010), and further implicate its role in regulating affect during emotionally arousing events.

Neural Mechanisms underlying the Perception of Control

To better understand affective experiences of control, it is necessary to probe the neural correlates of control experiences underlying maladaptive behavior and healthy functioning. Over the past two decades, imaging studies have begun to explore this

relationship by examining brain regions involved in the affective and motivational influence of perceiving control. Some of the earliest studies examining perceived contingency between one's actions and rewards have demonstrated a role for the striatum (i.e., Bjork & Hommer, 2007; O'Doherty, Critchley, et al., 2003; O'Doherty et al., 2004; Tricomi et al., 2004), a key region involved in reward processing (i.e., Robbins & Everitt, 1996). The striatum receives projections from several brain structures including the cortical and midbrain dopaminergic regions, putting it in an optimum location to process affective and reward-related information (Haber, 2003; Haber & Knutson, 2010). Striatal activity responds to differing aspects of reward processing, such as during the anticipation of impending rewards (Knutson, Taylor, Kaufman, Peterson, & Glover, 2005; O'Doherty, Deichmann, Critchley, & Dolan, 2002) or during the receipt of reinforcers (Berridge, 1996; J. P. O'Doherty, Rolls, Francis, Bowtell, & McGlone, 2001). Further, its activation increases when processing primary rewards such as food or drinks (Gottfried, O'Doherty, & Dolan, 2003; Pagnoni, Zink, Montague, & Berns, 2002) and secondary rewards such as monetary incentives (Delgado, Nystrom, Fissell, Noll, & Fiez, 2000).

Reward contingencies on behavior have implicated a role for the striatum, consistent with findings that suggest that an experience of control is rewarding. Specifically, striatal activation is increased for instrumentally delivered rewards compared to rewards that are passively received (Bjork, Smith, Danube, & Hommer, 2007; O'Doherty, Critchley, Deichmann, & Dolan, 2003; O'Doherty et al., 2004; Tricomi, Delgado, & Fiez, 2004). For instance, Tricomi and colleagues (2004) investigated brain activity that responds to contingency between choice opportunity and

outcomes. In the choice condition, participants believed that a reward outcome was dependent upon their button press response, whereas during no-choice conditions, participants believed their actions did not influence the reward outcome. In this study, participants showed increased levels of control over outcomes during the choice compared to no-choice trials, and heightened motivation levels to earn monetary rewards. Importantly, the choice condition led to an activation of the caudate nucleus, a portion of the striatum when participants perceived a contingency between their behavior and reward outcome. Additional studies have found striatal involvement in computing contingency (O'Doherty et al., 2004; Tanaka, Balleine, & O'Doherty, 2008), highlighting the role of striatum in processing action contingency and perception of control.

Studies demonstrating striatal involvement in behavior contingency and perceiving control suggest the region may be critical for choice processing. Recent fMRI data support this idea, providing support that choice is desirable and recruits the striatum. For example, in a simple decision-making paradigm, Leotti & Delgado (2011) examined whether expectancies of choice opportunities are rewarding, focusing on cues indicative of free- or forced-choice opportunity. This study found that participants reported greater liking of cues predictive of free choice compared to forced choice, which was linked with heightened activations in the ventral striatum. Additional neuroimaging data have reported similar results, such that striatal activity is enhanced during the anticipation of choice opportunity (Leotti & Delgado, 2014; Murty, DuBrow, & Davachi, 2015) and tracks choice-induced preference (Cockburn et al., 2014; Fujiwara et al., 2013; Izuma et al., 2010; Sharot, De Martino, & Dolan, 2009). Evidence from fMRI data suggest merely choosing an item (relative to rejecting) enhances its subjective rating and recruits reward-

related activity in the striatum (Sharot, De Martino, & Dolan, 2009), and these post-choice changes in preference are associated with levels of striatal activations (Sharot, De Martino, & Dolan, 2009; Sharot et al., 2010). These results suggest that the need for choice is intrinsically motivated (Leotti et al., 2010), and further implicate its role in influencing affective processes.

When examining how individuals respond to opportunities for choice, one important factor to consider is individual differences in reward sensitivity. Reward sensitivity refers to individual responsiveness to rewards and the positive affect derived from engaging in reinforcing behaviors (Gray, 1987). If choice is desirable, we could expect individual sensitivity for rewards to influence how people respond to choice opportunity. People with high sensitivity for reward exhibit a tendency to engage in goal-directed behavior and to experience pleasure when exposed to reward cues (Carver & White, 1994; Gard, Gard, Kring, & John, 2006), and recruit reward-processing brain regions (Beaver et al., 2006; Hahn et al., 2009). Reward-motivated trials have been shown to enhance activity in the ventrolateral prefrontal cortex (VLPFC) (Taylor et al., 2004; Baxter et al., 2009), a region involved in cognitive control processes (Badre & Wagner, 2007; Bunge, Burrows, & Wagner, 2004; Duncan & Owen, 2000). This suggests a potential role for the VLPFC in encoding reward sensitivity which might show a particular sensitivity for opportunities for free versus forced choices. To test this prediction, Aim 2 investigated how reward sensitivity contributes to neural responses associated with free and forced choice. Based on motivation and cognitive control literature, we expected the VLPFC to modulate reward-related circuitry during free-choice trials in reward sensitive individuals.

Neural Evidence for Perceived Control Modulating Affective Processing

Over the past decade, researchers have found regions within the prefrontal cortex to be involved in perceptions of control, suggesting interactions between cortical and subcortical regions might be important for modulating affective experiences of control. PFC regions such as the lateral and medial prefrontal regions have been implicated in diminishing negative affect via inhibiting responses in affect and motivational processing regions (McRae et al., 2010). The dorsolateral prefrontal cortex (DLPFC) is implicated in regulating negative emotions by modulating activity in subcortical regions involved in affect processing such as the amygdala, insula, and striatum (Green & Malhi, 2006; Ochsner & Gross, 2008) and directing attention to goals and reappraisal-relevant features (Ochsner, Silvers, & Buhle, 2012). If perceiving control involves modifying the aversiveness or meaning of affective stimuli (Averill, 1973; Miller, 1979), we could hypothesize the presence of control to engage the DLPFC, hence bolstering the idea that the perception of control can serve as a means for affect regulation.

In support of affect modulation via experiences of control, regions within the prefrontal cortex are involved in attenuation of emotional experiences such as pain. Exerting control over painful stimuli such as heat and shock decreases neural responses in pain-processing regions (Salomons et al., 2004, 2007; Wiech et al., 2006). Increased activity in the prefrontal cortex during expectations of control may contribute to these positive effects of control, resulting in lowered pain processing and subjective ratings of pain. In a recent fMRI study, Bräscher et al. (2016) probed the neural circuitry underlying the influence of control on the affective experience of physical pain. In this study,

participants underwent a series of painful or warm stimuli to regulate (controllable trials) or rate (uncontrollable trials) the given temperature. The authors found reduced reported perceptions of pain during controllable relative to uncontrollable trials. Further, when pain was controllable, pain-related anterior insula region exhibited an inverse connectivity with the dorsolateral prefrontal cortex (DLPFC), an area associated with cognitive control and emotion regulation. This brain response may suggest exerting control may support reinterpreting a potentially threatening stimulus, thus altering the meaning or significance of the stimulus (Averill, 1973), indicating the presence of control is essential for regulating affective processing. Further, the experience of control may require actively monitoring, decision making, and response selection that rely on the executive control network, hence recruiting the lateral PFC (Badre & Wagner, 2004). These data implicate a role for lateral PFC involvement in regulating emotional experiences when perceiving control.

While the neuroimaging literature converges on the regulatory role of lateral PFC in modulating affective experiences during control, the role of medial PFC influencing control experiences has been less clear and rather complex. For example, Bräscher and colleagues (2016) found that mPFC connectivity with pain-related anterior insula increased in the uncontrollable condition, suggesting that mPFC may facilitate pain by increasing sensitivity to heat during uncontrollable conditions. However, in this study, the authors did not directly compare between controllable vs. uncontrollable trials, which made it difficult to determine whether the observed activities were due to uncontrollability. A potential alternative is that mPFC is involved in affect regulation via top-down control of regions involved in affective processing (i.e., amygdala and insula)

(Davidson, 2000; Kim, Gee, Loucks, Davis, & Whalen, 2011), possibly to a greater degree for more distressing uncontrollable trials. Indeed, the ventral and perigenual regions of MPFC detected by Bräscher and colleagues (2016) have been associated with emotion regulation functions such as reinterpreting, reversing, and extinguishing affective associations (Schiller & Delgado, 2010). Such findings call for a necessity to examine the functions of distinct regions within the mPFC determining affective experiences of control.

Importantly, rodent research supports the critical role of vmPFC for the beneficial influence of controllability (e.g., improved escape learning) and blunting aversive effects of a stressor (i.e., escape deficits, freezing) (Baratta, Lucero, Amat, Watkins, & Maier, 2008; S F Maier, Amat, Baratta, Paul, & Watkins, 2006). A related study by Delgado and colleagues (2008) demonstrated a critical function of the vmPFC in diminishing fear responses by inhibiting amygdala activity in humans. In that study, diminishing fear responses via extinction training and emotion regulation revealed a similar pattern of enhanced activity in the vmPFC, a region identified as critical for assisting controllability effects on regulation of stress (Kerr et al., 2012; Maier et al., 2006). Such evidence implicates the vmPFC in supporting emotion regulation perhaps by computing the contingency information between one's behavior and outcome (Dickinson, Balleine, Watt, Gonzalez, & Boakes, 1998; Maier & Watkins, 2010) and forming adaptive behavioral responses (Bhanji & Delgado, 2014). As a result, an enhanced connectivity between the mPFC and affect processing areas during uncontrollable contexts (Brascher, Becker, Hoeppli, & Schweinhardt, 2016) might suggest a role for the region encoding

contingency, hence modulating activity in regions associated with emotional processing (i.e., amygdala and insula).

In sum, evidence suggests that the anticipation of control influence brain activity involved in generating and regulating affective experiences. Further work is needed to identify the neural mechanisms associated with the influence of perceiving control on affective processes. Future investigations could probe connectivity patterns of cortical and subcortical regions depending on controllability. However, functional connectivity analyses do not allow for inferring causations; thus, implementation of alternative approaches are necessary for delineating causal inferences between regions. In particular, the employment of dynamic causal modeling (DCM) may help identify context-specific variations in effective connectivity between brain regions (Friston, 2011). Therefore, the goal of Aim 3 was to probe the directionality of cortical regions influencing affect-processing regions (i.e., striatum) as a function of perceiving choice. Given previous neuroscientific model characterizing reward motivation (Ballard et al., 2011), we hypothesized anticipation of choice to directly impact our regions of interest, which will affect strength of corticostriatal connectivity.

Overview of Proposed Experiments

We develop beliefs in our ability to exercise control over the environment by exerting choice. Research suggests such beliefs in control are highly adaptive in our psychosocial functioning and well-being, indicating perceiving control has important consequences on behavior as well as affective processing. However, the influence of behavioral control and subjective perceptions of control on general negative affective

processing is yet unclear. Thus, the current set of experiments investigated whether the two types of control – subjective perceived control (decisional control) vs. objective controllability (instrumental control) can serve as means to dampen negative emotions, and further examined the neural circuitry underlying effects of controllability on decision making and affective processing. In this research, control is operationalized as conditions that allow for individuals to exert free choices during which they perceive control over their outcome, hence choices are not externally forced by the experimenter. The current set of experiments investigated the influence of perceived control on decision making and affective processing.

Specifically, Aim 1 explored the effect of choice on affective processing. To investigate this idea, the first experiment probed the influence of choice on evaluating negative outcomes, and the Experiments 2—4 assessed the role of perceived control on regulating affective experiences. We hypothesized exercising choice will dampen emotional responses to aversive stimuli (e.g., negative emotional pictures). Then, Aim 2 examined the neural correlates of free choice involving reward options in individuals particularly prone to reward sensitivity. Based on previous research demonstrating the involvement of the striatum in the value of choice, we hypothesized reward sensitivity to be linked with reward signals in the striatum during free choice. In addition, we expected attentional control regions to show increased activity during exercise of free choice in reward sensitive individuals. Lastly, Aim 3 further examined the directionality of neural circuitry of choice opportunity. We hypothesized information about controllability may enter through the neural system via regions previously associated with perceptions of

control and reward motivation, and further predicted connectivity between regions would be modulated by choice anticipation.

Chapter 2

AIM 1: To investigate the influence of choice on affective processing

Negative emotions may induce adverse effects on human cognition and memory (Dolcos & McCarthy, 2006) potentially by impairing goal-directed attentional systems (Eysenck et al., 2007). Once negative emotions arise, regulating such maladaptive response is critical for successfully accomplishing desired outcomes. One strategy that could help regulate negative emotions is enhancing one's control beliefs via exerting choice. Findings from perceived controllability research are indicative of a strong link between control beliefs and emotional responses, which suggests control beliefs can have significant consequences on affective processing. For example, beliefs of control can influence tolerance for pain, motivation, and the ability to cope with chronic pain (Mineka & Henderson, 1985; Maier & Watkins, 1998; Jensen & Karoly, 1991; Jensen et al., 2001). These studies suggest negative events are experienced as less distressful when we perceive a means to control a threatening stimulus, and underscore the significance of understanding the relationship between perception of control and negative emotions.

Although evidence suggests perceiving control has a buffering effect on specific domains such as fear conditioning (Hartley et al., 2014) and pain (Brascher et al., 2016, Salomons et al., 2004, 2007, Wiech et al., 2007), the mechanism underlying its impact on broader emotions is yet unclear. A number of studies indicate that a lack of control over aversive stimuli induce exaggerated fear responses, greater negative affect, enhanced stress levels (Amat et al., 2005; Maier & Watkins, 2005; Mohr et al., 2012), and even lead to psychiatric disorders (Weiss & Simson, 1986). These results support the idea that perceiving increased control may protect against adverse effects of stress (Amat et al.,

2006; Christianson et al., 2008). For instance, patients who receive patient-controlled analgesia under extreme pain report reduced pain, use less pain-alleviating medications, and have greater functional capacity (Ballantyne et al., 1993). Such findings converge on the idea that perceived controllability has significant consequences on mental health and well-being (Jensen, Turner, & Romano, 2001; Maier & Watkin, 1998), and highlight its role in the regulation of negative emotions.

When examining the impact of perceived control on affective processing, it is important to consider the different types of control (i.e., behavioral control vs. decisional control) and their influence on emotional systems. Behavioral control refers to the ability to modify an event outcome through behavioral response (Maier & Seligman, 1976). For instance, individuals are able to avoid negative stimuli via performance on a task, terminate an aversive stimulus, or limit the intensity of a negative stimulus or shock (Averill & Rosenn, 1972; Hokanson et al., 1971; Geer & Maisel, 1972). Behavioral control has been shown to diminish arousal during anticipation of noxious noise (Glass, Singer, & Friedman, 1969) or photographs (Geer & Maisel, 1972), and to increase tolerance to electric shock (Staub, Tursky, & Schwartz, 1971), and pain (Kanfer & Seider, 1973), supporting the idea that exercising behavioral control reduces emotional responses to negative stimuli.

Another way of exerting control over our environment is by exerting decisional control via making choice. Decisional control is the ability to select a single course of action from potential alternatives (Averill, 1973). Therefore, perceptions of control can be enhanced even when there is no immediate contingency between one's behavior and outcome. Research suggests exercising decisional control may impact emotional

processing by allowing an individual to act as a causal agent to accomplish a goal. Control beliefs are critical to individuals' well-being (Bandura, 2006; Ryan & Deci, 2006), and individuals seek to exercise control over their environment by means of having choice. The opportunity for choice can be a powerful motivator (DeCharms, 2013; Lewin, 1951), and enhance motivation and performance on tasks by allowing one to assert their preference (Patall, 2013; Patall, Cooper, & Robinson, 2008). When people are able to express their will through choice, people feel more satisfied, competent, and engaged (Cordova & Lepper, 1996; Grolnick & Ryan, 1987; Langer & Rodin, 1976; Patall, et al., 2008; Patall, Cooper, & Wynn, 2010; Ryan & Deci, 2000). Having an opportunity to choose over something inconsequential can even influence quality and duration of life (Langer & Rodin, 1976), providing evidence that exercising decisional control can influence our well-being and emotional systems.

Moreover, evidence suggests exerting choice could impact responses to affective events. A study by Sharot and colleagues (2010) probed whether choosing to go through an aversive medical condition reduces expected aversiveness of the condition. In this study, individuals reported medical conditions as less aversive after choosing to go through them compared to their initial ratings before choosing to go through the conditions, indicating expectations of negative events are less aversive if they had made a choice to encounter them in the future. Altogether, these findings provide evidence that by exercising choice, perceiving greater control could modulate behavioral and emotional responses towards affective stimuli. Although recent work has begun exploring the effects of perceived control on painful experiences such as heat (Mohr et al., 2012),

shock (Hartley et al., 2014) and medical conditions (Sharot et al., 2010), its role as a means for regulating general negative emotions has been less well studied.

Thus, the overarching goal of Aim 1 was to examine how exercising decisional control and instrumental control interact with emotional processing in a simple choice paradigm. More specifically, we conducted a set of four experiments in which participants were exposed to pictures that evoked negative emotions under contexts in which they were able to exercise control or not. Experiments 1 probed the impact of exerting decisional control on evaluating negative outcomes, to test whether exercising choice may serve as an emotion regulation strategy when receiving feedback about one's behavioral response. In contrast to evaluating outcomes associated with one's response, Experiments 2 through 4 examined how indirectly raising levels of control via exercising choice modulates one's own emotional processing of aversive stimuli (i.e., how does the picture make you feel?). Experiment 2 examined whether enhancing decisional control impacts emotional responses to negative outcomes. Experiments 3 and 4 probed whether exercising behavioral control impacts emotional responses to aversive pictures. In a simple decision-making task, participants were given an opportunity to make a choice in free-choice trials, whereas participants were instructed to select the key chosen by the computer during forced-choice trials. After a button press, participants observed an emotional picture and rated their feelings. We hypothesized affective ratings on negative pictures would be diminished during free relative to forced choice, revealing a greater decrease in negative feelings when control beliefs are enhanced.

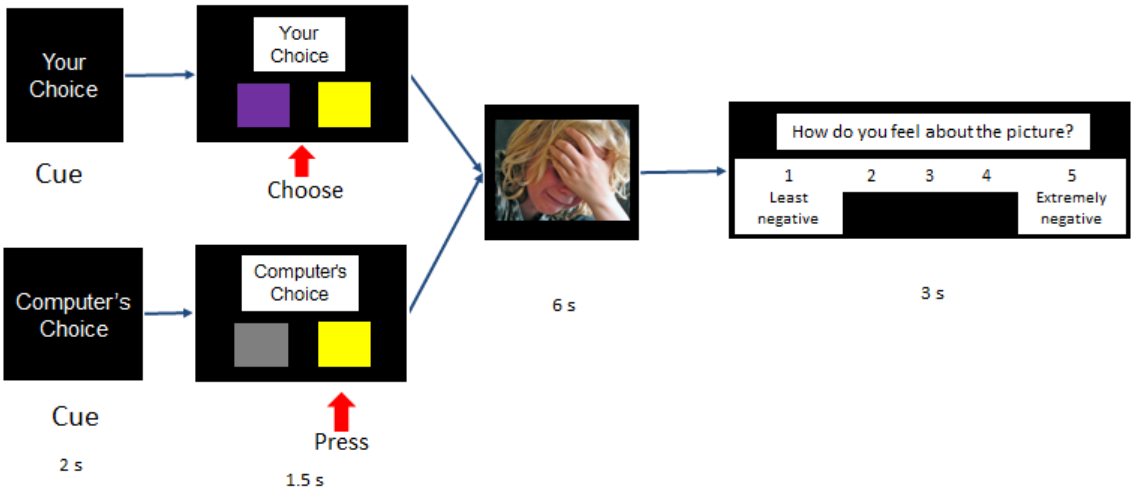
Experiment 1: Evaluating negative outcomes under choice

Methods

Participants

Thirty-seven healthy individuals (32 female, mean age = 21.2, *SD* = 2.9, range = 18 – 33) from Rutgers University-Newark participated in this study in exchange for course credit in psychology courses. Six participants were excluded from analyses due to failure to comply with task requirements (e.g., use of cellphones, failure to remain awake during the duration of the experiment, failing to respond on more than one third of trials). Thus, the final sample included in the following analyses consisted of thirty-one participants. Participants gave informed consent according to the Rutgers University Institutional Review Board.

Figure 2.1 Experimental design for Experiment 1. Each trial presented two colored keys, followed by a negative or neutral image.



Experimental task

In a simple choice paradigm, participants were given an option to choose between two colored keys that led to an emotional picture (Fig. 1.1). Each colored key was associated with either a negative or neutral picture, and the goal in each trial was to select the correct key to avoid seeing a negative image. Participants had 1.5 seconds to make a response. Failure to respond on a trial led to a key selected by the computer at random. Each trial began with a 2 second cue indicating whether it was a free-choice ("Your choice") or forced-choice ("Computer's choice") trial. In free-choice trials, subjects had the option to choose between red and blue keys to avoid receiving a negative picture, hence resulting in a neutral image. Choosing a specific key on one occasion did not guarantee seeing a neutral picture on another trial, hence individuals were encouraged to maximize their chance of avoiding the negative picture through trial and error. Nonetheless, individuals had decisional control over negative pictures during free choice because they had an option to choose between two cues. In forced-choice conditions, however, participants were forced to select the key determined by the computer (the other option was denoted in gray), thus removing the ability to control the outcome in these trials. After a button press, either a negative or neutral image was presented on screen for 6 seconds. Participants rated their feelings on a 5-point scale (1 = not at all negative, 5 = extremely negative).

Images were taken from the International Affective Picture System (IAPS, Lang et al., 1999), which uses standardized photographs matched for content, luminance, and color. The entire task consisted of 100 trials, divided into 20 blocks of 5 free- or forced-choice trials presented at random within each block. Neutral and negative images were

intermixed within a block, and no more than three of the same image type (negative or neutral) were presented consecutively. Finally, after completing the task, subjects rated how much control they felt in each free- and forced-choice condition (1 = not at all, 5 = extremely).

Results

Behavioral results

Making choices might be associated with cognitive effort, which may yield different mean reaction times between free and forced-choice trials. To test for differences in time lag as a function of free and forced choice, a paired-sample *t*-test was conducted at the decision making phase. Average reaction times were slower when subjects responded to free choice (M = 791 ms, SD = 101.99 ms) than when they responded to forced choice trials (M = 738 ms, SD = 116.16 ms), $t(30) = 2.061$, $p < 0.05$.

Figure 2.2 Results from a paired-sample t-test on feelings of control between free-choice and forced-choice trials.

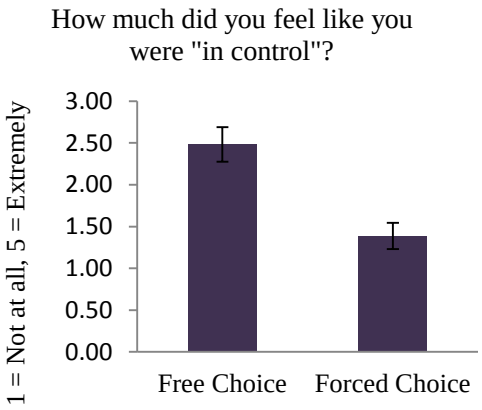
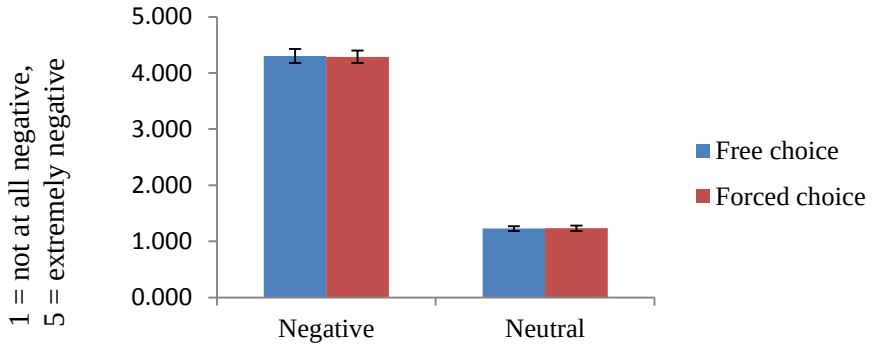


Figure 2.3 Results from a repeated measures ANOVA with image valence and choice as factors.



Next, a paired-sample *t*-test was conducted to test whether levels of perceived control differed between free- relative to forced-choice trials. Our analyses indicated that participants felt more in control during free choice (M = 2.48, SD = 6.4) compared to forced choice (M = 1.39, SD = 4.9), $t(30) = 4.52$, $p < 0.001$ (Fig 2.2). Subsequently, subjective ratings for images in free and force choices were entered into a repeated measures analysis of variance (ANOVA), with image valence (negative and neutral) and choice (free and forced) as factors. A main effect of valence was found, which indicated ratings of negative images (M = 4.294, SD = .64) as significantly more negative than neutral pictures (M = 1.231, SD = .23), $F(1,30) = 870$, $p < .001$). However, participants did not report differences in ratings of pictures between free (M = 2.764, SD = .412) and forced choice (M = 2.761, SD = .373), $F(1,30) = .015$, $p > .05$ (Fig 2.3). There was no interaction between image valence and choice factors. Taken together, these observations suggest although perceived control differed between free and forced choice, their levels of control did not modulate their responses to emotional outcomes.

Summary

Experiment 1 examined the effect of free choice on evaluating emotional outcomes. Consistent with existing research implicating increased feelings of control when exerting choice, participants felt greater control during free relative to forced choices. Furthermore, participants took longer to respond when exerting choice, which could be an indication of increased levels of cognitive effort and attention involved in making the best course of actions to achieve one's desired goal (e.g., avoiding the negative picture). However, contrary to our hypothesis, we did not find that an increased perception of control modified emotional experiences. One explanation that might account for these results is the valence of images used in the current task. Although images in the current experiment were purposefully selected to be highly aversive (average valence of 1.9) in order to effectively dissociate free and forced choice, the pictures may have been too extreme to regulate or alter one's emotional responses. Hence, subsequent task called for a new set of images to be selected that are in line with an average valence of 2.5 – 2.6 typically used in previous emotion regulation studies.

An alternative explanation might account for associations of negative and neutral images as failure or success of one's decisions in a given trial. In such case, individuals might have attributed negative images as failure due to one's bad decisions (e.g., "I failed because I chose the wrong key"). Thus, the tendency for a status quo bias could increase because individuals felt responsible for the consequences of their own decisions (Samuelson and Zeckhauser, 1988), hence developing a preference for the computer selected key which does not demand responsibility. According to Baron and Ritov (1994), a status quo bias may reflect a regret-minimizing strategy. Individuals may be

inclined to accept the status quo for reasons such as an enhanced sense of accountability for an error (Ritov and Baron, 1990) and feelings of regret from resulting error (Kahneman and Tversky, 1982). Therefore, our results suggest evaluating positive or negative outcomes may be dependent on one's interpretations of feedback about one's responses and suggests a need to dissociate outcomes from influencing processing of affective stimuli. In a subsequent experiment (Experiment 2), we modified our task to dissociate feelings of failure or success from processing affective stimuli.

Experiment 2: Regulating negative emotions via choice

In the second study, several modifications were applied to examine whether the opportunity for decisional control (having opportunity for choice irrespective of outcome) alters emotional responses towards negative stimuli. In contrast to the image set used in the previous experiment (average valence= 1.9; lower value denotes higher negative valence), new sets of images of lower negative intensity (average valence = 2.5) were selected. Additionally, to dissociate valence of pictures from perceiving success or failure, a training session was included in this study. During training, participants could learn which key was associated with greater reward value, which helps them select a better key in the choice phase. Thus, in the choice phase each key was associated with a reward value that was dissociated from the affective nature of pictures. In a simple decision-making task, participants were given an opportunity to make a choice in free-choice trials, whereas participants were instructed to select the key chosen by the computer during forced-choice trials. Thus, the current experiment tested whether experiencing choice modulates emotional responses.

Consistent with our previous findings, we expect participants to report greater control during free versus forced choices. When participants are viewing negative images, we predict participants will show decreased ratings of negative feelings during free-choice compared to forced-choice trials. We do not expect to see differences in ratings between free and forced choice while participants are viewing neutral images.

Methods

Participants

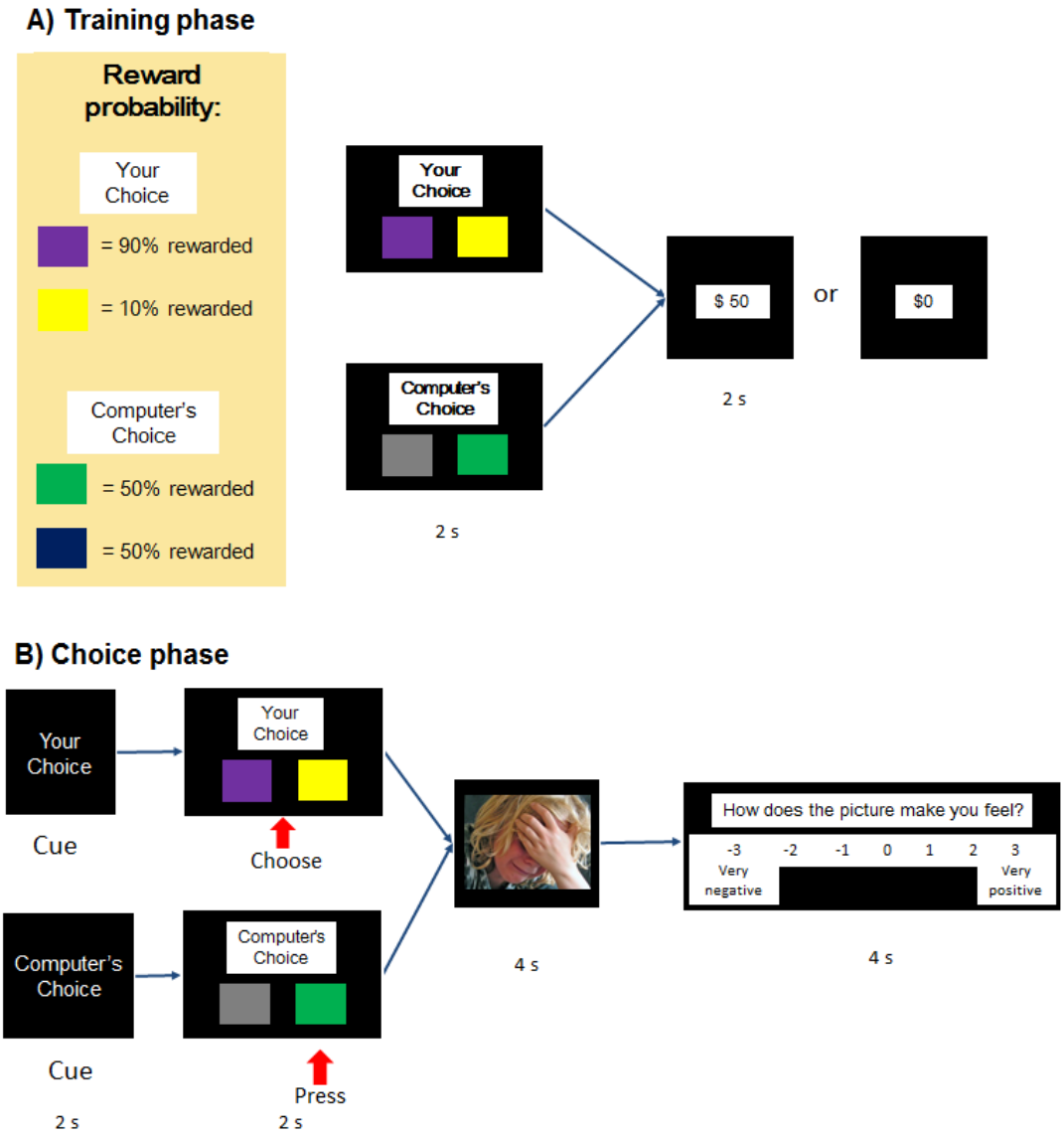
Twenty-six healthy subjects (17 female, mean age = 21.0, SD = 3.2, range = 18 – 34) from Rutgers University-Newark participated in the current study in exchange for course credit. One subject was excluded from subsequent analyses due to failure to learn the task. Therefore, the final sample included in the analysis consisted of twenty-five subjects. Participants gave informed consent according to the Rutgers University Institutional Review Board.

Experimental task

In the beginning of the experiment, participants were informed that they will be playing several games with monetary consequences. These experimental dollars would be translated into real bonus money at the end of the experimental session. This experimental paradigm consisted of two phases: a training phase and a choice phase (Fig. 2.4). During the training phase, participants responded to two colored keys (2 sec) to learn which key was associated with a greater monetary reward. On every trial,

participants could win either $0 or $50 and their goal was to win as much money as possible.

Figure 2.4 Experimental design for Experiment 2. (A) Training phase, B) choice phase.



During free-choice trials, subjects could decide which one of two keys to choose, and could perceive decisional control even though their behavior did not impact the resulting picture, whereas during forced-choice trials subjects must select the key

determined by the computer. If participants failed to respond to a key or chose the nonselected key during forced-choice trials, no reward was given in that trial. In the free-choice condition, a colored key (i.e., purple) was rewarded during 90% of the trials whereas the other key (i.e., yellow) was rewarded only 10% of the time. In the forced-choice condition, each colored key (blue or green) was rewarded with a 50% probability. Immediately after training, participants were asked to indicate which color they preferred in each trial type to examine whether they had learned the reward contingency. Subjects performed twenty free- and forced-choice trials each.

Participants then proceeded to the choice phase of the experiment in which they were encouraged to use their knowledge from training to earn bonus money. Participants could win $50 or $0 on each trial depending on which color they selected. In the choice phase, monetary feedback in each trial was not provided until the very end of the experiment. Importantly, participants were told that these experimental dollars will be translated into real bonus money at the end of the game. Upon selecting a key, either a neutral or negative image was displayed on screen for 4 seconds. After looking at each picture, participants were asked to rate how the picture made them feel, on a 7-point scale (-3 = very negative, +3 = very positive). Participants completed 80 trials in total separated by 4 blocks of free- or forced-choice trials. Each block was composed of 20 trials in each free- and forced-choice condition. Neutral and negative images were randomly presented in each block. No more than three of the same consecutive image types (negative or neutral) were presented.

Results

Behavioral results

Behavioral analyses primarily focused on three phases of the experiment: the training phase, choice phase, and post-experimental questions. Immediately after completing the training phase, participants were asked which colored key they preferred over the other. In the training phase, 84% of participants preferred the more rewarded (90%) key compared to the less rewarded (10% reward) key, which was significantly different from 50% chance, $t(24) = 11.225$, $p < .001$.

To measure whether engaging in free or forced choice induced differences in reaction times, a paired t-test was conducted in the choice phase. Mean reaction times in free-choice (M = 874 ms, SD = 165 ms) did not differ from forced-choice trials (M = 866 ms, SD = 190 ms), $t(24) = .464$, $p = .647$. Further, subjects reported negative images (M = 2.286, SD = .495) as more negative than neutral pictures (M = 3.921, SD = .595), $F(1,24) = 127.376$, $p < .001$. Differences in ratings between free-choice (M = 3.082, SD = .435) and forced-choice (M = 3.126, SD = .415) trials were nonsignificant, $F(1,24) = .834$, $p = .37$. Results were identical in 21 subjects that learned the correct behavioral response for the choice task.

Next, after completing the choice task, all participants answered a post-experiment questionnaire which addressed whether they had felt “in control” during the free-choice condition. Participants felt more in control during free choice (M = 3.08, SD = .91) compared to forced choice (M = 2.16, SD = 1.07), $t(24) = 3.994$, $p < 0.001$.

Summary

This study investigated how the experience of choice alters emotional responses. Consistent with findings from the previous study, we found that opportunity for choice increases feelings of control compared to forced choices. However, results from reaction times and behavioral ratings suggest levels of control did not influence emotional reactions to affective pictures. An explanation of these results might account for issues associated with the current experimental paradigm, such as complexity of our design. Even when one key was rewarded with a 90% probability, four out of twenty-five subjects responded they did not prefer the rewarded key over the other during the training phase. Failure to associate the better key with a potential reward may have influenced subjects' responses, especially during the choice phase when feedback on reward outcome was not presented on a trial-by-trial basis.

Contrary to Study 1, we did not find differences in reaction times. A potential interpretation is that the keys associated with rewards during training were not related to outcomes of pictures – hence might explain not observing differences in reaction time between the two trial types. Further, there is a possibility that free and forced choices were more difficult to differentiate due to the addition of the training phase. Therefore, the following study examines the effect of choice on affective processing by simplifying the experimental paradigm.

Experiment 3: Regulating negative emotions via choice (Modified version)

As a subsequent step, a new task was designed to simplify the choice paradigm and also test whether behavioral control (instrumental control) can influence emotional processing. In this study, subjects were shown two scenarios (i.e., accident, threat) to choose from, and on each trial indicated their preference for picture by pressing a button. Contrary to previous experimental designs, in which participants' button press did not impact the resultant picture, in this new paradigm, participants could directly select a picture to watch, hence following an instrumental conditioning paradigm.

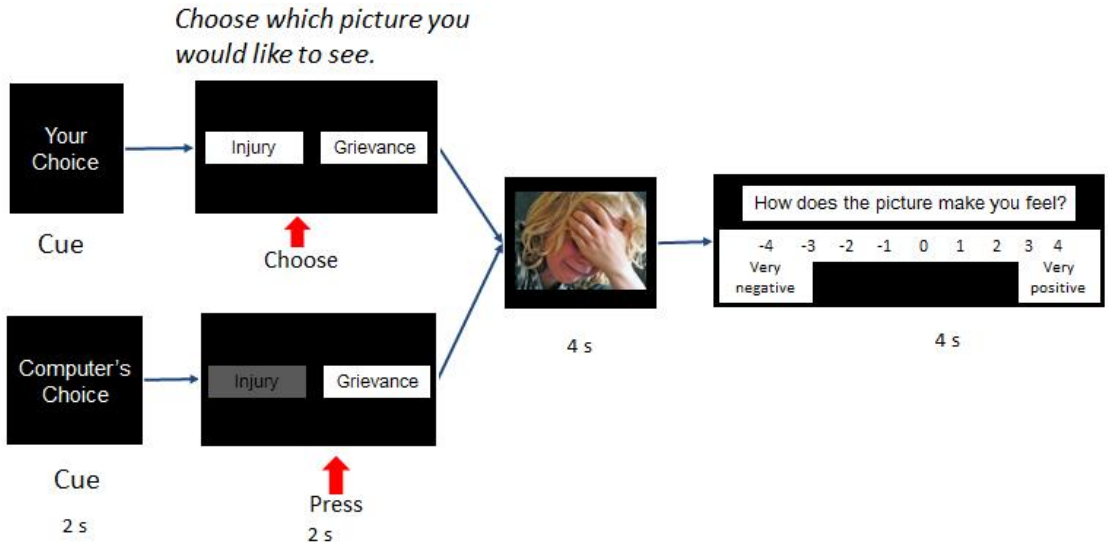
After viewing a corresponding image, subjects rated their feelings in response to the negative or neutral images. The present study tested whether choosing to look at a picture reduces emotional responses to those images. This experimental paradigm provided a benefit over the previous version because it allowed participants to directly choose a preferred category of picture without including an extra decision making process that might have complicated choice processing.

Methods

Participants

Twenty-nine individuals (22 female, mean age = 24.7, SD = 6.8, range = 18 – 54) from Rutgers University-Newark participated in this study in exchange for course credit. Two subjects were excluded from analyses due to technical difficulties (e.g., malfunction in the computer). Therefore, the final sample included in the analyses consisted of twenty-seven participants. Participants gave informed consent according to the Rutgers University Institutional Review Board.

Figure 2.5 Experimental design for Experiment 3. In each trial, participants were presented with two options. Upon making a response, participants saw a corresponding image.



Experimental task

On each trial, subjects were provided with two scenarios to choose from, such as accident vs. threat (Fig. 2.5). Subjects were given 4 seconds to press a button (left or right) to select which picture they would like to see. Upon making a response, a corresponding picture was shown for four seconds. Each block began with a 2 second cue phase indicating whether it was a free-choice ("Your choice") or forced-choice ("Computer's choice") trial. During free-choice trials, subjects had freedom to choose between the two categories to select the picture they wished to see. In these trials, subjects had direct control over the type of images that would appear on screen. During forced-choice trials, subjects had no option but to choose the category selected by the computer, thus removing personal preference for an image type. Subjects selected the option chosen by the computer and waited for the corresponding image to appear. Each image was

followed by a question asking how the picture made them feel on a 9-point scale (-4 = very negative, +4 = very positive).

All images were taken from the IAPS (Lang, Bradley, & Cuthbert, 1999), and were matched in valence for either negative or neutral condition. Negative categories included accident, threat, injury, and grievance, whereas neutral categories consisted of tool, person, abstract art, and face. A negative trial only presented categories from the negative scenario, and neutral condition only presented neutral pairs. There were a total of 72 trials in the experiment, equating to about 28 minutes.

Results

Behavioral Results

Subjects responded significantly slower during free-choice (M = 1775 ms, SD = 364ms) relative to forced-choice (M = 1125 ms, SD = 249 ms) trials, $F(1,26) = 116.231$, $p < .001$. Responses during negative trials (M = 1521 ms, SD = 275 ms) were slower than responses for neutral trials (M = 1379 ms, SD = 281 ms), $F(1,26) = 25.169$, $p < .001$.

Participants felt more in control during free choice (M = 2.67, SD = .78) compared to forced choice (M = 1.56, SD = 1.01), $t(26) = 5.151$, $p < 0.001$. As expected, subjects rated negative pictures (M = 2.796, SD = .816) as more negative compared to neutral pictures (M = 5.583, SD = .478), $F(1,26) = 172.266$, $p < .001$. However, there were no differences in ratings between choice (M = 4.182, SD = .359) and nochoice (M = 4.197, SD = .468) trials, $F(1,26) = .047$, $p = .830$.

Summary

In a simplified choice paradigm, the present study examined whether choosing to look at a picture reduces emotional responses to those images. Contrary to previous studies that have found a decrease in aversive value of negative events as a function of one's choice (Sharot et al., 2010), we did not find differences in emotional responses from perceiving control. An explanation for this difference in results might stem from differences in ratings used to measure people's feelings. Whereas Sharot and colleagues (2010) examined the influence of choice on expectancy of future events that have not yet occurred, the current study tested whether perceiving control modulates actual affective experiences in the moment. Hence, choice opportunity may incur different results on momentary and anticipatory responses to negative stimuli.

An alternative explanation for results from the current study might suggest perceiving control has a greater influence on expectancy of outcomes rather than the actual affective experience per se. Consistent with this idea, although opportunity for choice modulates expectancy of outcomes (Leotti et al., 2014, Murty et al., 2015), studies have reported inconsistencies on the effect of choice on the subjective experience of affective stimuli such as pain (Borckardt et al., 2011; Maier & Watkins, 1998; Salomons et al., 2007; Staub et al., 1971; Weich et al., 2006). Additionally, previous work did not explicitly compare subjective ratings between free and forced choices but measured changes in emotional responses to stimuli before and after choice (Sharot et al., 2010).

Importantly, during forced choices in the current version of task, participants were exposed to both options (i.e., accident vs. injury) allowing participants to compare values between the two choices. If this is the case, it is possible that even though participants

could only physically choose the computer-chosen option, they could be engaging in self-serving bias within a trial that the items chosen by the computer is better than the unchosen option. Previous literature has shown these results such that options that are chosen as opposed to rejected are rated as higher in value after selection (Brehm, 1956), hence suggesting the need to eliminate the possibility for value comparisons between options during forced choices. Therefore, additional work was required to delineate the effects of free and forced choices on experiences of affective processing in a revised choice paradigm.

Experiment 4: Regulating negative emotions via choice

In Experiment 4, participants performed the choice task with the inclusion of three key changes in the design. First, in previous experimental designs 1—3, participants were able to view both options during forced-choice trials (i.e., injury vs. accident) even if they could only select the computer-chosen option. The current version of experiment provided two of the same options (i.e., injury vs. injury) during forced choices. The rationale for this modification is that participants could potentially compare and compute values for both options if they could visually see both cues, which could enhance their feelings of control during forced-choice trials. Therefore, the present version aimed to remove any value comparisons between the options by restricting cues to a single option during forced choices.

Second, baseline measures of images in each category were collected prior to the choice task. These pre-choice ratings provide additional measures that allow us to examine the effect of choice on modulating responses to negative events. Both baseline

and post-task measures are subjective ratings that rely on participants' own awareness of emotional reactions to pictures. Third, to probe whether subliminal responses to emotional events are altered by choice opportunity, we included an additional 'Go' phase immediately prior to picture presentation to test whether reaction times for events changed as a function of free and forced choice. Therefore, upon making a choice between two categories of negative pictures, participant saw the word 'Go!', signaling that the picture they've chosen would appear once the participant pressed a button in each trial. Each go phase was followed by a corresponding image for four seconds. Finally, participants rated how the image made them feel on a 5-point scale.

Methods

Participants

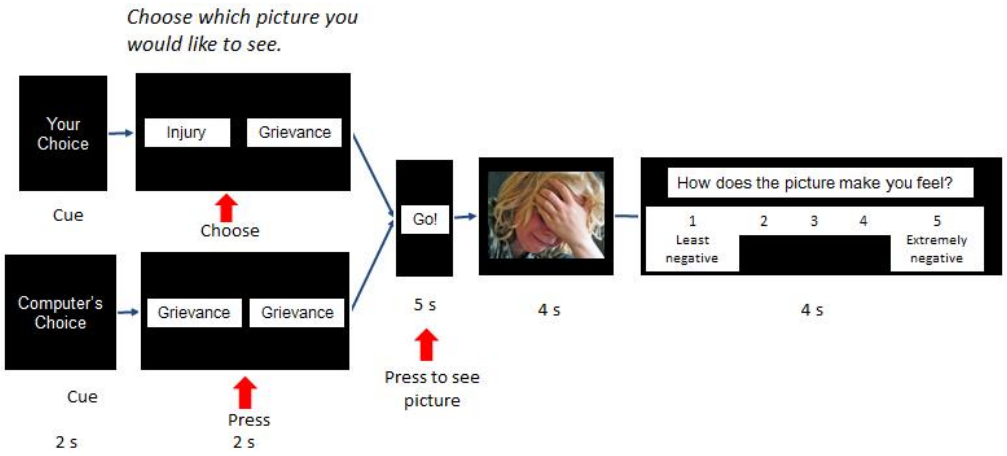
Thirty-four individuals (22 female, mean age = 20.0, SD = 2.26, range = 18 – 28) from Rutgers University-Newark participated in this study in exchange for course credit. Two subjects were excluded from analyses due to failure to comply with task requirements (e.g., pressing the same button throughout the entire task) and malfunction in computer. Therefore, the final sample included in the analyses consisted of thirty-two participants. Participants gave informed consent according to the Rutgers University Institutional Review Board.

Experimental task

First, to measure participants' baseline ratings of images in each category, participants rated a series of pictures in each category consisting of accident, grievance,

injury, and threat. Subsequently, participants underwent a choice task which began with a 2-second cue indicating whether it was a free-choice ("Your choice") or forced-choice ("Computer's choice") trial.

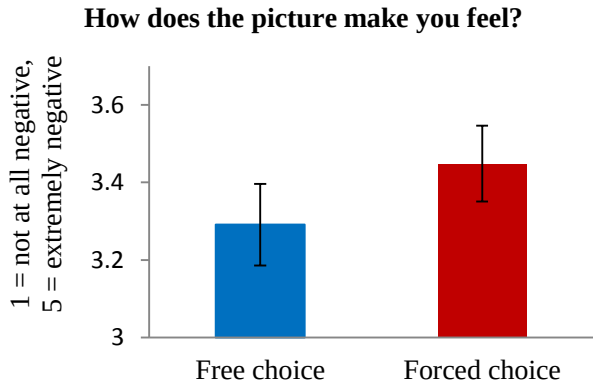
Figure 2.6 Experimental design for Experiment 4. Participants chose between two options/keys in each trial. Choice trials presented different options, whereas no-choice trials showed the same option on left and right of the screen. A corresponding image was displayed upon making a button response.



On free-choice trials, participants were able to freely choose which picture they would like to see by choosing between two scenarios (i.e., injury vs. grievance) (Fig. 2.6). In these trials, participants had direct control over the type of image that they would see. Subjects were given 4 seconds to press a button (left or right) to select which picture they would like to see. Upon selecting a category, the word ‘Go!’ appeared, signaling that the picture they’ve chosen would appear once the participant pressed a button. This phase was intended to measure a subliminal approach or avoidance response towards seeing the

picture in each category. Next, a corresponding picture was shown for four seconds. On forced-choice trials, participants had no option but to choose the pre-determined category, thus removing personal freedom to choose preferred picture category. In these trials, participants were presented with the same option on either side of the screen (See Figure 2.6). Upon a button press, participants waited for the corresponding image to appear. After each image, participants rated their feelings on a 5-point scale (1 = not at all negative, 5 = extremely negative).

Figure 2.7 Average ratings of pictures in free-choice vs. forced-choice trials.



Results

To measure whether engaging in free or forced choice induced differences in reaction times, a paired t-test was conducted in the choice phase. Subjects responded significantly slower during free (M = 1793 ms, SD = 446 ms) relative to forced-choice (M = 1313 ms, SD = 364 ms) trials, $t(33) = 8.44$, $p < 0.001$. Next, the Go phase was analyzed to test whether there were differences in reaction times between free and forced choice as a function of differences in subliminal approach or avoidance response towards seeing a picture. There were no differences in mean reaction times times between free- (M = 1008

ms, *SD* = 255 ms) and forced-choice trials (*M* = 1070 ms, *SD* = 490 ms), *t*(30) = -0.946, *p* = .35.

Upon completing the choice task, participants answered a post-experimental questionnaire asking how much they preferred and how much participants felt "in control" during the two trial types. On average, participants liked free choice (*M* = 4.26, *SD* = 1.26) more compared to forced choice (*M* = 3.13, *SD* = .96), *t*(30) = 4.799, *p* < 0.001, and felt more in control during free choice (*M* = 3.26, *SD* = .93) compared to forced-choice trials (*M* = 1.52, *SD* = .88), *t*(30) = 7.84, *p* < 0.001.

Next, average ratings between free- and forced-choice conditions were compared to test whether there were differences in perceived negativity of picture between the two trial types across pictures. Subjects rated images as significantly less negative in the free-choice trials (*M* = 3.29 , *SD* =0.59) relative to forced-choice trials (*M* = 3.45, *SD* =0.55), *t*(31) = -2.646, *p* = 0.013 (Fig 2.7).

To test whether ratings of categories differed between before and during (time) the choice task within each category of pictures, a repeated measures ANOVA (time x category) was implemented. Significant main effects were found for time *F*(1.392, 99.694) = 4.903, *p* < 0.05, and category *F*(2.765, 99.694) = 13.137, *p* < 0.001. There was a significant interaction between time and category *F*(4.335, 99.694) = 6.585, *p* < 0.001. Whereas ratings in the accident and injury categories did not reveal differences before and during the choice task, ratings for threat pictures were lower during free- and forced-choice trials compared to initial baseline. Ratings for grievance were lowest during free-choice trials, higher during forced-choice trials, and greatest during initial baseline.

Reward sensitivity was moderately correlated with free (r = .404, n = 31, p = .024) and forced choices (r = .461, n = 31, p = .009).

Summary

The present study probed whether exercising choice over negative stimuli modulates affective responses by using a simple choice paradigm using negative stimuli. Consistent with previous experimental designs 1—3, participants felt greater in control and preference for free choice over negative pictures, in line with studies demonstrating people feel increased sense of control and confidence when allowed to make choices and practice personal freedom (Langer, 1975; Langer & Rodin, 1976; Rotter, 1966; Taylor, 1989). Moreover, participants took longer to make decisions when exerting choice. These results may be suggestive of deliberate attention and enhanced cognitive effort towards making a response to achieve one's goal when provided with the option to choose. Importantly, in the current experimental design, we found a decrease in subjective ratings of negative images when participants were given the option to choose a negative picture to watch. These findings give support to the idea that the provision of choice may serve as a means to regulate emotions in aversive circumstances.

Furthermore, a benefit of the current experimental design was that we were able to explicitly compare subjective ratings of pictures before and during the choice task. From this analysis, we found an interesting pattern that emerged such that ratings before and during the task was influenced by specific contexts of pictures. For instance, while ratings for *injury* and *accident* categories did not show differences before and during the task, participants rated *threat* pictures much greater during initial baseline compared to

during the task. When participants chose pictures of *grievance*, they rated those pictures as less negative during free choice, higher during forced choice and greatest during initial baseline. These findings are consistent with the idea that effects of controllability on emotional responses may vary as a function of contextual factors (Wood et al., 2015; Salomons et al., 2007), suggesting certain domains within negative contexts compared to others could be more easily regulated by an opportunity for choice.

The revised choice task consisted of a few major modifications which included the addition of a 'Go' phase that aimed to measure participants' subliminal approach and avoidance responses towards pictures. In the previous version of choice task, whereas both options (i.e., accident vs. injury) were visible during forced choice conditions, the revised task presented two of same options to emphasize that there were no other options available during forced-choice trials. Contrary to expectations, subliminal responses to pictures were non-distinguishable during the 'Go' phase between the two trial types. However, as described above, we found free-choice trials to modify explicit emotional experiences towards aversive pictures. These contrasting results might suggest that having the option to choose a negative event alters perceptual meaning of the stimulus, hence affecting the emotional significance of an event (Averill, 1973) rather than affecting one's emotional responses at the subliminal level (i.e., reaction time).

General Discussion

In the current set of studies, we examined how exercising choice over negative stimuli alters emotional processing by using a simple choice paradigm. We reliably found that exerting free choice relative to forced choice induced enhanced feelings of control

across experiments 1—4. This finding is consistent with previous research that indicate increases in sense of control and confidence by exercising choice (Langer, 1975; Langer & Rodin, 1976; Rotter, 1966; Taylor, 1989). Across the four studies we also found that individuals have a greater preference for free choice over forced choice, suggesting choice is inherently rewarding and may be biologically motivating (Leotti et al., 2015). When participants exercised decisional control in which their actions not influence the actual outcome, we did not find differences in ratings between free and forced choices. These results suggest that although merely having choice between options unrelated to the outcome enhances a sense of control, it does not affect emotional processing of stimuli. However, in Experiment 4, we found that exercising free choice via instrumental control reduces emotional reactions to negative pictures compared to forced choice. These findings bolster the idea that the ability to control the outcome may serve as an emotion regulation strategy in the face of distressful stimuli.

It is important to consider the different levels of control participants felt in each of our experiments. In experiments 1-3, forced choices involved presentation of two options in which both options were visually available to participants. The visual availability of both options might have induced psychological factors that may have influenced participants' levels of control within forced choices. One element to consider is that participants may have developed a status quo bias to avoid the responsibility of choosing a wrong option (Baron & Ritov, 1994; Kahneman & Tversky, 1982), and may have engaged in self-fulfilling bias such that the chosen option by the computer might be better than the unchosen one. Another possibility is comparison of values between the two options during forced choice, which could influence some levels of control. Related to

this point, we found that when two of same options were provided during forced choice, we found a significant difference in affective responses between free and forced choice. Altogether, these data suggest visual availability of options can play an important role in levels of perceived control which can further influence the way individuals process affective stimuli.

The first experiment tested whether free choice influences evaluation of emotional outcomes (e.g., success vs. failure). In this experiment, participants were given the option to choose between two colored keys that either led to a neutral or negative picture. Participants were told that the goal of the experiment was to avoid seeing a negative image, and that choosing the correct key would lead to a neutral picture. In these trials, it is likely that participants attributed negative images as a result of one's failure, hence potentially eliciting negative emotional arousal. Such conditions may induce the tendency for a status quo bias in order to avoid responsibility for making the wrong decision and minimize regret (Baron & Ritov, 1994; Kahneman & Tversky, 1982), hence developing a preference for computer-choice trials. Indeed, literature on status quo bias suggest individuals may be inclined to accept the status quo to avoid a sense of accountability for error and regret from making errors (Kahneman & Tversky, 1982; Ritov & Baron, 1990). These findings indicate emotional responses may depend on interpretations of the outcome, and attributing an outcome as one's failure may make it difficult to alter emotional responses. Altogether, these results suggest the need to control for the possibility of attributing an outcome as success or failure when viewing negative or positive outcomes.

Therefore, our choice task was modified in a subsequent experiment (Experiment 2) to dissociate feelings of failure or success from processing affective events. A training session was added in the beginning of the experiment, such that participants could learn explicitly which key would lead to a greater reward value prior to the choice task. Subsequently in the choice task, participants were given the opportunity to select a key in each trial without seeing feedback about the monetary outcome but were shown a negative or neutral picture presented at random. Hence, in the second phase of the experiment, participants' emotional responses to pictures were not associated with feelings of failure or success in a given trial.

Although participants' ratings of pictures were not influenced by attributions of failure or success in this version of choice task, our results may have been influenced by the complexity of our design. Contrary to all other studies (Experiments 1, 3, and 4), we did not find differences in reaction times between free- and forced-choice trials in Experiment 2, which might indicate that the current version may have been difficult to perform due to the addition of the training phase. Even though one key was rewarded with substantially high probability than the other key during training, a number of subjects reported they did not prefer the better key over the other after the training phase. Therefore, it was necessary for a subsequent experiment to simplify the choice paradigm without changing the nature of the study (examining the effect of choice on processing affective stimuli).

Consequently, a new task was designed to probe the idea of exercising choice as an emotion regulation strategy by simplifying the choice paradigm. In this version (Experiment 3), subjects were provided with two scenarios to choose from (i.e., injury vs.

accident). Selecting an option led to the presentation of corresponding picture. Hence, participants could directly choose which negative image to watch, enhancing the feeling of control in a simple choice paradigm. This design provided benefit over the previous version because it allowed individuals to directly choose a preferred type of picture without an extra phase that might complicate choice processing. Although people preferred and reported free-choice trials to enhance feelings of control, we did not find differences in ratings of pictures between free and forced choice (Experiment 3). An explanation for this result might account for allowing participants to see both options (i.e., accident vs. threat) during computer-choice trials, encouraging value comparisons between options. Seeing both options may facilitate value computations and influence processing of pictures thereby interfering with feelings of control during forced choices. Therefore, although reaction time data and ratings of perceived control between forced and free choice suggest people feel greater in control and are more attentive during free-choice trials, subsequent steps required testing a paradigm that did not involve value computations during forced-choice trials.

As a result, Experiment 4 investigated the influence of choice on affective responses by providing two of the same options (i.e., grievance vs. grievance) in forced-choice trials, effectively restricting choices to only one option. This design provided benefit over the previous task because it accentuated a lack of control component by removing the potential for value comparisons during forced choices. As originally expected, we found decreased negative emotions when people exercised choice over distressing pictures. These results are consistent with previous research indicating control beliefs may incur important consequences on emotional processes. Prior studies have

demonstrated the influence of control beliefs on different domains of affect such as on pain (Jensen & Karoly, 1991; Salomons et al., 2004, 2007), medical conditions (Sharot et al., 2010), and fear conditioning (Hartley et al., 2014), indicating distressful events are experienced as less aversive when we perceive a means to control the stimulus. However, the in contrast to the specific domains, the precise mechanism underlying the impact of exercising choice on broader negative emotions has been unclear.

Findings from the current set of experiments provide evidence that exerting choice over negative stimuli may alter emotional responses. Importantly, contrary to Experiments 1–3, results from Experiment 4 showed that having the option to choose a category of picture reduces negative significance of the event. Previous studies have also reported inconsistencies on the effect of choice on subjective experiences of affective stimuli (Borckardt et al., 2011; Maier & Watkins, 1998; Salomons et al., 2007; Staub et al., 1971; Weich et al., 2006). The current study adds another layer to previous studies such that even when individuals perceive greater control as found in experiments 1–3, contextual factors play an important role in influencing emotional significance of an event. Collectively, our data suggest that context influences controllability, and the opportunity for choice plays a significant role in modulating emotions in distressing circumstances.

Chapter 3

AIM 2: To examine the neural mechanisms underlying perceived control in reward sensitive individuals

(Published in the Frontiers in Decision Neuroscience)

Perceiving control via exercising choice, affects the ways in which we make decisions. For instance, individuals report an overall decrease in liking and consumption of rewards when they are forced as opposed to free (Catley & Grobe, 2008a; Oliveto et al., 1992). Neuroimaging studies also support this idea, such that individuals report greater rewarding feelings and recruit the striatum when anticipating the opportunity for choice (Leotti & Delgado, 2011, 2014). Although previous work investigating benefits of control have focused on the striatal-dependent anticipatory effects of choice (Leotti & Delgado, 2011, 2014; Sharot et al., 2009, 2010), the present study examined the neural circuitry of choice during the decision-making phase in which participants made choices between rewards. Therefore, the current study probed whether free choice recruits neural activity in the striatum modulated by other areas involved in reward processing, particularly in individuals sensitive to rewards.

Reward sensitivity refers to individual responsiveness to rewards and the positive affect derived from engaging in reinforcing behaviors (Gray, 1987). Sensitivity to reward can be influenced by the biological mesocorticolimbic system (Di Chiara et al., 2004; Kelley, Schiltz, & Landry, 2005) and psychological traits (Cohen, Young, Baek, Kessler, & Ranganath, 2005), which suggests it can vary significantly among individuals (Carver & White, 1994). Upon encountering stimuli with appetitive properties (i.e., food or

drugs), reward sensitivity may predict responses to obtain such cues, reflected by heightened activations in reward-related brain regions (Beaver et al., 2006; Carter, Macinnes, Huettel, & Adcock, 2009; Volkow et al., 2002). For instance, those with a high sensitivity to reward are more likely to experience greater cravings (Franken & Muris, 2005), recruit reward-related brain activity (Beaver et al., 2006; Hahn et al., 2009), and exhibit appetitive responses towards cues with greater reinforcement value (Davis, Strachan, & Berkson, 2004; Volkow et al., 2002). These findings highlight how reinforcers tend to promote approach behavior that lead to the seeking and consumption of incentives—effects that are more pronounced in humans with greater reward sensitivity (Stephens et al., 2010).

An important way of understanding responses to reward cues is to compare decisions voluntarily made by the individual (i.e., free choice) versus predetermined choices (i.e., forced choice). Expressing one's preference via choice can be rewarding, particularly when decisions are freely made as opposed to being forced (Lieberman, Ochsner, Gilbert, & Schacter, 2001; Sharot et al., 2009; Sharot, Velasquez, & Dolan, 2010). For instance, participants who were prompted to smoke on a predetermined schedule (forced choice) experienced significantly lower rewarding effects from smoking compared to those who were free to smoke (free choice) on their own schedule (Catley & Grobe, 2008b). In these types of choice studies, free-choice behavior is compared to forced-choice procedure that is experimenter-determined and the resulting outcome is measured. Such studies converge on the idea that exerting control via choice enhances a) motivation and performance (Patall, 2013; Ryan & Deci, 2000) and b) positive feelings and neural activity in reward-related brain regions such as the striatum when anticipating

an opportunity to exert control (Leotti and Delgado, 2011, 2014). Importantly, these findings suggest having the opportunity to choose (free choice) relative to being forced to choose (forced choice) between reward options may engage distinct behavioral and neural patterns in reward sensitive individuals. Although previous work examining benefits of choice have focused on neural responses during the anticipation of choice (Leotti and Delgado, 2011, 2014; Sharot et al., 2009, 2010), the present study investigates the period of choice itself and whether engaging in choices involving rewards recruits distinct neural systems as a function of reward sensitivity.

Implementing decisional control via choice augments general motivation and performance (Patall, 2013; Ryan & Deci, 2000). Decisional control is the ability to select a single course of action from potential alternatives (Averill, 1973). Thus, the opportunity for choice facilitates motivation to engage in behavior by allowing an individual to act as a causal agent to accomplish a desired goal. Prior research has suggested that the ventrolateral prefrontal cortex (VLPFC) may be sensitive to manipulations of motivation and performance (Taylor et al., 2004; Baxter et al., 2009). The VLPFC receives input from the orbitofrontal cortex and subcortical areas such as the midbrain and amygdala (Barbas & De Olmos, 1990) linked with motivational and affective information (Paton, Belova, Morrison, & Salzman, 2006; Tremblay & Schultz, 1999). The VLPFC has also been associated with cognitive control processes that guide access to relevant information (Badre & Wagner, 2007; Bunge, Burrows, & Wagner, 2004; Duncan & Owen, 2000; Petrides, Alivisatos, & Evans, 1995; Petrides, 2002) and is more activated during conditions that require goal-directed behavior (Sakagami & Pan, 2007). Interestingly, the VLPFC interacts with motor regions to orient attention (Corbetta & Shulman, 2002),

suggesting increased connectivity with VLPFC might be important for directing attention to relevant stimuli in reward sensitive individuals. Altogether, these findings suggest responses to choice may vary due to individual traits such as reward sensitivity, which can be tracked by the VLPFC (Mullette-Gillman, Detwiler, Winecoff, Dobbins, & Huettel, 2011). Other regions have also been associated with value computations, such as the striatum and ventromedial prefrontal cortex (Hare et al., 2008, 2009; Kable & Glimcher, 2007; Knutson et al., 2007; Lim et al., 2011). However, given that these regions are more closely related with intrinsic value signals in individuals without considering their sensitivity for rewards, we focused primarily in the VLPFC, which is often involved in anticipation of rewards in reward sensitive individuals (Chase et al., 2016; Whitton, Treadway, & Pizzagalli, 2015).

Here, we investigated how reward sensitivity contributes to neural responses associated with free and forced choices. For example, how does reward sensitivity interact with forced choices within a category (for example, broccoli and Brussels sprouts) versus free choices across categories (i.e., vegetables and snacks)? Will reward sensitive individuals demonstrate different patterns of brain activity during free relative to forced choices? In this study, we presented participants with two cues that were predictive of distinct classes of outcomes in each trial. Specifically, participants could earn points or information, both of which were tied to a monetary reward at the end of the experiment (Smith, Rigney, & Delgado, 2016). We presented these cues in two distinct formats. On free-choice trials, the cues were mixed (for example, subjects were free to choose between points or information), thus allowing participants to freely express their preference between points and information. On forced-choice trials, both cues were

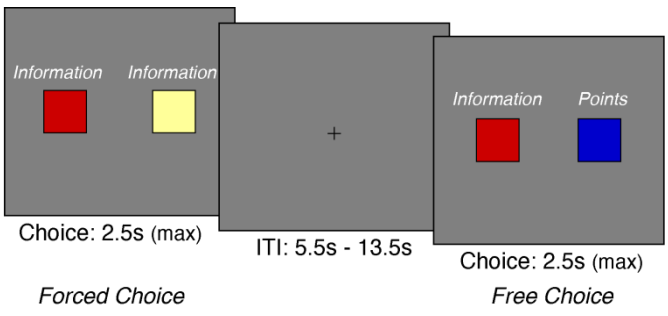
predictive of points or information, thus forcing the participant to choose within the given option (i.e., forced to choose within information or information), hence limiting their freedom to choose across cues. The goal of the task was to choose the option that maximized monetary reward to be obtained at the end. We focused on two key hypotheses. Based on prior studies demonstrating striatal involvement in the value of choice, we hypothesized reward sensitivity to be linked with reward signals in the striatum during free choice. Second, based on motivational control literature, we expected the VLPFC to modulate reward-related circuitry during free-choice trials in reward sensitive individuals.

Methods

Participants

Thirty-three healthy subjects participated in the current study (mean age = 24, range: 18-39, 18 females). Written informed consent was acquired from each subject for a protocol approved by the Institutional Review Board of Rutgers University.

Figure 3.1 Sequence of experimental task for Experiment 5 (Aim 2).



Stimuli and Task

In an experiment prior to this task (Smith et al., 2016), subjects performed a card task that involved learning about colors that were associated with either points or information. A *points trial* presented three cold colors, in which each color was associated with a point value (1, 2, or 3). An *information trial* presented three warm colors, and each color was probabilistically linked with a letter (D, K, or X). Upon selecting a color in each trial, participants received a feedback representing the value (either a point or letter) of the color. Participants performed 36 trials of each points and information trial types. Both types of trials were important because 1) subjects needed to accrue enough points to play a bonus game at the end to earn extra money, and 2) the bonus game presented a letter in each trial and subjects needed to answer correctly to win money. This task allowed participants to develop preferences for either points or information as a means to acquire reward. Because participants developed their own subjective preference for either points or information in this task, participants cared about their decisions in the subsequent session.

Next, we proceeded with the choice task, which provided opportunities for participants to choose their preferred cue (free choice) or computer-chosen options (forced choice). Our goal was to measure differences in neural activity in response to free and forced choices that varied as a function of reward sensitivity (Fig. 3.1). On free-choice trials, participants chose freely between a cue that delivered points and a cue that delivered information. Because participants had developed a preference for either points or information in order to obtain rewards, it was important for them to be able to choose their preferred cue during free-choice trials. On forced-choice trials, participants were

presented with two cues that delivered either points or information. This procedure blocked the participant from choosing between points and information—which effectively forced them to choose the presented option (cf. Lin et al., 2012). Hence, participants were unable to choose their preferred cue in these trials, and either cue type was randomly presented. The goal of the task was to maximize monetary reward to be received at the end of the task.

Each trial was separated by a random intertrial interval from 5.5 s to 13.5 s. At the end of the task, a randomly chosen trial from each subject's response was presented with an associated monetary reward. The present experimental task was programmed using the Psychophysics Toolbox 3 in MATLAB (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007).

Temporal Experience of Pleasure Scale (TEPS)

To probe individuals' sensitivity to rewards, we implemented the Temporal Experience of Pleasure Scale (TEPS; Gard et al., 2006). The scale is composed of two subscales measuring anticipatory (10 items) and consummatory (8 items) pleasure. Anticipatory pleasure reflects positive feelings derived from anticipation of a reinforcer, whereas consummatory pleasure measures in-the-moment feelings of joy in response to a pleasurable cues (Gard et al., 2006; Treadway & Zald, 2011). Based on previous literature which suggests perceiving control via choice is rewarding (Leotti and Delgado, 2011, 2014), we focused on the consummatory subscale as subjects were expected to increase feelings of joy upon being presented with an option of control.

fMRI Data Acquisition and Preprocessing

Functional magnetic resonance imaging data were acquired on a 3T Siemens MAGNETOM Trio scanner using a 12-channel head coil at the Rutgers University Brain Imaging Center (RUBIC). Whole-brain functional images were collected using a T2*-weighted echo-planar imaging (EPI) sequence. The parameters for the functional measurement were as follows: GRAPPA with R = 2; repetition time (TR) = 2000 ms; echo time (TE) = 30 ms; flip angle = 90°; matrix size = 68 x 68; field of view (FOV) = 204 mm; voxel size = 3.0 x 3.0 x 3.0 mm; with a total of 37 slices (10% gap). High-resolution T1-weighted structural scans were collected using a magnetization-prepared rapid gradient echo (MPRAGE) sequence (TR: 1900 ms; TE: 2.52 ms; matrix 256 x 256; FOV: 256 mm; voxel size 1.0 x 1.0 x 1.0 mm; 176 slices; flip angle: 9°). B0 field maps were also obtained following the same slice prescription and voxel dimensions as the functional images (TR: 402 ms; TE1: 7.65 ms; TE2: 5.19 ms; flip angle: 60°).

Imaging data were preprocessed using Statistical Parametric Mapping software (SPM12; Wellcome Department of Cognitive Neurology, London, UK [http://www.fil.ion.ucl.ac.uk/spm/software/spm12]). Each image was aligned with the anterior commissure posterior commissure plane for better registration. To correct for head motion, each time series were realigned to its first volume. Using the B0 maps, we spatially unwarped each dataset to remove distortions from susceptibility artifacts. Prior to normalization of the T1 anatomical image, mean EPI image was coregistered to the anatomical scan. A unified segmentation normalization was performed on the anatomical image, which was used to reslice EPI images to MNI stereotactic space using 3-mm isotropic voxels (Ashburner & Friston, 2005). Normalized images were spatially

smoothed using a 4-mm full-width-half-maximum Gaussian kernel. Additional corrections were applied to control for motion using tools from FSL (FMRIB Software Library), given that connectivity results can be particularly vulnerable to severe distortion by head motion. Motion spikes were identified by calculating the differences between the reference volume and 1) root-mean-square (RMS) intensity difference of each volume, and 2) mean RMS change in rotation/translation parameters. A boxplot threshold (i.e., 75 percentile plus 1.5 times the interquartile range) was applied to classify volumes as motion spikes. Once identified, all spikes and the extended motion parameters (i.e., squares, temporal differences, and squared temporal differences) were removed via regression (Power, Schlaggar, & Petersen, 2015). Next, non-brain tissue was segmented and removed using robust skull stripping with the Brain Extraction Tool (BET), and the 4D dataset was globally normalized with grand mean scaling. Low frequency drift in the MR signal was removed using a high-pass temporal filter (Gaussian-weighted least-squares straight line fit, with a cutoff period of 100 s).

FMRI Analyses

Imaging data were analyzed using the FEAT (fMRI Expert Analysis Tool) module of FSL package, version 6.0. A general linear model (GLM) with local autocorrelation correction was used for our model (Woolrich, Ripley, Brady, & Smith, 2001). First, we generated a model to identify brain regions that showed increased BOLD signal as a function of free and forced choice conditions. Our GLM included five regressors to model two cues (i.e., points or information) presented to subjects during the two conditions (free and forced choice): free choice (points), forced choice (points), free

choice (information), forced choice (information), and missed responses. Therefore, each condition (forced or free) consisted of two regressors (points and information). Our main contrast of interest was free > forced choice. The goal of this analysis was to identify brain regions that respond to free choice as a function of reward sensitivity. Therefore, individual scores of TEPS were entered as a covariate in identifying a region in the free – forced choice.

Using the output from free- vs. forced-choice contrast, we selected a seed region to conduct a psychophysiological interaction analysis (PPI; Friston et al., 1997). Recent meta-analytic work has demonstrated that PPI produces consistent and specific patterns of task-dependent brain connectivity across studies (Smith & Delgado, 2016; Smith, Gseir, Speer, & Delgado, 2016). The primary purpose of conducting PPI analysis is to detect regions that show increased functional connectivity with the seed region as a function of an experimental manipulation. For each individual, we extracted BOLD time-series from the peak voxel within a mask of the VLPFC cluster. The whole cluster was identified using the contrast of the regressor during free-choice vs. forced-choice trials. Next, we generated a single-subject GLM consisting of the following regressors: five main regressors/conditions, a physiological regressor representing the time course of activation within the VLPFC ROI, and interactions with VLPFC activity with each of the four main regressors. Importantly, modeling PPI effects separately for each condition (i.e., a generalized PPI model) has been shown to result in improved sensitivity and specificity (McLaren, Ries, Xu, & Johnson, 2012). We included nuisance regressors in our model to account for missed responses during the decision-making phase. All task regressors were convolved with the canonical hemodynamic response function. We

modeled group-level analyses using a mixed-effects model in FLAME 1 (FMRIB's Local Analysis of Mixed Effects), treating subjects as a random effect (Beckmann, Jenkinson, & Smith, 2003). All z-statistic images were thresholded and corrected for multiple comparisons using an initial cluster-forming threshold of $z > 2.3$ and a corrected cluster-extent threshold of $p < 0.05$ (Worsley, 2001).

Results

In aim 2, we addressed the question whether individual differences in reward sensitivity are associated with behavioral and neural responses to free and forced choice. Our behavioral analyses focused on evaluating individual difference scores in reward sensitivity with TEPS. Subsequently, we analyzed differences in reaction times in free and forced choice trials.

Individual differences in reward sensitivity

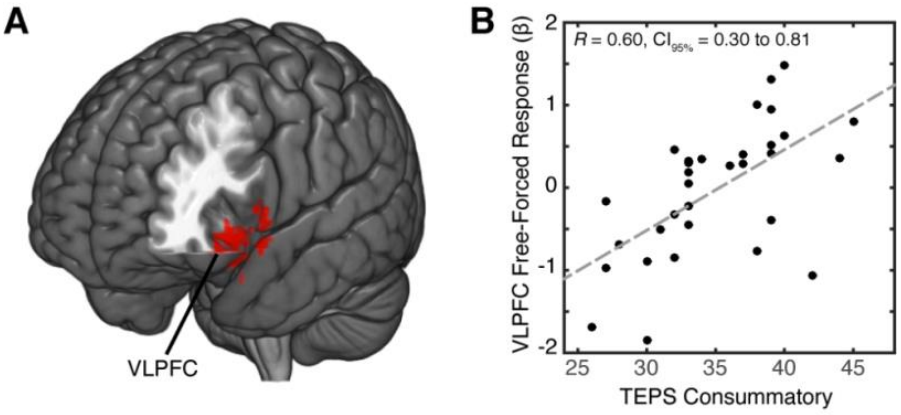
From an experiment preceding the choice task, we found that subjects were more likely to prefer affective choices (M = .607, SD = .182) compared to informative choices (M = .393, SD = .182); $t(32)$= -3.367, p = .002. They were successful at obtaining relevant information as indicated by performance in the bonus task (M = 69.36%; SE = 3.45%). The bonus task assessed the extent to which the participants learned the associations between the colors and letters, which led to a monetary bonus.

Consistent with previous research (Carter et al., 2009; Chan et al., 2012), we quantified reward sensitivity with TEPS (Gard et al., 2006). Given that our primary goal was to examine how reward sensitivity interacts with responses to free and forced choices

during the decision-making phase, our subsequent analyses focused on the consummatory component of the TEPS. Individuals varied in the consummatory reward sensitivity score (TEPS-c) from 34.91 ± 4.89 (mean ± SD, ranging from 26 to 45), which was positively related with TEPS-a, $r(31) = .42$, $p < .05$.

Making decisions during free and forced choices might be associated with different levels of difficulty in decision making, which may yield slower or faster reaction times between conditions. To test whether subjects perceived differences in difficulty between the two trial types, we conducted a paired-sample t-test to measure differences in response times between free and forced-choice trials. Reaction times between free (M = 1.1700 s, SD = 0.279 s) and forced choice (M = 1.166 s, SD = 0.2697 s) were not significant ($t(32) = -0.131$, p = 0.45). Hence, our reaction time results suggest 1) participants perceived both types of trials as similar in difficulty, and 2) further differences in neural activity were not driven by participants' reaction times between free and forced choice trials. Nevertheless, individual differences in response times could be tied to reward sensitivity. We therefore examined whether response times for free and forced choice were correlated as a function of individual reward sensitivity (TEPS-c). We did not find a relationship between reward sensitivity scores and response times (TEPS-a and reaction time during free choice, r = -.15, n.s.; TEPS-a and reaction time during forced choice, r = -.08, n.s.; TEPS-c and reaction during free choice, r = -.18, n.s.; and TEPS-c and reaction time during forced choice, r = -.16, n.s.). Taken together, these observations suggest both types of trials did not reveal any differences in response times that could be attributed to further differences in neural activations.

Figure 3.2 Increased VLPFC activity in reward sensitive individuals during free vs. forced choice.

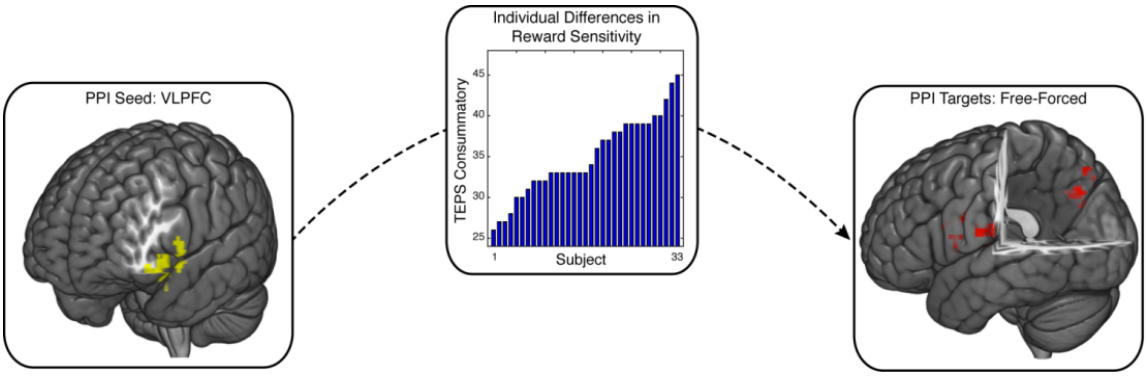


Reward sensitivity engages the VLPFC during choice

Perceiving a freedom for choice enhances positive feelings and is rewarding (Leotti, Iyengar, & Ochsner, 2010; Leotti & Delgado, 2011). If choice is truly rewarding, we could predict individuals particularly sensitive to rewards would recruit regions involved in anticipation of rewards in individuals prone to reward sensitivity. The VLPFC has been implicated in anticipation of rewards in reward sensitive individuals (Chase et al., 2016; Whitton et al., 2015). Hence, we predicted VLPFC recruitment would vary along scores of reward sensitivity during free-choice trials. A region previously associated with cognitive control, response selection, and reward motivation (Badre & Wagner, 2007; Baxter et al., 2009; Taylor et al., 2004), previous findings support the engagement of VLPFC in reward-motivated trials. To test our hypothesis of whether individual differences in reward sensitivity modulated distinct brain regions in response to free choice, we examined neural patterns that covaried as a function of reward sensitivity during free vs. forced choice. In our whole-brain analysis of free vs. forced

choice contrast, we identified a cluster within the left ventrolateral prefrontal cortex (VLPFC) (MNIx,y,z, = -48, 23, -19; 140 voxels, p = 0.011) (Fig. 3.2a) that covaried with individuals' reward sensitivity scores (Fig. 3.2b). Specifically, individuals who reported greater reward sensitivity scores exhibited greater activation in the VLPFC during free choice compared to forced-choice trials. We did not observe any activations from the forced vs. free contrast that covaried with reward sensitivity scores, even at a lower uncorrected-threshold.

Figure 3.3 Enhanced VLPFC connectivity with PCC and precentral gyrus during free choice compared to forced choice.



Enhanced connectivity of the attentional systems and the ventrolateral prefrontal cortex during free choice

Our whole-brain cluster analysis suggests a role for the VLPFC in processing free choice in reward sensitive individuals. The VLPFC is densely connected with a number of structures associated with cognitive control and motivational systems (Petrides & Pandya, 2002; Sakagami & Pan, 2007). One potential idea is that connectivity of VLPFC

with these regions may support response selection and goal-directed behavior during free-choice trials. We tested this idea using a psychophysiological interaction (PPI) analysis with the VLPFC defined by the cluster analysis as our seed region (Friston et al., 1997). By implementing PPI analyses, our goal was to identify regions that exhibit increased functional connectivity with the VLPFC in reward sensitive individuals during opportunities for free compared to forced choice. Our PPI analysis identified two clusters in the posterior cingulate cortex (PCC) (MNIx,y,z = 18, -73, 41; 103 voxels, $p = 0.043$) and the precentral gyrus (MNIx,y,z = -39, -19, 35; 156 voxels, $p = 0.0035$), which showed enhanced connectivity with VLPFC as a function of individuals' reward sensitivity (Fig. 3.3).

Discussion

The present study investigated the influence of free choice on individual differences in reward sensitivity. When given free choice, individuals high in reward sensitivity revealed enhanced VLPFC activation, a region known to be involved in attentional control and response selection. Further, our PPI analyses found increased VLPFC connectivity with the PCC and precentral gyrus that might be involved in motor processing during free-choice trials in reward sensitive individuals. These observations suggest reward sensitivity may recruit VLPFC-related attentional control processes during free choice that relate to goal-directed behavior and action selection.

Individuals high in reward sensitivity show a tendency to engage in goal-directed behavior and to experience pleasure when exposed to cues of impending reward (Carver & White, 1994; Gard et al., 2006). When given an opportunity to freely choose between

options, individuals sensitive to rewards may more readily orient to an option that leads to maximizing their goal (i.e., increasing chances of reward). The VLPFC has been associated with computing behavioral significance by integrating input from regions processing motivational and affective information (Sakagami & Pan, 2007). Experiencing control via exerting self-initiated choice is motivating and can be rewarding in it of itself (Bhanji & Delgado, 2014; L. A. Leotti, Cho, & Delgado, 2015; R M Ryan & Deci, 2000). A region linked with tracking reward expectancy value (Pochon et al., 2002), the recruitment of VLPFC during free choice in reward sensitive individuals might suggest a role for the region in increasing attentional control (Badre & Wagner, 2007; Bunge et al., 2004; Duncan & Owen, 2000) and guiding goal-directed behavior (Sakagami & Pan, 2007). Consistent with this idea, greater VLPFC activation is observed when individuals make decisions between consequential choices (i.e., choosing with whom to date) relative to inconsequential choices (i.e., choosing between same-sex faces) (Turk et al., 2004). Our results suggest that an opportunity for free choice enhances attentional biases to maximize goals (i.e., reward maximization) by increasing VLPFC activation in reward sensitive individuals. Exerting control by expressing one's choice has been linked with adaptive consequences (Bandura, 1997; L A Leotti et al., 2010; Richard M Ryan & Deci, 2006), and one's ability to choose between alternatives modulates expectancy towards hedonic and/or aversive outcomes (Leotti & Delgado, 2014; Sharot et al., 2009, 2010). Our findings may extend to interpretations of motivational influences of free choice on reward sensitivity by modulating cognitive control regions that may facilitate goal-directed behavior.

A novel aspect of our study was that when individuals chose freely between options, we observed increased VLPFC connectivity with the precentral gyrus and the PCC/precuneus. Although the PCC is commonly associated with the default-mode network (Buckner, Andrews-Hanna, & Schacter, 2008), recent findings have suggested that the PCC can also participate in the cognitive control network (Leech, Braga, & Sharp, 2012; Leech, Kamourieh, Beckmann, & Sharp, 2011; Utevsky, Smith, & Huettel, 2014). This observation has led some researchers to argue that the PCC is involved in detecting and responding to stimuli that demand behavioral modifications (Leech & Sharp, 2014; Pearson, Heilbronner, Barack, Hayden, & Platt, 2011). By interacting with regions involved in cognitive control, the PCC might help individuals more readily orient to options during free choice and increase efficacy of behavioral responses promoting maximization of one's goals (i.e., earning rewards). In line with this explanation, our results indicate making a choice between two attributes is facilitated by increased VLPFC connectivity with the PCC. This finding yields a potential interpretation that free choice enhances VLPFC region connectivity with target PCC and precentral regions to support motor responses in reward sensitive individuals. A recent meta-analysis of PPI studies found PCC was a reliable target of studies examining cognitive control, but only when the dorsolateral prefrontal cortex was used as the seed region (Smith, Gseir, et al., 2016). This discrepancy could be due to the fact that our results are based on individual differences in reward sensitivity, which were explicitly ignored in the recent PPI meta-analysis. In addition, because our analyses are limited to connectivity between regions and not directionality, an alternative explanation accounts for VLPFC region modulating PCC in response to context-specific factors (i.e., free choice) modulated by individual

differences in reward sensitivity. The brain engages in multiple processes of valuation when deciding between different options. Once the sensory information is computed, signals are integrated with other motivational and contextual factors, which are then used to guide choices (Grabenhorst & Rolls, 2011; Kable & Glimcher, 2009). The interactions between the VLPFC and PCC increased during free choice, suggesting cognitive resources are made accessible via enhanced connectivity of the PCC with the cognitive control network (Leech et al., 2012; Utevsky et al., 2014).

Contrary to our hypothesis, we did not observe an association between reward sensitivity and reward signals in the striatum during free choice. Studies suggest striatal recruitment can depend on variables such as individual differences (i.e., preference for choice) and can be influenced by contextual factors (such as gain or loss context) (Leotti & Delgado, 2014). It is possible that individuals value opportunity for choice because they believe such choice will provide them access to the best option available. Consistent with this idea, previous studies found reward-related striatal activation is limited to free-choice biases primarily predicting positive outcomes (Cockburn et al., 2014; Lauren A Leotti & Delgado, 2011, 2014). Hence, it is possible that the striatum did not dissociate between free and forced choices because value across both conditions were similar. It is also noteworthy that we did not observe neural activations involved in value computation in our contrasts that correlated with reward sensitivity scores. In our experimental design, there were no differences in value representation between points and information because they both led to monetary rewards. Therefore, a potential explanation for not finding value modulated brain areas as a function of reward sensitivity might account for similarity of value associated with each option.

The purpose of the current study was to compare free vs forced choices involving rewards not necessarily prescribed to negative or positive outcomes, and both types of choice trials were related to accomplishing the goal of the task (i.e., accruing monetary outcomes). The opportunity to choose involves making a decision by selecting a response necessary for obtaining one's goals, processes supported by VLPFC (Badre & Wagner, 2007; Bunge et al., 2004; Duncan & Owen, 2000; Sakagami & Pan, 2007). Consistent with this perspective, the VLPFC emerged as a key region in our paradigm that tracked the opportunity for choice in reward sensitive individuals. In sum, our results suggest goal-directed behavior (i.e., increasing chances of reward) might be facilitated in reward sensitive individuals by enhanced attentional and cognitive control network in response to trials that afford them free choice.

We note that our reward sensitivity findings may have important clinical implications. Psychiatric patients often show deficits in decision-making tasks involving rewards (Parvaz, MacNamara, Goldstein, & Hajcak, 2012). For instance, substance abuse and psychopathy are related to high levels of responsiveness to rewards (Buckholtz et al., 2010; Schneider et al., 2012; Tanabe et al., 2013; Yau et al., 2012). Reward sensitivity is also associated with negative mental-health outcomes such as greater risks for addictions (Kreek, Nielsen, Butelman, & LaForge, 2005), alcohol abuse (Franken, 2002), eating disorders (Davis et al., 2004; Franken & Muris, 2005), and depressive disorders (Alloy, Olino, & Freed, 2016). Consistent with our findings from reward sensitivity, bipolar patients show hypersensitivity to rewards and recruit VLPFC when anticipating rewards (Chase et al., 2016; Whitton et al., 2015), and pathological gamblers tend to reveal hyposensitivity to rewards and fail to activate the VLPFC in response to monetary

rewards (de Ruiter et al., 2009). The close association between levels of sensitivity for rewards and psychiatric disorders may implicate failures in the executive control network during affective and motivational processing (Heatherton & Wagner, 2011; Johnstone, van Reekum, Urry, Kalin, & Davidson, 2007). An exciting direction for future research is with respect to understanding networks and the specific connectivity affected by reward in/sensitivity that govern decision-making processes.

Although our results may have implications for clinical research, we note that a number of limitations accompany our results. First, in our design, free choice offered individuals a choice between dissimilar options, whereas forced-choice trials provided participants with similar options. It is possible that subjects perceived forced-choice trials as easier than choice trials upon making decisions. However, analyses on reaction times did not reveal significant differences between free- vs. forced-choice trials, which suggest our findings were not due to differences in perceived difficulty between trial types. Also, an alternative approach to human behavior of preferring forced choice could be explained by the regret theory (Loomes & Sugden, 1982), which suggests feelings of regret are enhanced when the option taken leads to a worse outcome than the alternative option. Therefore, humans may have a tendency for a status quo bias to minimize a feeling of regret (Nicolle, Fleming, Bach, Driver, & Dolan, 2011). Moreover, although some aspects of our design did not measure forced choice explicitly in line with conventional free vs. forced choice framework, given that reward sensitive regions are context specific and varies in accordance with the range of possible options available (Nieuwenhuis et al., 2005), the current study tested whether brain activations in reward sensitivity would dissociate responses to free choices between categories compared with forced choices

within a category. Second, it is also worth noting that the VLPFC has been implicated in a number of roles including incentive motivation (Baxter et al., 2009; Taylor et al., 2004), cognitive regulation (Lopez, Hofmann, Wagner, Kelley, & Heatherton, 2014), response inhibition (Aron, Robbins, & Poldrack, 2004), and task switching (Braver, Reynolds, & Donaldson, 2003). Therefore, there may be alternative explanations for the VLPFC activation in reward sensitive individuals. However, research demonstrates consistency of VLPFC activation patterns in response to rewarding stimuli as a function of reward sensitivity (de Ruiter et al., 2009; Whitton et al., 2015; Yokum, Ng, & Stice, 2011), suggesting a role for the region in modulating attentional control in response to rewarding contexts particularly for reward sensitive individuals. Finally, we note that complex personality traits such as reward sensitivity can be difficult to quantify. Although TEPS provides one validated approach for measuring reward sensitivity, we note that other scales have also been used to relate brain responses to personality traits associated with reward and motivation. For instance, recent work has demonstrated that individual differences in regulatory focus are associated with PCC responses to promotion goals (Strauman et al., 2013) and ventral striatal responses to reward (Scult et al., 2016). These observations suggest that future work may be able to build on our findings be integrating regulatory focus theory and other personality measures with classical measures of reward sensitivity (e.g., TEPS and BIS/BAS).

Despite these caveats, our findings suggest that reward sensitivity may be an important factor in determining one's responses to rewarding stimuli. This can extend to intrinsically rewarding stimuli, such as the opportunity to exert control. When given an opportunity to make a free choice, high reward sensitive individuals might demonstrate

enhanced reactivity and engage greater attentional and motor control necessary for achieving one's goals (i.e., accruing more money).

Chapter 4

AIM 3: To investigate the dynamic patterns of neural circuitry associated with perceiving control

Perceiving control over our environment is a critical determinant of our health and psychosocial well-being (Bandura, 2006; Ryan & Deci, 2006). Linked with a wide range of positive outcomes, perception of control has been associated with factors such as academic achievement and persistence (Multon, Brown, & Lent, 1991), child development (Bandura, Caprar, Barbaranelli, Gerbino, & Pastorelli, 2003), work-related performances (Stajkovic & Luthans, 1998), and health functioning (Holden, 1992). Exercising decisional control via choice augments general motivation and performance (Patall, 2013; Ryan & Deci, 2000). Decisional control refers to the ability to select a single course of action from potential alternatives (Averill, 1973). Hence, the opportunity for choice facilitates motivation to engage in behavior by allowing an individual to act as a causal agent to accomplish a desired goal. Having an opportunity to choose increases competence, satisfaction, and engagement in various tasks (Cordova & Lepper, 1996; Grolnick & Ryan, 1987; Langer & Rodin, 1976; Patall, et al., 2008; Patall, Cooper, & Wynn, 2010; Ryan & Deci, 2000), suggesting that opportunities for decisional control can be a powerful motivator.

Consistent with behavioral data indicating desirability for choice, neural evidence supports the idea that anticipation of choice is inherently rewarding. A key region involved in reward processing, the striatum is recruited during anticipation of choice (Frank, Doll, Oas-Terpstra, & Moreno, 2009; Leotti & Delgado, 2011, 2014; Murty et al.,

2015), suggesting opportunity for choice can be desirable and enhances positive feelings. Located in a prime area for processing affective and reward-related information that may be linked with perceiving control, the striatum receives projections from cortical and midbrain dopaminergic structures (Haber, 2003; Haber & Knutson, 2010). Specifically, the striatum exhibits connectivity with regions such as the vmPFC and DLPFC implicated in value computation and emotion regulation, which could influence how one perceives control. In this study, we investigated the dynamic interplay between cortical (i.e., DLPFC and vmPFC) connectivity with the striatum underlying affective processes of choice anticipation.

Neuroimaging literature supports striatal involvement in different components of controllability. For example, the striatum is recruited when one perceives contingency between one's actions and rewards (Bjork & Hommer, 2007; O'Doherty, Critchley, et al., 2003; O'Doherty et al., 2004; Tricomi et al., 2004). Striatal activity tracks choice-induced preferences (Cockburn et al., 2014; Fujiwara et al., 2013; Izuma et al., 2010; Sharot, De Martino, & Dolan, 2009) and is recruited by merely choosing, as opposed to rejecting an item (Sharot, De Martino, & Dolan, 2009; Sharot et al., 2010). Consistent with the notion that choice is rewarding, more recent evidence suggests the striatum is involved during the anticipation of choice (Frank, Doll, Oas-Terpstra, & Moreno, 2009; Leotti & Delgado, 2011, 2014; Murty et al., 2015). However, it is unclear from which neural input it receives information about controllability in the environment, and motivates the need to examine coupling with other cortical regions involved in perceiving control. Given that the striatum is a multifaceted structure that receives input from cortical regions, we could expect the striatum to show differential connectivity with regions within the prefrontal

cortex that are involved in aspects of control (i.e., vmPFC, DLPFC). Therefore, the following hypotheses were tested in the current study.

The first hypothesis is that there will be enhanced coupling between the DLPFC and striatum in response to choice anticipation. Neuroimaging studies have implicated the prefrontal regions such as the dorsolateral prefrontal cortex (DLPFC) when perceiving control (Borckardt et al., 2011; Brascher et al., 2016; Wiech et al., 2006). The DLPFC is associated with regulating negative emotions by directing attention to goals and reinterpreting the meaning of a stimulus (Ochsner, Silvers, & Buhle, 2012). Enhanced DLPFC activations during controllable conditions may support the idea that exerting control involves reinterpreting a potentially threatening stimulus and changing the meaning of a noxious stimulus (Averill, 1973). Therefore, if perceiving control via choice opportunity facilitates cognitive reinterpretations of stimuli, we could expect enhanced coupling between the DLPFC and striatum in response to choice anticipation.

The second hypothesis is that information about controllability enters the neural system via input into the vmPFC. While previous studies converge on the regulatory role of the lateral PFC in modulating affective experiences during control, the role of medial PFC influencing control experiences is rather complex. The vmPFC is associated with the detection of controllability (Amat et al., 2005; Maier et al., 2006; Maier & Watkins, 2010), and increased activity in this region is associated with guarding against negative effects from a stressor (Baratta et al., 2008; Maier et al., 2006). Studies have found increased ventromedial PFC activity during anticipation of control over negative stimuli/threat (Kerr et al., 2012; Wood et al., 2016) and during diminishing fear responses through extinction training and emotion regulation (Delgado et al., 2008). Such evidence

implicates the vmPFC in computing the contingency information between one's behavior and outcome (Dickinson, Balleine, Watt, Gonzalez, & Boakes, 1998; Maier & Watkins, 2010) and forming adaptive behavioral responses (Bhanji & Delgado, 2014). Consequently, given that the ventromedial PFC is critical for supporting controllability effects (Maier, Amat, Baratta, Paul, & Watkins, 2006), we could expect information about controllability to enter the neural system via input into the vmPFC, hence modulating activity in regions associated with emotional and motivational processes such as the striatum.

A third hypothesis is that choice anticipation involves a modulatory signal from the vmPFC to the striatum for an accurate update of expected value. Studies examining valuation processes implicate the ventromedial PFC in computations of value that drive choice (Hare et al., 2008, 2011; Levy et al., 2010), and increased activity in this region is associated with subjective value of rewards (Cohen et al., 2008; Gottfried et al., 2003; Kable & Glimcher, 2007; Kim et al., 2006). As mentioned above, choice anticipation is inherently rewarding and enhances responses in the striatum. Therefore, we could make two different hypotheses regarding directionality of modulatory signal from the vmPFC to striatum during choice anticipation. If value representations for choice enhances rewarding feelings, we could expect a positive modulatory input of vmPFC on the striatum. Accurate representations of value are critical for learning (Sutten & Barto, 1998) and decision making, which guides adaptive behavior (Cohen, 2008; Montague et al., 2004). Thus, when progressing from a trial to another, it is necessary to update expected value of stimuli that is encoded in the striatum (Kahnt et al., 20011; O'Doherty et al., 2003; Pessiglione et al., 2006). Thus, an alternative hypothesis is that choice

anticipation enhances an inhibitory signal into the striatum for an accurate representation of expected value, which is encoded in the vmPFC (Kable and glimcher, 2007; Montague and Berns, 2002).

Research suggests that control experiences recruit regions consisting of vmPFC, DLPFC, and the striatum. However, the dynamics of the network underlying affective experiences of control has been yet to be explored. In the current study, we tested where information about choice anticipation enters the system and how it modulates the neural network involved in perceiving control. The employment of dynamic causal modeling (DCM) may help investigate directionality of cortical regions influencing affect-processing regions (i.e., striatum) when perceiving choice opportunity. To understand effective connectivity among a priori brain regions linked with choice opportunity, the current study compared hypothesized models using DCM. Given their involvement in perceiving choice, the following key regions were selected: the vmPFC, DLPFC, and the striatum (Ballard et al., 2011; Brascher et al., 2016; Kerr, McLaren, Mathy, & Nitschke, 2012; Leotti & Delgado, 2011; Maier et al., 2006; Salomons et al., 2004, 2007; Wiech et al., 2006) to examine their causal relationships supporting choice anticipation.

First, we constructed a model space consisting of reciprocal connections between all regions (vmPFC, DLPFC, and striatum) driven by our context modulation (anticipation of free or forced choice) (Fig 4.2). We hypothesized anticipation of free or forced choice (driving input) to enter the system through its input via one of our tested regions, and anticipation of free choice specifically would modulate connectivity between our regions of interest. Then, a Bayesian model comparison was conducted to compare and identify the model that provides the best model fit for our data (BMS, Stephan,

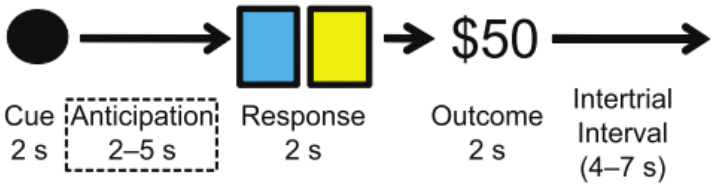
Penny, Daunizeau, Moran, & Friston, 2009) characterizing choice anticipation. The following questions were addressed in the current study. First, where does information about free and forced choice (driving input) enter the system? Second, which coupling between regions is influenced by anticipation of free choice?

Methods

Participants

Neuroimaging data set from a prior study from our group (Leotti & Delgado, 2011) was used to analyze connectivity patterns among a priori brain regions by implementing DCM. Twenty-seven healthy individuals were recruited via posted advertisements from Rutgers University-Newark and the surrounding area. Two subjects were excluded from analyses due to excessive motion, two subjects were excluded due to scanner hardware malfunction, and five were excluded due to failure to comply with task requirements (e.g., failure to respond on more than 3 SDs above the mean number of missing trials). Thus, the final sample of subjects included in the analyses included eighteen subjects. Participants gave informed consent according to the Rutgers University Institutional Review Board for the Protection of Human Subjects in Research and the Newark Campus Institutional Review Board of the University of Medicine and Dentistry of New Jersey.

Figure 4.1 Sequence of experimental task for Experiment 6 (Aim 3). On each trial, participants viewed a cue indicating free or forced choice and made a response. Monetary outcome was presented upon response choice.



Procedure

A simple choice paradigm was implemented in the fMRI scanner to probe affective experience when anticipating choice opportunity (Fig 4.1). Participants were presented with two colored (blue and yellow) keys, in which a response led to a potential monetary reward of $0, $50, or $100, with each outcome occurring on 33% of trials. Participants were unaware of these reward probabilities. Each trial began with a cue (2 sec) informing of free or forced choice. In some trials, participants could freely choose between the keys (free choice), whereas in other trials, participants were forced to accept a computer-chosen key (forced choice). The goal of the task was to earn as much experimental reward as possible, which would be translated to real bonus money at the end of the experiment. Although both keys were available in free-choice trials, their choices did not impact the outcome because each reward outcome occurred at random. Nonetheless, participants believed they had control over the outcome and were encouraged to select the option that maximized their reward outcome. Participants were given 2 seconds to respond, which was followed by a monetary feedback (2 sec). Upon

completing the choice task, participants were asked how much they liked or disliked the free and forced-choice cues on a scale from 1 (*disliked a lot*) to 5 (*liked a lot*).

Neuroimaging Data Acquisition and Analyses

Images were acquired using a 3T Siemens Allegra head-only scanner at Rutgers University. Anatomical images were collected using a T1-weighted MPRAGE sequence (256 x 256 matrix, 176 1 mm sagittal slices). Functional images were acquired using a single-shot gradient echo-planar imaging (EPI) sequence (TR = 2000 ms, TE = 25 ms, FOV = 192 cm, flip angle = 80˚, bandwidth = 2604 Hz/px, echo spacing = 0.29 ms), which comprised of thirty-five contiguous oblique-axial slices (3 x 3 x 3 mm voxels) parallel to the anterior commissure-posterior commissure (AC-PC) line.

Imaging data were analyzed using Statistical Parametric Mapping software (SPM12; Wellcome Department of Cognitive Neurology, London, UK [http://www.fil.ion.ucl.ac.uk/spm/software/spm12]). Each time series were corrected for head motion via realignment and slice-time corrected. Next, T1 anatomical image were coregistered to participants' mean functional reference images. Using the coregistered T1 image, we conducted a unified segmentation and normalization using forward deformation on the anatomical image, which was used to reslice EPI images to Montreal Neurological Institute (MNI) template space using 3 mm isotropic voxels (Ashburner & Friston, 2005). Subsequently, normalized functional images were spatially smoothed using a 8 mm full-width-half-maximum Gaussian kernel along with a high-pass filtering of frequencies (three cycles per time course).

A general linear model (GLM) was constructed for each participant across sessions. Our GLM consisted of the following regressors of interest: four indicators to model four anticipatory cues (free choice cue, forced choice cue, non-informative cue, and predictive cue), a regressor for decision making phase, and three outcome regressors including no reward ($0), small reward ($50), and large reward ($100). Our main contrast focused on identifying brain regions that showed increased BOLD signal as a function of free choice compared to forced choice.

Psychophysiological Interaction Analysis

To identify regions showing increased functional connectivity with the striatum in response to free choice, psychophysiological interaction (PPI) analyses were conducted. We identified a region in the left ventral striatum from the main contrast of interest (free vs. forced choice), which was used as a seed region to conduct PPI (Friston et al., 1997). The ventral striatum was chosen as the seed region because it has been previously associated with anticipation of choice (Leotti et al., 2011, 2014) and anticipation of rewards (Knutson et al., 2001; O'Doherty et al., 2002). For each participant, we created a BOLD time-series of the striatum from the subject-specific peak voxel within a 3-mm mask of the left ventral striatum (nucleus accumbens defined by the Harvard Oxford atlas) cluster. To identify activity in the striatal cluster for each subject, we examined the contrast between free- vs. forced-choice conditions. Next, we generated a single-subject GLM consisting of the following regressors: a physiological regressor representing the time course of activation within the ventral striatum, a psychological variable of interest (free vs. forced choice contrast), an interaction of the two variables between striatal time

series and free vs. forced choice contrast, and six motion parameters were included for each session.

Dynamic Causal Modeling

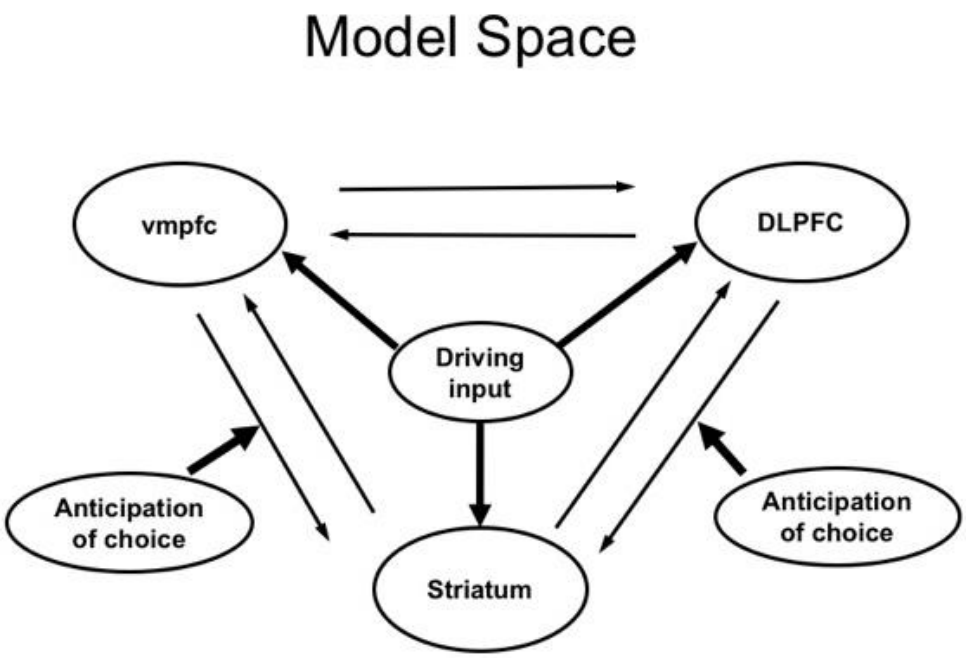
To test for changes in coupling strengths between regions under specified experimental manipulations, we conducted an effective connectivity using DCM as implemented by SPM 12. DCM is used to make inferences about neural responses that underlie measured time series by estimating the parameters of a neuronal system model. Given a set of regional responses and connections, dynamic causal modeling estimates the parameters of a meaningful neuronal system model by converting modeled neural dynamics into hemodynamic responses, which aims to match predicted BOLD responses to actual observed BOLD time series (Ashburner et al., 2014). Using a biophysical forward model, measured data are decomposed into a predicted BOLD signal (Friston et al., 2000; Stephan et al., 2007). Functional imaging data are used to make inferences about the causal relationships of activation patterns between different brain regions (Friston et al., 2003). A benefit to using DCM is that it is not restricted to linear systems and allows an examination of dynamic nature of neuronal interactions to infer the hidden activity of brain responses in difference experimental contexts (Friston et al., 2003). While other conventional methods, such as structural equation modeling (SEM), assume interactions are linear and treat inputs as unknown, DCM accommodates nonlinear and dynamic aspects of neuronal communications, and estimate parameters via perturbations that take into account experimentally manipulated input (Friston et al., 2003). In this way, DCM is a causal modeling that is a more advanced analysis method of effective

connectivity compared to conventional methods, and allows analyses of region-specific effects.

Volumes of Interest (VOI)

For construction of DCMs, an additional first-level analysis was run that included a regressor with free and forced choice combined. Time series were extracted from three a priori regions of interest (ROIs): the striatum, DLPFC, and vmPFC. Automated anatomical labeling (AAL) structural anatomical masks of vmPFC (10 mm) were created including bilateral rectus and medial orbitofrontal gyrus, and a DLPFC (10 mm) mask was created consisting of BA 8, 9, and 46 using WFU PickAtlas Tool (Wake Forest University School of Medicine, Winston-Salem, NC). A ventral striatum ROI (4 mm sphere) was constructed using the Harvard-Oxford Atlas. Then, time series for each subject were extracted from the free and forced choice combined contrast from a 4-mm sphere around the individually defined peak voxel within each VOI.

Figure 4.2 Schematic illustrating the model space that will be tested. The model space tests where information about perceiving choice enters the system and how the system is modulated by anticipating choice.

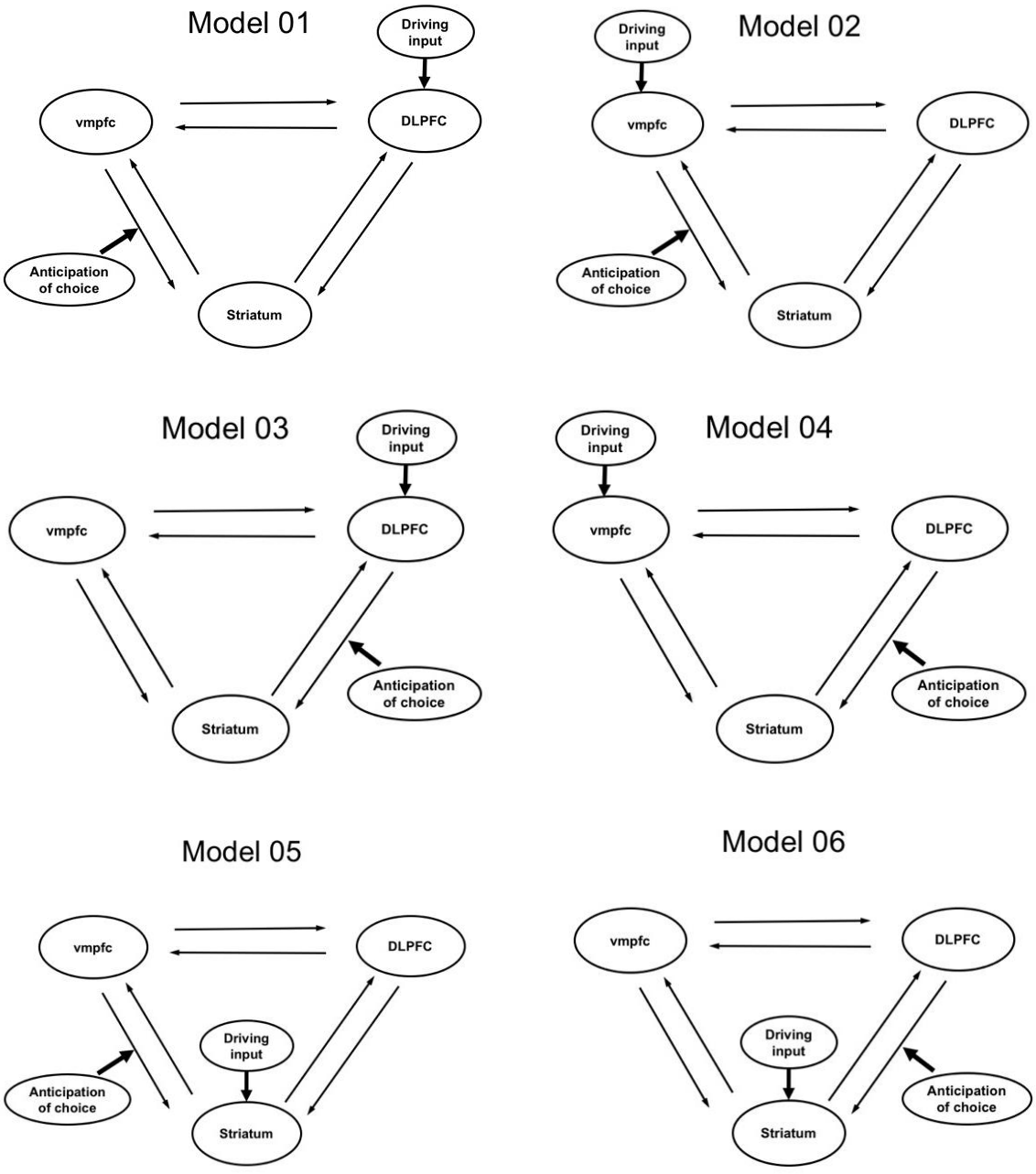


Construction of DCMs

DCM consists of three primary components that describe modeled neural dynamics: the intrinsic connections between regions that are independent of context, the direct inputs of conditions that drive regional activity, and context-dependent modulations in effective connectivity induced by the experimental design. To examine where information about anticipating choice enters the system and how the system is modulated by choice opportunity, we constructed a model space based on findings from the perceptions of control literature. This model space (Fig 4.2) consists of reciprocal

intrinsic connections between all regions of interest, vmPFC, DLPFC, and striatum, driven by anticipation of free or forced choice (driving input). The driving input represents contextual information about anticipation of either free or forced choice. To test from which region the contextual information is entered into the network, all three regions were selected as candidates for driving input in our models (Fig 4.3). In DCM, the modulatory input represents an experimental manipulation that affects the strength of connections between two regions. Thus, modulatory input represents connections between two regions influenced by free-choice cues (anticipation of choice) in our study. The striatum receives anatomical projections from the prefrontal cortex and has been previously associated with choice anticipation (Leotti & Delgado, 2011, 2014). Hence, given that modulation assumes that a signal from another region sends an input to a target region (i.e., striatum), only pathways from the vmPFC or DLPFC to the striatum were considered as modulatory inputs in our tested models. Thus, in total, six models per subject were fitted and compared using Bayesian model comparison (See Figure 4.3).

Figure 4.3 Schematic of Models 1-6. Information about free or forced choice enters the system through one of our tested regions, with anticipation of choice modulating connectivity between regions of interest.



Bayesian model comparison

We constructed and compared six DCM models using Bayesian model selection, which considers the relative fit and complexity of competing models (Penny et al., 2004) to identify the probability that a given model explains our data better than all other models (Stephan et al., 2009). This method involves comparison of model evidence, which takes into account the likelihood of data and prior probability of parameters. The models varied in terms of through which region the driving input enters the system and which coupling between regions are modulated as a function of choice anticipation (modulatory input). All models tested are illustrated in Figure 4.3. A model was chosen based on Bayesian model comparison, and parameters for inputs, endogenous connections, and modulatory effects were acquired for the chosen model.

Results

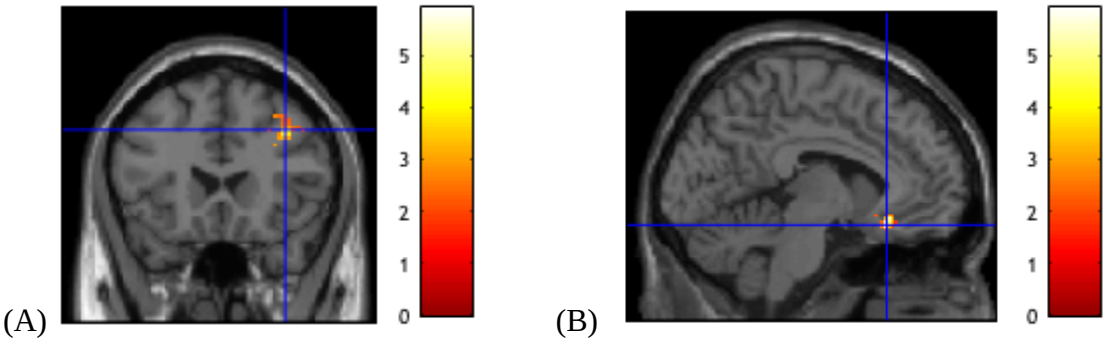
Anticipation of choice engages the striatum

We first identified regions that increased activity during free-choice relative to forced-choice trials. To do this, we estimated a GLM of BOLD activity during which neural responses increased from free – forced choice contrast. In our whole-brain analysis of free choice – forced choice, we found enhanced activity in the left ventral striatum (MNIx,y,z = -12, 8, -4; $t(17) = 5.74$, $p = 0.001$), right ventral striatum (MNIx,y,z = 16, 8, 4; $t(17) = 5.45$, $p = 0.001$), right superior frontal gyrus (MNIx,y,z = 6, 24, 42; $t(17) = 7.06$, $p = 0.001$), and left middle frontal gyrus (MNIx,y,z = -30, -4, 46; $t(17) = 4.41$, $p = 0.007$).

Regions showing enhanced connectivity with the striatum

Consistent with previous studies examining the effect of choice (Leotti & Delgado, 2011, 2014), we found activity in the ventral striatum which showed enhanced activity from free–choice vs. forced–choice trials. The striatum has rich anatomical connections with brain regions within the prefrontal cortex, which may facilitate perceptions of control. We tested this idea using a psychophysiological interaction analysis with the left ventral striatum (MNIx,y,z = -12, 8, -4) defined by whole-brain analysis as our seed region. Using PPI analysis, we identified regions whose connectivity with the left ventral striatum increased as a function of free relative to forced choice. We identified activation in the DLPFC (MNIx,y,z = 38, 22, 38, $t(17) = 4.84$, $p = 0.045$), and activity in the vmPFC (MNIx,y,z = -6, 26, -16, $t(17) = 5.46$, $p = 0.006$) by performing small volume corrections (Fig 4.4). Additional significant activations were observed in the right posterior cingulate cortex (MNIx,y,z = 4, -16, 26, $t(17) = 5.48$, $p = 0.001$) and left posterior cingulate cortex (MNIx,y,z = -6, -44, 30, $t(17) = 5.82$, $p = 0.001$).

Figure 4.4 Increased connectivity in the right dorsolateral prefrontal cortex (A) and the left ventromedial prefrontal cortex (B) with the left striatum seed region during anticipation of choice.



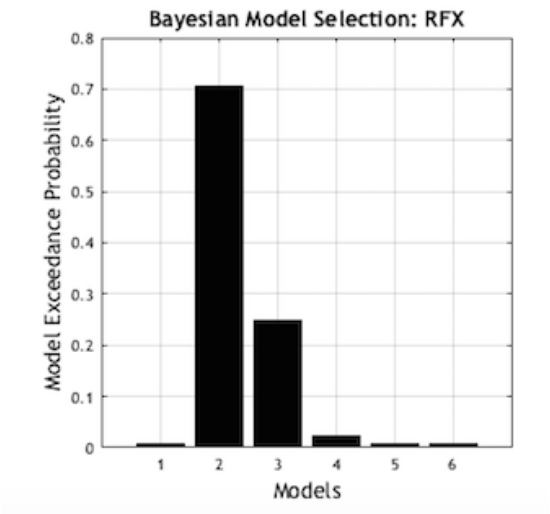
Interactions between prefrontal cortices and the striatum during anticipation of choice

We used DCM to examine the mechanisms through which coordinated activity in the three regions are modulated by choice anticipation. All models consisted of fixed reciprocal connections between the three regions involved in perceptions of control. Each model allowed for the driving input to enter the system via one of the three regions. In addition to specifying the driving input, we tested for which coupling between regions is influenced by anticipation of choice (modulatory input). Then, we used Bayesian model selection to detect the most likelihood model given our data by calculating exceedance probability. Exceedance probability is a measure of posterior belief that given a set of models, one model is more likely than others. Exceedance probabilities across models sum to 1, hence information regarding relative probabilities of models are more useful than the absolute probability (Penny et al., 2010). In the current model comparison, model 2 was identified as the most probable (Fig 4.5), with an EP of 0.7 relative to other 5 models, which ranged in EP from 0.006 to 0.26). Therefore, model comparison results suggest that information about free and forced choice enters through the vmPFC, and connections from the vmPFC to the striatum is modulated by anticipation of choice.

Next, Bayesian model averaging was conducted to compute weighted average of modulatory effects of connectivity for model 2 (Stephan et al., 2009). Estimates of parameters were considered statistically significant if they exceeded a posterior probability threshold of 95%. At baseline examining intrinsic connections between regions that are independent of context, we found significant connections from vmPFC to DLPFC. This coupling was not significantly modulated by choice anticipation,

suggesting that this coupling is not influenced by choice. Anticipation of choice induced significant changes in connection strength only in the negative coupling from the vmPFC to the striatum.

Figure 4.5 Bayesian model comparisons showing results for each model exceedance probability.



Discussion

The present study examined the influence of anticipation of choice on dynamics of cortical-striatal connections in a network involving the striatum, vmPFC, and DLPFC. Importantly, our experimental design allowed us to isolate neural activity during the onset of choice expectancy phase, independent of reward outcomes. To examine where information about free or forced choice enters the network system and which coupling is affected by anticipation of choice, multiple models were compared to test their fit and complexity. Our results indicate that when anticipating choice, information about free or forced choice enters the system via vmPFC. Then, anticipation of free choice increased

the modulation of inverse connectivity from the vmPFC to the striatum, a region involved in reward processing (Berridge, 1996; Robbins & Everitt, 1996).

We found anticipation of free or forced choice enters the neural system solely through driving input to vmPFC. This finding is consistent with previous literature highlighting the critical role of vmPFC on detection of controllability (Amat et al., 2005; Maier et al., 2006; Maier & Watkins, 2010) and blocking against aversive effects of a stressor (Baratta et al., 2008; Maier et al., 2006). More precisely, blocking the activation of vmPFC during stressor in rodents resulted in responding to both escapable and inescapable stimuli as if they were uncontrollable, whereas activity in vmPFC led to reactions towards both escapable and inescapable stimuli as if they were controllable (Amat et al., 2008). Thus, although behavioral learning is intact during inhibition of vmPFC during controllable stress, blocking vmPFC activity disabled stressor controllability on those outcomes (Amat et al., 2005).

Neuroimaging studies in humans also demonstrate anticipation of control over an aversive event activates the vmPFC. For instance, snake phobic participants recruited greater activations in the vmPFC when they had the opportunity to terminate a threatening video as opposed to having no control over duration of stressful clips (Kerr et al., 2012). In a related study, Wood and colleagues (2016) demonstrated that individuals recruit activity in the vmPFC during predictable and controllable threat. Other studies have found increased ventromedial PFC activation during diminishing fear responses through extinction training and emotion regulation (Delgado et al., 2008). Such evidence implicates the vmPFC in computing the contingency information between one's behavior and outcome (Dickinson, Balleine, Watt, Gonzalez, & Boakes, 1998; Maier & Watkins,

2010) and forming adaptive behavioral responses (Bhanji & Delgado, 2014). Our results suggest information about free or forced choice is primarily processed in the ventromedial PFC, a region previously identified as critical for supporting controllability effects on stress regulation (Maier, Amat, Baratta, Paul, & Watkins, 2006). Importantly, whereas previous choice studies have relied on analyses comparing contrasts between choice and no-choice conditions, the current analyses allowed us to consider the effects of both controllable and uncontrollable entering into the neural system. Hence, results from our analyses suggest contextual information about controllability or uncontrollability in the environment is encoded in the vmPFC, whereas the striatum responds to the positive feelings associated with expectation for choice. As a result, an enhanced connectivity between the vmPFC and affect processing areas during controllable contexts (Brascher et al., 2016) might suggest a role for the region encoding anticipation of choice, hence modulating activity in regions associated with emotional and motivational processing such as the striatum.

Consistent with this notion, we found anticipation of choice increases an inverse modulation from the vmPFC to ventral striatum (VS). This finding is inline with anatomical data showing strong cortical input from the vmPFC to the ventral striatum (Haber & Knutson, 2009). The striatum is implicated in reward processing such as during anticipation of impending rewards (Knutson, Taylor, Kaufman, Peterson, & Glover, 2005; O'Doherty, Deichmann, Critchley, & Dolan, 2002). Studies examining perceived contingency between one's actions and rewards have demonstrated a role for the striatum, particularly when rewards are instrumentally delivered compared to rewards that are passively received (Bjork, Smith, Danube, & Hommer, 2007; O'Doherty,

Critchley, Deichmann, & Dolan, 2003; O'Doherty et al., 2004; Tricomi, Delgado, & Fiez, 2004). Hence, striatal activation is involved in computing contingency (O'Doherty et al., 2004; Tanaka, Balleine, & O'Doherty, 2008), highlighting the role of striatum in processing action contingency and perception of control when anticipating choice opportunity. These findings further support the idea that experiencing control via exerting choice is motivating and can be rewarding in it of itself (Bhanji & Delgado, 2014; L. A. Leotti et al., 2015; R M Ryan & Deci, 2000), consistent with our findings revealing increased striatal responses in free compared to forced choices.

Clinical studies demonstrate heightened prefrontal cortico-striatal reward circuit to reward-related cues and approach behavior (Alloy et al., 2015; Nusslock et al., 2014; Phillips & Swartz, 2014), highlighting an important role of vmPFC in correcting striatal activity in response to reward anticipation. Bipolar patients are characterized by hypersensitivity to reward cues, and neural evidence indicates these patients exhibit heighted activity in VS and vmPFC in response to anticipation of monetary rewards compared to healthy controls (Caseras et al., 2013; Nusslock et al., 2012). Moreover, patients with bilateral lesions in vmPFC have a preference for immediate rewards at the risk of negative consequences in the future (Bechara et al., 2001). As a result, elevated responses in the vmPFC and VS during reward anticipation may represent a predisposition for exaggerated mood and approach behavior underlying hypersensitivity to rewards (Alloy et al., 2016; Nusslock et al., 2012) and failure to inhibit amplified striatal responses. Thus, in healthy controls, we may expect vmPFC to dampen activity in the striatum to support accurate representations of value during the anticipation of choice. These findings provide support that vmPFC updates representation of value signals by

sending inhibitory input into the ventral striatum during anticipation of choice opportunity. Indeed, the vmPFC is implicated in computations of value that drives choices (Hare et al., 2008, 2011; Kable & Glimcher, 2007; Levy et al., 2010), integrates values across different stimuli (Blair et al., 2006) before choice (Glascher et al., 2009; Knutson et al., 2007), weighs benefits against cost when computing risky decisions potentially by integrating input from the VS (Bruguier et al., 2008). Therefore, while striatum responds to the positive nature of anticipating choice, inhibitory input from the vmPFC is critical for updating accurate representations of expected value of stimuli or actions in the striatum (Kahnt et al., 20011; O'Doherty et al., 2003; Pessiglione et al., 2006).

To characterize the directionality of dynamic interplay between brain regions involved in anticipation of choice, we implemented dynamic causal modeling. The use of DCM is relevant for analyses examining causal relationships among regions because it does not rely on temporal precedence for causality. While many connectivity analyses (i.e., structural equation modeling, psychophysiological interactions) infer coupling between regions from observed time-series, the causal architecture exists at the neuronal dynamic levels. Therefore, to make inferences about connectivity at the neural level, DCM estimates parameters of a neuronal system model such as the effective strength of synaptic connectivity among neuronal populations and their modulations from context-dependencies (Stephan et al., 2010). In DCM, measured data are decomposed into a predicted BOLD signal by using a biophysical forward model, (Friston et al., 2000; Stephan et al., 2007). Three key components in DCM are used to explain modeled neural dynamics: the intrinsic connections between regions that are independent of context, the

direct inputs of conditions that drive regional activity, and context-dependent modulations in effective connectivity induced by the experimental design. To investigate where information about anticipating choice enters the system and how the system is modulated by choice opportunity, we implemented DCM to make inferences about the causal relationships of activation patterns between regions involving vmPFC, DLPFC, and striatum based on perceptions of control literature. Taken together, our data supports an important role for vmPFC in detecting controllability (free or forced choice), which projects signals to the ventral striatum for accurate representation of expected value during anticipation of choice. Future studies may test whether hypersensitivity to rewards exhibit enhanced positive connectivity between the vmPFC and VS during anticipation of choice, an opposing pattern from the current study involving healthy controls.

Chapter 5

General Discussion

Summary and Significance

Overall summary

Perceiving control over our environment affects the way in which we interpret stimuli, which has significant influences on our decision making and affective processes. The current set of empirical experiments demonstrated these effects. The first four experiments investigated how exercising choice over negative stimuli modulates emotional processing by using a simple choice paradigm. The fifth experiment tested the influence of free vs. forced choice on neural responses associated with levels of reward sensitivity. The sixth experiment probed the causal relationships among brain regions associated with perceptions of control and anticipation of choice.

Across the first four experiments, we found that exerting free choice enhanced feelings of control, consistent with research suggesting exercising control enhances sense of control and confidence. In the first experiment, participants engaged in a simple choice task that gave options to choose between two keys that led to either a neutral or negative picture. Participants took longer to respond to the two keys when exerting choice, which may indicate increased cognitive effort and attention involving making decision making. Emotional ratings of pictures were not different between free and forced choices.

In Experiment 2, we employed a modified choice task to explore whether effects of choice influences affective processing when we dissociate success and failure outcomes from valence of pictures. Before engaging in the choice task, participants performed a training session to learn which key was associated with a greater reward

value. Learning this information helped participants select a better key in the subsequent task, which was dissociated with valence of pictures in the choice task. Results from reaction times and behavioral ratings suggest participants did not dissociate effects of free and forced choice, potentially due to complexity of the experimental design.

A simplified choice paradigm was tested in Experiment 3 to examine the effect of choice on processing emotional pictures. In each trial, participants were shown two scenarios to choose from, and making a choice resulted in the presentation of a corresponding picture. Ratings of pictures between free- and forced-choice trials were compared. Comparison of ratings of images between the two trial types did not reveal significant differences. Additional changes were made in the experimental design to limit comparison of choices in the forced-choice condition in Experiment 4. Hence, the modified task removed value comparisons between options by restricting cues to a single option during forced choices. We found decreased ratings of negative images during free vs. forced choice, supporting the idea that having choice over negative stimuli helps regulation of emotions within the context of the current experiment. Effects of choice on emotional processing were context-specific, such that modulation of ratings were stronger in certain types of categories relative to others.

Experiment 5 probed the influence of free choice on levels of reward sensitivity. Participants performed a choice task that presented free and forced choices between cues about monetary rewards. During free choices, participants were able to freely choose between different categories of options, whereas participants were forced to choose between the same category during forced choices. Individuals high in reward sensitivity recruited activity in the VLPFC, a region involved in attentional control and response

selection. In individuals with high reward sensitivity, PPI analyses demonstrated enhanced VLPFC connectivity with the PCC that may be involved in motor processing during free choice.

Lastly, Experiment 6 investigated the dynamic interplay between brain regions involved in affective processes underlying anticipation of choice. Dynamic causal modeling was implemented to investigate directionality of cortical regions influencing affect-processing regions (i.e., striatum) when perceiving choice opportunity. We examined where information about choice anticipation enters the system and how it modulates the neural network involved in perceiving control. Given their involvement in perceiving choice, three key regions were selected: the vmPFC, DLPFC, and the striatum. We found that information about free or forced choice enters the neural system via vmPFC. Anticipation of free choice enhanced the modulation of inverse connectivity from the vmPFC to the striatum, a region involved in reward processing.

Neural circuitry underlying perceived control

Studies five and six employed simple choice tasks involving monetary rewards to probe the neural responses associated with decision making and affective processing of exercising choice. In Experiment 5, when given an opportunity for choice, we found that individuals high in reward sensitivity recruit activity in the VLPFC, a region associated with increased attentional control and response selection. This research is significant as individual differences in sensitivity to rewards may be highly responsive to opportunities for choice.

However, in contrast to previous research suggesting vmPFC activity for encoding controllability, we did not find involvement of this region in our Experiment 5. We believe this could be due to the sensitivity of controllability effects to contexts in which individuals exercise control. In Experiment 5, the experimental task required participants to keep in mind information about different cues that were presented, in order to select the option that would maximize reward. Thus, these were more abstract forms of options that required cognitive control, which might explain recruitment of VLPFC in free choice conditions for individuals that were particularly sensitive to rewards.

Study 6 examined the causal directionality of neural responses associated with controllability effects on affective processing, and the results are consistent with previous control literature that controllability is detected at vmPFC (Maier et al., 2006). This study provides novel insights on the relationship between the vmPFC and the striatum during anticipation of choice opportunity, potentially supporting an update of value representation signals from vmPFC to the striatum.

Consistent with previous literature on controllability, our results indicate that information about controllability is processed in the vmPFC. Extant research has primarily focused on controllability effects on negative contexts such as pain and fear conditioning (Brascher et al., 2016, Hartley et al., 2014; Salomons et al., 2004, 2007, Wiech et al., 2007). Importantly, the current experiment informs that activity in the vmPFC also encodes controllability information during positive contexts (i.e., anticipating monetary rewards). Thus, the vmPFC might send input to the striatum when perceiving controllability in positive contexts, and may send information to regions

associated with processing salience and intensity of emotions such as the amygdala and insula when perceiving control during aversive contexts.

Significance

The experiments contribute additional knowledge to the perceived controllability and choice literature. Across our experiments, we found different effects of behavioral control (instrumental control) and subjective control (decisional control) on affective processing. For instance, in Experiments 1 and 2 in which free choice enhanced subjective perceptions of control by having choice between two cues regardless of actual outcome (decisional control), their perceptions of control did not dampen emotional responses to negative pictures. However, when participants exercised behavioral control (instrumental learning) by directly choosing a picture nonreliant on chance, we found their choices reduced negative emotional responses. These findings suggest behavioral control, which involves a true contingency between action and behavior, may be more effective at influencing emotional systems. Extant studies have found powerful influence of behavioral control over painful stimuli such as shock, heat, and chronic pain in reducing and buffering against negative emotional responses (Maier & Watkins, 1998; Jenson & Karoly, 1991; Jensen et al., 2001; Salomons et al., 2004, 2007; Wiech et al., 2006). According to the reinforcement learning theory (Skinner, 1953; Thorndike, 1933), a response that successfully achieves one's goal reinforces that behavior. Therefore, one potential explanation for our findings is that a behavior that results in a desirable outcome amplifies feelings of control and success. These enhanced sense of control over negative

outcomes, may lead to a cognitive change in one's belief that a behavior will lead to a desired outcome, which might be critical for supporting emotion regulation mechanisms.

Indeed, Averill (1973) has underscored the importance of cognitive control, which refers to regulating the way a potentially threatening stimulus is interpreted, such as altering the meaning or significance of the event or stimulus. In this way, cognitive control is important to consider because perceptions of pain may depend on the meaning or significance of distressful stimuli (Melzack & Casey, 1970). Moreover, the capacity for cognitive control is important for self-regulation (Baumeister, Heatherton, & Tice, 1994; Ochsner & Gross, 2005; Vohs & Baumeister, 2011), and may be critical for fostering self-efficacy beliefs. Therefore, one way in which increased control impacts affective processing is through reinterpretations of negative events in a way that dampens emotional responses to those stimuli, consistent with the mechanisms of emotion regulation strategies (i.e., cognitive reappraisal; Ochsner & Gross, 2002). From our data, we may infer that one potential way in which behavioral control (instrumental control) impacts emotional processing is through changes in cognitive control. A behavior that reinforces successful outcomes is likely to strengthen one's belief about controllability by modifying the meaning of a stimulus. Thus, undergoing cognitive change via instrumental learning could be an important mechanism that supports altering emotional responses to distressful stimuli.

Yet, we note that these effects were restricted to behavioral control over aversive stimuli. While Aim 1 concentrated on the effects of perceiving control over negative stimuli, Aims 2 and 3 explored the neural circuitry underlying decisional control over positive outcomes involving monetary outcomes. Given our results indicating the

involvement of cognitive control network and reward-related circuitry during subjective experiences of control, we could infer that perceiving decisional control over positive outcomes can influence affective processing. These findings are consistent with previous literature on self-determination theory underscoring autonomy that underlies intrinsic motivation (Ryan & Deci, 2000). People's general positive feelings are enhanced when they feel their actions are freely determined by the self as opposed to by others, whereas motivation is diminished when the environment is perceived as controlling or forced. Opportunities for choice increase competence, satisfaction, and engagement in various tasks (Cordova & Lepper, 1996; Grolnick & Ryan, 1987; Langer & Rodin, 1976; Patall, et al., 2008; Patall, Cooper, & Wynn, 2010; Ryan & Deci, 2000), suggesting that decisional control can be a powerful motivator. Consistent with behavioral findings indicating desirability for choice, neural evidence supports the idea that anticipation of choice is inherently rewarding. Such studies converge on the idea that exerting decisional control via choice enhances positive feelings and neural activity in reward-related brain regions such as the striatum when anticipating an opportunity to exert control (Leotti and Delgado, 2011, 2014). Thus, although decisional control can have limited influences on regulating negative emotions, findings from our studies converge on the idea that exercising decisional control via choice enhances positive feelings. One explanation for this finding is that despite its increase in positive affect, merely having decisional control does not induce changes in cognitive belief that one's behavior will definitely impact the outcome. Thus, modifications in cognitive belief could be a critical element for altering emotional responses to stimuli, which is insufficient in the case of decisional control which may or may not produce desired outcome.

Altogether, given our findings that cognitive change could be a critical component underlying changes in affective responses in stressful contexts, one important direction to pursue for future research is to examine whether reevaluations of cognitive judgments in the face of distressful contexts effectively alters emotional processing. For instance, even when a situation is deemed as uncontrollable, individuals may exercise changes in cognitive appraisal of the given context to regulate emotions. Studies on emotion regulation have found decreases in negative emotions by practicing cognitive reappraisal strategy (Ochsner & Gross, 2002). However, effects of such strategies depend on contextual elements (Troy et al., 2013) and demand cognitive effort that competes with maintaining and achieving a desired goal. Therefore, future studies could test other means of undergoing cognitive change (i.e., mindfulness), that is effortless. For example, practices of mindfulness-based strategies have shown to no longer engage cognitive effort (Chiesa, Serretti, & Jakobsen, 2013), and are effective at reducing ruminative thinking and risk of depressive relapses (Segal, 2002), demonstrating a potential avenue for future research examining benefits of cognitive change that are less effortful.

Our findings indicating the influence of behavioral control on emotional processing are consistent with previous learned helplessness literature. Subjective helplessness linked with electric shock has been associated with greater ratings of pain (Muller & Netter, 2000). In animal studies, rats exposed to uncontrollable shocks revealed exaggerated fear conditioning and were more likely to develop negative health consequences (Amat et al., 2006; Grissom et al., 2008). Similar effects have been reported across studies in both humans and animals, indicating that learned helplessness (lack of behavioral control over a stressor) is associated with negative consequences

(Amat et al., 2005; Maier & Watkin, 1998; Salomons et al., 2004; Salomons, Johnstone, Backonja, Shackman, & Davidson, 2007) and behavioral control is critical for regulating emotional responses (Jensen & Karoly, 1985; Jensen et al., 2001). It would be interesting for future studies to test whether behavioral control (instrumental control) has similar effects on positive outcomes (increasing positive affect), and whether it compares to the effects of decisional control (merely having choice that is not contingent on the outcome).

Furthermore, the present research has important clinical implications. Effects of perceiving control via exercising choice may not have similar effects on all participants. Results from this study suggest sensitivity for rewards may be an important factor to consider that may modulate effects of perceiving control. Reward sensitivity is associated with many psychiatric disorders, such as substance abuse, eating disorders, depression, bipolar disorders. For example, bipolar disorder is characterized by hypersensitivity to rewards, whereas depression is associated with hyposensitivity to rewards. Therefore, the current research provides important implications for clinical disorders. Future work could explore how perceptions of control mediate responses to emotional events in these populations.

Although previous imaging studies on controllability have primarily relied on direct contrasts or neural correlates associated with perceiving control, Experiment 6 is the first study to examine causal directionalities of neural mechanisms underlying choice anticipation. Results from this study implicate an important causal link between vmPFC to striatum during anticipation of choice, potentially supporting update of value representations in the striatum.

Context-specific effects of control

The current set of experiments provide novel insights on controllability research. Previous research examining controllability effects on negative stimuli have focused on specific domains such as pain, fear conditioning, and medical conditions. To test whether controllability can serve as means for regulating broader negative affect, Experiments 1—4 examined whether perceiving choice over stimuli can dampen affective responses to aversive pictures. Although initial Experiments 1—3 did not reveal modulations in affective processing from choice, after a number of modifications in the experimental design we found that exercising choice helps diminish negative emotions under limited contexts (Experiment 4). Specifically, among four categories of pictures, effects of choice were greatest for pictures in the *grievance* category and then for *threat*. Ratings for *injury* and *accident* categories did not show differences from baseline and choice trials. A potential explanation for these results is that although the valence across categories were matched, certain contexts may be easier to regulate emotions, hence revealing greater decreases in negative emotions from having choice. Indeed, previous findings support this idea, such that adaptiveness of emotion regulation strategies depend on the contexts in which they are used (Cheng et al., 2001), and that effects of controllability on emotional responses may vary as a function of contextual factors (Wood et al., 2015; Salomons et al., 2007; Troy, Shallcross, & Mauss, 2013). Therefore, our findings indicate certain domains within negative contexts compared to others may be more easily regulated by an opportunity for choice, underscoring the context specificity of controllability effects.

Type of emotional stimuli

When examining responses towards negative events, it is important to consider the type of stimuli used in the experiment. In our set of behavioral studies (Experiments 1—4), we focused on using images to measure changes in responses to those pictures using choice manipulation. This is one the common ways in which previous experimenters have examined the effects of emotion regulation strategies on emotional processing (Ochsner et al., 2002; McRae et al., 2009; Wager et al., 2008). While using IAPS pictures may be useful and reliable for measuring affective responses, certain limitations remain. For example, although aversive pictures may induce negative emotions in an individual, they may not be the best indicator of one's emotions due to less personal connections with the participant. Thus, it is possible that pictures may not be as useful for assessing how one responds to emotional events in certain individuals, and other measures such as response to pain measures could be more relevant (Salomons et al., 2004, 2007, Wiech et al., 2007). Moreover, Likert rating self-reports on pictures requires additional level of cognitive processing on top of intrinsic emotional reactions to stimuli. Therefore, it is possible that people's ratings of pictures have greater variability and reliability as a measurement for emotions, compared to other measures such as responses to pain (i.e., shock, heat) (Brascher et al., 2016, Hartley et al., 2014; Salomons et al., 2004, 2007, Wiech et al., 2007).

Potential limitations of choice manipulation

There are several limitations of controllability manipulations employed in our studies. According to motivational theories, autonomy is one of fundamental needs that

underlie people's motivation (Ryan & Deci, 2000), and exercising choice is a powerful motivator (DeCharms, 2013; Lewin, 1951). However, not all choices are rewarding or have motivational values. For instance, previous research indicates having too many options for choice can be overwhelming and stressful (Schwartz, 2000), thus exposure to many opportunities for choice may discourage subsequent consumption (Iyengar & Lepper, 2000).

Moreover, researchers have suggested that making a choice requires cognitive resource, hence could be ego-depleting (Baumeister et al., 1998). However, a subsequent study by Moller and colleagues (2006) found that true choice did not deplete cognitive resources, suggesting differences in manipulations of choice can affect results. Taken together, these findings indicate choice can have different meanings such that having too many options can deteriorate the positive effects of choice, and having only a few options can still be meaningful if one feels choice is truly emanating from the self (Ryan & Deci, 2006). Thus, we emphasize that choice effects are specific to contexts in which it is employed, and choice manipulation needs to take into account whether individuals feel that the experimental choice enhances their sense of control or free-will.

Overall conclusions and future directions

Perceiving control is a critical determinant of our health and well-being. The current set of experiments demonstrates a significance of behavioral control via instrumental conditioning on regulating negative emotions. These findings are consistent with previous literature outlining detrimental affective outcomes of learned helplessness, in which there is no behavioral response available for controlling the outcome.

Interestingly, in the context of positive outcomes, we find that neural responses from perceiving decisional control have effects on emotional processing regions. Therefore, context specificity is an important factor that can modulate effects of control on affective processing. Consistent with our findings, previous studies on perceptions of control have focused on domain specific effects such as pain (i.e., heat, shock), fear conditioning, and imagining medical conditions. This research demonstrates that behavioral control and subjective experiences of control have different influences on emotions, and that controllability may support emotion regulation under specific contexts. Future research should probe specific domains in which controllability is effective or non-effective at modulating emotional responses to aversive stimuli. Moreover, we discovered certain individual differences are more responsive to effects of controllability, such as sensitivity for rewards, which is closely related to psychiatric symptoms. Thus, given that controllability is at the core of various psychiatric disorders, it is important to test the influence of control beliefs in clinical populations such as in depressive and bipolar disorders.

References

Alloy, L. B., Olino, T., & Freed, R. D. (2016). Role of Reward Sensitivity and Processing in Major Depressive and Bipolar Spectrum Disorders. *Behavior Therapy*, *January 29*(online), 1–68. http://doi.org/10.1016/j.beth.2016.02.014

Amat, J., Baratta, M. V, Paul, E., Bland, S. T., Watkins, L. R., & Maier, S. F. (2005). Medial prefrontal cortex determines how stressor controllability affects behavior and dorsal raphe nucleus. *Nat Neurosci*, *8*(3), 365–371.

Amat, J., Paul, E., Zarza, C., Watkins, L. R., & Maier, S. F. (2006). Previous experience with behavioral control over stress blocks the behavioral and dorsal raphe nucleus activating effects of later uncontrollable stress: role of the ventral medial prefrontal cortex. *J Neurosci*, *26*(51), 13264–13272.

Aron, A. R., Robbins, T. W., & Poldrack, R. A. (2004). Inhibition and the right inferior frontal cortex. *Trends in Cognitive Sciences*, *8*(4), 170–177. http://doi.org/10.1016/j.tics.2004.02.010

Ashburner, J., & Friston, K. J. (2005). Unified segmentation. *NeuroImage*, *26*(3), 839–851. http://doi.org/10.1016/j.neuroimage.2005.02.018

Averill, J. R. (1973). Personal control over aversive stimuli and its relationship to stress. . *Psychological Bulletin*, *80*(4), 286.

Badre, D., & Wagner, A. D. (2004). Selection, Integration, and Conflict Monitoring. *Neuron*, *41*(3), 473–487. http://doi.org/10.1016/S0896-6273(03)00851-1

Badre, D., & Wagner, A. D. (2007). Left ventrolateral prefrontal cortex and the cognitive control of memory. *Neuropsychologia*, *45*(13), 2883–2901. http://doi.org/10.1016/j.neuropsychologia.2007.06.015

Balcetis, E., & Dunning, D. (2007). Cognitive dissonance and the perception of natural environments. *Psychological Science*, *18*(10), 917–921. http://doi.org/10.1111/j.1467-9280.2007.02000.x

Ballantyne, J. C., Carr, D. B., Chalmers, T. C., Dear, K. B., Angelillo, I. F., & Mosteller, F. (1993). Postoperative patient-controlled analgesia: meta-analyses of initial randomized control trials. . *Journal of Clinical Anesthesia*, *5*(3), 182–193.

Ballard, I. C., Murty, V. P., Carter, R. M., MacInnes, J. J., Huettel, S. A., & Adcock, R. A. (2011). Dorsolateral Prefrontal Cortex Drives Mesolimbic Dopaminergic Regions to Initiate Motivated Behavior. *Journal of Neuroscience*, *31*(28), 10340–10346. http://doi.org/10.1523/JNEUROSCI.0895-11.2011

Bandura, A. (1977). Bandura (1977), *84*(2), 191–215. http://doi.org/10.1037/0033-295X.84.2.191

Bandura, A. (1997). *Self-efficacy: the exercise of control.* New York: Freeman.

Bandura, A. (2014). Toward a Psychology of Human Agency. *Perspectives on Psychological Science*, *1*(2), 164–180. http://doi.org/10.1111/j.1745-6916.2006.00011.x

Baratta, M. V, Lucero, T. R., Amat, J., Watkins, L. R., & Maier, S. F. (2008). Role of the ventral medial prefrontal cortex in mediating behavioral control-induced reduction of later conditioned fear. *Learning {&} Memory (Cold Spring Harbor, N.Y.)*, *15*(2), 84–87. http://doi.org/10.1101/lm.800308

Barbas, H., & De Olmos, J. (1990). Projections from the amygdala to basoventral and mediodorsal prefrontal regions in the rhesus monkey. *The Journal of Comparative Neurology*, *300*(4), 549–571. http://doi.org/10.1002/cne.903000409

Baumeister, R. F., Heatherton, T. F., & Tice, D. M. (1994). *Losing control: How and why people fail at self-regulation.* . Academic Press.

Baxter, M. G., Gaffan, D., Kyriazis, D. a., & Mitchell, A. S. (2009). Ventrolateral prefrontal cortex is required for performance of a strategy implementation task but not reinforcer devaluation effects in rhesus monkeys. *European Journal of Neuroscience*, *29*(10), 2049–2059. http://doi.org/10.1111/j.1460-9568.2009.06740.x

Beaver, J. D., Lawrence, A. D., van Ditzhuijzen, J., Davis, M. H., Woods, A., & Calder, A. J. (2006). Individual differences in reward drive predict neural responses to images of food. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *26*(19), 5160–6. http://doi.org/10.1523/JNEUROSCI.0350-06.2006

Beckmann, C. F., Jenkinson, M., & Smith, S. M. (2003). General multilevel linear modeling for group analysis in FMRI. *NeuroImage*, *20*(2), 1052–1063. http://doi.org/10.1016/S1053-8119(03)00435-X

Berridge, K. C. (1996). Food reward: brain substrates of wanting and liking. *Neurosci Biobehav Rev*, *20*(1), 1–25. http://doi.org/0149-7634(95)00033-B [pii]

Bhanji, J. P., & Delgado, M. R. (2014). Perceived control influences neural responses to setbacks and promotes persistence. *Neuron*, *83*(6), 1369–1375. http://doi.org/10.1016/j.neuron.2014.08.012

Bjork, J. M., Smith, A. R., Danube, C. L., & Hommer, D. W. (2007). Developmental differences in posterior mesofrontal cortex recruitment by risky rewards. *J Neurosci*, *27*(18), 4839–4849. http://doi.org/27/18/4839 [pii] 10.1523/JNEUROSCI.5469-06.2007

Borckardt, J. J., Reeves, S. T., Frohman, H., Madan, A., Jensen, M. P., Patterson, D., … George, M. S. (2011). Fast left prefrontal rTMS acutely suppresses analgesic effects of perceived controllability on the emotional component of pain experience. *Pain*, *152*(1), 182–7. http://doi.org/10.1016/j.pain.2010.10.018

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433–436. http://doi.org/10.1163/156856897X00357

Brascher, A.-K., Becker, S., Hoeppli, M.-E., & Schweinhardt, P. (2016). Different Brain Circuitries Mediating Controllable and Uncontrollable Pain. *Journal of Neuroscience*, *36*(18), 5013–5025. http://doi.org/10.1523/JNEUROSCI.1954-15.2016

Braver, T. S., Reynolds, J. R., & Donaldson, D. I. (2003). Neural mechanisms of transient and sustained cognitive control during task switching. *Neuron*, *39*(4), 713–726. http://doi.org/10.1016/S0896-6273(03)00466-5

Brehm, J. W. (1956). Post-decision changes in the desirability of alternatives. *Journal of Abnormal and Social Psychology*, *52*, 384–389.

Buckholtz, J. W., Treadway, M. T., Cowan, R. L., Woodward, N. D., Benning, S. D., Li, R., … Zald, D. H. (2010). Mesolimbic dopamine reward system hypersensitivity in individuals with psychopathic traits. *Nature Neuroscience*, *13*(4), 419–421. http://doi.org/10.1038/nn.2510

Buckner, R. L., Andrews-Hanna, J. R., & Schacter, D. L. (2008). The brain's default network: Anatomy, function, and relevance to disease. *Annals of the New York Academy of Sciences*, *1124*, 1–38. http://doi.org/10.1196/annals.1440.011

Bunge, S. A., Burrows, B., & Wagner, A. D. (2004). Prefrontal and hippocampal

contributions to visual associative recognition: Interactions between cognitive control and episodic retrieval. *Brain and Cognition*, *56*(2 SPEC. ISS.), 141–152. http://doi.org/10.1016/j.bandc.2003.08.001

Carter, R. M., Macinnes, J. J., Huettel, S. a, & Adcock, R. A. (2009). Activation in the VTA and nucleus accumbens increases in anticipation of both gains and losses. *Frontiers in Behavioral Neuroscience*, *3*(August), 21. http://doi.org/10.3389/neuro.08.021.2009

Carver, C. S., & White, T. L. (1994). Behavioral inhibition, behavioral activation, and affective responses to impending reward and punishment: The BIS/BAS Scales. *Journal of Personality and Social Psychology*, *67*(2), 319–333. http://doi.org/10.1037/0022-3514.67.2.319

Catley, D., & Grobe, J. E. (2008a). Using basic laboratory research to understand scheduled smoking: A field investigation of the effects of manipulating controllability on subjective responses to smoking. *Health Psychology*, *27*(3, Suppl), S189–S196. http://doi.org/10.1037/0278-6133.27.3(Suppl.).S189

Catley, D., & Grobe, J. E. (2008b). Using basic laboratory research to understand scheduled smoking: A field investigation of the effects of manipulating controllability on subjective responses to smoking. *Health Psychology*, *27*(3, Suppl), S189–S196. http://doi.org/10.1037/0278-6133.27.3(Suppl.).S189

Chan, R. C. K., Shi, Y. F., Lai, M. K., Wang, Y. N., Wang, Y., & Kring, A. M. (2012). The temporal experience of pleasure scale (TEPS): Exploration and confirmation of factor structure in a healthy Chinese sample. *PLoS ONE*, *7*(4). http://doi.org/10.1371/journal.pone.0035352

Chase, H. W., Phillips, M. L., Friston, K. J., Chen, C. H., Suckling, J., Lennox, B. R., … Huang, L. (2016). Elucidating Neural Network Functional Connectivity Abnormalities in Bipolar Disorder: Toward a Harmonized Methodological Approach. *Biological Psychiatry: Cognitive Neuroscience and Neuroimaging*, *1*(3), 288–298. http://doi.org/10.1016/j.bpsc.2015.12.006

Chiesa, A., Serretti, A., & Jakobsen, J. C. (2013). Mindfulness: top-down or bottom-up emotion regulation strategy? *Clinical Psychology Review*, *33*(1), 82–96. http://doi.org/10.1016/j.cpr.2012.10.006

Cockburn, J., Collins, A. G. E., & Frank, M. J. (2014). A Reinforcement Learning Mechanism Responsible for the Valuation of Free Choice. *Neuron*, *83*(3), 551–557. http://doi.org/10.1016/j.neuron.2014.06.035

Cohen, M. X., Young, J., Baek, J. M., Kessler, C., & Ranganath, C. (2005). Individual differences in extraversion and dopamine genetics predict neural reward responses. *Cognitive Brain Research*, *25*(3), 851–861. http://doi.org/10.1016/j.cogbrainres.2005.09.018

Corbetta, M., & Shulman, G. L. (2002). Control of Goal-Directed and Stimulus-Driven Attention in the Brain. *Nature Reviews Neuroscience*, *3*(3), 215–229. http://doi.org/10.1038/nrn755

Davidson, R. J. (2000). Dysfunction in the Neural Circuitry of Emotion Regulation--A Possible Prelude to Violence. *Science*, *289*(5479), 591–594. http://doi.org/10.1126/science.289.5479.591

Davis, C., Strachan, S., & Berkson, M. (2004). Sensitivity to reward: Implications for overeating and overweight. *Appetite*, *42*(2), 131–138.

http://doi.org/10.1016/j.appet.2003.07.004

de Ruiter, M. B., Veltman, D. J., Goudriaan, A. E., Oosterlaan, J., Sjoerds, Z., & van den Brink, W. (2009). Response perseveration and ventral prefrontal sensitivity to reward and punishment in male problem gamblers and smokers. *Neuropsychopharmacology : Official Publication of the American College of Neuropsychopharmacology*, *34*(4), 1027–1038. http://doi.org/10.1038/npp.2008.175

DeCharms, R. (2013). *Personal causation: The internal affective determinants of behavior*. Routledge.

Delgado, M. R., Nearing, K. I., LeDoux, J. E., & Phelps, E. a. (2008). Neural Circuitry Underlying the Regulation of Conditioned Fear and Its Relation to Extinction. *Neuron*, *59*(5), 829–838. http://doi.org/10.1016/j.neuron.2008.06.029

Delgado, M. R., Nystrom, L. E., Fissell, C., Noll, D. C., & Fiez, J. a. (2000). Tracking the hemodynamic responses to reward and punishment in the striatum. *Journal of Neurophysiology*, *84*(6), 3072–7. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11110834

Di Chiara, G., Bassareo, V., Fenu, S., De Luca, M. A., Spina, L., Cadoni, C., … Lecca, D. (2004). Dopamine and drug addiction: The nucleus accumbens shell connection. *Neuropharmacology*, *47*(SUPPL. 1), 227–241. http://doi.org/10.1016/j.neuropharm.2004.06.032

Dickinson, A., Balleine, B., Watt, A., Gonzalez, F., & Boakes, R. A. (1998). Motivational control after extended instrumental training. *Animal Learning and Behavior*, *23*(2), 197–206.

Dolcos, F., Kragel, P., Wang, L., & McCarthy, G. (2006). Role of the inferior frontal

cortex in coping with distracting emotions. *NeuroReport*, *17*(15), 1591.

Duncan, J., & Owen, A. M. (2000). Common regions of the human frontal lobe recruited by diverse cognitive demands. *Trends Neurosci*, *23*(10), 475–483. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve%7B&%7Ddb=PubMed%7B&%7Ddopt=Citation%7B&%7Dlist%7B_%7Duids=11006464

Eysenck, M., Derakshan, N., Santos, R., & Calvo, M. (2007). Anxiety and cognitive performance: attentional control theory. *Emotion*, *7*(2), 336–53. http://doi.org/10.1037/1528-3542.7.2.336

Frank, M. J., Doll, B. B., Oas-Terpstra, J., & Moreno, F. (2009). Prefrontal and striatal dopaminergic genes predict individual differences in exploration and exploitation. *Nature Neuroscience*, *12*(8), 1062–8. http://doi.org/10.1038/nn.2342

Franken, I. H. a. (2002). Behavioral approach system (BAS) sensitivity predicts alcohol craving. *Personality and Individual Differences*, *32*(2), 349–355. http://doi.org/10.1016/S0191-8869(01)00030-7

Franken, I. H. a, & Muris, P. (2005). Individual differences in reward sensitivity are related to food craving and relative body weight in healthy women. *Appetite*, *45*(2), 198–201. http://doi.org/10.1016/j.appet.2005.04.004

Friston, K. J., Buechel, C., Fink, G. R., Morris, J., Rolls, E., & Dolan, R. J. (1997). Psychophysiological and modulatory interactions in neuroimaging. *NeuroImage*, *6*(3), 218–229. http://doi.org/10.1006/nimg.1997.0291

Friston, K. J., Harrison, L., & Penny, W. (2003). Dynamic causal modelling. *NeuroImage*, *19*(4), 1273–1302. http://doi.org/10.1016/S1053-8119(03)00202-7

Fujiwara, J., Usui, N., Park, S. Q., Williams, T., Taira, M., Iijima, T., … Tobler, P. N.

(2013). Value of freedom to choose encoded by the human brain. *Journal of Neurophysiology*, *110*(8), 1915–1929.

Gard, D. E., Gard, M. G., Kring, A. M., & John, O. P. (2006). Anticipatory and consummatory components of the experience of pleasure: A scale development study. *Journal of Research in Personality*, *40*(6), 1086–1102. http://doi.org/10.1016/j.jrp.2005.11.001

Gottfried, J. a, O'Doherty, J., & Dolan, R. J. (2003). Encoding predictive reward value in human amygdala and orbitofrontal cortex. *Science (New York, N.Y.)*, *301*(5636), 1104–1107. http://doi.org/10.1126/science.1087919

Grabenhorst, F., & Rolls, E. T. (2011). Value , pleasure and choice in the ventral prefrontal cortex. *Trends in Cognitive Sciences*, *15*(2), 56–67. http://doi.org/10.1016/j.tics.2010.12.004

Gray, J. A. (1987). The neuropsychology of emotion and personality. In S. M. Stahl, S. D. Iverson, & E. C. Goodman (Eds.), *Cognitive neurochemistry* (pp. 171–190). New York: Oxford University Press.

Green, M. J., & Malhi, G. S. (2006). Neural mechanisms of the cognitive control of emotion. *Acta Neuropsychiatrica*, *18*(3–4), 144–153. http://doi.org/10.1111/j.1601-5215.2006.00149.x

Grissom, N., Kerr, W., & Bhatnagar, S. (2008). Struggling behavior during restraint is regulated by stress experience. *Behavioural Brain Research*, *191*(2), 219–226. http://doi.org/10.1016/j.bbr.2008.03.030

Haber, S. N. (2003). The primate basal ganglia: parallel and integrative networks. *Journal of Chemical Neuroanatomy*, *26*(4), 317–330.

http://doi.org/S0891061803001078 [pii]

Haber, S. N., & Knutson, B. (2009). The Reward Circuit: Linking Primate Anatomy and Human Imaging. *Neuropsychopharmacology : Official Publication of the American College of Neuropsychopharmacology*, *35*(1), 1–23. http://doi.org/10.1038/npp.2009.129

Haber, S. N., & Knutson, B. (2010). The reward circuit: linking primate anatomy and human imaging. *Neuropsychopharmacology*, *35*(1), 4–26. http://doi.org/10.1038/npp.2009.129

Hahn, T., Dresler, T., Ehlis, A. C., Plichta, M. M., Heinzel, S., Polak, T., … Fallgatter, A. J. (2009). Neural response to reward anticipation is modulated by Gray's impulsivity. *NeuroImage*, *46*(4), 1148–1153. http://doi.org/10.1016/j.neuroimage.2009.03.038

Hartley, C. a., Gorun, A., Reddan, M. C., Ramirez, F., & Phelps, E. a. (2014). Stressor controllability modulates fear extinction in humans. *Neurobiology of Learning and Memory*, *113*, 149–156. http://doi.org/10.1016/j.nlm.2013.12.003

Heatherton, T. F., & Wagner, D. D. (2011). Cognitive neuroscience of self-regulation failure. *Trends in Cognitive Sciences*, *15*(3), 132–9. http://doi.org/10.1016/j.tics.2010.12.005

Izuma, K., Matsumoto, M., Murayama, K., Samejima, K., Sadato, N., & Matsumoto, K. (2010). Neural correlates of cognitive dissonance and choice-induced preference change. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(51), 22014–9. http://doi.org/10.1073/pnas.1011879108

Jensen, M. P., Turner, J. A., & Romano, J. M. (2001). Changes in beliefs,

catastrophizing, and coping are associated with improvement in multidisciplinary pain treatment. *Journal of Consulting and Clinical Psychology*, *69*(4), 655–662. http://doi.org/10.1016/j.pain.2004.06.003

Johnstone, T., van Reekum, C. M., Urry, H. L., Kalin, N. H., & Davidson, R. J. (2007). Failure to regulate: counterproductive recruitment of top-down prefrontal-subcortical circuitry in major depression. *The Journal of Neuroscience*, *27*(33), 8877–8884.

Kable, J. W., & Glimcher, P. W. (2009). Review The Neurobiology of Decision : Consensus and Controversy. *Neuron*, *63*(6), 733–745. http://doi.org/10.1016/j.neuron.2009.09.003

Kelley, A. E., Schiltz, C. a., & Landry, C. F. (2005). Neural systems recruited by drug- and food-related cues: Studies of gene activation in corticolimbic regions. *Physiology and Behavior*, *86*(1–2), 11–14. http://doi.org/10.1016/j.physbeh.2005.06.018

Kerr, D. L., McLaren, D. G., Mathy, R. M., & Nitschke, J. B. (2012). Controllability modulates the anticipatory response in the human ventromedial prefrontal cortex. *Frontiers in Psychology*, *3*(DEC). http://doi.org/10.3389/fpsyg.2012.00557

Kim, M. J., Gee, D. G., Loucks, R. a, Davis, F. C., & Whalen, P. J. (2011). Anxiety dissociates dorsal and ventral medial prefrontal cortex functional connectivity with the amygdala at rest. *Cerebral Cortex (New York, N.Y. : 1991)*, *21*(7), 1667–1673. http://doi.org/10.1093/cercor/bhq237

Kleiner, M., Brainard, D., & Pelli, D. G. (2007). What's new in Psychtoolbox-3. *Perception*, *36*(14), 1. http://doi.org/10.1016/S0140-6736(13)62162-5

Knutson, B., Taylor, J., Kaufman, M., Peterson, R., & Glover, G. (2005). Distributed neural representation of expected value. *J Neurosci*, *25*(19), 4806–4812. http://doi.org/25/19/4806 [pii] 10.1523/JNEUROSCI.0642-05.2005

Kreek, M. J., Nielsen, D. a, Butelman, E. R., & LaForge, K. S. (2005). Genetic influences on impulsivity, risk taking, stress responsivity and vulnerability to drug abuse and addiction. *Nature Neuroscience*, *8*(11), 1450–1457. http://doi.org/10.1038/nn1583

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1999). International Affective Picture System (IAPS): Technical Manual and Affective Ratings. *NIMH Center for the Study of Emotion and Attention*, 39–58. http://doi.org/10.1027/0269-8803/a000147

Langer, E. J. (1975). The Illusion of Control. *Journal of Personality and Social Psychology*, *32*(2), 311–328.

Langer, E. J., & Rodin, J. (1976). The effects of choice and enhanced personal responsibility for the aged: a field experiment in an institutional setting. *J Pers Soc Psychol*, *34*(2), 191–198. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=1011073

Leech, R., Braga, R., & Sharp, D. J. (2012). Echoes of the brain within the posterior cingulate cortex. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *32*(1), 215–222. http://doi.org/10.1523/JNEUROSCI.3689-11.2012

Leech, R., Kamourieh, S., Beckmann, C. F., & Sharp, D. J. (2011). Fractionating the default mode network: distinct contributions of the ventral and dorsal posterior cingulate cortex to cognitive control. *The Journal of Neuroscience : The Official*

Journal of the Society for Neuroscience, *31*(9), 3217–3224. http://doi.org/10.1523/JNEUROSCI.5626-10.2011

Leech, R., & Sharp, D. J. (2014). The role of the posterior cingulate cortex in cognition and disease. *Brain*, *137*(1), 12–32. http://doi.org/10.1093/brain/awt162

Leotti, L. A., Cho, C., & Delgado, M. R. (2015). The Neural Basis Underlying the Experience of Control in the Human Brain. In P. Haggard & B. Eitam (Eds.), *The Sense of Agency* (p. 145). UK: Oxford University Press.

Leotti, L. A., & Delgado, M. R. (2011). The inherent reward of choice. *Psychological Science*, *22*(10), 1310–8. http://doi.org/10.1177/0956797611417005

Leotti, L. A., & Delgado, M. R. (2014). The value of exercising control over monetary gains and losses. *Psychological Science*, *25*(2), 596–604. http://doi.org/10.1177/0956797613514589

Leotti, L. A., Iyengar, S. S., & Ochsner, K. N. (2010). Born to Choose: The Origins and Value of the Need for Control. *Trends in Cognitive Sciences*, *14*(10), 457–463.

Lewin, K. (1951). Field theory in social science.

Lewinsohn, P. M., Mischel, W., Chaplin, W., & Barton, R. (1980). Social competence and depression: The role of illusory self-perceptions. *Journal of Abnormal Psychology*, *89*(2), 203–212.

Lieberman, M. D., Ochsner, K. N., Gilbert, D. T., & Schacter, D. L. (2001). Do amnesics exhibit cognitive dissonance reduction? The role of explicit memory and attention in attitude change. *Psychol Sci*, *12*(2), 135–140. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=11340922

Lin, A., Adolphs, R., & Rangel, A. (2012). Social and monetary reward learning engage overlapping neural substrates. *Social Cognitive and Affective Neuroscience*, *7*(3), 274–281. http://doi.org/10.1093/scan/nsr006

Loomes, G., & Sugden, R. (1982). Regret Theory : An Alternative Theory of Rational Choice Under Uncertainty. *The Economic Journal*, *92*(368), 805–824.

Lopez, R. B., Hofmann, W., Wagner, D. D., Kelley, W. M., & Heatherton, T. F. (2014). Neural Predictors of Giving in to Temptation in Daily Life. *Psychological Science*, *25*(7), 1337–44. http://doi.org/10.1177/0956797614531492

MacNamara, A., Ferri, J., & Hajcak, G. (2011). Working memory load reduces the late positive potential and this effect is attenuated with increasing anxiety. *Cognitive, Affective & Behavioral Neuroscience*, *11*(3), 321–31. http://doi.org/10.3758/s13415-011-0036-z

Maier, S. F., Amat, J., Baratta, M. V, Paul, E., & Watkins, L. R. (2006). Behavioral control, the medial prefrontal cortex, and resilience. *Dialogues Clin Neurosci*, *8*(4), 397–406. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=17290798

Maier, S. F., & Seligman, M. E. (1976). Learned helplessness: Theory and evidence. *Journal of Experimental Psychology: General*, *105*(1), 3–46. http://doi.org/10.1037//0096-3445.105.1.3

Maier, S. F., & Watkin, R. (1998). Stressor Con trollability , An xiety , an d Seroton in, *22*(6), 595–613.

Maier, S. F., & Watkins, L. R. (2010). Role of the medial prefrontal cortex in coping and

resilience. *Brain Research*, *1355*, 52–60. http://doi.org/10.1016/j.brainres.2010.08.039

McLaren, D. G., Ries, M. L., Xu, G., & Johnson, S. C. (2012). A generalized form of context-dependent psychophysiological interactions (gPPI): a comparison to standard approaches. *NeuroImage*, *61*(4), 1277–1286. http://doi.org/10.1016/j.neuroimage.2012.03.068

Melzack, R., & Casey, K. L. (1970). The affective dimension of pain. In M. B. Arnold (Ed.), *Feelings and emotions*. New York: Academic Press.

Miller, S. M. (1979). Controllability and human stress: Method, evidence and theory. *Behaviour Research and Therapy*, *17*(4), 287--304.

Mullette-Gillman, O. a., Detwiler, J. M., Winecoff, A., Dobbins, I., & Huettel, S. a. (2011). Infrequent, task-irrelevant monetary gains and losses engage dorsolateral and ventrolateral prefrontal cortex. *Brain Research*, *1395*, 53–61. http://doi.org/10.1016/j.brainres.2011.04.026

Murty, V. P., DuBrow, S., & Davachi, L. (2015). The simple act of choosing influences declarative memory. *Journal of Neuroscience*, *35*(16), 6255–6264. http://doi.org/10.1523/JNEUROSCI.4181-14.2015

Nicolle, A., Fleming, S. M., Bach, D. R., Driver, J., & Dolan, R. J. (2011). A regret-induced status quo bias. *Journal of Neuroscience*, *31*(9), 3320–3327. http://doi.org/31/9/3320 [pii]10.1523/JNEUROSCI.5615-10.2011

Nieuwenhuis, S., Heslenfeld, D. J., von Geusau, N. J. A., Mars, R. B., Holroyd, C. B., & Yeung, N. (2005). Activity in human reward-sensitive brain areas is strongly context dependent. *NeuroImage*, *25*(4), 1302–1309.

http://doi.org/10.1016/j.neuroimage.2004.12.043

O'Doherty, J., Critchley, H., Deichmann, R., & Dolan, R. J. (2003). Dissociating valence of outcome from behavioral control in human orbital and ventral prefrontal cortices. *J Neurosci*, *23*(21), 7931–7939. http://doi.org/23/21/7931 [pii]

O'Doherty, J. P., Dayan, P., Schultz, J., Deichmann, R., Friston, K., & Dolan, R. J. (2004). Dissociable roles of ventral and dorsal striatum in instrumental conditioning. *Science*, *304*(5669), 452–454. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=15087550

O'Doherty, J. P., Deichmann, R., Critchley, H. D., & Dolan, R. J. (2002). Neural responses during anticipation of a primary taste reward. *Neuron*, *33*(5), 815–826. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=11879657

O'Doherty, J. P., Rolls, E. T., Francis, S., Bowtell, R., & McGlone, F. (2001). Representation of pleasant and aversive taste in the human brain. *J Neurophysiol*, *85*(3), 1315–1321. Retrieved from http://www.jn.physiology.org/cgi/content/full/85/3/1315

Ochsner, K. N., & Gross, J. J. (2005). The cognitive control of emotion. *Trends in Cognitive Sciences*, *9*(5), 242–249. http://doi.org/10.1016/j.tics.2005.03.010

Ochsner, K. N., & Gross, J. J. (2008). Cognitive emotion regulation insights from social cognitive and affective neuroscience. *Current Directions in Psychological Science*, *17*(2), 153–158.

Ochsner, K. N., Silvers, J. a, & Buhle, J. T. (2012). Functional imaging studies of emotion regulation: a synthetic review and evolving model of the cognitive control of emotion. *Annals of the New York Academy of Sciences*, *1251*, E1-24. http://doi.org/10.1111/j.1749-6632.2012.06751.x

Oliveto, A. H., Hughes, J. R., Higgins, S. T., Bickei, W. K., Pepper, S. L., Shea, P. J., & Fenwick, J. W. (1992). Psychopharmacology Forced-choice versus free-choice procedures : caffeine self-administration in humans, *109*, 85–91.

Pagnoni, G., Zink, C. F., Montague, P. R., & Berns, G. S. (2002). Activity in human ventral striatum locked to errors of reward prediction. *Nat Neurosci*, *5*(2), 97–98. http://doi.org/10.1038/nn802 nn802 [pii]

Parvaz, M. a, MacNamara, A., Goldstein, R. Z., & Hajcak, G. (2012). Event-related induced frontal alpha as a marker of lateral prefrontal cortex activation during cognitive reappraisal. *Cognitive, Affective & Behavioral Neuroscience*, *12*(4), 730–40. http://doi.org/10.3758/s13415-012-0107-9

Patall, E. A. (2013). Constructing motivation through choice, interest, and interestingness. . *Ournal of Educational Psychology*, *105*(2), 522.

Paton, J. J., Belova, M. A., Morrison, S. E., & Salzman, C. D. (2006). The primate amygdala represents the positive and negative value of visual stimuli during learning. *Nature*, *439*(7078), 865–870. http://doi.org/nature04490 [pii] 10.1038/nature04490

Pearson, J. M., Heilbronner, S. R., Barack, D. L., Hayden, B. Y., & Platt, M. L. (2011). Posterior cingulate cortex: Adapting behavior to a changing world. *Trends in Cognitive Sciences*, *15*(4), 143–151. http://doi.org/10.1016/j.tics.2011.02.002

Petrides, M. (2002). The mid-ventrolateral prefrontal cortex and active mnemonic retrieval. *Neurobiology of Learning and Memory*, *78*(3), 528–538. http://doi.org/S1074742702941079 [pii]

Petrides, M., Alivisatos, B., & Evans, a C. (1995). Functional activation of the human ventrolateral frontal cortex during mnemonic retrieval of verbal information. *Proceedings of the National Academy of Sciences of the United States of America*, *92*(13), 5803–5807. http://doi.org/10.1073/pnas.92.13.5803

Petrides, M., & Pandya, D. N. (2002). Comparative cytoarchitectonic analysis of the human and the macaque ventrolateral prefrontal cortex and corticocortical connection patterns in the monkey. *The European Journal of Neuroscience*, *16*, 291–310. http://doi.org/10.1046/j.1460-9568.1999.00518.x

Pochon, J. B., Levy, R., Fossati, P., Lehericy, S., Poline, J. B., Pillon, B., … Dubois, B. (2002). The neural system that bridges reward and cognition in humans: an fMRI study. *Proceedings of the National Academy of Sciences of the United States of America*, *99*(8), 5669–5674. http://doi.org/10.1073/pnas.082111099

Power, J. D., Schlaggar, B. L., & Petersen, S. E. (2015). Recent progress and outstanding issues in motion correction in resting state fMRI. *NeuroImage*, *105*, 536–551. http://doi.org/10.1016/j.neuroimage.2014.10.044

Rapee, R. M., Craske, M. G., Brown, T. a., & Barlow, D. H. (1996). Measurement of perceived control over anxiety-related events. *Behavior Therapy*, *27*(2), 279–293. http://doi.org/10.1016/S0005-7894(96)80018-9

Robbins, T. W., & Everitt, B. J. (1996). Neurobehavioural mechanisms of reward and motivation. *Current Opinion in Neurobiology*, *6*(2), 228–236. http://doi.org/S0959-

4388(96)80077-8 [pii]

Rotter, J. B. (1966). Generalised expectancies for internal versus external control of reinforcement. *Psychological Monographs*, *80*(1, NaN 609), 1–28.

Ryan, R., & Deci, E. (2000). Intrinsic and Extrinsic Motivations: Classic Definitions and New Directions. *Contemporary Educational Psychology*, *25*(1), 54–67. http://doi.org/10.1006/ceps.1999.1020

Ryan, R. M., & Deci, E. L. (2000). Self-determination theory and the facilitation of intrinsic motivation, social development, and well-being. *The American Psychologist*, *55*(1), 68–78. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11392867

Ryan, R. M., & Deci, E. L. (2006). Self-regulation and the problem of human autonomy: does psychology need choice, self-determination, and will? *Journal of Personality*, *74*(6), 1557–85. http://doi.org/10.1111/j.1467-6494.2006.00420.x

Sakagami, M., & Pan, X. (2007). Functional role of the ventrolateral prefrontal cortex in decision making. *Current Opinion in Neurobiology*, *17*(2), 228–233. http://doi.org/10.1016/j.conb.2007.02.008

Salomons, T. V, Johnstone, T., Backonja, M.-M. M., & Davidson, R. J. (2004). Perceived controllability modulates the neural response to pain. *J Neurosci*, *24*(32), 7199–7203. http://doi.org/10.1523/JNEUROSCI.1315-04.2004

Salomons, T. V, Johnstone, T., Backonja, M. M., Shackman, A. J., & Davidson, R. J. (2007). Individual differences in the effects of perceived controllability on pain perception: critical role of the prefrontal cortex. *J Cogn Neurosci*, *19*(6), 993–1003. http://doi.org/10.1162/jocn.2007.19.6.993

Schiller, D., & Delgado, M. R. (2010). Overlapping neural systems mediating extinction, reversal and regulation of fear. *Trends in Cognitive Sciences*, *14*(6), 268–276. http://doi.org/10.1016/j.tics.2010.04.002

Schneider, S., Peters, J., Bromberg, U., Brassen, S., Miedl, S. F., Banaschewski, T., … Büchel, C. (2012). Risk taking and the adolescent reward system: A potential common link to substance abuse. *American Journal of Psychiatry*, *169*(1), 39–46. http://doi.org/10.1176/appi.ajp.2011.11030489

Scult, M. A., Knodt, A. R., Hanson, J. L., Ryoo, M., Adcock, R. A., Hariri, A. R., & Strauman, T. J. (2016). Individual Differences in Regulatory Focus Predict Neural Response to Reward. *Social Neuroscience*, *919*(April), 1–11. http://doi.org/10.1080/17470919.2016.1178170

Seligman, M. E., & Maier, S. F. (1967). Failure to escape traumatic shock. *Journal of Experimental Psychology*, *47*(1), 1–9. http://doi.org/10.1037/h0024514

Sharot, T., De Martino, B., & Dolan, R. J. (2009). How choice reveals and shapes expected hedonic outcome. *J Neurosci*, *29*(12), 3760–3765. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=19321772

Sharot, T., De Martino, B., & Dolan, R. J. (2009). How choice reveals and shapes expected hedonic outcome. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *29*(12), 3760–3765. http://doi.org/10.1523/JNEUROSCI.4972-08.2009

Sharot, T., Fleming, S. M., Yu, X., Koster, R., & Dolan, R. J. (2012). Is Choice-Induced Preference Change Long Lasting? *Psychological Science*, *23*(10), 1123–1129.

http://doi.org/10.1177/0956797612438733

Sharot, T., Shiner, T., & Dolan, R. J. (2010). Experience and choice shape expected aversive outcomes. *J Neurosci*, *30*(27), 9209–9215. http://doi.org/30/27/9209 [pii]10.1523/JNEUROSCI.4770-09.2010

Sharot, T., Velasquez, C. M., & Dolan, R. J. (2010). Do decisions shape preference? Evidence from blind choice. *Psychological Science*, *21*(9), 1231–1235. http://doi.org/10.1177/0956797610379235

Skinner, B. F. (1953). Operant behavior. *Science and Human Behavior*, 59–90. http://doi.org/10.3390/ijerph8093528

Smith, D. V., & Delgado, M. R. (2016). Meta-analysis of psychophysiological interactions: Revisiting cluster-level thresholding and sample sizes. *Human Brain Mapping*, *0*(August). http://doi.org/10.1002/hbm.23354

Smith, D. V., Gseir, M., Speer, M. E., & Delgado, M. R. (2016). Toward a cumulative science of functional integration: A meta-analysis of psychophysiological interactions. *Human Brain Mapping*, *37*(8), 2904–2917. http://doi.org/10.1002/hbm.23216

Smith, D. V., Rigney, A. E., & Delgado, M. R. (2016). Distinct Reward Properties are Encoded via Corticostriatal Interactions. *Scientific Reports*, *6*(August 2015), 20093. http://doi.org/10.1038/srep20093

Stephan, K. E., Penny, W. D., Daunizeau, J., Moran, R. J., & Friston, K. J. (2009). Bayesian model selection for group studies. *NeuroImage*, *46*(4), 1004–1017. http://doi.org/10.1016/j.neuroimage.2009.03.025

Stephens, D. N., Duka, T., Crombag, H. S., Cunningham, C. L., Heilig, M., & Crabbe, J.

C. (2010). Reward sensitivity: Issues of measurement, and achieving consilience between human and animal phenotypes. *Addiction Biology*, *15*(2), 146–168. http://doi.org/10.1111/j.1369-1600.2009.00193.x

Strauman, T. J., Detloff, A. M., Sestokas, R., Smith, D. V., Goetz, E. L., Rivera, C., & Kwapil, L. (2013). What shall I be, what must I be: neural correlates of personal goal activation. *Frontiers in Integrative Neuroscience*, *6*(January), 123. http://doi.org/10.3389/fnint.2012.00123

Tanabe, J., Reynolds, J., Krmpotich, T., Claus, E., Thompson, L. L., Du, Y. P., & Banich, M. T. (2013). Reduced neural tracking of prediction error in Substance-dependent individuals. *American Journal of Psychiatry*, *170*(November), 1356–1363. http://doi.org/10.1176/appi.ajp.2013.12091257

Tanaka, S. C., Balleine, B. W., & O'Doherty, J. P. (2008). Calculating consequences: brain systems that encode the causal effects of actions. . *The Journal of Neuroscience*, *28*(26), 6750–6755.

Taylor, S. F., Welsh, R. C., Wager, T. D., Phan, K. L., Fitzgerald, K. D., & Gehring, W. J. (2004). A functional neuroimaging study of motivation and executive function. *NeuroImage*, *21*(3), 1045–54. http://doi.org/10.1016/j.neuroimage.2003.10.032

Thorndike, E. L. (1933). Special articles, 75–76.

Treadway, M. T., & Zald, D. H. (2011). Reconsidering anhedonia in depression: Lessons from translational neuroscience. *Neuroscience and Biobehavioral Reviews*, *35*(3), 537–555. http://doi.org/10.1016/j.neubiorev.2010.06.006

Tremblay, L., & Schultz, W. (1999). Relative reward preference in primate orbitofrontal cortex. *Nature*, *398*(6729), 704–708. http://doi.org/10.1038/19525

Tricomi, E. M., Delgado, M. R., & Fiez, J. A. (2004). Modulation of caudate activity by action contingency. *Neuron*, *41*(2), 281–292. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=14741108

Troy, A. S., Shallcross, A. J., & Mauss, I. B. (2013). A Person-by-Situation Approach to Emotion Regulation: Cognitive Reappraisal Can Either Help or Hurt, Depending on the Context. *Psychological Science*, *24*(12), 2505–14. http://doi.org/10.1177/0956797613496434

Turk, D. J., Banfield, J. F., Walling, B. R., Heatherton, T. F., Grafton, S. T., Handy, T. C., … Macrae, C. N. (2004). From facial cue to dinner for two: The neural substrates of personal choice. *NeuroImage*, *22*(3), 1281–1290. http://doi.org/10.1016/j.neuroimage.2004.02.037

Utevsky, A. V., Smith, D. V., & Huettel, S. A. (2014). Precuneus Is a Functional Core of the Default-Mode Network. *The Journal of Neuroscience*, *34*(3), 932–940. http://doi.org/10.1523/JNEUROSCI.4227-13.2014

Vohs, K. D., & Baumeister, R. F. (Eds. . (2011). *Handbook of self-regulation: Research, theory, and applications*. Guilford Press.

Volkow, N. D., Wang, G. J., Fowler, J. S., Logan, J., Jayne, M., Franceschi, D., … Pappas, N. (2002). "Nonhedonic" food motivation in humans involves dopamine in the dorsal striatum and methylphenidate amplifies this effect. *Synapse*, *44*(3), 175–180. http://doi.org/10.1002/syn.10075 [pii] 10.1002/syn.10075

Weiss, J. A. Y. M. (1968). EFFECTS OF COPING RESPONSES ON STRESS 1 A subsequent study on monkeys by, *65*(2), 251–260. http://doi.org/10.1037/h0025562

Whitton, A. E., Treadway, M. T., & Pizzagalli, D. A. (2015). Reward processing dysfunction in major depression, bipolar disorder and schizophrenia. *Current Opinion in Psychiatry*, *28*(1), 7–12. http://doi.org/10.1097/YCO.0000000000000122

Wiech, K., Kalisch, R., Weiskopf, N., Pleger, B., Stephan, K. E., & Dolan, R. J. (2006). Anterolateral prefrontal cortex mediates the analgesic effect of expected and perceived control over pain. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *26*(44), 11501–9. http://doi.org/10.1523/JNEUROSCI.2568-06.2006

Woolrich, M. W., Ripley, B. D., Brady, M., & Smith, S. M. (2001). Temporal autocorrelation in univariate linear modeling of FMRI data. *NeuroImage*, *14*(6), 1370–86. http://doi.org/10.1006/nimg.2001.0931

Worsley, K. J. (2001). Statistical Analysis of Activation Images. In P. Jezzard, P. M. Matthews, & S. M. Smith (Eds.), *Functional MRI: an introduction to methods* (pp. 251–270). New York: Oxford University.

Yau, W. Y., Zubieta, J. K., Weiland, B. J., Samudra, P. G., Zucker, R. A., & Heitzeg, M. M. (2012). Nucleus accumbens response to incentive stimuli anticipation in children of alcoholics: relationships with precursive behavioral risk and lifetime alcohol use. *J Neurosci*, *32*(7), 2544–2551. http://doi.org/10.1523/JNEUROSCI.1390-11.2012

Yokum, S., Ng, J., & Stice, E. (2011). Attentional bias to food images associated with elevated weight and future weight gain: an fMRI study. *Obesity (Silver Spring, Md.)*, *19*(9), 1775–83. http://doi.org/10.1038/oby.2011.168