CHAPTER 4

The neural basis of self-control

4.1 Introduction

The ability to exert self-control over one's thoughts and behaviors is crucial to successfully navigating the real world in a variety of domains, such as motor control (remaining in your seat during a boring lecture instead of jumping up and running outside), control over risky behavior (taking a sure option so as not to risk losing money), control over immediate temptation (choosing to delay a payment so as to receive a larger one), and emotional control (remaining composed and suppressing the desire to yell at someone who angered you). Each of these examples requires different actions to successfully exert control over the more desirable yet detrimental action. It is under debate in both the human and animal literature whether self-control and its inverse, impulsivity, even with these different varieties, is a general concept subserved by a single system (Monterosso & Ainslie, 1999; Muraven & Baumeister, 2000), or whether each type of control/impulsivity is separable (Evenden, 1999; G. T. Smith et al., 2007).

Behavioral studies tend to support the theory that self-control is a unitary concept in humans. Results of a series of studies comparing multiple forms of self-control indicate that if one exerts self-control in any domain, he or she is impaired at any future attempts at self-control, regardless of which domain it involves (for a review, see: Muraven & Baumeister, 2000). The domains studied are as varied as squeezing a resistant handgrip, motor response inhibition, the Stroop incongruency effect, resisting alcohol, and emotion regulation. The conclusion from this line of research is that self-control is a limited resource subserved by a

single system and that it can therefore be fatigued by effort in any self-control domain (Muraven & Baumeister, 2000; Muraven et al., 2006, 1998).

Another manner through which to determine whether different forms of self-control are related is to directly compare performance on two different forms of self-control in a single group of participants. For example, poorer self-control as measured by worse motor response inhibition has been correlated with increased risk-taking in healthy and obese children (Nederkoorn et al., 2006) and in poorer ability to regulate emotions in healthy children (Hoeksma et al., 2004; Lewis et al., 2006). Additionally, the ability to suppress risky behavior has been associated with increased emotion regulation in healthy adults (Leith & Baumeister, 1996) and a greater ability to delay gratification in participants with cocaine dependence (Monterosso et al., 2001). A variety of groups at risk for impaired self-control have poorer motor response inhibition than controls, such as adults that are high in impulsivity (Logan et al., 1997) and who abuse substances (Fillmore & Rush, 2002; Monterosso et al., 2005), individuals with ADHD (Lijffijt et al., 2005; Logan et al., 2000), and children (B. Williams et al., 1999). Lastly, populations at risk for impaired self-control, such as individuals who abuse substances, have been found to behave more poorly than control participants in behavioral choice tasks probing risky behavior (Grant et al., 2000; Monterosso et al., 2001; Rogers, Everitt, et al., 1999) and the ability to delay gratification (for a review, see: Bickel & Marsch, 2001).

The current literature exploring the neural basis of self-control overwhelmingly focuses on individual tasks that require self-control for successful performance.

Virtually every task requiring self-control finds right ventrolateral prefrontal cortex (rVLPFC) involvement in the contrasts requiring control, including in the motor (Aron & Poldrack, 2006; Aron et al., 2004; Elliott et al., 2000; Garavan et al., 2002; Kringelbach & Rolls, 2003), risk-taking (Ernst et al., 2002; Rogers, Owen, et al., 1999), delaying gratification (McClure et al., 2004; Monterosso et al., 2007), and emotion regulation (Kalisch et al., 2005; Levesque et al., 2003; Lieberman et al., 2007; Ochsner & Gross, 2005; Ochsner et al., 2004; Phan et al., 2005) domains. None of these studies, however, compares the task of interest to other forms of self-control, so whether different areas within the rVLPFC or a single locus are involved in these tasks is unknown.

The rVLPFC is well suited to serving a key role in exerting self-control over actions. It has close anatomical associations with other control areas in the prefrontal cortex, such as the dorsolateral prefrontal cortex (DLPFC), medial prefrontal cortex (mPFC) including the anterior cingulate cortex (ACC), and the orbitofrontal cortex (OFC; Miller & Cohen, 2001). Evidence that the rVLPFC is linked to the amygdala via the mPFC comes from affect labeling studies, which find increased rVLPFC activity associated with decreased amygdala activity (Hariri, Bookheimer, & Mazziotta, 2000; Hariri, Mattay, Tessitore, Fera, & Weinberger, 2003; Lieberman et al., 2007), likely through mediation by the mPFC, which has dense reciprocal connections with both structures (Lieberman et al., 2007).

Recently, white matter connections identified using Diffusion Tensor Imaging (DTI) have been noted between the rVLPFC and the pre-supplementary motor

area (preSMA), an area thought to be involved in conflict detection (Aron et al., 2007). Crucially, the rVLPFC also has direct connections with motor output control areas of the basal ganglia such as the subthalamic nucleus (STN; Aron et al., 2007). This may be the means through which the rVLPFC may send a signal to exert behavioral control and therefore underlie an act of self-control.

The current study sought to directly compare performance on four different tasks requiring very different forms of self-control both behaviorally and during a functional MRI scan in order to determine whether there is a common network or region across all the tasks that may subserve self-control generally, or whether the different forms of self-control are fully dissociable. It also related task performance to various self-report measures of impulsivity and risk-taking. While some studies already have attempted to look at the purported relationship between control-related tasks, the tasks used in these studies were very similar to each other, such as comparing the go/no-go task with the flanker task (Bunge et al., 2002; Wager et al., 2005) or the Wisconsin Card Sorting Task (Konishi et al., 1999). Each of these tasks requires inhibition of a prepotent response in order to either not respond or to make the correct response. We attempted to extend this literature by exploring tasks with very different control requirements on very different timecourses (i.e., rapid motor control or control over risky choices as compared to slower, more deliberate control over emotions or delaying gratification). The tasks included in this study were the stop-signal task (SS, motor control; Logan et al., 1994), the balloon analogue risk task (BART, control over risky behavior; Lejuez et al., 2002), the temporal discounting task (TD, control

in order to delay gratification; Kable & Glimcher, 2007; McClure et al., 2004), and the emotion regulation task (ER, emotional control; Ochsner et al., 2004). The SS task tests ones ability to exert self-control by inhibiting a button press to a stimulus at the occurrence of a signal to immediately stop responding. The dependent variable is stop-signal reaction time (SSRT), a measure of the time a participant needs to be able to inhibit his or her response. The BART examines the degree to which individuals will accept increasing risk of a monetary loss in order to obtain greater monetary gains as compared to exerting control over risky button presses and cashing out with less money on a trial. The TD task tests one's tendency to choose a small reward immediately instead of exerting control over the desire for immediate payoff to wait for a larger reward at a later time, which would result in a larger payoff overall. The ER task requires participants to suppress an initial negative emotional response to aversive images. In independent neuroimaging studies, contrasts requiring control in each of these tasks has revealed activity in the rVLPFC (Aron & Poldrack, 2006; Kalisch et al., 2005; Levesque et al., 2003; McClure et al., 2004; Monterosso et al., 2007; Ochsner et al., 2004; Phan et al., 2005; Rao, Korczykowski, Pluta, Hoang, & Detre, 2008; Rubia et al., 2003), although performance has never been directly compared to determine whether there is overlap within the rVLPFC or if the regions involved are dissociable.

4.2 Materials and Methods

4.2.1 Participants.

89 healthy adults were recruited from UCLA's campus via posted advertisements for a behavioral study exploring the relationship between different forms of self-control. Participants were eligible if they were between the ages of 18 and 40, right-handed, not currently taking psychoactive medication or illegal substances, had no history of neurological illness, and had a social security number (necessary for payment, see below). Of these participants, 11 were excluded because of: incomplete data (7) or poor performance defined a priori for each task (4). The remaining 78 participants had a mean age of 21.3 (range 18-34) and there were 39 females. Each of these 78 participants was invited back to participate in the MRI study if they were eligible to participate in an MRI scan (i.e., not claustrophobic, not pregnant, and no metal in their bodies). Of these 78, 29 participated in the MRI study. Five participants were excluded because of: technical issues (2; artifacts due to a loose head coil and field of view did not cover the entire brain) or poor behavioral performance defined a priori for each task (3). Therefore, 24 participants with a mean age of 20.8 (range 18-33, 10 females) were included in the MRI study. All participants provided written informed consent according to the procedures of the UCLA Institutional Review Board.

4.2.2 Experimental Design and Procedure.

Stop-Signal: Behavioral participants performed three runs of the SS task (Logan et al., 1994) and MRI participants performed two more during MRI scanning. The primary task was a simple two-choice reaction time task with spatially compatible stimulus-response mappings. On go trials, participants pressed the right button with their right middle finger if an arrow pointed rightwards and the left button with their right index finger if the arrow pointed leftwards. On each go trial, an open circle appeared on the computer monitor for 500 ms to indicate that the primary stimulus was about to appear (visual angle subtended 4.9 x 4.9). Then the arrow, pointing left or right, appeared in the center of the circle until the participant responded or 1000 ms elapsed. The duration of the blank screen between the trials was 500 ms for the behavioral version and was jittered between 500 and 4000 ms (mean 1000 ms, sampled from an exponential distribution) for the MRI version so as to optimize our ability to compare successful inhibition trials to go trials with fMRI.

On 25% of the trials, a tone was sounded (stop trials) and participants tried to inhibit their already initiated response to the arrow. The tone was presented at varying delays (the stop-signal delay; SSD) after the onset of the go stimulus. If participants responded on a stop trial, the trial proceeded as if it were a go trial. If participants inhibited their response, the arrow remained on the screen for 1000 ms, followed by the jittered interval between trials (Figure 4.1).

An adaptive, tracking staircase procedure was used to adjust the SSD at which

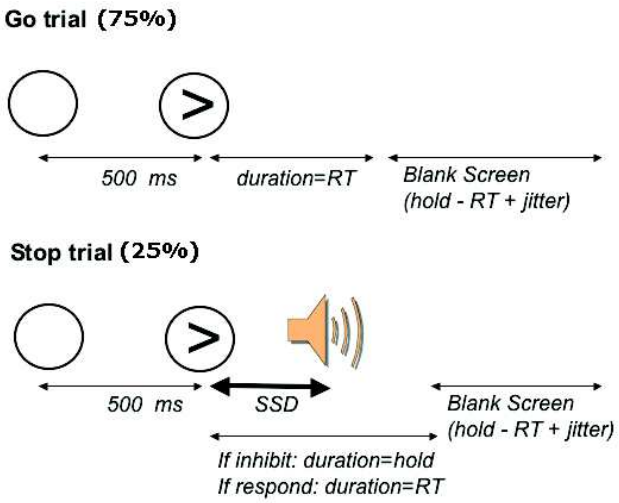

Figure 4.1: Schematic of go and stop trials on the stop-signal task. Timing reflects that of the MRI version.

the presentation of the stop-signal resulted in approximately 50% inhibition of responses. Two independent staircase functions with a step size of 50 ms were used to determine SSD. Starting delays for the two ladders on the first run of the stop-signal task were 250 ms and 350 ms respectively. The delay of each staircase was increased by 50 ms if a participant successfully inhibited his or her response to make it more difficult to inhibit a response on the next stop trial. If a participant responded on a stop trial, however, the delay was decreased by 50 ms to make it easier to inhibit a response on the next stop trial. For each subsequent run, the last SSD of each staircase on the previous block was used as each staircase's starting value. By using a dynamic SSD, we ensured that each participant was able to successfully inhibit his or her responses on approximately 50% of the stop trials. The two staircases began at slightly different delays in order to maximize the chance that at least one would begin close to a participant's ideal SSD.

Each run had 128 trials: 96 go trials and 32 stop trials and lasted between 352 and 362 seconds, depending on the length of the jittered inter-trial intervals. For each eight trials, there were four left arrows and four right arrows. There were also two stop trials (one for each ladder). Order of arrow direction, stop-trial ladder, and on which trials the stop-signal occurred were randomized. For behavioral trials there were four different list orders and for MRI trials each participant had a unique list order to ensure that there were no order effects.

BART: Behavioral participants performed one run of the BART (Lejuez et al., 2002) and MRI participants performed one additional run during MRI scanning. Participants saw a balloon on the monitor and were given the option to either inflate it by pressing the left button with their right index finger or to stop inflating it by pressing the right button with their right middle finger. For the behavioral version, the balloon began at a value of 5 cents and each pump of the balloon added one cent to a temporary pool of winnings. For the MRI version, the balloon began at a value of 50 cents and its value was increased by 25 cents for each pump. If the participant decided to stop inflating the balloon, the accrued money was moved to a permanent store of winnings and a new balloon was presented. After a variable number of pumps the balloon exploded, in which case the participant lost all the money in the temporary pool. The actual number of pumps before an explosion followed a uniform distribution across trials, with an average of 32 pumps for the behavioral version (SD = 10 pumps) and 6 pumps for the MRI version (SD = 2 pumps). There were two balloon colors for the behavioral version (blue and red) and only one for the MRI version (blue). Each

balloon color was presented 36 times for a total of 72 trials for the behavioral version and 36 trials for the MRI version.

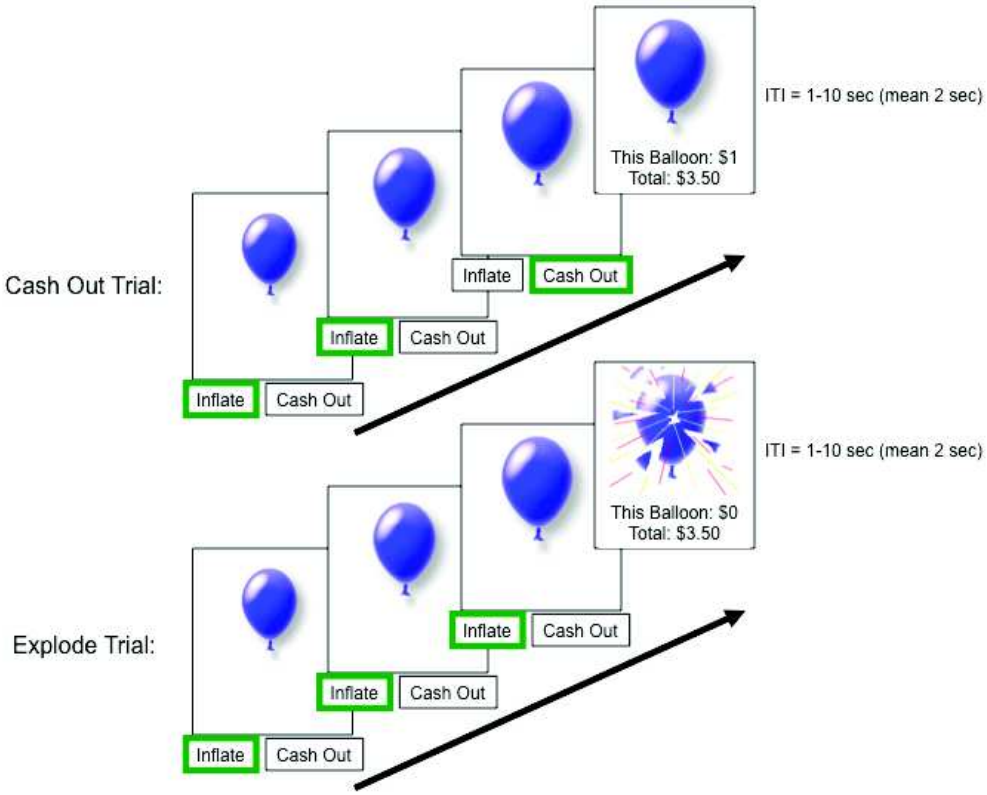

Figure 4.2: Example of a cash out trial and an explode trial on the balloon analogue risk task. Timing reflects that of the MRI version.

The number of trials and the average number of pumps before explosion varied between the behavioral and MRI versions because the timing for each version was quite different from that of the other. For the behavioral version, the balloon remained on the monitor until the participant made a choice. If the choice was to inflate the balloon, the next balloon appeared after 100 ms. After each pump, the balloon size increased by 2%. If the balloon exploded, after a delay of 100

ms the participant saw an image of an exploded balloon for 1500 ms, along with the amount of money won so far. If the participant chose to cash out and stop inflating the balloon, the balloon remained on the screen with the updated amount of money earned for 1500 ms. The next trial began after a delay of 500 ms. There were two brief breaks during the behavioral version.

For the MRI version, the balloon once again remained on the monitor until the participant made a choice. The time between events was longer than during the behavioral version and variable so we could pull apart neural responses to each of the event types. If the choice was to inflate the balloon, the next balloon appeared after a jittered delay of between 1000 ms and 3000 ms (mean 2000 ms, uniform distribution). After each pump, the balloon size increased by 15%. If the balloon exploded, after a jittered delay from the same distribution as used when inflating the balloon, the participant saw an image of an exploded balloon for 2000 ms, along with the amount of money won so far. If the participant chose to cash out and stop inflating the balloon, the balloon remained on the screen with the updated amount of money earned for 2000 ms. The next trial began after a jittered delay of between 1000 ms and 12000 ms (mean 2000 ms, exponential distribution). Run length was variable for this task since it was based on participant responses, but the maximum length was capped at 600 seconds (mean = 500 seconds [SD = 30 seconds]; Figure 4.2).

Participants received the actual amount of money earned during this task in order to ensure that they took the task seriously and viewed pumping the balloon as risky.

Temporal Discounting: Behavioral participants performed one run of the TD task (Kable & Glimcher, 2007; McClure et al., 2004) and MRI participants performed one additional run during MRI scanning. Participants made a series of decisions regarding whether they would prefer to receive a smaller amount of money immediately or a larger, variable amount of money after a variable delay. For all trials, the two payment/delay options were presented adjacent to each other on the computer monitor and participants were instructed to press the left of two buttons with their right index finger if they preferred the option displayed on the left of the monitor (the immediate option) and to press the right button with their right middle finger if they preferred the option displayed on the right of the monitor (the delayed option). The behavioral and MRI versions were very different from each other because we took advantage of learning about the individual discounting parameter for each participant during the behavioral version to determine the choices presented during the MRI version.

For the behavioral version, the immediate amount was either $5 or $10. There were six possible delays (2 days, 1 week, 3 weeks, 2 months, 4 months & 1 year). The delays were evenly distributed along a log scale then adjusted to give delays that would be easily interpreted (i.e., 2 months instead of 71 days). The dollar amount of the delayed option ranged from $5 to $120 and was determined adaptively with a staircasing procedure (Du, Green, & Myerson, 2002; Estle, Green, Myerson, & Holt, 2007). Based on previous literature, it was assumed that each participant's pattern of discounting the value of the delayed option followed a hyperbolic curve (Kable & Glimcher, 2007; Monterosso et al., 2007). The parameter

describing the steepness of the curve (k; discounting parameter) has an average value of approximately 0.013 based on previous results from studies in healthy adults (Kable & Glimcher, 2007; Kirby, Petry, & Bickel, 1999; Monterosso et al., 2007). Assuming a hyperbolic discounting function, the equation to determine the subjective value of a delayed option is:

$$SV = V/(1 + kD)$$

where SV = the subjective value of the payment after accounting for its discounted value, V = the numerical value of the payment, k = the individual's discounting parameter, and D = the delay in days of the payment. We calculated the indifference point of each option, where the subjective value of the delayed amount was equal to the actual value of the immediate amount; this would result in an option where a person with the same discounting parameter would feel that the two options were equivalent. This allowed us to calculate the actual value of the delayed amount given the delay and the immediate amount:

$$V = SV * (1 + kD)$$

where SV is equal to the immediate amount on any given trial. There were 96 adaptive trials: 50% with each immediate value ($5 and $10) and 8 occurrences of each delay for each starting value. The order of trials was random. The task began by assigning a k-value of 0.013 (the average in the healthy adult population)

to each of two staircases, one assigned to all immediate $5 options and a second assigned to all immediate $10 options. A combination of the k-value, the delay, and the immediate amount was used to determine the delayed amount presented to the participant. The only constraint to this approach was that the maximum delayed amount was capped at $120. After each trial, the k-value was updated based on the QUEST toolbox in MATLAB (A. B. Watson & Pelli, 1983). The QUEST parameters were as follows: starting estimate (0.013), standard deviation (.02), probability of choosing delayed (0.5), Weibull function parameters (beta = 5, delta = 0.01, gamma = 0.01), step size (0.001), and range of responses (1). If a participant chose the immediate amount, the indifference k-value on that trial was smaller than the person's actual k-value and it was increased on the next trial. If a participant chose the delayed amount, the indifference k-value was decreased on the next trial. This procedure was used so that the staircases would converge at the person's indifference k-value by the end of the run. Order of immediate amount and delay was random. As a check of this adaptive procedure, 54 trials with a set indifference k-value were randomly interspersed throughout the task. There were nine pre-defined k-values (.005, .0075, .01, .02, .03, .04, .05, .075, .1; Kirby et al., 1999). Each k-value was tested once per delay and randomly assigned to a starting value of $5 or $10, since pilot testing showed no difference between the converged k-values for the two starting values. Order of k-value, delay, and immediate amount was random. This allowed us to compare the k-values determined through the adaptive and through the set method, which were highly correlated ($r = 0.89$, $p < .00001$). The means of the two values were

not significantly different from each other (t(76)=0.95, p = .3). Two different list orders were used to ensure that there were no order effects.

Each choice was displayed to participants until a choice was made or 8000 ms. After 3000 ms if no response was made, a prompt appeared underneath the options to remind participants to respond. After the choice was made, a fixation crosshair was displayed for 1000 ms before the next trial began. There was one brief break in the middle of the run.

For the MRI version, we took advantage of having an estimate of each participant's discounting parameter (k). We defined trials as hard or easy based on each person's previously estimated indifference k-value. Hard trials gave choices that were only a small amount different from the indifference delayed amount (1% or 5%). Easy trials gave choices that were quite different from the indifference delayed amount (95%, 99%, 190%, or 200%). The same immediate amounts and delays were used as in the behavioral version. There were 96 trials. For each of the two immediate values each delay was tested 8 times at different degrees of difficulty. For each immediate value/delay combination, there were two hard amounts that were less than the indifference delayed amount (1% and 5%; hard immediate), two hard amounts that were more than the indifference delayed amount (1% and 5%; hard delayed), two easy amounts that were less than the indifference delayed amount (95% and 99%; easy immediate), and two easy amounts that were more than the indifference delayed amount (190% and 200%; easy delayed). Note that for the easy amounts the percent change was different for easy immediate and easy delayed trials. This is because if the easy immediate

amount was more than 100% less than the indifference value, then the delayed amount could be less than the immediate amount. We constrained the minimum delayed amount so it could be no less than the immediate amount. Trial order was generated using an m-sequence (Liu, 2004; Liu & Frank, 2004), a pseudorandom sequence optimized to maximize the tradeoff between power and efficiency, with 13 trial types (6 delays x hard vs. easy + null events). Because no differences were seen between immediate values of $5 or $10, order of those was pseudorandom, constrained so that 50% of hard immediate, 50% of hard delayed, 50% of easy immediate, and 50% of easy delayed had immediate values of $5 and 50% of each had immediate values of $10. Four different list orders were used to ensure that there would not be order effects.

At the beginning and end of the task a fixation crosshair was displayed on the screen for 16 seconds to get a baseline comparison. Each choice was displayed to participants for 4500 ms regardless of when they made their choice. There was a fixation crosshair between trials for 750 ms. There were eight null events (fixation crosshair) with a duration of 5250 ms randomly interspersed throughout the task. The run lasted 580 seconds (Figure 4.3).

Participants received the actual amount of money at the delay chosen for one randomly selected trial on this task (with the delayed amount capped at $120) to ensure that they took the task seriously. Participants were briefed on the payment procedure before the task and all stated in a debriefing questionnaire after the study that they believed it would occur as explained.

Figure 4.3: Example trial on the temporal discounting task. Timing reflects that of the MRI version.

Emotion Regulation: Behavioral participants performed one run of the ER task (Ochsner et al., 2004) and MRI participants performed two additional runs during MRI scanning. Before the task, participants were trained on the technique of cognitive reappraisal to teach them how to reduce their negative affect when viewing aversive images. Cognitive reappraisal involves redefining the image in a non-emotional, less negative manner and has been used successfully in previous studies to reduce negative affect (Gross, 1998a, 2002; Ochsner, Bunge, Gross, & Gabrieli, 2002; Ochsner et al., 2004; Phan et al., 2005). For example, an image of a person with a gruesome bullet wound may be described as an actor in a movie where the person is covered in fake blood. Participants were trained until they understood the concept of cognitive reappraisal and were able to successfully reappraise aversive images without the help of the experimenter.

Participants saw 60 novel images from the International Affective Picture Sys-

tem (IAPS; Lang, Greenwald, Bradley, & Hamm, 1993). 20 images were neutral and 40 were aversive. IAPS images are rated on a 9-point likert scale for both valence and arousal, with most unpleasant and least arousing corresponding to the lowest ratings. Neutral images were chosen from those rated between 4.38 and 6.53 for valence (mean = 5.03 [SD = 0.50]) and 1.72 and 3.85 for arousal (mean = 2.81 [SD = 0.42]). Negative images were rated between 1.31 and 4.60 for valence (mean = 2.36 [SD = 0.76]) and 4.45 and 7.35 for arousal (mean = 5.93 [SD = 0.79]). There were two instruction conditions in this experiment: suppress and attend. In the suppress condition, participants were instructed to attempt to suppress any negative emotions they may feel using cognitive reappraisal. Crucially, participants were told not to take their eyes off the images or to distract themselves with irrelevant thoughts. During attend trials, participants were instructed to look at the images and respond naturally. 20 trials were attend to neutral images (attend neutral trials), 20 were attend to negative images (attend negative trials), and 20 were suppress to negative images (suppress negative trials). Trial order was randomized for the behavioral version and optimized to detect differences in BOLD response to suppress negative trials as compared to attend negative trials for the MRI version. Average IAPS image ratings were equivalent for the behavioral and MRI runs for each participant, as were the average ratings for the attend negative images and the suppress negative images within each run (ANOVA comparing suppress negative and attend negative for behavioral and MRI runs: $F(3,76) = .02$, $p > .99$ for valence and $F(3,76) = .004$, $p > .99$ for arousal; t-test comparing attend neutral images between the

behavioral and MRI runs: $t(38) = .49$, $p = .63$ for valence and $t(38) = .03$, $p = .98$ for arousal). Each group of images contained 50% faces and 50% non-faces. There were four different list orders, each containing a different combination of images, to ensure that there were no order effects.

During the task, each trial began with the instructions for that trial (suppress or attend) displayed for 1 second. Participants were instructed to view the images as they were for the "attend" trials and utilize cognitive reappraisal for the "suppress" trials. They then viewed the image (either aversive or neutral) for 5 seconds. There was then a fixation crosshair for 2 seconds, followed by a self-report screen for 3 seconds, which asked the participants how negative they felt after either suppressing or attending to the image on a 4-point likert scale from 1 (very slightly or not at all negative) to 4 (extremely negative). The trial ended with a 3 second fixation crosshair before the next trial began. The only difference between the behavioral and MRI versions was that the behavioral version was one run with two brief breaks, whereas the MRI version was separated into two runs of 392 seconds each (Figure 4.4). Before and after the task, participants were administered the Positive and Negative Affect Schedule (PANAS; D. Watson, Clark, & Tellegen, 1988), which asks people to report the extent to which they are currently experiencing 20 emotions in order to assess changes in mood. After the MRI scan, MRI participants viewed all images they had seen during the scan and rated the negativity of each one (when attending to the image) on a 7-point likert scale from 1 (not at all negative) to 7 (extremely negative).

In order to minimize demand characteristics, participants were instructed

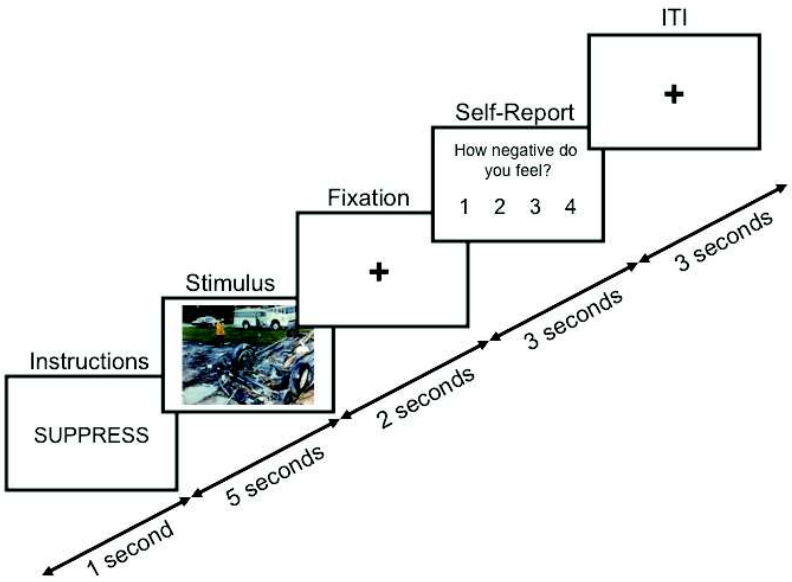

Figure 4.4: Example of a suppress trial on the emotion regulation task. Attend trials had an identical timecourse.

before the task that emotion regulation is not always successful and that we specifically chose difficult images so they may not always be able to suppress their negative emotions. It was emphasized that they should rate the strength of their negative emotion honestly and not worry about whether they were successful in decreasing their negative emotions.

The MATLAB (The MathWorks, Inc., Natick, MA) Psychophysics Toolbox (Brainard, 1997) version 7.5 was used to present the stimuli to participants and to record their responses for all tasks.

Self-Report Questionnaires: A battery of pen and paper self-report questionnaires was administered to behavioral participants to tap the presence or absence of various aspects of self-control, including impulsivity, behavioral inhi-

bition, and risky behavior. The following questionnaires were administered (all questionnaires included in full form in appendix). The Barratt Impulsiveness Scale, Version 11 (BIS-11; Patton, Stanford, & Barratt, 1995) measures one's overall level of impulsivity along three dimensions (attention, motor, and non-planning) in 30 items. The Behavioral Inhibition/Approach Scale (BIS/BAS; Carver & White, 1994) measures one's tendency to avoid (inhibit) or approach various situations in 20 items. Approach behaviors cover three dimensions: reward responsivity, fun seeking, and drive. The Cognitive Appraisal of Risky Events (CARE; Fromme, Katz, & Rivet, 1997) measures one's perception of the positive and negative consequences of engaging in certain risky events, as well as how likely one is to engage in such events in 34 items. The Domain-Specific Risk Taking (DOSPERT; Blais & Weber, 2006; Weber, Blais, & Betz, 2002) measures one's perceived risk of, benefit of, and likelihood of engaging in risky events in 30 items. The Sensation Seeking Scale (Zuckerman, Eysenck, & Eysenck, 1978) measures how much one enjoys participating in risky events in 40 items. The Need for Cognition (Cacioppo, Petty, & Kao, 1984) measures the extent to which people prefer situations where they must think and challenge themselves in 18 items. The Gambling Attitudes and Beliefs Survey (GABS; Breen & Zuckerman, 1999) measures the extent to which one enjoys gambling and is superstitious while gambling in 35 items. The Cognitive Reflection Task (Frederick, 2005) asks participants to solve three problems in which the intuitive answer is not accurate. Participants record their answer, rate the likeliness that it is accurate, and note if they had seen the problem before.

Procedure: Behavioral participants took part in two sessions separated by 2-3 weeks and MRI participants did a third MRI session 1-9 months later (mean = 4.5 months [SD = 1.4 months]). During the first behavioral session, which lasted 60-90 minutes, participants were consented then shown examples of the negative images they would see during the emotion regulation task to ensure that they would be able to view aversive images. Next, they were given one run of the stop-signal task for practice. The session ended with the participants completing the self-report questionnaires.

The next session was 2-3 weeks later to allow time for the prepaid debit cards, which were used for payment, to be ordered and received for each participant. It lasted approximately two hours. During this session, the participant performed the four behavioral tasks, filled out debriefing questionnaires about strategy for each task, and were paid.

If a participant consented to take part in the MRI session as well, they returned 1-9 months later for their scan. They were given a urine screen to ensure that they had not used any illegal substances or alcohol before the scan. During the scan, they were administered the MRI versions of the four self-control tasks, along with structural scans to register the data. Participants viewed the tasks through LCD goggles and responded using an MR-compatible button box. After the scan, they were asked to rate the negativity of each of the images they observed during the emotion regulation task, filled out debriefing questionnaires for each task, and were paid.

Payment Procedure: Participants were paid $10/hour to fill out the self-report questionnaires and paid based on task performance on the BART and TD tasks for the other sessions, ensuring that they received at least $10/hour for the behavioral session and $20/hour for the MRI session. They were paid the total amount of money they earned on the BART and their choice for one trial chosen at random from the TD task. Participants were paid separately for performance on the behavioral version of the tasks and the MRI version of the tasks. In order to make the payment cost equivalent for choosing the delayed or the immediate option on the TD task, participants were paid with prepaid debit cards. Therefore, if they chose $5 or $10 immediately on the trial chosen as payment for the TD task, they had that amount on the card the day they participated. If they chose a larger, delayed amount, that amount was added to the same debit card on the date they were to receive their payment. BART payment was done through a combination of money on the card and cash the day of participation to ensure they were paid the appropriate amount. To order cards for people, we had to provide their name, birth date, and social security number to the prepaid debit card company.

4.2.3 fMRI Data Acquisition.

Imaging data were collected with a 3T Siemens Trio scanner at the Ahmanson-Lovelace Brain Mapping Center at the University of California, Los Angeles. For each functional run we collected T2*-weighted echoplanar images (34 slices, slice thickness 4 mm, TR = 2000 ms, TE = 30 ms, flip angle = 90°, matrix 64 x

64, field of view 192 mm). A T2-weighted matched-bandwidth high-resolution anatomical scan with the same slice prescription as the functional images was also acquired. Lastly, a magnetization-prepared rapid-acquisition gradient echo (MPRage; 176 sagittal slices, slice thickness 1 mm, TR = 1900 ms, TE = 2.26 ms, matrix 256 x 256, field of view 250) was collected.

4.2.4 Behavioral Data Analysis.

Stop-Signal: Go task response time (RT) and accuracy, percent successful inhibition, average SSD, and SSRT were calculated for each participant. Only correct go trials were included in the go RT analyses. SSRT was calculated according to the race model of stopping (Logan & Cowan, 1984). The race model assumes that the go and stop processes occur in parallel and are stochastically independent (although when using the tracking method this assumption is not critical; see: Band et al., 2003). The go process begins when the go task stimulus appears on the screen and ends with the participant's response, which falls within an RT distribution. The stop process begins when the stop-signal occurs and ends after a duration termed the stop-signal reaction time (SSRT) that is assumed to be constant. This is a measure of the time it takes for a participant, once hearing the tone, to be able to suppress his or her response (Logan et al., 1994). The two processes are in a race; whichever finishes first determines the outcome of the trial. To calculate SSRT, first all correct RTs were arranged in an assumption-free distribution in ascending order. Then the proportion of failed inhibition (i.e., the proportion of stop trials on which the participant responded)

was determined. The RT corresponding to that proportion was computed (i.e., if failed inhibition was .55, the RT corresponding to 55% of the area under the RT distribution curve): the quantileRT. SSRT was calculated as the difference between the quantileRT and the average SSD.

BART: Average number of pumps for each balloon, number of exploded balloons, and amount of money won across the run were calculated for each participant. For the behavioral version with two balloon colors, the three variables were calculated separately for each balloon color and then averaged.

Temporal Discounting: The steepness of each participant's discounting curve (k-value) was calculated. For the behavioral version, if the participant's adaptive k-staircases converged, the average of the 10 steps of the ladder around the convergence point was taken. If the staircases did not converge (9 of 78 participants), the k-value from the set k trials was calculated (Kirby et al., 1999). The geometric means between each two consecutive tested k-values, plus the lowest and highest tested k-values, were the possible k-values a participant could have. Each mean was given a point if a participant responded consistently with that k-value (i.e., k-values higher than the indifference k on an immediate choice or lower than the indifference k on a delayed choice were considered consistent). The mean with the highest number of points was considered the participant's actual k-value. If there was more than one, the geometric mean of all options with the same number of points was taken. For the MRI version, logistic regression was used to calculate each participant's k-value.

Emotion Regulation: Amount of reported regulation was calculated for participants by subtracting the average of their rating scores after all the suppress negative images from the average of their rating scores after all the attend negative images.

Behavioral Relationships: In order to determine whether there were any relationships in behavioral performance across tasks or between task performance and self-reports on the questionnaires, we conducted a series of Pearson correlations between variables of interest.

4.2.5 fMRI Data Analysis.

Imaging data were processed and analyzed using FSL 4.1 (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl). Steps included BET to extract the brain from the skull and McFLIRT for motion correction.

Statistical analysis was conducted using FEAT 5.98. The statistical models varied depending on the task. For the SS task, the model included events for successful go responses, successful stop responses, and unsuccessful stop responses. Incorrect and missed go trials were included in a nuisance regressor. All events began at fixation onset and lasted through the duration of the stimulus (1.5 seconds). For the BART, the model included events for inflating the balloon (all but the last inflation of each trial), the last inflation before an explosion, cashing out, and a balloon explosion. The three response-related events began at stimulus onset and lasted the duration of the participant's RT. The explosion event

began at the time of the explosion and lasted the amount of time the exploded balloon was on the screen (2 seconds). For the temporal discounting task, the model included events for trials predefined as hard choices and trials predefined as easy choices. It also included parametric regressors weighting each of those trial types by delay. All events began at stimulus onset. The duration of all events was the participant's RT on that trial. Nuisance regressors included trials with no response (duration 4.5 seconds) and the remainder of each trial itself after a decision had been made (4.5 seconds - RT). For the emotion regulation task, the model included events for viewing the attend instructions, viewing the suppress instructions, viewing the three different image types (attend neutral, attend negative, and suppress negative), viewing the rating screen, and a demeaned parametric regressor weighted by the participant's response. All events began at stimulus onset and lasted either the duration of the stimulus (1 second for instructions, 5 seconds for images) or the participant's RT (viewing the rating screen and the parametric regressor of the participant's rating). Missed rating trials were included in a nuisance regressor with a duration of 3 seconds. For the image regressors, only images rated as 1-3 (all neutral images) or 5-7 (all negative images) were included. Three participants had less than two instances of at least one of the events and were therefore excluded from the analysis.

For the first level analysis, images were spatially smoothed using a Gaussian kernel of FWHM 5 mm. Time-series statistical analysis was carried out using FILM (FMRIBs Improved Linear Model) with local autocorrelation correction after highpass temporal filtering (Gaussian-weighted least-squares straight line

fitting, with sigma = 33.0s). Regressors of interest were created by convolving a delta function representing each event of interest with a canonical (double-gamma) hemodynamic response function (Woolrich et al., 2001). Parametric regressors were created by modulating the amplitude of a delta function using a demeaned version of the parameter of interest. In addition to regressors of interest, estimated motion parameters and their temporal derivatives (i.e., displacement) were included as nuisance regressors. Linear contrasts were performed for comparisons of interest.

A 3-step registration process was applied using FSL's FNIRT module for nonlinear registration. EPI functional images were first registered linearly to an inplane T2-weighted structural image (matched bandwidth; 7 DOF). The inplane structural image was registered linearly to the high-resolution structural image (MPRage; 7 DOF), and the high-resolution image was registered to standard MNI152 space using nonlinear registration with 12 degrees of freedom (warp resolution 10 mm). These transformation matrices were combined to provide the transform from EPI to MNI space, and this transform was applied to the results from the first-level analysis.

For the two tasks that had more than one run (SS and ER), data were combined across the two runs using a fixed effects model, and then modeled using mixed effects at the group level with FSL's FLAME model (Stage 1 only). The model for each task included a regressor modeling mean activity and demeaned regressors for SSRT (SS), number of pumps (BART), k (TD), and amount of reported regulation (ER). Outlier deweighting was performed using a mixture

modeling approach (Woolrich, 2008). Results were thresholded at a whole-brain level using cluster-based Gaussian random field theory, with a cluster-forming threshold of $z > 2.3$ and a whole-brain corrected cluster significance level of $p < .05$ unless otherwise noted in the text. Results of the ROI analysis were thresholded within that ROI using a threshold-free cluster enhancement method (TFCE; S. M. Smith & Nichols, 2009) and a corrected significance level of $p < .05$ unless otherwise noted. The conjunction analysis found areas that were significantly active within that ROI for at least two of the tasks. Cortical surface renderings were performed using CARET software (http://brainmap.wustl.edu). Group statistical maps were mapped to the Population Average Landmark and Surface-based (PALS) atlas using the multifiducial mapping technique described by Van Essen (Van Essen, 2005). For the purposes of presentation, data are overlaid on the average atlas surface.

4.3 Results

4.3.1 Behavioral Analyses

First, we explored potential relationships in behavioral performance across the tasks. We found no relationships in performance between the tasks for the MRI participants (all $ps > .17$). Given the small number of participants in that study ($n = 24$), we then looked at correlations in the 78 behavioral participants to increase our power to find any relationships. Once again, there were no significant relationships between tasks (all $ps > .37$). There were some relationships

between behavioral performance on tasks and self-report measures of risk-taking and impulsivity (see Table 4.1). However, only one of these survived correction for the number of comparisons conducted (Bonferroni-corrected p-value threshold = .0009); people who pumped the balloon more times on the BART task were more likely to think there would be positive outcomes after engaging in real-world risky activities on the DOSPERT scale (r = 0.37, p = .0009). Therefore, we focus the rest of this manuscript on MRI analyses exploring potential overlap in neural networks involved when exerting control.

Questionnaire Subscales	**Task**							
	SS		**BART**		**TD**		**ER**	
	r	p	r	p	r	p	r	p
BIS-11: Attentional	0.24	0.04			0.25	0.03		
BIS-11: Non-Planning					-0.24	0.03		
BIS-11: Total	0.23	0.04			0.30	0.007		
BIS/BAS: Reward Responsiv.	0.23	0.04						
DOSPERT (RP): Ethical	0.23	0.04	-0.34	0.003				
DOSPERT (RP): Total			-0.25	0.03				
DOSPERT (EB): Ethical			0.34	0.002				
DOSPERT (EB): Financial			0.30	0.008			0.25	0.03
DOSPERT (EB): Recreational			0.35	0.002				
DOSPERT (EB): Total			0.37	0.0009				
CARE (Engaging): Sports							0.24	0.04
GABS: Total			0.28	0.01				
Cognitive Reflect.: Num Corr			0.34	0.002				
Cognitive Reflect.: Confidence			0.35	0.002				
Need For Cognition: Total					0.24	0.04		

Table 4.1: Significant Pearson correlations between behavioral tasks and subscales of self-report questionnaires. These are not corrected for multiple comparisons. r = correlation, p = significance value, RP = risk perception, EB = expected benefits.

4.3.2 Whole-Brain fMRI Analysis

For each of the tasks we explored the whole-brain main effect for the contrast requiring self-control. Whole-brain results were corrected for multiple comparisons using cluster-based Gaussian random field theory (cluster-forming threshold of $z > 2.3$, whole-brain FWE-corrected $p < .05$) unless otherwise noted.

Region	**Coordinates (x,y,z in mm)**	**Max z**	**Extent (voxels)**
Stop-Signal Task			
R frontal pole, R inferior frontal gyrus, R orbitofrontal gyrus, R anterior insula, R frontal opercular cortex, B ACC, B paracingulate gyrus, R middle frontal gyrus, B superior frontal gyrus, B preSMA, R supramarginal gyrus, R angular gyrus, R temporal pole, R superior temporal gyrus, R middle temporal gyrus	62, -38, 10	6.56	20291
L inferior frontal gyrus, L orbitofrontal gyrus, L anterior insula, L frontal opercular cortex, L striatum, L thalamus, L STN, L supramarginal gyrus, L angular gyrus, L temporal pole, L superior temporal gyrus, L middle temporal gyrus	-44, -32, 8	6.72	9454
R striatum, R thalamus, R STN, R brainstem	8, 6, 0	4.97	2329
L lateral occipital cortex, L occipital pole	-26, -96, 8	4.61	1808
R lateral occipital cortex, R occipital pole	28, -90, 8	5.09	1700

Table 4.2: Clusters associated with successful stopping - going on the SS task. All clusters survived whole-brain correction at $z > 2.3$, $p < .05$. Clusters are reported in MNI space (mm). B = bilateral, L = left, R = right.

Stop-Signal: For the SS task, the contrast requiring self-control compared successful stopping to successful going. This controlled for stimulus events such as seeing the go stimulus and preparing for a motor response while focusing on activity related to successful inhibition of a motor response. We found activity in the right lateral frontal pole, right inferior frontal gyrus, bilateral orbitofrontal gyrus, bilateral anterior insula, bilateral ACC, bilateral paracingulate gyrus, right

middle frontal gyrus, bilateral superior frontal gyrus, bilateral preSMA, bilateral striatum, bilateral thalamus, bilateral STN, bilateral supramarginal gyrus, bilateral temporal pole, bilateral superior temporal gyrus, and bilateral occipital pole during successful motor control (Figure 4.5a; Table 4.2). Many of these areas are those that have been consistently seen in other SS studies (Aron & Poldrack, 2006; Rubia et al., 2003).

Region	**Coordinates (x,y,z in mm)**	**Max z**	**Extent (voxels)**
Balloon Analogue Risk Task			
R precentral gyrus, B postcentral gyrus, L ventral striatum, B thalamus, B STN, B hippocampus, R parahippocampal gyrus, B supramarginal gyrus, B superior parietal lobule, B fusiform cortex, B lateral occipital cortex, B occipital pole	28, -78, -14	6.70	38070
R lateral frontal pole, R inferior frontal gyrus, R orbitofrontal gyrus, R anterior insula, R middle frontal gyrus	50, 16, 28	5.34	4754
B ACC, B paracingulate gyrus, B superior frontal gyrus	4, 22, 46	4.74	1949
L inferior frontal gyrus, L middle frontal gyrus, L precentral gyrus	-38, 10, 28	4.80	1891

Table 4.3: Clusters associated with cashing out - inflating the balloon on the BART. All clusters survived whole-brain correction at $z > 2.3$, $p < .05$. Clusters are reported in MNI space (mm). B = bilateral, L = left, R = right.

BART: For the BART task, the contrast requiring self-control compared trials on which the participants chose to cash out to those on which the participants chose to inflate the balloon. This focused on when participants exerted self-control to stop themselves from inflating the balloon more even though it became worth more money with more pumps. During control over risky decisions we saw activity in many of the same regions seen during motor control, including the right lateral frontal pole, bilateral inferior frontal gyrus, right orbitofrontal

gyrus, right anterior insula, bilateral ACC, bilateral paracingulate gyrus, right middle frontal gyrus, left precentral gyrus, right postcentral gyrus, left striatum, bilateral thalamus, bilateral STN, bilateral hippocampus, bilateral supramarginal gyrus, bilateral superior parietal lobule, bilateral fusiform cortex, bilateral lateral occipital cortex, and bilateral occipital pole (Figure 4.5b; Table 4.3).

Region	**Coordinates (x,y,z in mm)**	**Max z**	**Extent (voxels)**
Temporal Discounting Task			
B frontal pole, R dorsal inferior frontal gyrus, B caudal ACC, B paracingulate gyrus, R middle frontal gyrus, R superior frontal gyrus,	2, 46, 20	3.86	5629
B cerebellum	10, -84, -42	3.51	2180
L supramarginal gyrus, L angular gyrus, L superior lateral occipital cortex	-52, -46, 54	3.47	1637
R supramarginal gyrus, R angular gyrus, R superior lateral occipital cortex	40, -64, 42	3.82	1538
B precuneus cortex	20, -62, 26	4.13	1184
B caudal ACC, B posterior cingulate cortex	2, -30, 34	3.87	1166
L occipital fusiform cortex, L occipital pole	-36, -90, -8	3.35	1066
R occipital fusiform cortex, R occipital pole	40, -90, -10	3.43	979

Table 4.4: Clusters associated with hard trials parametrically varying by delay on the TD task. All clusters survived whole-brain correction at $z > 2.3$, $p < .05$. Clusters are reported in MNI space (mm). B = bilateral, L = left, R = right.

Temporal Discounting: For the TD task, there were multiple contrasts that could be argued required greater self-control of participants. Since the goal of this study was to examine potential overlap in rVLPFC regions in tasks requiring self-control, we chose the contrast with maximal rVLPFC activity to be able to best test the hypothesis in which we were interested. Therefore, we examined the parametric neural response to difficult trials (defined a priori based on the pre-testing of participants) with increasing delays. More difficult decisions during TD tasks have been associated with longer RTs (McClure et al., 2004; Monterosso et

al., 2007). We found a significant increase in RT with increasing delays ($F(5,115) = 3.39$, $p = .007$), thus we are confident that the choices became more difficult with longer delays. Presumably the more difficult the choice, the more self-control necessary to make the decision. During decision-making with increasing difficulty, we saw activity in right lateral frontal pole, right dorsal inferior frontal gyrus, bilateral caudal ACC, bilateral paracingulate gyrus, right middle frontal gyrus, right superior frontal gyrus, bilateral posterior cingulate cortex, bilateral supramarginal gyrus, bilateral angular gyrus, bilateral fusiform cortex, bilateral precuneus cortex, bilateral lateral occipital cortex, and bilateral occipital pole. Many of the active regions were also active in the other tasks requiring self-control, although there was less overlap between the TD task and the SS and BART tasks than between the SS and BART tasks themselves (Figure 4.5c; Table 4.4).

Another contrast that could involve self-control is comparing trials on which participants chose the delayed amount over the immediate amount, implying that they were able to control the temptation to receive money immediately. Unexpectedly, we did not see any significant differences in neural activity when comparing delayed choices to immediate choices. Unfortunately, our participants chose the immediate option significantly more often than the delayed option ($t(23) = 2.11$, $p = .04$; mean % delayed responses = 40.4%), with 7 participants choosing fewer than 25% delayed responses so they had to be excluded from the analysis, which greatly limited our power to detect such a difference. That could explain the null results.

Emotion Regulation: For the ER task, once again there were multiple con-

Region	Coordinates (x,y,z in mm)	Max z	Extent (voxels)
Emotion Regulation Task			
B ACC, B paracingulate gyrus, B posterior cingulate gyrus, B preSMA	-6, -28, 38	3.74	1848
R middle frontal gyrus, R precentral gyrus, R postcentral gyrus, R superior parietal lobule, B precuneus cortex	28, 8, 52	4.10	1770
R supramarginal gyrus, R angular gyrus, R parietal operculum, R middle temporal gyrus, R inferior temporal gyrus, R inferior lateral occipital cortex	64, -26, 42	3.89	1378
B cuneal cortex, B precuneus cortex	8, -74, 40	4.06	756
L supramarginal gyrus	-32, -44, 40	3.49	646
L fusiform cortex, L inferior lateral occipital cortex	-44, -74, -2	3.99	469
L superior lateral occipital cortex	-36, -78, 40	4.54	445
L inferior frontal gyrus, L precentral gyrus	-58, 6, 40	3.85	415
L superior frontal gyrus	-28, -6, 48	3.74	363
R superior lateral occipital cortex	44, -76, 32	3.65	336
L thalamus	-10, -22, 14	3.38	275
L occipital fusiform gyrus, L occipital pole	-22, -88, -6	4.50	234
R thalamus	16, -18, 8	3.05	222
R fusiform cortex	32, -54, -6	3.50	216
R inferior frontal gyrus, R orbitofrontal gyrus	46, 24, -6	3.34	186
R middle frontal gyrus	44, 12, 36	3.24	118

Table 4.5: Clusters associated with regions correlated with self-reported emotion regulation during suppression of negative images in the ER task. All clusters survived whole-brain correction at $z > 2.0$, $p < .05$. The cluster-forming threshold was lowered from $z > 2.3$ because of the lack of power to detect a correlation between behavior and brain activity. Clusters are reported in MNI space (mm). Clusters listed here are larger than 100 voxels. B = bilateral, L = left, R = right.

trasts that could reflect greater control in participants. As with the TD task, we chose the contrast with maximal rVLPFC activity to best test our hypothesis. We examined the neural response to viewing images on suppress negative trials. We focused on areas that were more active with greater self-reported regulation, implying greater emotional control. Because of low power to view correlations in our data (we only included participants who rated enough negative images as at least a 5 out of 7 [7 being extremely negative] in a post-scan rating, therefore

only 21 were included in this analysis), we lowered the cluster-forming threshold to $z > 2.0$, while keeping the whole-brain FWE-corrected significance threshold at $p < .05$. When exploring areas related to increasing control over negative emotions, we found activity in the right lateral frontal pole, left inferior frontal gyrus, bilateral orbitofrontal gyrus, bilateral anterior insula, right posterior insula, bilateral ACC, bilateral paracingulate gyrus, bilateral middle frontal gyrus, bilateral superior frontal gyrus, bilateral preSMA, bilateral precentral gyrus, bilateral postcentral gyrus, bilateral putamen, bilateral thalamus, right STN, right amygdala, right hippocampus, bilateral superior parietal lobule, bilateral fusiform cortex, bilateral lateral occipital cortex, and right occipital pole. Again, many of the regions active during control in the other tasks were seen when successfully regulating negative emotion (Figure 4.5d; Table 4.5).

Another contrast that could involve self-control is comparing suppress negative images to attend negative images. Unfortunately, we did not see significant differences between these two event types, possibly due to the fact that many of the images were not viewed as negative enough by our participants (mean rating of negativity of images = 4.40 out of 7 [SD = 0.93]), so regulation was not necessary for all the suppress negative images. Examining the correlation between reported regulation and neural activity, therefore, takes into account that some images had less of a need to be regulated than others.

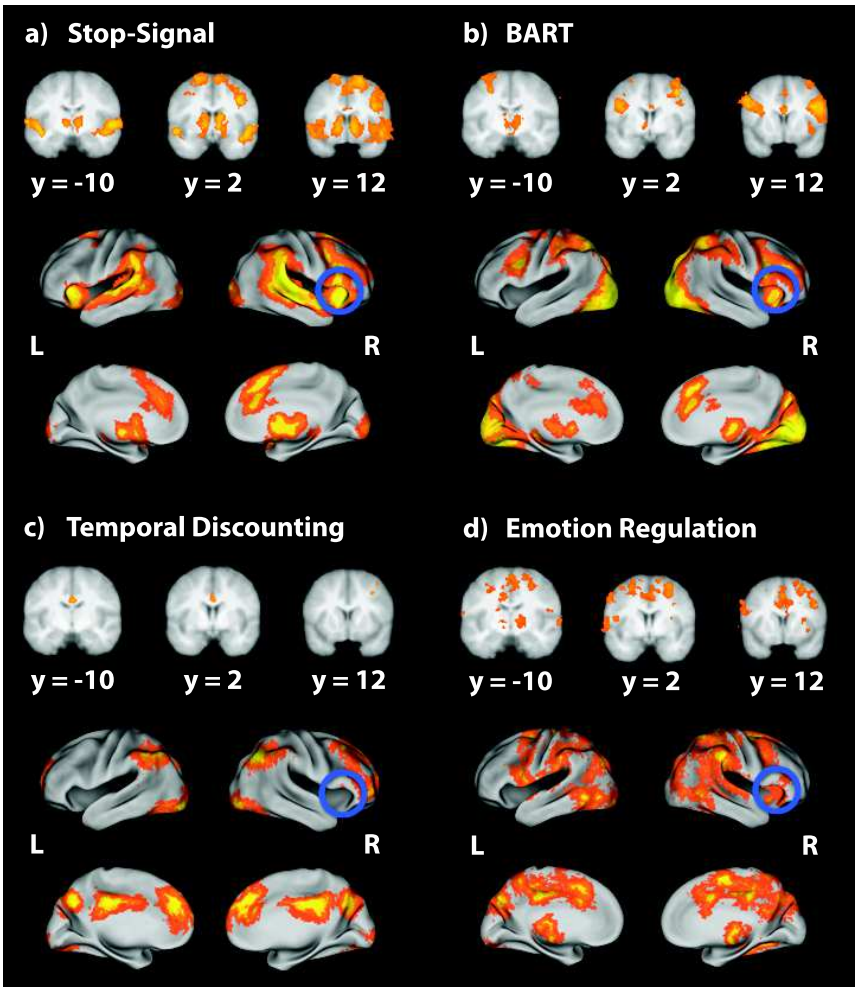

Figure 4.5: Whole-brain main effects involving self-control for each of the four tasks: a) successful stopping - going for the SS task, b) cashing out - inflating the balloon for the BART, c) hard trials parametrically varying by delay for the TD task and d) regions correlated with self-reported emotion regulation during suppression of negative images during the ER task. All clusters survived whole-brain correction at $z > 2.3$, $p < .05$ for the SS, BART, and TD tasks. The cluster–forming threshold was lowered to $z > 2.0$, $p < .05$ for the ER task because of the lack of power to detect a correlation between behavior and brain activity. See Tables 4.2-4.5.

4.3.3 Right VLPFC ROI Analysis

For the rVLPFC ROI we included the entire areas opercularis and triangularis of the inferior frontal gyrus, the anterior insula (anterior to y = 0), and the

lateral orbitofrontal gyrus (lateral to x = 32). We chose these regions because much of the literature examining control in the rVLPFC has reported activity in some combination of these areas (Aron & Poldrack, 2006; Kalisch et al., 2005; Levesque et al., 2003; McClure et al., 2004; Monterosso et al., 2007; Ochsner et al., 2004; Phan et al., 2005; Rao et al., 2008; Rubia et al., 2003). We used the Harvard-Oxford Probabilistic Atlas (FSL; provided by the Harvard Center for Morphometric Analysis) to define these regions, thresholded at 25% probability of being in each structure. For the SS, BART, and TD tasks, we thresholded activity within this ROI at a TFCE-corrected significance level of $p < .05$. For the ER task, we thresholded activity within this ROI at a TFCE-corrected significance level of $p < .1$. We raised the significance threshold for this task because we had less power to detect a correlation in only 21 participants than to detect a main effect in 24 participants as we did in the other tasks. We found robust activity across the entire ROI for the SS task and much of the ROI (except for the pars triangularis of the inferior frontal gyrus) for the BART. For the TD task, we saw activity in much of the lateral orbitofrontal gyrus, the most anterior part of the insula, and the dorsal aspect of the inferior frontal gyrus (including portions of both the pars opercularis and, to a lesser extent, the pars triangularis). Lastly, for the ER task, we saw a small amount of activity contained to the lateral orbitofrontal gyrus (Figure 4.6).

Next, we did a conjunction analysis examining regions within the rVLPFC ROI that were significantly active in all tasks. This analysis confirmed that the lateral orbitofrontal gyrus region active during emotion regulation was active in

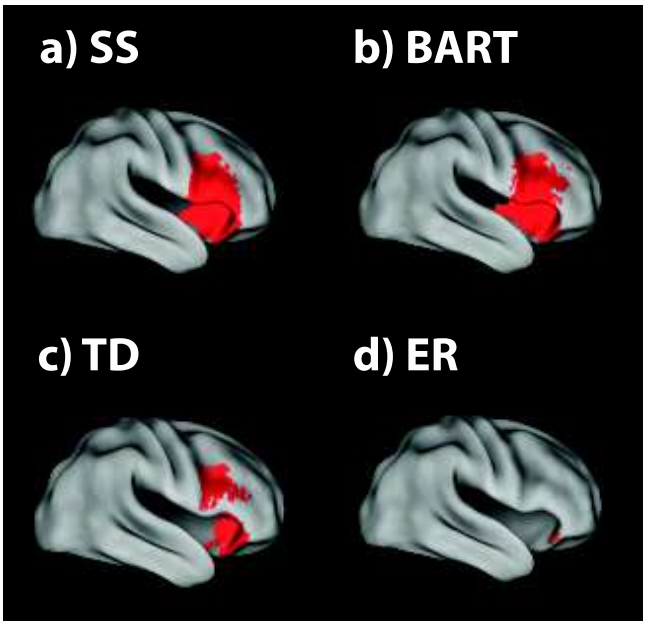

Figure 4.6: ROI analysis in the rVLPFC including inferior frontal gyrus, anterior insula, and lateral orbitofrontal gyrus for each of the four tasks: a) successful stopping - going for the SS task, b) cashing out - inflating the balloon for the BART, c) hard trials parametrically varying by delay for the TD task and d) regions correlated with self-reported emotion regulation during suppression of negative images during the ER task. Activity was thresholded at a TFCE-corrected significance level of $p < .05$ for the SS, BART, and TD tasks. The threshold was raised to $p < .1$ for the ER task because of the lack of power to detect a correlation between behavior and brain activity.

all four tasks requiring self-control. There was more overlap when examining the TD, BART, and SS tasks without the ER task. In this conjunction, we saw much of the orbitofrontal gyrus, the most anterior aspect of the insula, and the dorsal inferior frontal gyrus was commonly active in all three tasks. Lastly, we compared just the SS and BART tasks, as those two showed the most overlap. In support of this, a much greater region of the rVLPFC was commonly active across these two tasks, including much of the inferior frontal gyrus pars opercularis, a greater

portion of the anterior insula, and most of the lateral orbitofrontal gyrus (Figure 4.7).

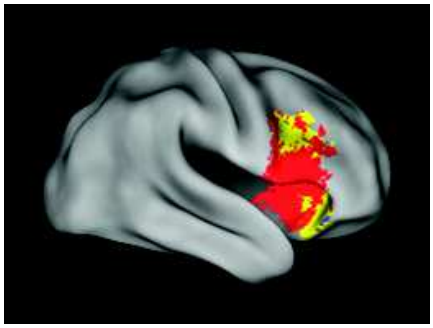

Figure 4.7: Conjunction analysis within the rVLPFC ROI. Blue = conjunction including all four tasks (SS, BART, TD and ER). Yellow = overlap of SS, BART, and TD, excluding ER. Red = overlap between SS and BART.

4.4 Discussion

We administered four very different tasks requiring very different forms of self-control to our participants in order to determine whether behavioral performance and neural regions involved were similar across the tasks. We did not find any relationships in behavioral performance between the tasks. We did find some relationships (albeit relatively weak) between task performance and various measures of impulsivity and risk-taking, such as the BIS-11 and the DOSPERT, implying that people who were better able to exert self-control were less impulsive and less risky than those were less able to exert self-control in the tasks. For example, participants who inflated the balloon fewer times on the BART and were therefore less risky were more likely to view risky behaviors as less beneficial to engage in

on the DOSPERT than those who were riskier on the BART. Much research has focused on how impulsive populations (i.e., those with ADHD or substance abuse problems) are more impulsive, more risk-taking, and perform worse on a number of these tasks (Baicy & London, 2007; Bickel & Marsch, 2001; Durston et al., 2006; Fillmore & Rush, 2002; Grant et al., 2000; Lijffijt et al., 2005; Logan et al., 1997, 2000; Monterosso et al., 2001, 2005, 2007; Nederkoorn et al., 2006; Rogers, Everitt, et al., 1999). Moreover, some studies have found relationships between poor self-control on these tasks and greater impulsivity (Logan et al., 1997) and risk-taking (Lejuez et al., 2002) in healthy populations, although these results are inconsistent (see: Hunt, Hopko, Bare, Lejuez, & Robinson, 2005; Lijffijt et al., 2004). It therefore seems as though the relationship between laboratory-based measures of self-control and self-report measures of real-world impulsivity and risk-taking is tenuous at best in healthy populations, even though it may be robust in clinically impulsive populations. It is possible that the mechanism that causes people to have clinical levels of impulsivity may also cause people to perform worse on multiple of these tasks even though that relationship does not hold for healthy adults.

Neurally, we found that while each of the tasks had unique activity associated with the contrast requiring control, there were varying degrees of overlap in the rVLPFC. The SS task and the BART had the most overlap, while the ER had the least overlap with the other three tasks. The SS task and the BART both required rapid decision-making and responses, whereas the TD and ER tasks required slower, more deliberate decision-making, so that could explain the in-

creased similarity between the SS task and the BART. Both the TD and ER tasks utilized more orbital areas. The lateral OFC has close ties to the limbic system, which is involved in evaluating and responding to both rewards (such as the payment in the TD task) and emotions (which were the focus of the ER task; Kringelbach & Rolls, 2004). The results of the conjunction analysis in combination with the lack of behavioral relationship between the tasks implies that while the rVLPFC may be involved generally in exerting self-control, there are multiple dissociable components of control.

While these results are interesting, they must be taken cautiously. First, the rVLPFC has been associated with a number of diverse tasks and cognitive processes in addition to control, such as stimulus-driven, bottom-up attention and automatic alerting to unexpected, salient stimuli (Corbetta & Shulman, 2002), memory retrieval when one must differentiate between relevant and irrelevant aspects of a stimulus (Kostopoulos & Petrides, 2003), and both object-oriented (Courtney, Ungerleider, Keil, & Haxby, 1996) and spatially-oriented (Rizzuto, Mamelak, Sutherling, Fineman, & Andersen, 2005) working memory. Its involvement in attention and memory can be ruled out as a common component of each of the tasks in the current study (i.e., trials where one cashed out on the BART did not appear any different or require more attention than those on which participants chose to inflate the balloon and each trial on the TD task was independent, thus did not require more attention or memory than any other trial). However, it is possible that in addition to requiring more control, each of the control conditions was more difficult than the condition to which it was

compared. For example, the stop task in the SS task is more difficult than the go task, making a decision to cash out may be more difficult than continuing to make the same, inflate response as on the previous trial in the BART, making a decision as delay increases may require more thought and be more difficult than with shorter delays in the TD task, and regulating one's emotion to an image that requires more regulation may be more difficult than if the image requires less regulation and is therefore less negative to begin with in the ER task. A future study needs to be designed that dissociates difficulty from self-control in order to better test this hypothesis.

Additionally, not all of the contrasts thought to require self-control in the TD and ER tasks showed activity in the rVLPFC. It is assumed that because some do, the relationship between control and the rVLPFC exists. It is possible that due to the self-selection of participants and study design that some contrasts had less power to detect activity then others. This is supported by the fact that the contrasts showing a lack of rVLPFC activity (delayed - immediate choices on the TD task and suppress negative - attend negative trials on the ER task) showed a lack of activity everywhere in the brain, not just in the rVLPFC. For the TD task we chose participants who showed consistent responding on the behavioral version of the task. However, calculated discounting parameters, while they were highly correlated on the behavioral and MRI versions ($r = 0.86$, $p < .0001$), tended to be lower on the behavioral version ($t(23) = 1.36$, $p = .19$; mean behavioral $k = .008$ [$SD = .014$]; mean MRI $k = .013$ [$SD = .027$]). It is possible that the MRI environment made people less comfortable and therefore a bit more

impulsive. Alternatively, the behavioral version with its staircasing procedure may have eased people into making more patient choices than they would when asked randomly. Regardless, the difference in discounting parameters may have made most of the trials difficult for participants. In support of that, RTs were slower for all trial types (including pre-defined "easy" trials that anticipated participants would choose the delayed option: easy delayed) than easy trials where it was expected participants would choose the immediate option (easy immediate; most of those trials were between $10 immediately and $10 at a later date and it was easy for everyone to choose the immediate option). We conducted paired t-tests between easy immediate and easy delayed ($t(23) = 3.24$, $p = .004$), easy immediate and hard immediate ($t(23) = 3.35$, $p = .003$) and easy immediate and hard delayed ($t(23) = 3.63$, $p = .001$) in order to quantify that difference. With most trials being difficult for participants, the decision-making process may have been different than if 50% of the trials were easy for participants. Lastly, the participants were a self-selecting, less impulsive group; people who responded more impulsively on the behavioral TD task tended not to want to return to participate in the MRI study (two-sample t-test comparing behavioral k-value of behavioral-only participants with that of MRI participants: $t(73) = 2.02$, $p = .047$, mean behavioral-only participants k-value = .02 [SD = .026], mean MRI participants k-value = .008 [SD = .014]). All of these reasons, in addition to the fact that participants tended to choose more immediate versus delayed options, may have caused us not to see any neural differences when participants chose the delayed, as compared to the immediate, option.

For the ER task, anecdotally, behavioral participants who felt the aversive images were most negative and therefore most needed to regulate negative emotion tended not to be comfortable performing the task again and therefore did not participate in the MRI study. Additionally, due to the fact that MRI participants performed this task twice (once in the behavioral study and once in the MRI study) and we did not want any images repeated, there was great variability in how negative the aversive IAPS pictures were, which may have resulted in less overall regulation during the suppress negative condition. In support of this, there was a correlation between how negative participants rated the images after the MRI scan and how much regulation they reported ($r = 0.45$, $p = .03$). Less regulation during the suppress negative condition could have translated to less of a difference in neural processes between the suppress negative and attend negative conditions.

Given the above limitations of this study, no firm conclusions can be drawn from the results. The results imply that there is some overlap in the rVLPFC during vastly different self-control processes, but the lack of a behavioral relationship across the tasks and the lack of differential activity during alternative contrasts related to self-control underscores the importance of future studies that more carefully control for conditions and effort and that recruit a more variable sample of participants. Fully understanding an intact control mechanism and whether it is the same for different forms of self-control in healthy adults may help to elucidate how control is exerted and why it appears to be impaired universally in some clinically impulsive populations.