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Intrinsic Reward Motivates Large-Scale Shifts Between Cognitive Control and Default Mode
Networks During Task Performance

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Communication

by

Richard W. Huskey

Committee in charge:

Professor René Weber, Chair

Professor Michael Miller

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June 2016

The dissertation of Richard W. Huskey is approved.

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June 2016

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by

Richard W. Huskey

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My sincere gratitude to everyone who has helped in the realization of this project,

Richard W. Huskey

P.S. So long and thanks for all the shoes.

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ABSTRACT

Intrinsic Reward Motivates Large-Scale Shifts Between Cognitive Control and Default Mode Networks During Task Performance

by

Richard W. Huskey

Cognitive control is an important framework for understanding the neuropsychological processes that underlie and enable the successful completion of everyday tasks. Only recently has research in this area investigated motivational contributions to control allocation. An important gap in our understanding is the way in which intrinsic rewards associated with a task motivate the sustained allocation of cognitive control. In three behavioral and one functional magnetic resonance imaging studies, we use a naturalistic and open-sourced simulator to show that changes in the balance between task difficulty and an individual's ability to perform the task result in different levels of intrinsic reward, which motivates dynamic shifts between networked brain states. Specifically, high levels of intrinsic reward associated with a balance between task difficulty and individual ability are associated with increased connectivity between cognitive control and reward networks. By comparison, a mismatch between task difficulty and individual ability is associated with lower levels of intrinsic reward and corresponds to increased activity within the default mode network. Insular activation suggests that motivational salience, as defined by the level of intrinsic

reward, drives shifts between networked brain states associated with task engagement or disengagement. These results implicate reward processing as a critical component of cognitive control.

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Foreword

“As best I can figure out, luck is a big part of a life in science.”

Michael S. Gazzaniga

The project described in this report represents the culmination of a five-year research program. It also hints at where my research is headed. As is the convention, this manuscript presents my project in a linear and orderly manner as if this is exactly what I had planned all along. Although, and as any seasoned investigator will attest, this is almost never the normal progression of science. My project is no different. It is the result of careful advising, chance encounters, a broad reading of interdisciplinary literatures, luck, fortunate timing, and determination in the face of obstacles that (on several occasions) threatened to derail the entire endeavor. This report is among the first to integrate two literatures from disciplines that currently share little interaction. To that end, and as Kuhn (1962) has noted, it is written in a technical style that makes it all but uninterruptable to anyone without advanced training in Media Neuroscience, a subfield that lies at the intersection of Media Psychology and the Cognitive Neurosciences (Weber, Eden, Huskey, Mangus, & Falk, 2015). A regrettable few within my chosen discipline of Communication have sufficient training to interpret the results reported herein, or clearly see how these results bear on the scientific study of Communication. This forward situates my narrow project within these two larger disciplines, thereby explicating otherwise obscure connections. It is the first in what will undoubtedly be a career-long goal: inspiring my colleagues to see Media Neuroscience as a valuable contribution to the scientific investigation of Communication.

Understanding why people enjoy media was my motivation for pursuing graduate training in Communication. My advisor, René Weber, turned me on to flow theory (Csikszentmihalyi, 1975) and suggested that I consider it as a framework for answering my question. Flow is a positively valenced and intrinsically rewarding psychological state that results from a balance between task difficulty and an individual's ability at the task. Communication scholars have long thought of flow as a useful framework for understanding media selection and enjoyment (Sherry, 2004). However, conceptual and measurement ambiguities have severely hamstrung empirical attempts to specify how variation in media content contributes to flow (Weber, Tamborini, Westcott-Baker, & Kantor, 2009). With a first-year graduate student's level of optimism and naiveté, I settled on solving the following question: How do media contribute to flow?

I was immediately confronted with the enormity of this question. Accordingly, our first study investigated the narrower topic of how attention is allocated during flow experiences. Consistent with predictions based on the limited capacity model of motivated mediated message processing (LC4MP; Lang, 2006), we found that flow required more attention than less motivationally relevant experiences as measured using a secondary task reaction time (STRT; Lang, Bradley, Park, Shin, & Chung, 2006). However, just-published results had suggested that attention is capacity-limited by modality (Keitel, Maess, Schröger, & Müller, 2013), thereby suggesting a natural follow-up study. In a second study using both visual and auditory STRTs, we showed that attentional demand during flow required high levels of attention regardless of modality.

At this point, we were confident that we had identified a behavioral correlate of flow that would allow us to tackle some of Sherry's (2004) untested predictions about moment-by-

moment contributions of a media stimulus to flow. We submitted our work for publication and were quickly rejected. The reviewers felt we were fooling ourselves. The paradigm lacked sufficient control, we had not fully accounted for alternate explanations, and our manipulation checks were not as convincing as we thought. Accordingly, we designed a third study to address these concerns. Our results showed robust evidence for our effect, even when stringent controls were administered. Over the course of three studies, long hours in the lab, and several hundred subjects, we had developed a high-control experimental paradigm for manipulating and measuring flow.

Encouraged, we continued in our investigations of the neurocognitive basis of flow. At the time, a recent paper in *Communication Theory* (Weber et al., 2009) made the case that conceptual ambiguities related to flow could be mitigated by adopting a Media Neuroscience perspective. Specifically, the Synchronization Theory of Flow predicted that intrinsically rewarding flow experiences resulted from a synchronization process between structures in cognitive control and reward networks. At the time, this prediction remained untested. The results from our three behavioral studies indicated that we had a procedure that would allow us to test this prediction. We began to plan the follow-up functional magnetic resonance imaging (fMRI) study.

Around this time, I was taking a cognitive neuroscience class with Michael Miller in the Department of Psychological and Brain Sciences at the University of California, Santa Barbara. Mike told me that flow sounded very similar to a problem in the Cognitive Neurosciences known as cognitive control (Miller & Cohen, 2001). Like flow, cognitive control was also interested in processes such as goal planning, goal maintenance, performance monitoring, response inhibition, and reward processing during task execution.

One of the unsolved problems within this literature was how intrinsic reward contributes to the allocation of cognitive control during task performance (Braver et al., 2014). Encouraged by the opportunity to consider flow from a broader interdisciplinary perspective, we dove into the literature. The first outcome of this effort was the development of a theoretical case for integrating flow and cognitive control. We argued that flow is a subtype of cognitive control where a balance between task demands and individual abilities contributes to the perception that a flow task requiring cognitive control is intrinsically rewarding (Weber, Huskey, & Craighead, 2016). Moreover, we made the case that Communication scholars were well positioned to test how variation in media content contributed to intrinsically rewarding flow experiences (specifically) and cognitive control (more generally).

These ideas persisted during the design and execution of our fMRI investigation of flow. Once the study was complete, we were even more convinced that our ideas about the integration of flow and cognitive control were on track. Consistent with sync theory predictions, we found that cognitive control and reward structures were functionally connected during a balance between task difficulty and individual ability (flow). Moreover, we found that a mismatch between difficulty and ability resulted in a brain state that commonly characterizes task disengagement (Raichle et al., 2001). We also replicated our STRT findings four a fourth time.

By integrating Media Psychology and Cognitive Neuroscience, we were able to show that variation in intrinsic reward of a media stimulus motivated differential levels of task engagement and cognitive control. Importantly, we demonstrated this effect in four studies using self-reports, behavioral measures, and neuroimaging data. This study addressed an important gap in the cognitive control literature by showing that intrinsic reward motivates

large-scale shifts in brain-network connectivity. For Communication scholars, our results suggest behavioral and neural correlates of the flow experience that provide a path for testing Sherry's (2004) predictions about the dynamic relationship between media content, the individual, and flow. They also provide compelling support for sync theory's central predictions. Lastly, our development of a novel paradigm, which includes an open source and high-control stimulus, provides both fields with a new tool for empirical research.

Interdisciplinary projects often underscore instances where different disciplines use distinct terminology to describe similar cognitive processes. This project is no different. But this project also demonstrates that integrating diverse fields can contribute meaningfully to broader research questions. Our hope is that Communication scholars will increasingly adopt a Media Neuroscience perspective, thereby integrating our field within the larger scholarly community.

Introduction

Planning, goal maintenance, performance monitoring, response inhibition, and reward learning are key features of cognitive control (Miller & Cohen, 2001). However, much of the work in this area has largely ignored motivation despite the fact that it is theorized to play a role in control allocation and task performance (Braver et al., 2014; Pessoa, 2008). Recent attempts at integrating these two constructs two have largely focused on the ways in which reward expectation motivates the allocation of control (Botvinick & Braver, 2014). A key finding demonstrates that control allocation is a function of anticipated task difficulty and expected rewards where humans strive to find an optimal balance between the two (Kool & Botvinick, 2014). Upon task completion, consummatory reward mechanisms track task-related outcomes and motivate subsequent behavior in order to maximize future rewards (O’Doherty et al., 2004). By comparison, the way in which task-related *intrinsic* rewards (Deci & Ryan, 1985) motivate the *sustained* allocation of cognitive control *during* task execution remains largely unknown (Braver et al., 2014). Illuminating this relationship has important implications for our understanding of cognitive control, particularly for the growing body of work showing that intrinsically rewarding, and thereby motivationally relevant, tasks contribute to better cognitive control training outcomes (Anguera et al., 2013).

Mounting evidence demonstrates that increased *extrinsic* rewards (e.g., monetary payments) facilitate increases in sustained task performance and activity in attentional, reward, and cognitive control networks (Engelmann, Damaraju, Padmala, & Pessoa, 2009; Locke & Braver, 2008). Similarly, the intrinsically rewarding nature of self-determined choice has been shown to elicit activity in reward-network structures and corresponds with increases in task enjoyment and performance (Kang et al., 2009; Leotti & Delgado, 2011;

Murayama et al., 2015). In order to evaluate intrinsic rewards resulting from task engagement (and not from choice), we draw on evidence showing that the sustained execution of a task can be intrinsically rewarding, particularly when there is a balance between the task's difficulty and an individual's ability to meet the task's demands (Csikszentmihalyi, 1975). Experimental manipulations that allow for task difficulty to vary in relationship to subject ability show a curvilinear relationship where intrinsic reward is low when difficulty \neq ability and high when difficulty \approx ability (Keller & Bless, 2008). In a follow-up study, Ulrich and colleagues (2013) replicated this finding by having subjects answer to math problems while undergoing functional magnetic resonance imaging (fMRI). Problems that matched subject's ability corresponded to the highest levels of intrinsic reward compared to problems that were too easy or difficult. This difficulty/ability balance was also associated with increased activity in attentional and cognitive control structures, particularly the inferior frontal gyrus (IFG) as well as the superior and inferior parietal lobes (SPL, IPL). Increased activity was also observed in the putamen, a region implicated in consummatory reward processing (Satterthwaite et al., 2007) and performance monitoring during cognitive control (Berkman, Falk, & Lieberman, 2012). Similar experimental paradigms using video game stimuli indicate that a balance between difficulty and ability corresponds with activation in attentional (lateral prefrontal cortex, cerebellum, thalamus, SPL) and reward (caudate nucleus, nucleus accumbens, putamen) structures (Klasen, Weber, Kircher, Mathiak, & Mathiak, 2012; Yoshida et al., 2014).

By comparison, a mismatch between difficulty and ability has been shown to result in lower levels of intrinsic reward and increased levels of activity within the default mode network (DMN; Raichle et al., 2001; Ulrich et al., 2013). Similar findings were also observed

in a study using a naturalistic video game stimulus (Mathiak, Klasen, Zvyagintsev, Weber, & Mathiak, 2013). Moreover, sustained performance on difficult cognitive tasks has been shown to exhaust subjects, resulting in a shift from activity in fronto-parietal control networks to the DMN (Esposito, Otto, Zijlstra, & Goebel, 2014). These results suggest that intrinsic reward may motivate task engagement and be a key factor driving shifts in brain-network organization between one optimized for cognitive control and one that characterizes task disengagement. Converging evidence suggests that the insula plays a key role in shifting between these networks (Chang, Yarkoni, Khaw, & Sanfey, 2013) where changes in activity within this structure predict task disengagement (Meyniel, Sergent, Rigoux, Daunizeau, & Pessiglione, 2013). To date, no study has systematically evaluated (1) the way in which task-related intrinsic reward modulates the allocation of cognitive control during task performance, and (2) how variation in intrinsic reward magnitude impacts networked brain connectivity patterns.

To test these questions, a novel, high-control, and open-sourced simulator called *Asteroid Impact* (CC BY-SA 4.0) was developed. This allowed us to manipulate the balance between task difficulty and individual ability in three naturalistic and ecologically valid (Bohil, Alicea, & Biocca, 2011) experimental conditions: low-difficulty (ability > difficulty), high-difficulty (ability < difficulty), and balanced-difficulty (ability \approx difficulty). Three behavioral validation studies showed a curvilinear relationship where intrinsic reward was greatest when task difficulty was balanced with individual ability. A secondary task reaction time procedure (STRT; Lang et al., 2006) replicated this inverted U-shaped pattern. Next, this paradigm was adapted for an fMRI study. Here, we show that a balance between task difficulty and individual ability is associated with robust connectivity between structures in

cognitive control and reward networks. By comparison, a mismatch between difficulty and ability was associated with increased activity in key structures within the default mode network. Interestingly, connectivity patterns between the right dorsoanterior insula and frontocontrol structures during the balanced-difficulty condition suggests that the salience network (Elton & Gao, 2014; Ham, Leff, de Boissezon, Joffe, & Sharp, 2013) plays a role in switching between these different neurocognitive states (Gu et al., 2015). These results indicate that intrinsic reward motivates shifts between brain states optimized for cognitive control, or task disengagement.

Method

Three behavioral experiments were conducted to evaluate a novel procedure for manipulating and measuring the relationship between task difficulty, individual ability, and cognitive control.

Subjects

Subjects in each experiment were drawn from a pool of students at The University of California, Santa Barbara (Table 1). The University's Institutional Review Board approved all experiments. Subjects in the fMRI experiment were right-handed, had normal or corrected to normal vision, and did not demonstrate any contraindication to fMRI scanning. Previous behavioral research evaluating engagement with naturalistic simulators has shown considerable variability in effect sizes. Accordingly, small effects were assumed when calculating a power analysis for the first behavioral experiment with subsequent behavioral experiments seeking to maintain comparable sample sizes. The fMRI sample size corresponded to related studies reported in the literature.

Naturalistic Simulator

In experiments one and two, subjects played *Star Reaction* (ABiGames, <http://loveisgames.com/Action/1979/Star-Reaction>), a point-and-click style simulator where subjects used their cursor to collect star-shaped targets that were displayed at different locations on a screen while avoiding rings that bounced around the screen. Thirteen levels incrementally manipulated difficulty by altering the number of targets a subject needed to collect, the number of objects to be avoided, and the rate at which these objects moved around the simulator window. While useful for initial testing, *Star Reaction* offered few options for interface customization, thereby limiting experimental control. To overcome this issue, an open-source variant called *Asteroid Impact* (CC BY-SA 4.0) was developed for experiment three and the subsequent fMRI experiment. *Asteroid Impact* was designed to have similar mechanics to *Star Reaction* while allowing for tight experimental control (see the simulator's documentation included in the supplemental materials).

Secondary Task Reaction Time Measurement

Subjects completed a STRT measure (Lang et al., 2006) while playing the experimental simulator (Figure 1). Reaction times (RTs) were defined as the latency between the onset time of a stimulus (trial) and the moment when a subject responded with a key press. For experiments one and two, each condition included 48 trials that lasted for 1500 ms. Only visual trials were used in experiment one while half of the visual trials were replaced with auditory trials (sine waveform, 440.0 Hz) in experiment two. The interstimulus interval (ISI) for each trial was calculated by adding a sample of normally distributed randomly generated numbers ($M = 1969$ ms, $SD = 1000$ ms) to a baseline of 1500 ms. In experiment three and the fMRI experiment, 24 visual trials were shown for each condition. The ISI for

these trials was jittered around a truncated Gaussian distribution with a floor of 1500 ms and a standard deviation of 2.0.

Measuring Intrinsic Reward

In experiments one and two, intrinsic reward was measured using a 4-item, 7-point scale (Bowman, Weber, Tamborini, & Sherry, 2013; Weber, Behr, & Bates, 2014).

Experiment three used a better validated and more widely used measure of intrinsic reward (Jackson & Marsh, 1996).

Measuring Simulator Ability

In experiments one and two, simulator ability was evaluated using a 4-point single-item measure. In experiment three and the fMRI study, this was changed to a 7-point single-item measure. In addition, and based on evidence that performance on different cognitive tasks correlates with simulator ability (Bowman et al., 2013), established behavioral measures of targeting (Watson & Kimura, 1989), attentional vigilance (Robertson, Manly, Andrade, Baddeley, & Yiend, 1997), dual-tasking ability (Erickson et al., 2007), and three-dimensional mental rotation (Peters et al., 1995) were collected as independent behavioral proxies for simulator ability (S1–S4).

Procedures

Self-reported simulator ability and baseline reaction times were collected at the beginning of each experiment. Subjects then familiarized themselves with the simulator stimulus by reading the rules and by repeatedly playing the simulator's first level for a period of two minutes. Subjects then played three randomly ordered conditions that manipulated low-difficulty, high-difficulty, and balanced-difficulty. The low-difficulty condition (ability > difficulty) was operationalized as repeated play of the simulator's first and least

challenging level while the high-difficulty condition (ability < difficulty) required repeated play of the most challenging level. In the balanced-difficulty condition (ability \approx difficulty), simulator difficulty and player ability were matched by asking subjects to complete as many successive levels (with increasing difficulty) as possible within the allotted time period. In experiments one and two, each condition lasted for a total of four minutes whereas each condition lasted for two minutes in experiment three and the fMRI experiment. Subjects completed each condition just once in experiments one, two, and three. In the fMRI experiment, subjects completed a total of four runs where each run included all three conditions in a counterbalanced order.

In experiment three, subjects then completed the three-dimensional mental rotation, attentional vigilance, dual-tasking, and targeting measures. In the fMRI experiment, subjects completed an n-back and gambling task in order to localize neural activity in key cognitive control and reward network regions of interest (S5–S8).

STRT and Self-Report Data Analysis

All STRT observations were capped at 1500 ms and the harmonic mean response time was calculated for each subject for each condition (Ratcliff, 1993). Repeated measures ANCOVAs were calculated to assess how intrinsic rewards and reaction times differed across experimental conditions. In each model, the variable of interest was included as a within-subjects factor and condition order was included as a between-subjects factor. Self-reported simulator ability and baseline reaction time covariates were also included in models evaluating reaction times.

fMRI Acquisition, Preprocessing, and Analysis

Data were acquired on a 3-tesla Siemens Magnetom Prisma scanner. Following recommendations established by the Human Connectome Project (Ugurbil et al., 2013), a multiband echo planar gradient sequence measured the blood oxygenated level dependent contrast (TR = 720.0 ms, TE = 37.0 ms, FA = 52 degrees, FOV = 208 mm, multi-band acceleration factor = 8) with each volume consisting of 72 interleaved slices with a 2 mm isotropic spatial resolution acquired parallel to the AC-PC plane. A high-resolution T1-weighted sagittal sequence of the whole brain (TR = 2500.0 ms, TE = 2.22 ms, FA = 7 degrees, FOV = 241 mm, .9 mm isotropic resolution) was collected prior to functional scanning.

Data preprocessing and analysis was performed using FEAT (fMRI Expert Analysis Tool v6.0) from the Oxford Center for Functional MRI of the Brain (FMRIB) Software Library (FSL v5.0 <http://www.fmrib.ox.ac.uk/fsl>) using a three-stage pipeline (Weber, Mangus, & Huskey, 2015). The first stage included brain extraction (BET; Smith, 2002), spatially aligning volumes to a common coordinate system (MCFLIRT; Jenkinson, Bannister, Brady, & Smith, 2002), and spatial smoothing (7 mm FWHM kernel). In the second step, an independent components analysis (ICA-AROMA; Pruim et al., 2015) was applied to the filtered data in order to remove motion artifacts. Finally, the functional data were high-pass filtered (sigma = 360.0 s), coregistered to T1-weighted anatomical scans (FLIRT; Jenkinson et al., 2002; Jenkinson & Smith, 2001), registered to the MNI152 standard template using a nonlinear transformation (FNIRT; Andersson, Jenkinson, & Smith, 2007a, 2007b), prewhitened, and fit to a general linear model (GLM).

A series of first-level GLMs were estimated for all subjects for all runs. Each model included an EV for each condition which was convolved with a hemodynamic response

function (gamma convolution = 6 s, $SD = 3$). Temporal derivatives of each EV were also included in as covariates of no interest. Planned contrasts modeled neural activations unique to each condition. These first-level models were then carried forward into a second-level mixed effects analysis (FLAME; Beckmann & Smith, 2004; Woolrich, Behrens, Beckmann, Jenkinson, & Smith, 2004). In line with recommendations for applying cluster-based corrections for multiple comparisons (Woo, Krishnan, & Wager, 2014), voxels were considered significant if they survived a stringent $Z = 3.1$, $p < .0001$ threshold (Worsley, 2001).

A series of psychophysiological interaction analyses (PPI; Friston et al., 1997) were then modeled to evaluate functional connectivity between structures in cognitive control and reward networks. Seed regions of interest (ROIs) were independently defined based on functional activations in the n-back and gambling localizer tasks. A 3 mm sphere was drawn around peak voxels for each ROI (in MNI152 space), warped to each subject's native space, and used to extract the neural timeseries from filtered functional data for each subject for each run. The first level PPI model included an indicator variable that encoded the balanced-difficulty > low-difficulty and high-difficulty contrast, a physiological regressor, and an interaction term. Second level mixed-effects models were then estimated for each seed ROI. Given that PPI analyses tend to suffer from decreased statistical power (Friston et al., 1997) FSL's default cluster correction threshold of $Z = 2.3$, $p < .05$ was applied.

Results

Behavioral Validation Experiments (Studies One, Two, and Three)

Experiments one and two tested if manipulating a naturalistic simulator stimulus modulated task engagement and intrinsic reward. Measures used to assess intrinsic reward

showed high internal consistency in both experiments one (Cronbach's $\alpha = .906$) and two (Cronbach's $\alpha = .896$) and the overall intrinsic reward models were significant for experiments one (Wilks' $\Lambda = .511$, $F(2,115) = 54.964$, $p < .001$) and two (Wilks' $\Lambda = .710$, $F(2,103) = 21.027$, $p < .001$). Significant results were also observed when modeling reaction times to visual trials in experiments one (Wilks' $\Lambda = .654$, $F(2,113) = 29.842$, $p < .001$) and two (Wilks' $\Lambda = .868$, $F(2,101) = 7.684$, $p < .001$), and for reaction times to auditory trials in experiment two (Wilks' $\Lambda = .822$, $F(2,101) = 10.937$, $p < .001$). In both experiments, and consistent with previous findings, intrinsic reward was the greatest in the balanced-difficulty condition. The reaction time data also showed an inverted U-shaped pattern where the longest reaction times were observed during the balanced-difficulty condition.

Experiment three tested whether the simulator ability covariate is best evaluated using self-report or behavioral measures. Bivariate Pearson correlations were calculated to assess the relationship between subject's performance on each behavioral measure of ability and the total number of targets they successfully collected while playing *Asteroid Impact* (a measure of simulator performance; see Table 2). Self-reported simulator ability ($r = .337$, $p < .01$) and the standard deviation of reaction times during the dual-mixed procedure ($r = -.221$, $p < .05$) were significantly correlated with *Asteroid Impact* performance. These two variables were then regressed on *Asteroid Impact* performance to further characterize the nature of this relationship. Self-reported simulator ability was entered into the first block (Adjusted $R^2 = .094$, $F(1,82) = 9.628$, $p = .003$) with dual-mixed standard deviation and an interaction term entered in a second block (Adjusted R^2 change = $.017$, $F(3,80) = 4.470$, $p = .006$). Self-reported simulator ability was the only variable that significantly predicted *Asteroid Impact*

performance ($B = .310, p = .004$). Therefore, it was again used as a covariate in subsequent reaction time analyses.

For experiment three, the items used to assess intrinsic reward showed acceptable internal consistency (Cronbach's $\alpha = .751$) and the overall repeated measures ANCOVA models were significant for intrinsic reward (Wilks' $\Lambda = .406, F(2,80) = 58.432, p < .001$) and reaction time (Wilks' $\Lambda = .310, F(2,78) = 86.698, p < .001$). Here again, intrinsic reward was the greatest and reaction times were longest in the balanced-difficulty condition (Figure 2; Table 3). Taken together, the results from these three studies demonstrate that the experimental paradigm successfully manipulated levels of intrinsic reward and task difficulty. These results also suggest that, within the context of this experimental procedure, the STRT measure may serve as a behavioral correlate of intrinsic reward.

Brain Imaging Results (Study 4)

As a manipulation check, and consistent with experiments one, two, and three, STRTs measured during the fMRI experiment were the longest in the balanced-difficulty condition (Wilks' $\Lambda = .095, F(2,9) = 42.96, p < .001$). Therefore, we infer that our experimental procedure successfully manipulated intrinsic reward in an fMRI context.

Brain-mapping results. Even with a stringent $Z = 3.1, p < .0001$ cluster correction, the brain mapping analysis yielded a small number of very large clusters (Table 4a). Given the issues associated with interpreting cluster corrected results that span across multiple anatomical structures (Woo et al., 2014), an FDR correction was applied to provide better anatomical specificity (Table 4b). Consistent with previous findings (Klasen et al., 2012; Ulrich et al., 2013; Yoshida et al., 2014), results show that the balanced-difficulty condition elicited robust neural activity in cognitive control, attentional, and reward structures.

Specifically, the balanced-difficulty > low-difficulty and high-difficulty contrast (Figure 3a) revealed broad activity in structures associated with cognitive control (thalamus, dorsolateral prefrontal cortex; DLPFC), orienting attention (SPL, precentral gyrus), and attentional alerting (middle frontal gyrus, dorsoanterior insula). Neural activity was also observed in the putamen, a structure implicated in processing consummatory rewards during cognitive control tasks (Satterthwaite et al., 2007). By comparison, the low-difficulty > balanced-difficulty contrast (Figure 3b) showed activity in structures commonly implicated in the default mode network, particularly the dorsal and ventral medial prefrontal cortex (PFC), ventral posteromedial cortex, temporal pole, and hippocampus. Finally, the high-difficulty > balanced-difficulty contrast (Figure 3c) revealed activity in the occipital fusiform gyrus, temporal pole, orbitofrontal cortex, and inferior temporal gyrus.

PPI results. A series of PPI analyses was then conducted to characterize functional connectivity patterns between key cognitive control and reward structures during the balanced-difficulty condition. Seed ROIs were defined *a priori* for anticipatory (nucleus accumbens) and consummatory (putamen) reward structures as well as key cognitive control (dorsolateral prefrontal cortex, thalamus) ROIs. *A posteriori* seed ROIs were also evaluated for the right dorsoanterior insula and right central precuneus, two structures that were implicated in the brain mapping results.

During the balanced-difficulty condition, the bilateral nucleus accumbens showed functional connections with the occipital pole, paracingulate cortex, central operculum, DLPFC, MTG, and temporal-occipital fusiform cortex (Table 5) while the bilateral DLPFC seed exhibited connectivity with the orbitofrontal cortex (OFC), frontopolar cortex, STG, central precuneus, and occipital fusiform gyrus with several clusters extending into the

anterior cingulate (ACC) and paracingulate (PCC) cortices (Table 6). Significant results were not observed when seeding from the putamen or thalamus. Nevertheless, an analysis of 344 lesion patients demonstrates that damage to nearly all these areas is associated with behavioral deficits in cognitive control and value-based decision-making tasks (Gläscher et al., 2012).

The exploratory ROIs also exhibited robust connectivity patterns. A seed ROI in the right dorsoanterior insula showed connectivity with somatosensory cortices, medial PFC, temporal and occipital cortex (Table 7). This result is largely consistent with meta analytic results showing that dorsoanterior insula connectivity within these regions is associated with task switching and cognitive control (Chang et al., 2013). Similarly, while the precuneus is generally understood as a core structure in the default mode network (Utevsky, Smith, & Huettel, 2014), there is also evidence that central regions within this large structure are implicated in a variety of cognitive processing (Margulies et al., 2009). Seeding from the “cognitive” right central precuneus yielded one large cluster with peak voxels located primarily in posterior visual and occipital regions (Table 8). However, this cluster also extended into key subcortical regions (thalamus, dorsal/ventral striatum) as well as medial and lateral frontal cortex. Taken together, these results demonstrate that intrinsically rewarding tasks correspond to broad connectivity within cognitive control and reward structures.

Discussion

To date, research investigating cognitive control and motivation has largely ignored the way in which motivation contributes to sustained control during cognitively demanding tasks. We show that modulating the balance between task difficulty and individual ability

results in different levels of intrinsic reward, which motivates different levels of task engagement with a naturalistic simulator stimulus. This allowed us, for the first time, to evaluate the self-reported, behavioral, and neural contributions of motivation to the ongoing allocation of cognitive control during a continuous performance task. Three key findings shed light on this relationship. First, and consistent with previous research (Keller & Bless, 2008; Ulrich et al., 2013; Yoshida et al., 2014), a balance between task difficulty and individual ability results in the highest levels of intrinsic reward. Moreover, high levels of consummatory reward corresponded to increased task-related attentional engagement as measured by the STRTs. This result is also reflected in the neuroimaging data. Differential levels of motivation seem to drive shifts between brain states consistent with high levels of task engagement or disengagement. We now turn our focus to these key findings and their broader implications.

Motivation Drives Task-Related Attentional Engagement

One critique of the emerging cognitive control and motivation literature is that the highly controlled experimental tasks employed typically rely on extrinsic and not intrinsic rewards (Braver et al., 2014). In this study, we sacrifice some experimental control in favor of developing a task that allowed for modulating intrinsic rewards. As a failsafe, we used STRTs as a behavioral measure of the extent to which variation in intrinsic reward entrained attentional engagement with the task. The rationale for this measure capitalizes on the insight that motivation has a curvilinear influence on task-related attentional engagement (Lang, 2000). This result is borne out in our STRT data. Interestingly, both visual and auditory RTs were the longest during the balanced-difficulty condition, a result that casts doubt on the view that attentional resources are capacity-limited by modality (e.g., Keitel et al., 2013) in

favor of models that treat attention as a single pool of cognitive resources (Lang et al., 2006; Shomstein & Yantis, 2004; Strozak & Francuz, 2016). That our STRT data show the same inverted-U shaped pattern as our self-reported intrinsic reward measure suggest that STRTs may serve as a behavioral correlate of intrinsic reward, particularly during motivationally relevant tasks. With that said, two important constraints are worth noting. First, the absolute mean STRT differences between conditions are quite small, thereby obscuring inferences about the magnitude of intrinsic rewards. A second issue is that STRTs are only a useful index of intrinsic reward when there is a firm understanding of how the stimulus balanced task difficulty and individual ability.

Reward-Processing and Cognitive Control

While the behavioral and self-report measures suggest a successful experimental manipulation, the fMRI data provide additional clarity to the neuroimaging literature on cognitive control and motivation. First, our brain-mapping results confirm previous findings implicating reward processing during cognitive control tasks. Our novel contribution is in elucidating the functional connections between these structures. Of particular interest is the relationship between anticipatory and consummatory rewards during cognitive control. Our GLM-based results showed that the balanced-difficulty condition elicited the highest levels of activity in the putamen. This fits nicely with the notion this structure is implicated in consummatory reward processing (O'Doherty et al., 2004; Satterthwaite et al., 2007) and that a balance between task difficulty and individual ability elicits strong activity in this structure (Ulrich et al., 2013). However, a balance between difficulty and ability has also been shown to elicit activity in the ventral striatum, particularly the nucleus accumbens (Klasen et al., 2012). Our PPI results when seeding from the ventral striatum add clarity here. We show that

the nucleus accumbens is functionally connected with the DLPFC when task difficulty is balanced with individual ability; a result consistent with the view that these two structures are implicated in reward anticipation and cognitive cost calculation (Botvinick, Huffstetler, & McGuire, 2009; Kool, McGuire, Wang, & Botvinick, 2013).

With that said, we did not design our study to directly manipulate reward expectation, so it is difficult to tell if our results support the view that reward anticipation and consumption is dissociated between the dorsal and ventral striatum (O’Doherty et al., 2004), or as some have suggested, if these structures subserve a common function related to evaluating the cognitive costs associated with earning a particular reward (Vassena et al., 2014) and even in consummatory reward processing (Pauli, O’Reilly, Yarkoni, & Wager, 2016). This common architecture view is also consistent with Braver and colleagues’ (2014) observation that intrinsic and extrinsic rewards may not be dissociable at the neuroanatomical level, but instead at the temporal level where extrinsic rewards are temporally immediate and tangible where intrinsic rewards are less tangible and more temporally disperse.

Nevertheless, we demonstrate that a balance between task difficulty and individual ability modulates reward-related subcortical processing and that these structures are functionally connected with frontocontrol structures during a cognitive control task; a finding that provides novel evidence that intrinsic reward motivates the allocation of cognitive control during sustained task performance.

Network-Level Effects of Motivation on Cognitive Control

More broadly, the observed connectivity patterns between lateral and medial PFC regions during the balanced-difficulty condition aligns with recent evidence suggesting that motivational influences on cognitive control emerge from hierarchical interactions between

structures within these regions (Kouneiher, Charron, & Koechlin, 2009). Moreover, our results observed during the balance condition map onto recent theorizing about the neural basis of so-called *flow* experiences (Csikszentmihalyi, 1975), an intrinsically rewarding motivational state which is thought to occur as the result of a network synchronization process between cognitive control and reward networks (Weber et al., 2009). In fact, the activity pattern observed during the balanced-difficulty condition was remarkably different from the low-difficulty and high-difficulty conditions. While the balanced-difficulty condition elicited activity consistent with reward-based cognitive control, the low-difficulty condition showed activations in the DMN. There is evidence that failures to suppress the DMN are associated with lapses in attention (Weissman, Roberts, Visscher, & Woldorff, 2006) and decreased performance during cognitive control tasks (Kelly, Uddin, Biswal, Castellanos, & Milham, 2008). The observed activations in the VMPFC may play a key role here, as this structure has been shown to suppress task-related attention with a bias towards rest or inward focused attention (Uddin, Kelly, Biswal, Castellanos, & Milham, 2009).

Interestingly, we also see that STRTs were generally faster and that game performance was high during the low-difficulty condition. This result, in conjunction with the observed activations in key DMN structures provides additional evidence that the low-difficulty condition required low levels of cognitive control. Moreover, it also contextualizes the extent to which low-difficulty tasks can be performed automatically, or at least with very low levels of cognitive control. This, combined with previous evidence showing that boring video game play (Mathiak et al., 2013) and a mismatch between difficulty and ability (Ulrich et al., 2013) is associated with DMN activity, provides evidence that motivation may be driving the shift between DMN activation during low-difficulty, and cognitive control

network activation during the balanced-difficulty conditions. An intriguing possibility implicated by our exploratory PPI analyses is that the dorsoanterior insula may be facilitating shifts between these brain states. A recent meta analysis using Neurosynth (Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011) data implicates this structure in shifts between cognitively demanding tasks and task disengagement (Chang et al., 2013). Additional research is needed to determine if momentary shifts in motivation drive dynamic shifts between these networks as facilitated by the insula.

Conclusion

In their earliest writings, Miller and Cohen (2001) indicated that motivation may play a role in cognitive control. In the decades that followed, most of the research in this area treated the two as separable processes by choosing to focus on cognition rather than motivation. However, an emerging perspective argues that higher order cognitions and their resulting behaviors are not easily reducible to their lower-level constitute parts, especially when considering the relationship between cognition and motivation (Pessoa, 2008). Our results fit within this framework by showing how task-elicited differences in motivation drive large-scale shifts in task-related reward perceptions, attentional allocation, and neural states. A recent focus has been on understanding how the somewhat ambiguously defined notion of stimulus salience facilitates dynamic shifts between network states. We propose that motivational salience, defined here as intrinsic reward resulting from a balance between task difficulty and individual ability, plays a role in facilitating these shifts.

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Appendix

Figure 1: *Schematic of the experimental paradigm. In all experiments, the subject's goal was to use their mouse to collect targets while avoiding asteroids and responding to STRT trials as quickly as possible. For the behavioral experiments (a), visual STRT trials appeared in one of five different locations on a second screen. In the fMRI experiment (b), STRT trials appeared on the same screen in one of four different locations.*

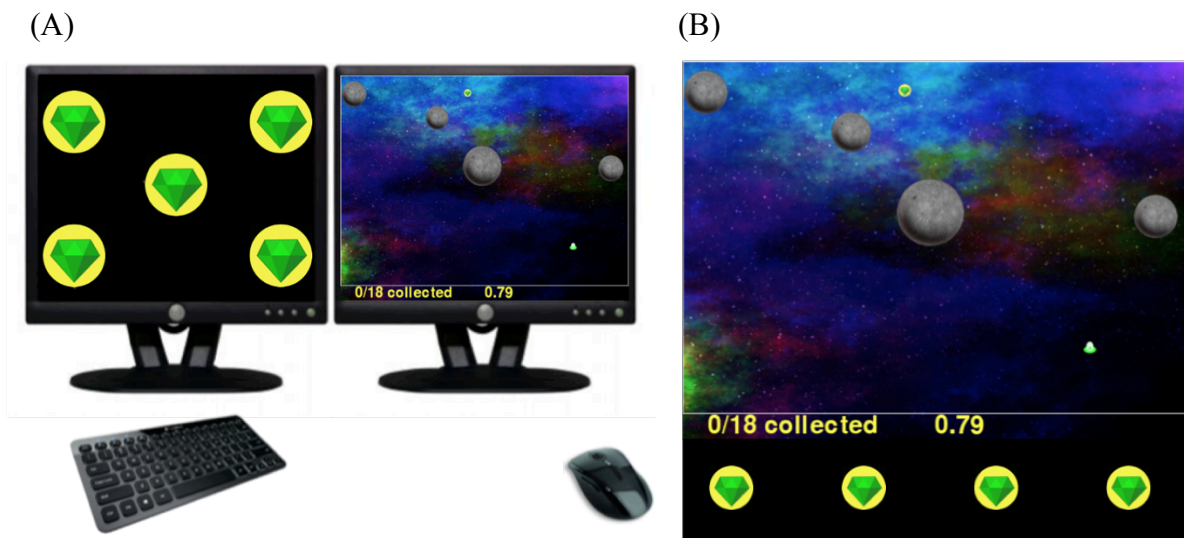


Table 1: *Summary statistics for describing the subject samples in all four experiments.*

	n	Mean Age (Std. Dev.)	% Female (% Male)	Mean Self-Reported Simulator Ability (Std. Dev.)*
Experiment 1	122	19.40 (1.21)	64.8 (35.2)	1.80 (1.21)
Experiment 2	110	20.48 (1.93)	70.9 (29.1)	1.64 (0.85)
Experiment 3	87	19.49 (1.44)	77.0 (23.0)	3.23 (1.63)
fMRI Experiment	18	22.83 (4.02)	77.8 (22.2)	3.00 (1.03)

* Self-reported simulator ability was measured using a 4-item scale in experiments one and two and a 7-item scale in experiment three and the fMRI study.

Table 2: *Pearson correlations between cognitive tasks and Asteroid Impact simulator performance.*

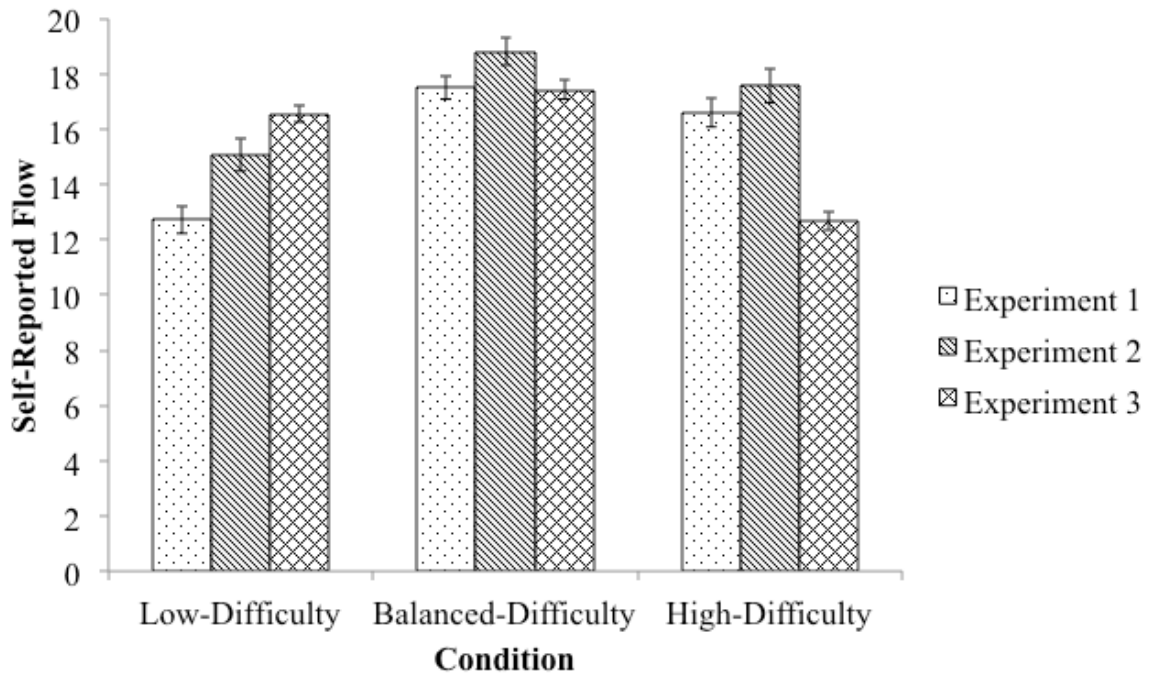
	1	2	3	4	5	6	7
1 Simulator performance	1						
2 Self-reported game ability	.337**	1					
3 Targeting	-.06	-.053	1				
4 Dual-mixed accuracy	.095	.045	-.042	1			
5 Dual-mixed std. dev.	-.221*	-.083	.150	-.609**	1		
6 SART accuracy	.187	.135	-.002	.368**	-.094	1	
7 SART std. dev.	-.001	-.147	.283**	-.063	.131	-.131	1

* Correlation is significant at the $p = .05$ level (two-tailed).

** Correlation is significant at the $p = .01$ level (two-tailed).

Figure 2: Means and standard errors for intrinsic-reward (a) and reaction times (b).

(A)



(B)

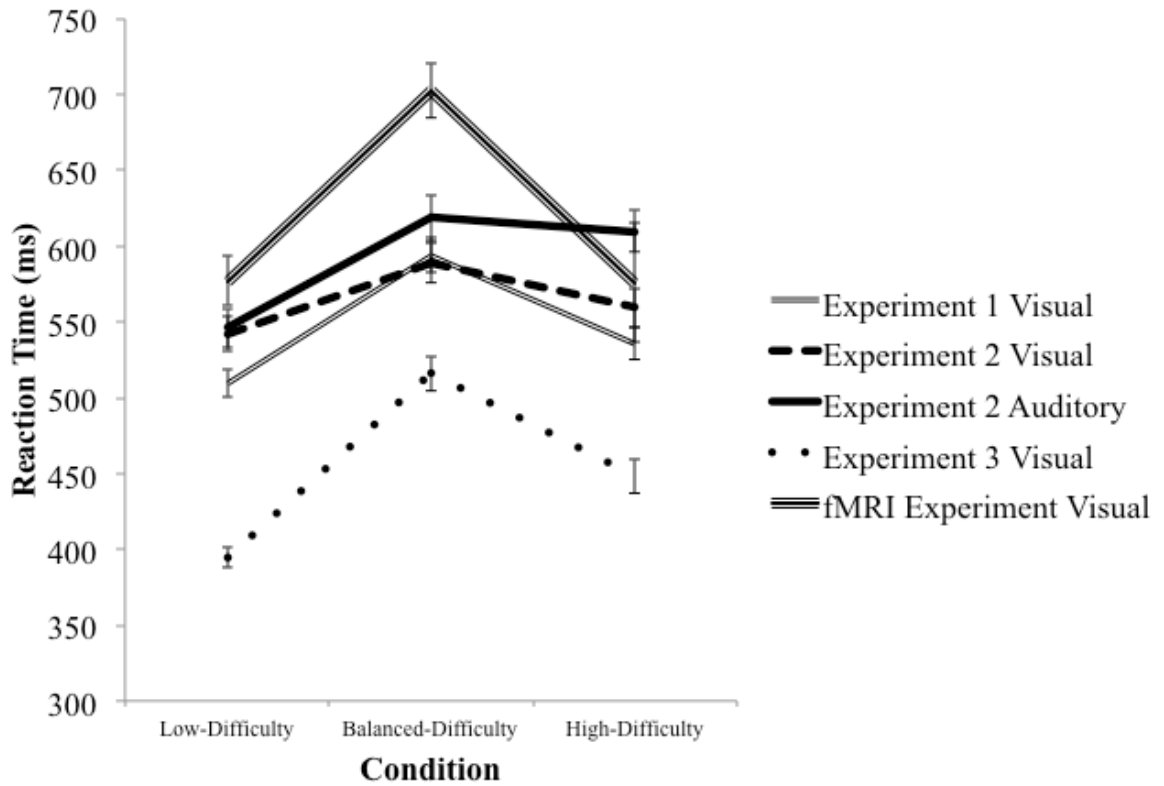


Table 3a: Means and standard errors for intrinsic reward (a) and reaction times (b).

(A)

	Low-Difficulty Condition Mean (Std. Error) (a)	Balanced-Difficulty Condition Mean (Std. Error) (b)	High-Difficulty Condition Mean (Std. Error) (c)
Experiment 1	12.721 (.487) ^{a,b}	17.523 (.426) ^a	16.617 (.528) ^a
Experiment 2	15.084 (.594) ^{b,c}	18.821 (.520) ^a	17.589 (.628) ^a
Experiment 3	16.562 (.298) ^{b,c}	17.431 (.333) ^{a,c}	12.694 (.339) ^{a,b}

For each row, superscripted text indicates statistically significant pairwise comparisons after a Bonferroni correction for multiple comparisons at the $p < .05$ level.

(B)

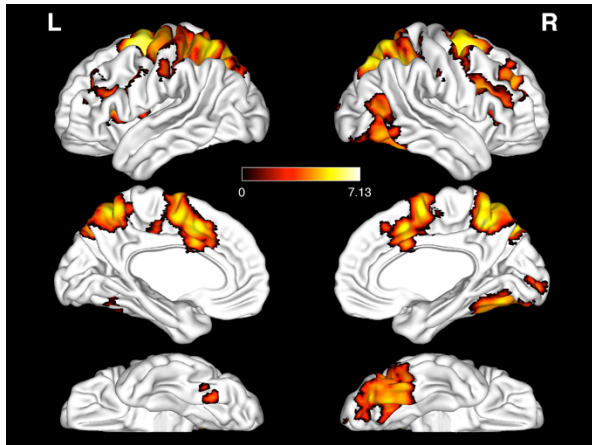
Table 3b: Means and standard errors for reaction times to visual and auditory trials.

	Low-Difficulty Condition Mean (Std. Error) (a)	Balanced-Difficulty Condition Mean (Std. Error) (b)	High-Difficulty Condition Mean (Std. Error) (c)
Experiment 1 Visual	509.491 (9.399) ^{b,c}	594.163 (11.624) ^{a,c}	536.250 (10.905) ^{a,c}
Experiment 2 Visual	542.059 (11.464) ^b	589.354 (13.357) ^a	559.434 (13.028)
Experiment 2 Auditory	546.189 (12.941) ^{b,c}	618.888 (15.367) ^a	609.970 (13.575) ^a
Experiment 3 Visual	394.638 (6.473) ^{a,b}	516.009 (11.398) ^{a,c}	448.549 (11.480) ^{a,c}
Experiment 4 Visual	577.022 (16.383) ^b	702.562 (17.768) ^{a,c}	575.727 (39.386) ^b

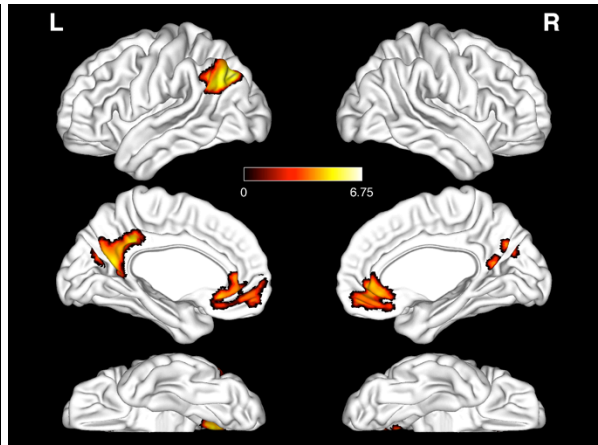
For each row, superscripted text indicates statistically significant pairwise comparisons after a Bonferroni correction for multiple comparisons at the $p < .05$ level.

Figure 3: Neural activations in the (a) *Balanced-difficulty > Low-Difficulty and High-Difficulty*, (b) *Low-Difficulty > Balanced-Difficulty*, and (c) *High-Difficulty > Balanced-Difficulty* contrasts; $Z = 3.1, p < .0001$.

(A)



(B)



(C)

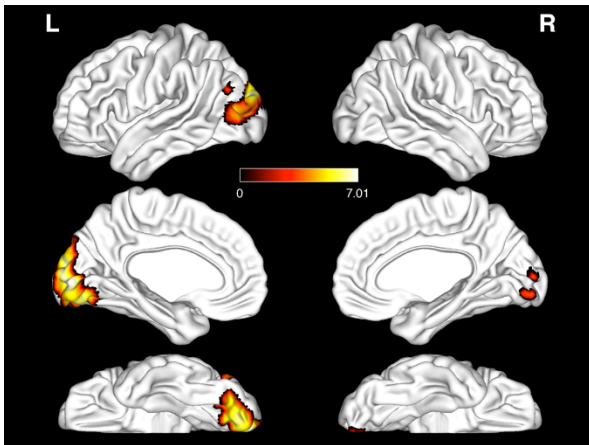


Table 4a: *Neural activity in the reported contrasts; cluster corrected $Z = 3.1$, $p < .0001$; coordinates are in MNI152 space.*

Structure	Laterality	Cluster Size	Maximum Z-score	Coordinates
Balanced-Difficulty > Low-Difficulty & High-Difficulty				
Superior Frontal Gyrus	Right	22775	7.13	24, 2, 50
Precentral Gyrus	Left		6.46	-26, -8, 48
Central Precuneus	Right		6.33	6, -50, 50
Superior Parietal Lobule	Right		6.19	28, -48, 66
Superior Parietal Lobule	Left		6.19	-32, -60, 64
Cerebellum	Right	6785	5.59	8, -62, -56
Cerebellum	Right		5.53	24, -56, -20
Cerebellum	Right		5.37	30, -54, -26
Cerebellum	Right		5.35	6, -70, -14
Occipital Fusiform Gyrus	Right		5.21	26, -64, -16
Cerebellum	Left		5.21	0, -76, -32
Dorsoanterior Insula	Left	615	4.83	-32, 12, 6
Putamen	Left		4.70	-22, -2, 4
Putamen	Left		4.68	-30, 20, 10
Putamen	Left		4.67	-26, 14, 0
Posterior Insula	Left		3.8	-42, -2, 6
Pallidum	Left		3.79	-22, -6, -4
Low-Difficulty > Balanced-Difficulty				
Superior Lateral Occipital Cortex	Left	1539	6.75	-42, -76, 42
Superior Lateral Occipital Cortex	Left		6.24	-54, -72, 36
Superior Lateral Occipital Cortex	Left		6.06	-44, -64, 30
Superior Lateral Occipital Cortex	Left		5.59	-54, -66, 34
Superior Lateral Occipital Cortex	Left		5.49	-48, -66, 38
Ventromedial Prefrontal Cortex	Left	1207	4.83	0, 28, -14
Paracingulate Cortex	Right		4.65	8, 42, -4
Anterior Cingulate Cortex	Right		4.5	2, 36, -8
Anterior Cingulate Cortex	Left		4.18	-2, 42, 4
Paracingulate Cortex	Left		4.15	-4, 44, -6
Ventromedial Prefrontal Cortex	Right		4.12	10, 48, -12
Posterior Cingulate Gyrus	Left	967	5.59	-10, -44, 34

Ventral Posteromedial Cortex	Left		5.07	-2, -60, 16
Ventral Posteromedial Cortex	Left		4.72	-4, -66, 24
Ventral Posteromedial Cortex	Left		4.47	-8, -54, 10
Posterior Precuneus	Right		4.42	2, -70, 30
Posterior Cingulate Gyrus	Left		4.41	-8, -54, 28
High-Difficulty > Balanced-Difficulty				
Visual Cortex	Left	4914	7.01	-12, -90, 4
Occipital Pole	Left		6.94	-6, -94, 14
Occipital Pole	Left		6.74	-20, -94, 24
Visual Cortex	Left		6.72	-14, -82, -10
Occipital Fusiform Gyrus	Left		5.60	-28, -76, -8
Occipital Pole	Left		5.19	-2, -92, 30

Table 4b: *Neural activity in the reported contrasts; activations are shown for clusters containing 25 or more voxels at the reported FDR correction.*

Structure	Laterality	q	Voxels	Coordinates
Balanced-Difficulty > Low-Difficulty & High-Difficulty				
Superior Parietal Lobule	Right	.0001	2768	28, -54, 42
Precentral Gyrus	Left	.0001	1706	-26, -8, 44
Paracingulate Cortex	Left	.0001	1565	-6, 8, 44
Cerebellum	Right	.0001	680	24, -56, -22
Cerebellum	Left	.0001	92	-12, -60, -52
Occipital Fusiform Gyrus	Right	.0001	63	40, -68, -12
Dorsolateral Prefrontal Cortex	Right	.0001	38	34, 44, 32
Middle Frontal Gyrus	Right	.0001	27	38, 18, 24
Dorsoanterior Insula	Right	.001	163	-32, 12, 6
Precentral Gyrus	Left	.001	112	-42, 4, 24
Cerebellum	Left	.001	60	-32, -52, -26
Middle Frontal Gyrus	Left	.001	57	-26, 30, 28
Putamen	Left	.001	44	-22, -2, 4
Putamen	Right	.001	20	28, 10, 2
Thalamus	Right	.01	144	10, -6, 4
Inferior Lateral Occipital Cortex	Left	.01	126	-52, -68, -4
Thalamus	Left	.01	67	-8, -6, 12
Occipital Pole	Right	.01	34	16, -98, 22
Primary Auditory Cortex	Left	.05	86	-46, -24, 12
Inferior Parietal Lobule	Right	.05	67	50, -42, 22
Superior Temporal Gyrus	Right	.05	58	46, -14, -14
Orbitofrontal Cortex	Right	.05	55	34, 50, -16
Temporal Fusiform Cortex	Right	.05	49	36, -24, -32
Low-Difficulty > Balanced-Difficulty				
Superior Lateral Occipital Cortex	Left	.0001	332	-46, -68, 38
Temporal Pole	Left	.001	81	-46, 2, -32
Ventral Posteromedial Cortex	Left	.001	65	-2, -60, 16
Posterior Cingulate Gyrus	Left	.001	43	-10, -44, 34
Ventromedial Prefrontal Cortex	Left	.01	531	0, 28, -14
Central Operculum	Right	.01	150	52, -10, 14

Hippocampus	Left	.01	140	-22, -18, -22
Superior Lateral Occipital Cortex	Right	.01	107	52, -62, 36
Inferior Temporal Gyrus	Right	.01	64	42, 4, -32
Middle Temporal Gyrus	Left	.05	155	-64, -38, -10
Primary Somatosensory Cortex	Right	.05	127	44, -24, 64
Middle Frontal Gyrus	Left	.05	94	-48, 18, 46
Inferior Frontal Gyrus	Left	.05	85	-54, 24, 8
Dorsomedial Prefrontal Cortex	Left	.05	44	-8, 62, 22
Dorsomedial Prefrontal Cortex	Left	.05	38	-10, 44, 48
Hippocampus	Right	.05	33	26, -6, -24
Hippocampus	Right	.05	25	28, -18, -22
High-Difficulty > Balanced-Difficulty				
Occipital Fusiform Cortex	Left	.0001	1790	-8, -90, -18
Temporal Pole	Left	.05	246	-44, 2, -34
Orbitofrontal Cortex	Left	.05	198	-30, 22, -22
Inferior Temporal Gyrus	Left	.05	29	-46, -24, -20

Table 5: *Psychophysiological interaction results when seeding from the bilateral (right: 10, 16, -6; left: -10, 16, -6) nucleus accumbens; cluster corrected $Z = 2.3$, $p < .05$; coordinates are in MNI152 space.*

Structure	Laterality	Cluster Size	Maximum Z-score	Coordinates
Balanced-Difficulty > Low-Difficulty & High-Difficulty				
Occipital Pole	Left	1442	6.18	-34, -96, 4
Superior Lateral Occipital Cortex	Left		3.96	-22, -74, 48
Paracingulate Cortex	Right	841	4.32	4, 22, 44
Middle Frontal Gyrus	Left		3.73	-34, 34, 34
Superior Frontal Gyrus	Left		3.67	-18, 26, 42
Paracingulate Cortex	Right		3.60	10, 36, 36
Central Operculum	Right	578	4.64	44, -12, 22
Precentral Gyrus	Right		3.42	34, 0, 36
Middle Frontal Gyrus	Right		3.19	44, 14, 32
Dorsolateral Prefrontal Cortex	Left	541	3.88	-30, 60, 8
Caudate Nucleus	Left		3.74	-8, 12, 12
Middle Temporal Gyrus	Right	398	4.23	52, -50, 6
Superior Temporal Gyrus	Right		3.40	58, -12, -8
Tempo-occipital Fusiform Cortex	Left	378	3.70	-30, -52, -20
Lingual Gyrus	Left		3.42	-20, -44, -14
Hippocampus	Left		2.93	-32, -34, -14

Table 6: *Psychophysiological interaction results when seeding from the bilateral (right: 32, 54, 10; left: -32, 54, 10) dorsolateral prefrontal cortex; cluster corrected $Z = 2.3$, $p < .05$; coordinates are in MNI152 space.*

Structure	Laterality	Cluster Size	Maximum Z-score	Coordinates
Balanced-Difficulty > Low-Difficulty & High-Difficulty				
Orbitofrontal Cortex	Left	6615	5.12	-36, 32, -8
Superior Temporal Gyrus	Left		4.97	-58, -10, -8
Middle Frontal Gyrus	Left		4.73	-46, 22, 26
Frontopolar Cortex	Left	6110	5.03	-8, 62, 28
Subcallosal Cortex	Right		4.78	2, 24, -12
Superior Frontal Gyrus	Right		4.48	10, 24, 60
Frontopolar cortex	Right		4.34	8, 52, 42
Superior Temporal Gyrus	Right	1887	5.10	54, -26, 0
Posterior Insula	Right		4.08	36, -16, 8
Secondary Somatosensory Cortex	Right		3.84	44, -14, 22
Broca's Area	Right	1271	4.16	58, 26, 22
Orbitofrontal	Left		3.91	24, 34, -10
Temporal Pole	Right		3.57	48, 24, -18
Central Precuneus	Left	754	4.12	-10, -48, 36
Ventral Posteromedial Cortex	Left		3.83	-4, -56, 14
Visual Cortex	Right		3.28	4, -66, 8
Anterior Precuneus	Left		3.13	-2, -48, 60
Occipital Fusiform Gyrus	Left	690	4.58	-16, -86, -18
Occipital Pole	Left		3.24	-12, -98, -4

Table 7: *Psychophysiological interaction results in the when seeding from the right (40, 16, -6) dorsoanterior insula; cluster corrected $Z = 2.3$, $p < .05$; coordinates are in MNI152 space.*

Structure	Laterality	Cluster Size	Maximum Z-score	Coordinates
Balanced-Difficulty > Low-Difficulty & High-Difficulty				
Primary Somatosensory Cortex	Right	15664	5.28	44, -22, 64
Primary Motor Cortex	Right		5.18	12, -30, 74
Inferior Frontal Gyrus	Right		5.00	56, 18, 26
Secondary Somatosensory Cortex	Right		4.93	44, -10, 20
Hippocampus	Left		4.89	-24, -30, -10
Dorsomedial Prefrontal Cortex	Right	4415	4.81	4, 62, 14
Superior Frontal Gyrus	Left		3.95	4, 28, 50
Ventromedial Prefrontal Cortex	Left		3.80	-8, 46, -16
Superior Lateral Occipital Cortex	Left	1096	3.98	-52, -72, 28
Angular Gyrus	Left		3.93	-52, -60, 28
Middle Temporal Gyrus	Left	724	4.12	-58, -52, 0
Superior Temporal Gyrus	Left		3.45	-50, -16, -10
Superior Lateral Occipital Cortex	Right	644	3.65	50, -62, 42
Inferior Parietal Lobule	Right		3.45	58, -58, 36
Inferior Frontal Gyrus	Left	544	3.53	-46, 32, -4
Orbitofrontal Cortex	Left		3.35	-24, 34, -14
Frontopolar Cortex	Left		2.97	-42, 40, -2
Subcallosal Cortex	Right	546	4.28	2, 30, -18
Caudate Nucleus	Left		2.71	-10, 14, 6

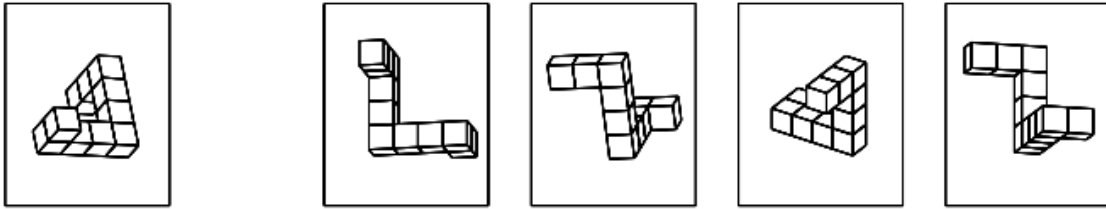
Table 8: *Psychophysiological interaction results in the when seeding from the right (8, -76, 52) central precuneus; cluster corrected $Z = 2.3$, $p < .05$; coordinates in MNI152 space.*

Structure	Laterality	Cluster Size	Maximum Z-score	Coordinates
Balanced-Difficulty > Low-Difficulty & High-Difficulty				
Visual Cortex	Left	58649	5.84	-2, -76, 16
Posterior Precuneus	Left		5.66	0, -52, 38
Posterior Cingulate Cortex	Left		5.65	-2, -44, 36
Ventral Posteromedial Cortex	Right		5.27	2, -66, 18
Occipital Fusiform Gyrus	Right		5.12	18, -86, -16
Ventral Posteromedial Cortex	Left		5.10	-4, -60, 14

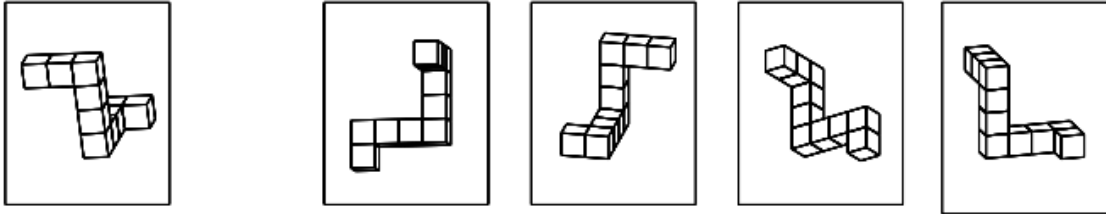
Supplemental Materials

Figure S1: The redrawn Vandenberg and Kuse mental rotations test (Peters et al., 1995) was administered in two three-minute runs. For each run, subjects were shown 12 three-dimensional reference shapes. For each reference shape, subjects were asked to identify which two (out of four) shapes matched the reference. Subjects were given a point if they correctly identified both shapes ($M = 7.298$, $SD = 3.894$, $Range = 0-22$).

2.a



3.a



4.a

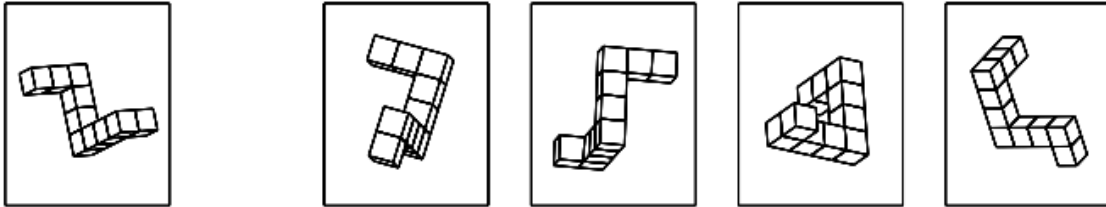


Figure S2: In the sustained attention response test (Robertson et al., 1997), subjects were shown a series of numbers (1–9) in five different font sizes for 250ms (font sizes were balanced across all values). The trial was then masked for 900 ms. Subjects were instructed to press a key as quickly as possible for all numbers (a *go* trial) except the number 3 (a *no-go* trial). A total of 225 trials were shown, 25 of which were *no-go* trials. Mirroring previous studies (Unsworth et al., 2015), the two dependent measures included: (1) accuracy – a frequency count of *no-go* trials where a key press was withheld ($M = 21.824$, $SD = 2.780$, $Range = 11–25$) and (2) the standard deviation of reaction times for correct *go* trials ($M = 453.012$, $SD = 87.169$, $Range = 102.07–544.40$).

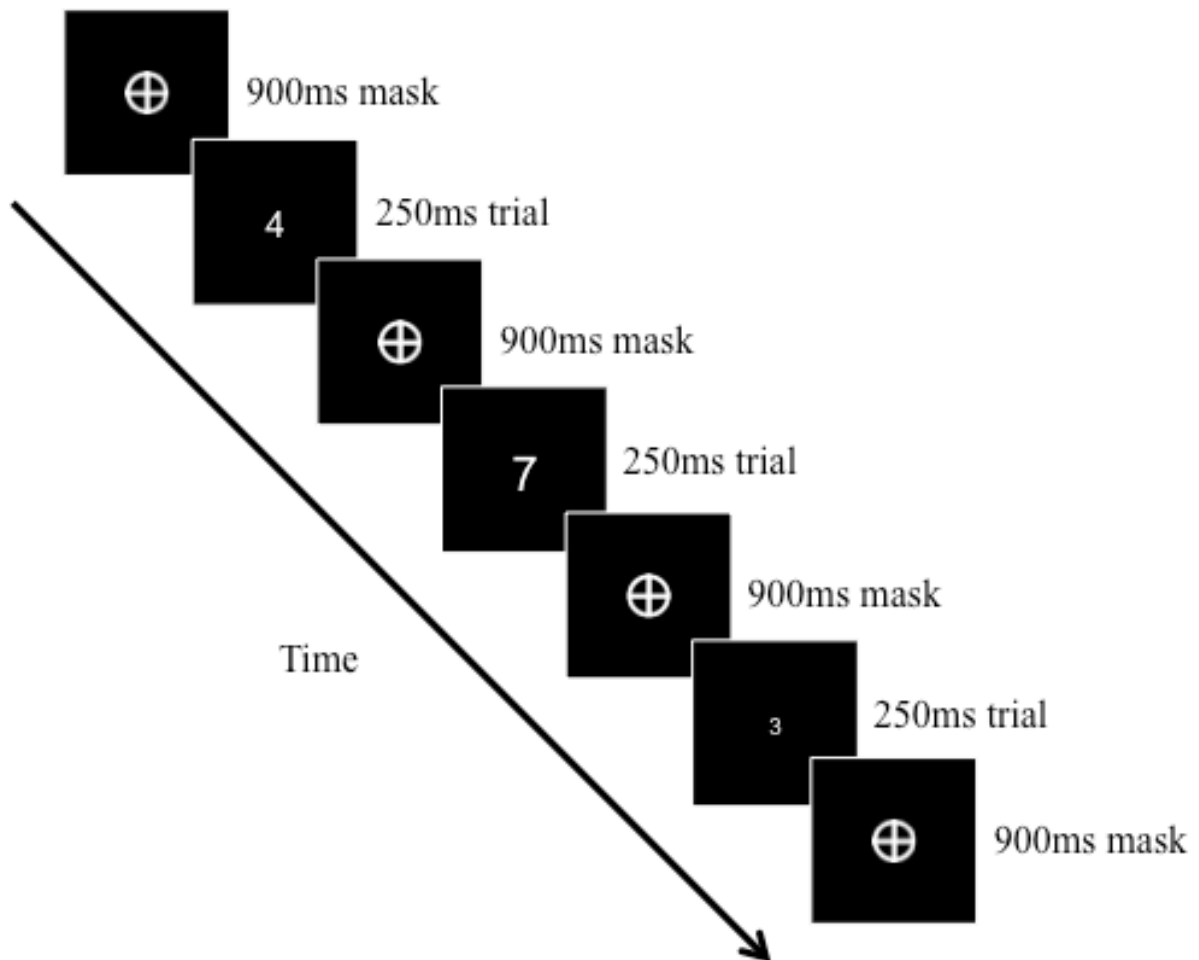


Figure S3: In the dual-task paradigm (Erickson et al., 2007), subjects were shown two types of trials (single-mixed, dual-mixed) which lasted for 2500ms and were separated by a 500ms fixation cross. In single mixed trials, subjects were shown one of four possible stimuli: >, <, a red square, or a green square. Each stimulus was mapped to a specific key and subjects were instructed to press the correct key as quickly as possible when a trial was shown without sacrificing accuracy. In the dual-mixed condition, two of four possible stimuli were shown and subjects were instructed to press the two keys that corresponded to each stimulus. A total of eight combinations of single- and dual-mixed trials were possible. Each was presented a total of 20 times in a randomized order.

Two dependent measures were assessed: (1) accuracy – the total number of dual-mixed trials where both keys were correctly pressed ($M = 67.279$, $SD = 13.495$, $Range = 5-79$), and (2) variability in task updating/monitoring – for dual-mixed trials, the standard deviation of Reaction Time 2 – Reaction Time 1 for all correct dual mixed trials ($M = 182.566$, $SD = 92.079$, $Range = 14.25-612.65$).

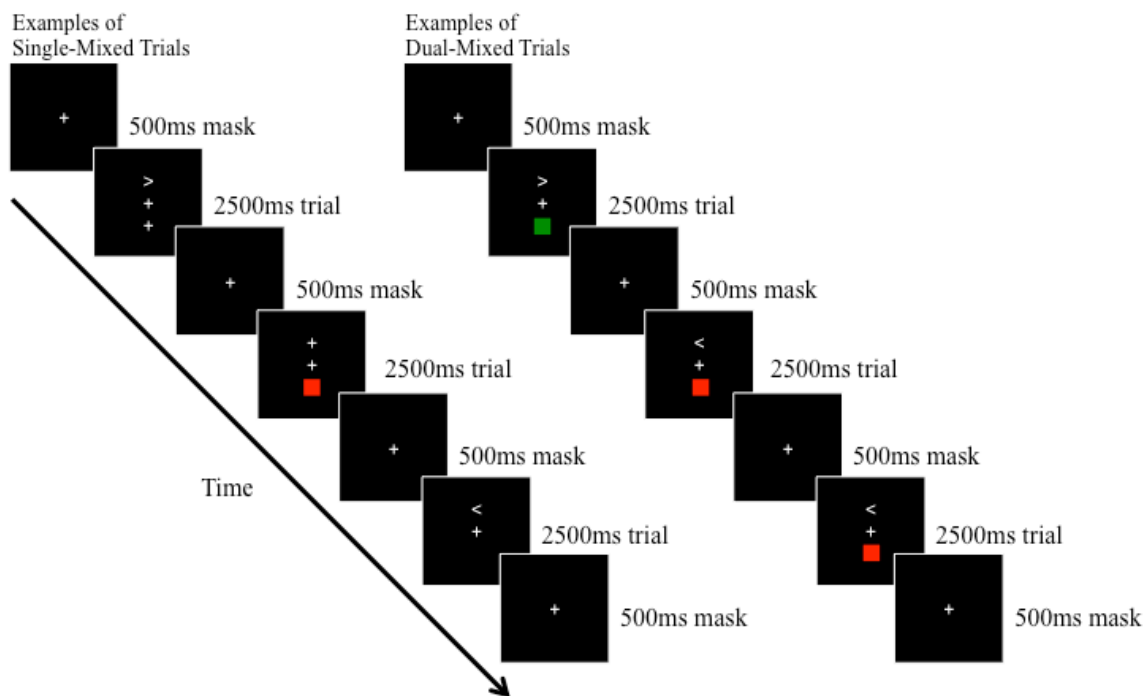


Figure S4: Subjects targeting abilities were evaluated using a dart-throwing procedure. (Watson & Kimura, 1989). A 60 cm diameter circular target with the bullseye 152 cm from the floor was fixed to a wall 3 m from where subjects stood. Subjects completed 25 overhand throws of a 25-gram dart using their dominant hand. The distance of each throw from the center was recorded in millimeters and averaged for each subject ($M = 137.838$, $SD = 27.085$, $Range = 70.89\text{--}207.00$). Smaller values indicated greater accuracy.

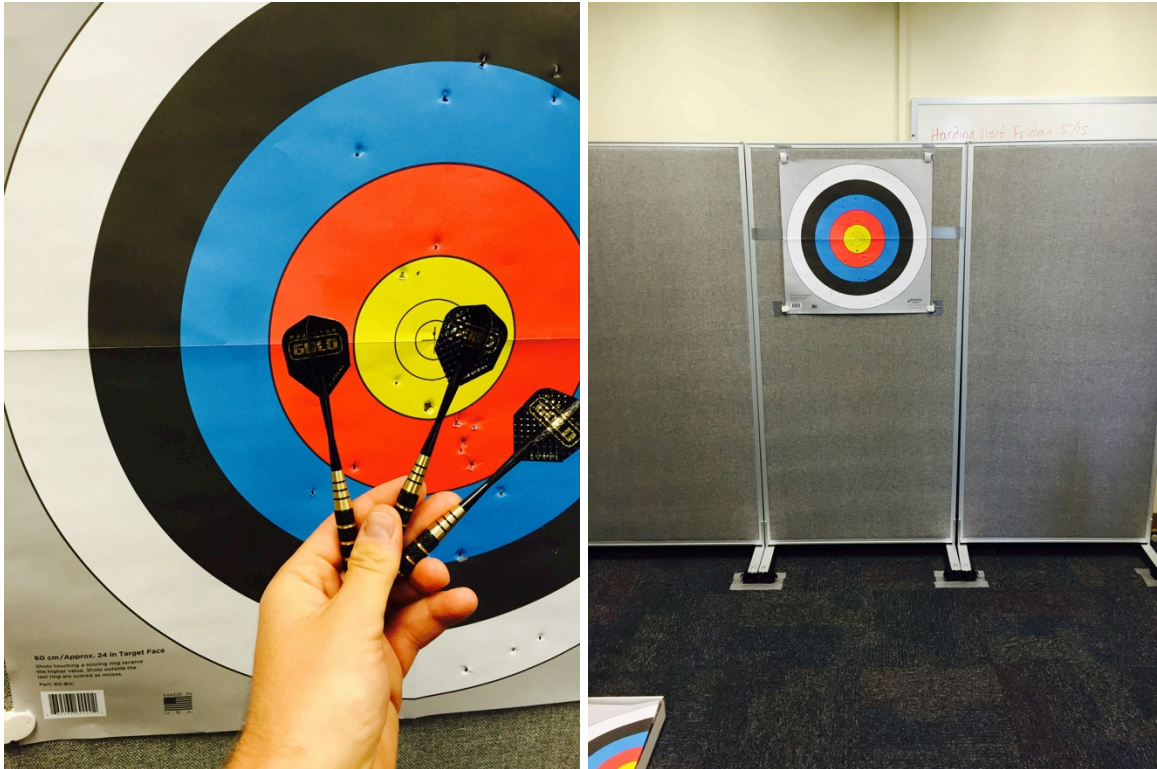


Figure S5: An n-back task was used to behaviorally localize functional activity in cognitive control regions of interest. The n-back task was selected as it shows reliable activation patterns across subjects (Drobyshevsky, Baumann, & Schneider, 2006), sessions (Caceres, Hall, Zelaya, Williams, & Mehta, 2009), and does not show gender differences (Schmidt et al., 2009). In a series of 2 runs, subjects were shown 320 trials where each trial was a randomly selected letter from A–Z that was shown for 1000 ms. In the 2-back condition, subjects were required to press a key when the letter shown was the same as one shown two trials back. In the 0-back condition, subjects pressed a key when the trial showed the letter “X”. Each run followed a 2-back (40 trials), 0-back (40 trials), 2-back (40 trials), 0-back (40 trials) pattern. Subjects were instructed to prioritize accuracy before speed. The 2-back and 0-back conditions were modeled in a block design with a 2-back > 0-back contrast in subsequent fMRI data analyses.

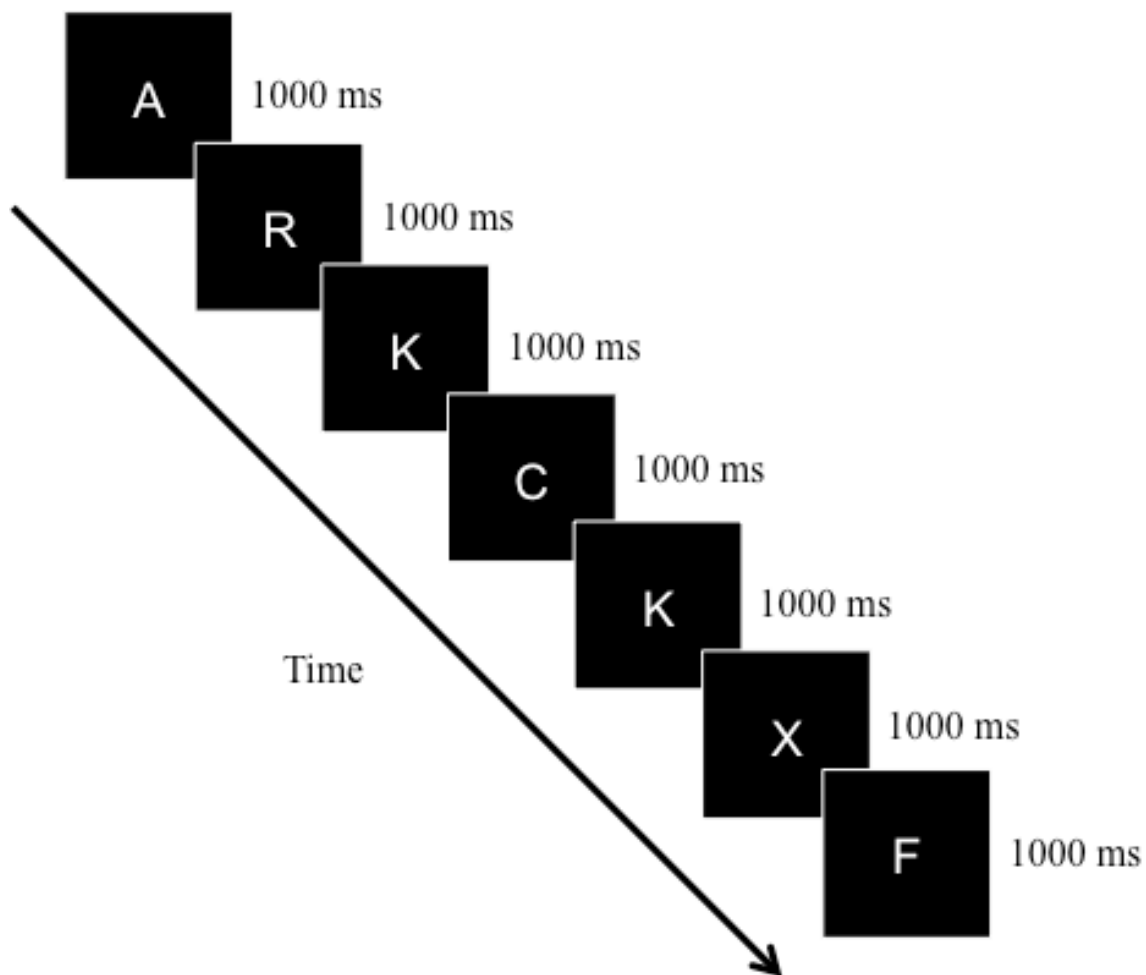
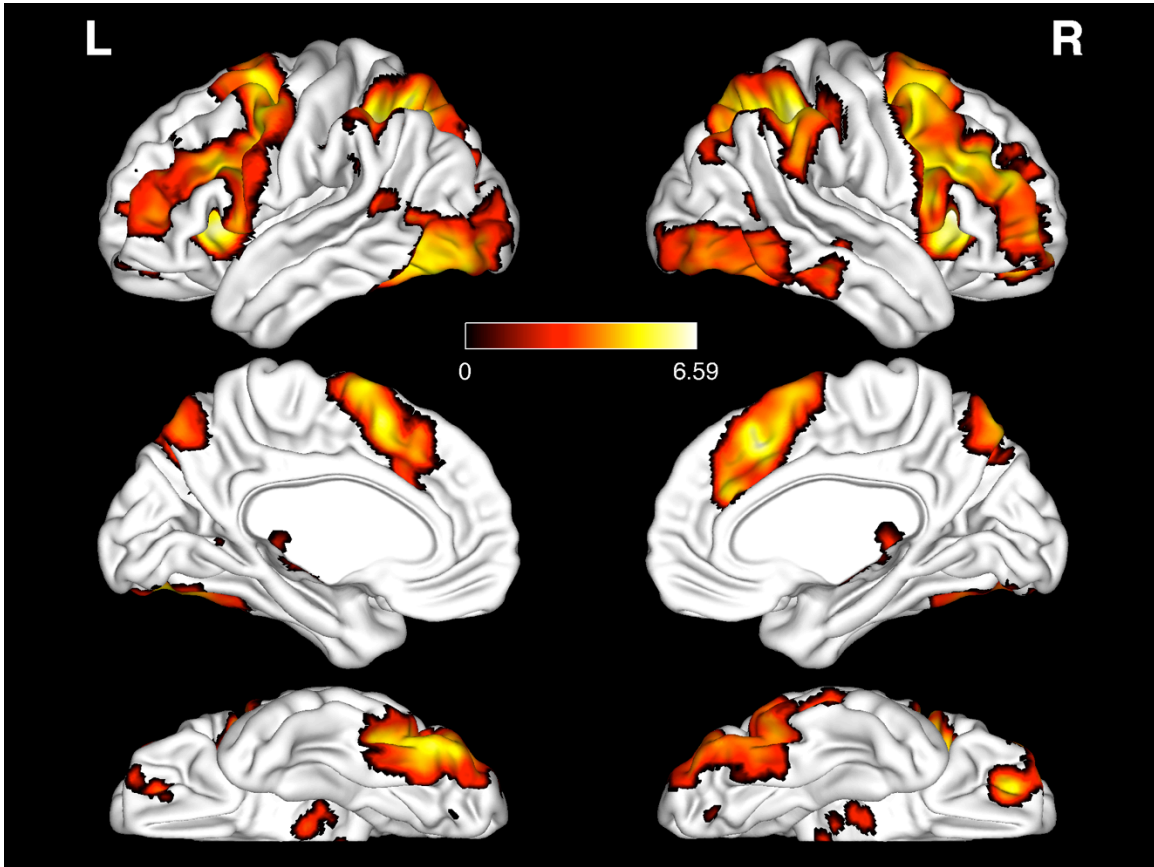


Figure S6: Activation and resulting seed ROIs in the 2-back > 0-back contrast; cluster corrected $Z = 2.3$, $p < .05$.



See ROIs (in MNI 152 space) for PPI analyses included:

Right DLPFC:	32, 54, 10
Left DLPFC	-32, 54, 10
Right Insula:	40, 16, -6
Right Thalamus:	16, -16, 10
Left Thalamus:	-8, -10, -2
Right Precuneus:	8, -76, 52

Figure S7: Structures within the reward network were behaviorally localized using a gambling task that has been shown to reliably activate structures in the basal ganglia (Delgado, Nystrom, Fissell, Noll, & Fiez, 2000; May et al., 2004; Tricomi, Delgado, & Fiez, 2004). In this task, subjects were shown a series of cards with a numeric value of 1–9. During an initial guessing period (2500 ms), subjects were asked to indicate if they thought value of the card was greater or less than 5. Subjects were then shown the outcome of their guess (1000 ms), and then a fixation cross during the post-outcome period (11500 ms) for a cumulative trial duration of 15,000 ms. A total of 100 trials were shown across 5 runs. Subjects were rewarded \$1.00 for correct guesses, lost \$0.50 for incorrect guesses, and did not win or lose any money for tie trials. The ratio of wins, losses, and ties was set at 40:40:20 (balanced across all runs). Neural activity during the post-outcome period was modeled in an event-related design with a wins > loss contrast.

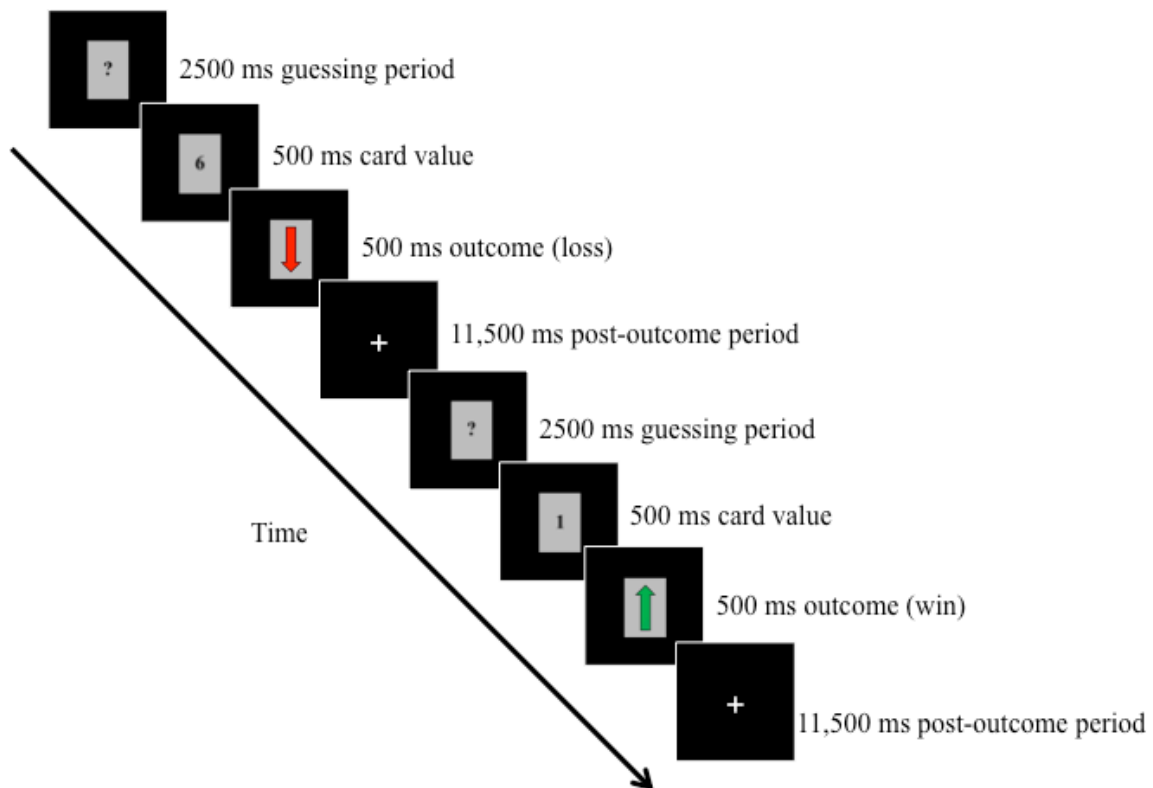
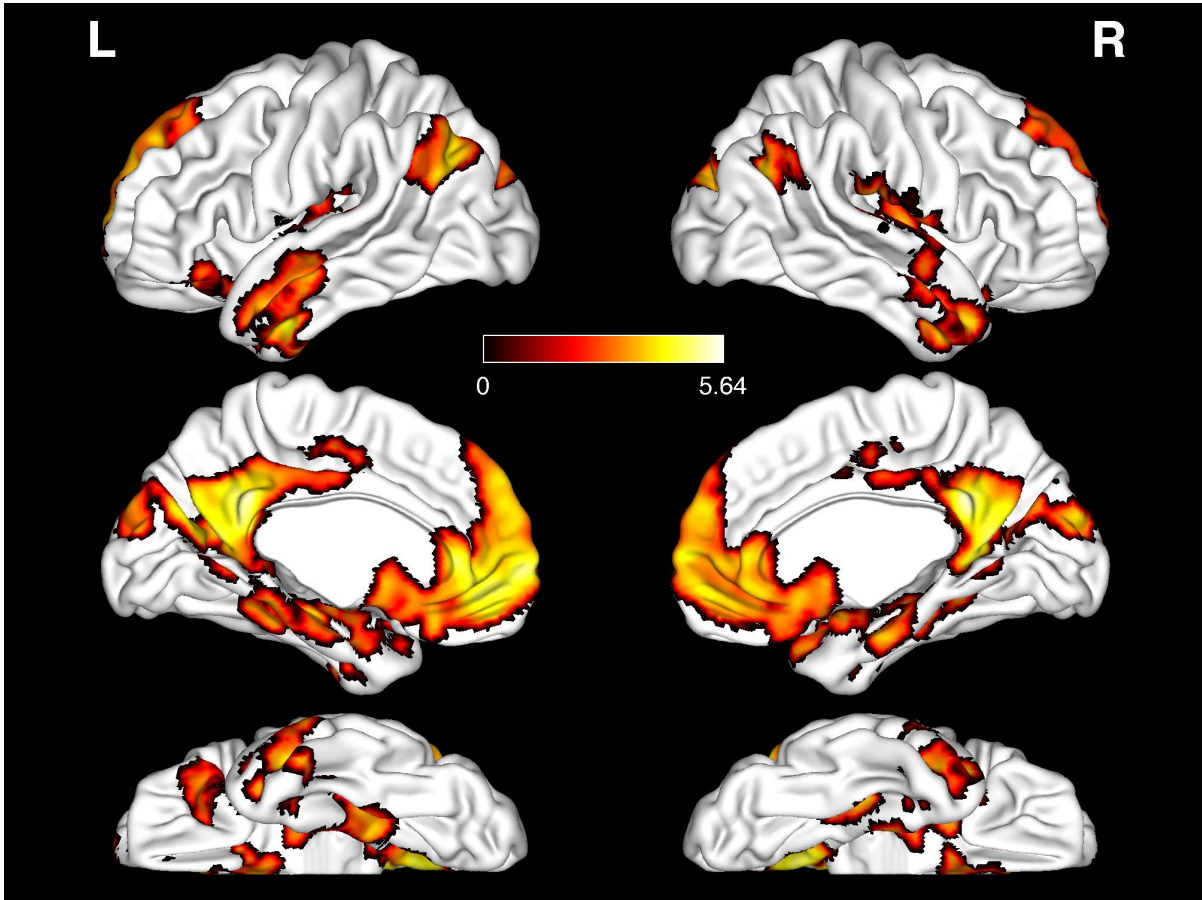


Figure S8: Activation and resulting seed ROIs in the win > loss contrast; cluster corrected $Z = 2.3, p < .05$.



See ROIs (in MNI 152 space) for PPI analyses included:

Right Ventral Striatum (Nucleus Accumbens):	10, 16, -6
Left Ventral Striatum (Nucleus Accumbens):	-10, 16, -6
Right Dorsal Striatum (Putamen):	16, 12, -6
Left Dorsal Striatum (Putamen):	-18, 12, 6