Striatal-frontal network activation during voluntary task selection under conditions of monetary reward

Joseph M. Orr[1,2], Michael J. Imburgio[1], Jessica A. Bernard[1,2], & Marie T. Banich[3,4]

[1]Department of Psychological and Brain Sciences, [2]Texas A&M Institute for Neuroscience, Texas A&M University, College Station, TX USA

[3]Institute of Cognitive Science, [4]Department of Psychology and Neuroscience, University of Colorado Boulder, Boulder, CO USA

Address correspondence to:

Joseph M. Orr, Ph.D.

Department of Psychological and Brain Sciences

515 Coke Street

Texas A&M University

College Station, TX 77843-4235

joseph.orr@tamu.edu

Abstract

During voluntary task selection there are a number of internal and external biases that guide such a choice. Previous work has shown that the rostrolateral prefrontal cortex is critical for overcoming such biases and maintaining long-term goals. However, it is not well understood how reward influences task selection when multiple options are possible. To address this issue, random rewards were occasionally presented after task performance in a voluntary task-switching paradigm while participants underwent fMRI scanning (n=19). To reinforce the overall goal to choose the tasks randomly, participants were told of a large bonus they would receive at the end of the experiment for making random task choices. We hypothesized that the transient rewards would increase the value of the just performed task and therefore bias participants to choose to repeat the same task on the subsequent trial. Contrary to expectations, transient reward had no consistent behavioral effect on subsequent task choice. Nevertheless, such rewards did influence activation in brain regions associated with reward processing as well as those associated with goal-directed control. In addition, reward on a prior trial was found to influence *activation* during task choice on a subsequent trial, with greater activation *in a number of executive function regions* as compared to no-reward trials. We posit that the global structure of the rewards (i.e., random presentation) and the bonus for random task choices together reinforced the goal to choose the tasks randomly, which influenced activation in reward-related regions and regions involved in abstract goal processing.

Introduction

Executive functioning underlies our ability to effortfully guide behavior towards goals. As executive functions require effort, which is aversive at some level (Kool, McGuire, Rosen, & Botvinick, 2010), motivation is often critical for deciding whether or not to exert effort and exercise executive control (Botvinick & Braver, 2014). Moreover, there is often some motivation towards goal-driven behavior. For example, the motivation to enjoy your favorite meal may engage executive processes to arrange for a reservation at the restaurant serving that meal or to organize your behavior so you can cook the meal yourself.

In fact, there is a growing literature on the relationship between reward-driven motivation and executive function. Motivation to rewards has been suggested to lead to enhanced proactive control that is associated with sustained goal maintenance, as opposed to more transient, reactive control mechanisms (Braver, 2012; Braver, Gray, & Burgess, 2007). As an example, Locke and Braver (2008) compared performance and BOLD activation during an AX-CPT task under conditions of reward and non-reward, and found that reward was associated with increased sustained activation of prefrontal and parietal cortices as well as improved proactive control. This behavioral finding was replicated by Chiew and Braver (2014) as well as by Fröber and Dresibach (2014, 2016a), but only when rewards were contingent on task performance and not random. It has been shown that such increased stability under conditions of reward has the concomitant effect of leading to decreased flexibility, which is the ability to adapt behavior to changing environmental information and goals (Müller et al., 2007).

One commonly-used task to examine cognitive flexibility is the task-switching paradigm, in which individuals switch between tasks on a trial-by-trial manner. Typically,

in such paradigms, a cue indicates which of the two tasks a participant should perform on that trial. In fact, several behavioral task-switching studies have now demonstrated that under certain reward structures, flexibility may be increased (Fröber & Dreisbach, 2016b; Kleinsorge & Rinkenauer, 2012; Shen & Chun, 2011). In all three studies, the increased prospect of a reward from one trial to the next was associated with increased flexibility, i.e., switch costs were reduced when reward value increased from the previous trial (e.g., low reward trial followed by a high reward trial) compared to when reward value remained the same; when reward prospects remain high from one trial to the next, stability is observed with behavioral benefit on task repeats at the expense of increase switch costs.

One limitation that arises when using standard task-switching paradigms to investigate the issue of flexibility is that while one can examine how quickly an individual switches from one task to the next, it is more limited with regards to investigating issues with regards to goal selection and maintenance. That is because in such paradigms the "goal" for the current trial is designated by a cue indicating which task should be performed on that trial. One way to overcome issue is to use a voluntary task switching (VTS) paradigm. In this paradigm, participants are free to choose which of two tasks to perform on every trial, and are typically instructed to choose the tasks equally often, yet in a random order (Arrington & Logan, 2004).

This paradigm was recently used in a series of behavioral studies with the addition of reward to determine how task choice might be affected by sequential changes in reward magnitude (Fröber & Dreisbach, 2016b). Four of these studies mixed cued and voluntary task switching, with an additional experiment that used a standard VTS paradigm with only voluntary choice trials. Across the studies, the magnitude of reward (low vs. high) was cued

at the beginning of a trial, and varied across trials such that reward magnitude could remain the same from one trial to the next, or increase/decrease in magnitude. It was found that participants were more likely to choose to switch tasks when reward increased or decreased from the previous trial, and conversely, they were biased to repeat the same task when reward magnitude was repeated from the previous trial. Thus, reward could either lead to increased flexibility (more frequent switches) or increased stability (more frequent repeats) depending on the recent reward history. Fröber & Dreisbach interpreted these findings as repeated high reward triggering exploitation and the possibility of a reward increase triggering exploration.

In the study by Fröber & Dreisbach (2016b), the reward structure likely only impacted the concrete task representation of the most recently performed task. On the other hand, a recent study by Braem (2017) demonstrated that reward could motivate abstract representations of repeating and switching. In this study, participants performed a block of explicit cued task switching trials followed by a block on voluntary task switching trials. The cued trials were rewarded, while the voluntary trials were not. One group of participants received more reward on switch trials than repeat trials while the other group received more reward for repeat trials. Participants who were rewarded more for cued task switches chose more voluntary task switches than participants who were rewarded more for cued task repeats. This pattern was found despite instructions to make random voluntary task choices, as well as a stipulation that deviating from random task choices would make participants ineligible for a contest for the person with the most points.

However, our current understanding of the brain's reward system circuitry suggests that it appears to be most sensitive to unexpected rewards (Schultz, Dayan, & Montague,

1997). Hence, in the current study, unlike Fröber & Dreisbach (2016), reward was presented infrequently and at the end of a trial in an unexpected, random manner. In addition to examining the effect of reward on task-switching ability (i.e., flexibility), we were also interested in whether reward at the end of one trial would bias voluntary task choice on the next trial. Task choice in the VTS paradigm has been shown in prior behavioral studies to be susceptible to influences that are both bottom-up (i.e., recent context) and top-down (i.e., overall goals) (Arrington, Weaver, & Pauker, 2010; Orr, Carp, & Weissman, 2012; Orr & Weissman, 2011). Our hypothesis was that by presenting a reward immediately after performing a given task, the value of that task would be temporarily increased (Schultz, 2006), and likewise, the strength of its goal representation. As such, we therefore predicted that reward would bias participants to choose that task again on the next trial.

With regards to the brain mechanisms that might be involved in strengthening such an association, we have previously argued that the rostral lateral prefrontal cortex (RLPFC) helps to maintain an abstract goal representation, which in the standard VTS paradigm is to choose between two tasks equally often and in a random order, so as to guide trial-by-trial task choices (Orr & Banich, 2014). The RLPFC is thought to lie at the apex of a gradient of abstraction within the PFC, with the most anterior regions controlling abstract, domain-general information and more posterior regions controlling domain-specific information like actions (Badre, 2008; O'Reilly, 2010); but see recent work suggesting that the dorsolateral PFC can also show "apex"-like characteristics (Nee & D'Esposito, 2016, 2017). More specifically, the RLPFC is thought to be involved in the high-level processing of goals, subgoals, and integrating information across time and stimulus dimensions (e.g., Charron &

Koechlin, 2010; Christoff et al., 2001; Koechlin, Basso, Pietrini, Panzer, & Grafman, 1999; Nee & D'Esposito, 2016). More recently, it has become clear that the RLPFC plays a role in decision-making. For example, Kovach and colleagues (2012) demonstrated that patients with RLPFC lesions have difficulty tracking recent trends in reward history. Furthermore, the RLPFC may be critical for considering alternatives to the chosen decision (Boorman, Behrens, Woolrich, & Rushworth, 2009) and exploring unfamiliar options (Daw, O'Doherty, Dayan, Seymour, & Dolan, 2006a).

Hence, we predicted that the effects of rewards would be two-fold. First, we predicted that the receipt of reward would be associated with increased activation in regions of the brain typically associated with processing immediate reward, such, as the ventral striatum and ventral medial PFC (McClure, Laibson, Loewenstein, & Cohen, 2004). The more interesting question is the degree to which such rewards would influence the activation RLPFC, which is involved in maintaining overall task goals. To the degree that RLPFC is involved in higher-order goals and considering temporal information that is required to meet such goals (e.g., Charron & Koechlin, 2010), its activation should also be influenced by rewards. However, we predicted that such influences would not be observed during receipt of reward, but rather have an influence during task choice on the subsequent trial after reward. This prediction was derived from the fact that RLPFC would need to integrate and balance information about the recent reward, that would likely bias to repeating the task choice, with the more long-term goal of a 50/50 distribution of task choice. To our knowledge, this is the first imaging study to examine the interactions of reward and voluntary task selection.

Method

Participants

Twenty-two young healthy adults were recruited from the University of Colorado Boulder community as part of a larger study of the individual differences on executive function (Orr, Smolker, & Banich, 2015; Reineberg, Andrews-Hanna, Depue, Friedman, & Banich, 2015; Reineberg & Banich, 2016; Smolker, Depue, Reineberg, Orr, & Banich, 2015). The median age was 20 years with a range of 19-27. Seven participants identified as female. We had intended on recruiting 25 participants based on an estimated power analysis but were only able to enroll 22 participants. There were technical problems for two participants and one participant only performed one task throughout the whole experiment, yielding useable data for a total of 19 participants.

Experimental Paradigm

Participants performed a double-registration variant of a voluntary task switching paradigm (Arrington & Logan, 2005; Orr et al., 2012). On each trial participants were allowed to voluntarily choose between two tasks: one involved making a decision about the numerical size of two digits while the other involved making a decision about the actual physical size of the font in which those two digits were presented. Task choices were made prior to the onset of the task stimuli, which consisted of two numbers; one number was larger than 6 and the other was smaller than 4, and one number was presented in a large font and the other in a small font. Participants were instructed to choose the tasks in a random order. To make this idea concrete, they were given examples of stereotyped task sequences and random sequences. After task performance, reward feedback was presented: on 25% of correct trials the feedback indicated that a 10-cent reward was earned and on the other trials the feedback indicated that 0 cents was earned. Reward was

pseudo-randomly presented such that there was an even distribution across the two tasks (within each run). The task was presented using E-Prime 2.10 (https://pstnet.com).

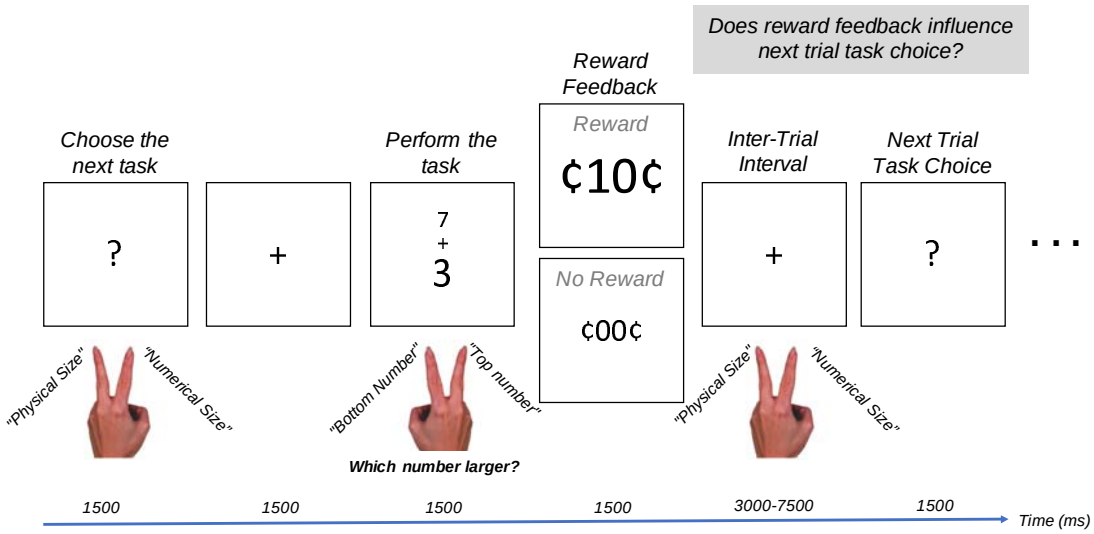

Figure 1. Example trial sequence. At the beginning of each trial participants were cued to choose the next task (either a numerical size comparison or a physical size comparison of two upcoming digits) with a '?'. After correct task performance, 25% of trials contained a reward, and the remaining trials did not. We predicted that the reward would increase the value of the just performed task, and would bias participants to choose to perform that task again on the next trial.

A prototypical trial is presented in Figure 1. The choice cue (i.e., ' ? ', presented in Calibri 24 size font) appeared for 350 ms followed by a fixation cross (presented in Calibri size 24 font) that appeared for 1150 ms. Participants chose the task by pressing a button with their left index or middle finger, with the task-button mapping being counterbalanced across participants. The target digits then appeared for 350 ms, followed by a fixation cross that appeared for 1150 ms. Participants responded to the task with their right index and middle fingers, with the index finger mapped to the bottom number and the middle finger mapped to the top number. The physically large number was presented in Calibri size 32 font and the physically small number was presented in Calibri size 18 font. The numerically large number was randomly selected from the set of 7, 8, and 9, and the numerically small number was randomly selected from the set of 1, 2, and 3. Physical size and numerical size

were counterbalanced across trials within each block. A reward feedback stimulus then appeared for 1500 ms, which indicated whether a reward was given or not. A reward was indicated by ¢10¢ (presented in Calibri in size 48 font) and no reward was indicated by ¢00¢ (presented in Calibri size 24 font). Each block consisted of 64 trials, with an equal number of congruent (correct answer is the same for both tasks, e.g., top number numerically and physically large) and incongruent trials (correct answer is different for both tasks, e.g., top number numerically large but physically small, as shown in Fig. 1), with the position of the numerically larger and physically larger digit being counterbalanced. The ITI was jittered between 3000 and 7500 ms according to a decreasing pseudo-exponential distribution that favored short ITIs (i.e., 57 trials at 3000 ms, 4 trials at 4500 ms, 2 trials at 6000 ms, and 1 trial at 7500 ms).

Participants were instructed that the trial rewards were random and were used to maintain motivation throughout the experiment. A running total of the rewards was updated at the end of each block. Participants were instructed that the maximum of these trial rewards would be $5. Participants were further instructed that a separate larger bonus, up to $10, would be determined based on how random their task choices were. They were told that the bonus would be delayed by two weeks. In this manner, we were attempting to provide more incentive for random task choices than for task choices biased by the transient rewards.

fMRI Data Collection

A Siemens Magnetom TIM Trio (3-Tesla) MRI system with a 12-channel head coil was used for data acquisition. Structural images were acquired with a T1-weighted 3D magnetization prepared rapid gradient multi-echo sequence (MPRAGE; sagittal plane;

repetition time [TR] = 2530 ms; echo times [TE] = 1.64 ms, 3.5 ms, 5.36 ms, 7.22 ms, 9.08 ms; GRAPPA parallel imaging factor of 2; 1 mm isotropic voxels, 192 interleaved slices; FOV = 256mm; flip angle = 7°; time = 6:03 min). Six functional task runs were collected with an EPI sequence from 26 interleaved slices (3 mm slice thickness, 3.4 x 3.4 mm in-place resolution) aligned parallel to orbital frontal cortex with the following parameters: [TR] = 1500 ms; [TE] = 25 ms; flip angle = 67 deg; 333 measurements; 0.53 ms echo spacing. In order to perform B0 unwarping, a gradient echo fieldmap was collected with the following parameters: TR = 400 ms; TE1 = 4.92 ms; TE2 = 7.38; 3 mm slice with 3.8 mm in-plane resolution. The fieldmap was processed in FSL to generate a phase difference image and a magnitude image for each echo time. B0 unwarping was performed in FEAT as described in more detail below. The structural images were collected in an earlier session occurring an average of 6 months prior.

fMRI Data Analysis

FMRI data processing was carried out using FEAT (FMRI Expert Analysis Tool) Version 6.00, part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl). The following pre-statistics processing was applied; motion correction using MCFLIRT (Jenkinson, Bannister, Brady, & Smith, 2002); slice-timing correction using Fourier-space time-series phase-shifting; non-brain removal using BET (Smith, 2002); B0 distortion unwarping (Jenkinson, 2003, 2004); spatial smoothing using a Gaussian kernel of FWHM 6.0mm; grand-mean intensity normalisation of the entire 4D dataset by a single multiplicative factor. Preprocessed data were then denoised with ICA-AROMA (Pruim, Mennes, van Rooij, et al., 2015; Pruim, Mennes, Buitelaar, & Beckmann, 2015), an automatic method of removing motion artifacts using ICA implemented with FSL MELODIC. After denoising, the data

underwent highpass temporal filtering (Gaussian-weighted least-squares straight line fitting, with sigma=45.0s).

First-level analyses were carried out using FEAT. Time-series statistical analysis was carried out using FILM with local autocorrelation correction (Woolrich, Ripley, Brady, & Smith, 2001). Two models were set-up for each run of the task: 1) BOLD activity associated with the reward feedback stimulus, and 2) BOLD activity associated with task choice as a function of whether participants chose to repeat or switch tasks and whether the previous trial was rewarded or not. Contrasts were defined for the mean of each level (e.g., reward, no reward, repeat, switch), Reward > No Reward, and Switch > Repeat. Thus, there were 3 contrasts for the first model, and 6 for the second model. Registration of the functional data to the T1w and MNI152_T1_2mm template was carried out using FLIRT with a Boundary Based Registration (BBR) cost function (Jenkinson et al., 2002; Jenkinson & Smith, 2001). Registration from the T1w to the MNI152_T1_2mm template was then further refined using FNIRT nonlinear registration (Andersson, Jenkinson, & Smith, 2007a, 2007b).

A second-level model was defined for each participant to average results across the five runs using fixed effect analysis in FEAT. Group-level analyses were performed in *randomize* using non-parametric permutation tests with cluster correction carried out with Threshold-Free Cluster Enhancement (TFCE) (Smith & Nichols, 2009; Winkler, Ridgway, Webster, Smith, & Nichols, 2014) with a cluster-level threshold of FWE-corrected $p < .05$. Note that as the name implies, TFCE does not used a voxel-level threshold and instead relies on a TFCE metric based on the height and width of activation. Some analyses are reported with a higher voxel-level t-statistic threshold in order to yield more separated clusters.

For display purposes, cortical volumetric statistics maps were projected to the HCP 900 Subject Group Average Midthickness Surface (Van Essen et al., 2017) using the Connectome Workbench v. 1.3.0 (https://www.humanconnectome.org/software/get-connectome-workbench), and 2-D slices were created using FSL's *fsleyes* (v. 0.23.0) on the MNI152_T1_1mm template. Cluster tables were generated using FSL's automated atlasquery (*autoaq*) using the volumetric data. Cluster labels come primarily from the Harvard-Oxford Cortical and Subcortical atlases, while the Oxford-GSK-Imanova Striatal Connectivity Atlas (Tziortzi et al., 2014) was used for labeling clusters in the striatum, and the Neubert Ventral Frontal Parcellation (Neubert, Mars, Thomas, Sallet, & Rushworth, 2014) and Sallet Dorsal Frontal Parcellation (Sallet et al., 2013) were used for labeling clusters in prefrontal cortex. As the Neubert and Sallet Parcellations were right lateralized, the thresholded t-stat maps were flipped to generate labels for the left hemisphere. Thus, the labels for the left prefrontal clusters may be approximate.

Regions of Interest

Region of interest (ROI) analyses were conducted in order to facilitate the detection of interactions between previous reward and current task choice, specifically, the decision to repeat or switch. Interactions are difficult to interpret with linear contrasts (e.g., a contrast for the interaction of previous reward and current task alternation is 0 1 -1 0 [Repeat-Reward Repeat-NoReward Switch-Reward Switch-NoReward]). Rather than setting up multiple simple effects contrasts, we chose to conduct a repeated measures ANOVA on Percent Signal Change (PSC) data extracted from *a priori* ROIs in the striatum and RLPFC. Striatal masks were created using the Oxford-GSK-Imanova Striatal Connectivity Atlas, an atlas based on cortical-striatal connectivity (Tziortzi et al., 2014). Striatal masks were

created for the executive subregion (connected to areas 9, 9/46 and area 10) and the limbic subregion (connected with orbitofrontal and ventromedial cortex). The atlas masks were thresholded at 60% and 70%, respectively, and binarized. For the RLPFC ROIs, we focused on the most anterior portion, the frontal pole (FP). Lateral and orbital FP masks were defined from our previous DTI-based connectivity parcellation of the FP (Orr et al., 2015). The FP masks consisted of spheres with a diameter of 10 mm centered on the center of mass from our k=6 parcellation in each hemisphere. Left and right masks were combined into bilateral masks. We previously showed that the lateral FP has more local connections within the PFC than other FP subregions and is functionally connected with the frontoparietal control network. We had previously found that the orbital FP is connected with visual cortex and temporal cortex, including the hippocampus and amygdala.

Results

Behavioral Results

Task Choice Behavior

We first examined whether the choice to repeat or switch tasks on the next trial (calculated as switch rate, i.e., the proportion of switch trials within a given cell) was influenced by whether or not the previous trial was rewarded. We had predicted that receiving a reward after performing a given task (compared with not receiving a reward) would bias participants to choose to repeat the same task on the next trial. Note that a 50% switch rate indicates a balance between repeating and switching tasks, a switch rate above 50% indicates a bias to switch tasks, and a switch rate below 50% indicates a bias to repeat tasks. Overall, participants showed a preference for switching tasks (M: 53.6% [CI: 50.1-

57.3%]; $t(18) = 2.2$, $p = .043$, Cohen's $d = 0.50$), contrary to most previous studies of voluntary task switching which show a strong repeat bias (e.g., Arrington & Logan, 2004, 2005; Mayr & Bell, 2006; Orr et al., 2012). However, previous studies have shown that even with response to stimulus there is a decreased (and sometimes absent) repetition bias at long vs. short response to stimulus intervals (Arrington & Logan, 2004, 2005; Liefooghe, Demanet, & Vandierendonck, 2009; Orr et al., 2012; Yeung, 2010); due to the nature of the slow BOLD response in fMRI, the target to choice stimulus interval was between 4500 and 10500 ms. Whether this long interval explains the switch bias observed here is unclear, and would require behavioral studies with variable intervals. Nevertheless, to our knowledge, no previous study using a standard VTS paradigm has shown a switch bias.

Furthermore, and contrary to our prediction, there was no main effect of whether or not the previous trial was rewarded (No Reward: 52.3% [CI: 48.1% - 56.4%]; Reward: 52.0% [CI: 46.0-58.0%]; $F(1,18) = 0.007$, *n.s.*, $\eta_p^2 = .000$). To further examine this null effect, we used the open source statistical program JASP (JASP Team (2018), Version 0.9 [Computer software]) to calculate the Bayes Factor BF_{01}, which quantifies the evidence for the null hypothesis vs. the alternative hypothesis (Rouder, Speckman, Sun, Morey, & Iverson, 2009). This analysis yielded $BF_{01} = 4.2$, suggesting these data are 4.2 times more likely to be observed under the null hypothesis, reflecting moderate support for accepting the null hypothesis that previous reward had no effect on switch rate.

In contemplating this unexpected outcome, we decided to consider whether the effect of reward on the previous trial affected switch rate based on whether the rewarded trial was a task repeat or task switch trials. We wondered whether participants may have thought that the reward was for repeating or switching tasks, rather than the specific task

choice (numerical size, physical size). There was a very large effect of whether or not the previous task had been repeated (Previous Repeat: 60.1%; Previous Switch: 44.8%; F(1,18) = 26.8, $p < .001$, $\eta_p^2 = .60$), with individuals more likely to switch tasks on the current trial if they had chosen to repeat on the previous trial (e.g., a task sequence such as Numerical-Numerical-Physical) than if they had chosen to switch on the previous trial (e.g., a task sequence such as Numerical-Physical-Numerical). Critically, however, there was no interaction of previous alteration and previous reward (F(1,18) = 0.24, *n.s.*, $\eta_p^2 = .013$). Thus, it does not appear that participants were guided by the strategy that the transient rewards were associated with the decision to repeat or switch tasks. Nevertheless, with neuroimaging we can look for evidence of reward mechanisms interacting with regions of the brain that underlie the decision to repeat or switch.

Task Choice Reaction Time

We considered the effects of task alternation (Repeat, Switch) and previous trial reward (No Reward, Reward) on how quickly a task was chosen (i.e., task choice reaction time). *The results are reported in Table 1.* The speed with which individuals chose a task showed a large effect of alternation (Repeat: 415 ms; Switch: 386 ms; F(1,18) = 15.3, $p < .001$, $\eta_p^2 = .46$) with participants being faster to choose on trials when they switched task than when they repeated the same tasks. While this finding is inconsistent with previous studies (Arrington & Logan, 2005; Orr & Weissman, 2011), this effect may be related to the switch bias described above. There was a moderate effect on whether the previous trial had been rewarded (No Reward: 392 ms; Reward: 409 ms; F(1,18) = 4.8, $p = .042$, $\eta_p^2 = .21$), with participants being slower to choose the next task following a reward as compared to

no reward. This suggests that rather than acting on fast heuristics to facilitate task choices, participants may have made more deliberate task choice decisions following a reward.

Target Performance

Response time and accuracy to the targets (i.e., the digit stimuli) was analyzed as a function of task alternation, *target congruency*, and previous trial reward. *See Table 2 for mean performance.* With regards to reaction time switch costs, participants showed a moderate sized switch cost with RT being longer for trials in which they switched tasks than repeated the same task, but the effect was only at a trend level (Repeat: 497 ms; Switch: 509 ms; $F(1,18) = 3.3$, $p = .085$, $\eta_p^2 = .16$). In terms of accuracy, there was not a significant switch cost (Repeat: 89.6%; Switch: 87.0%; $F(1,18) = 2.5$, $p = .128$, $\eta_p^2 = .12$), but there was a significant interaction of task alternation and target congruency ($F(1,18) = 4.9$, $p = .04$, $\eta_p^2 = .16$). The switch cost was larger for incongruent (-0.05%) compared to congruent trials (-3.99%), in line with at least one previous study (Orr et al., 2012).

Whole-Brain Imaging Results

To determine whether indeed our reward manipulation was effective, we first examined brain activation associated with the reward feedback phase of the trial. As expected, the contrast of Reward vs. No Reward feedback yielded significant clusters in the limbic subregion of the striatum, posterior hippocampus, area 47/ frontal operculum (FOp), medial FP, and other regions as reported in Table 1. Figure 2A shows the cortical surfaces while Figure 2B shows striatal slices of the contrast map overlaid on the limbic and executive subregions of the Oxford-GSK-Imanova connectivity striatal atlas (Tziortzi et al., 2014). As shown in Figure 2B, activation after reward feedback was fairly restricted to

the limbic subregion of the striatum. Thus, the reward feedback was associated with a number of regions implicated in the receipt of reward as well as internal monitoring of behavior, suggesting that our manipulation was effective in activating reward-related regions of the brain.

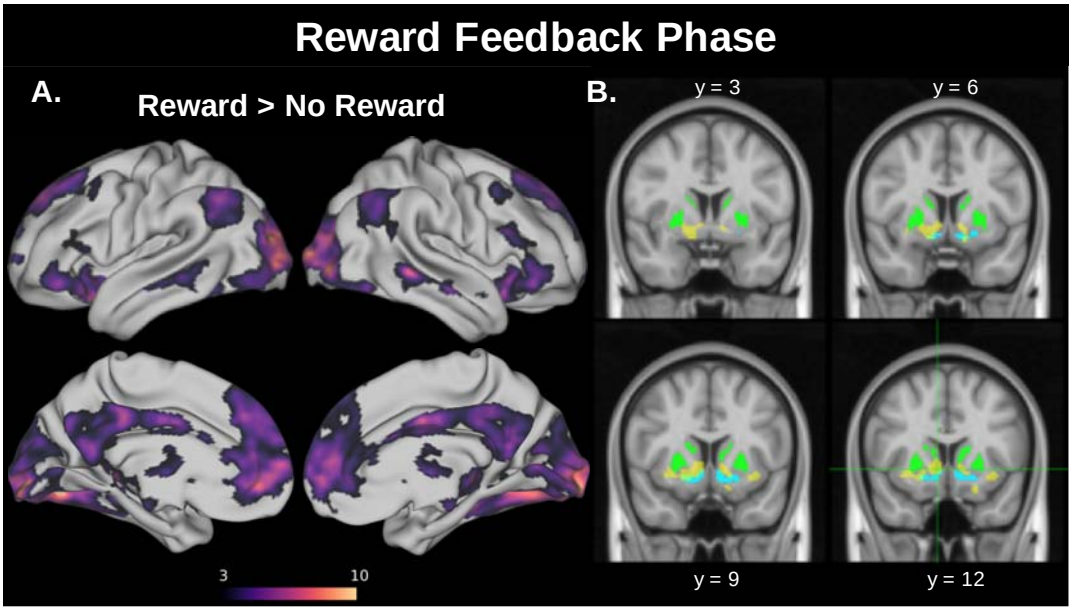

Figure 2. Cortical surface (A) and striatal slices (B) for activation associated with the reward feedback phase. Contrast of reward greater than no reward. Color bar represents t-values with a threshold of t > 5. B. Striatal slices depict activation (yellow) with the striatal executive subregion mask (60% threshold) shown in green and the striatal limbic subregion mask (70% threshold) shown in cyan.

Next, we examined activation for the contrast of switch and repeat trials, time-locked to the choice cue. Compared to repeat trials, switch trials showed greater activation of the Superior Parietal Lobule, Dorsal Premotor Cortex, Frontal Eye Fields, Dorsal Medial Frontal Cortex (including pre-supplementary motor area and cingulate), insula, and thalamus. These results are shown in Figure 3 and reported in Table 2. These regions have been implicated in task switching in a prior fMRI meta-analysis (Kim, Cilles, Johnson, & Gold, 2012). It is somewhat surprising that there was no dorsolateral FC activation in this

contrast, as this region is frequently associated with task switching and cognitive flexibility, more generally (e.g., Brass & von Cramon, 2002).

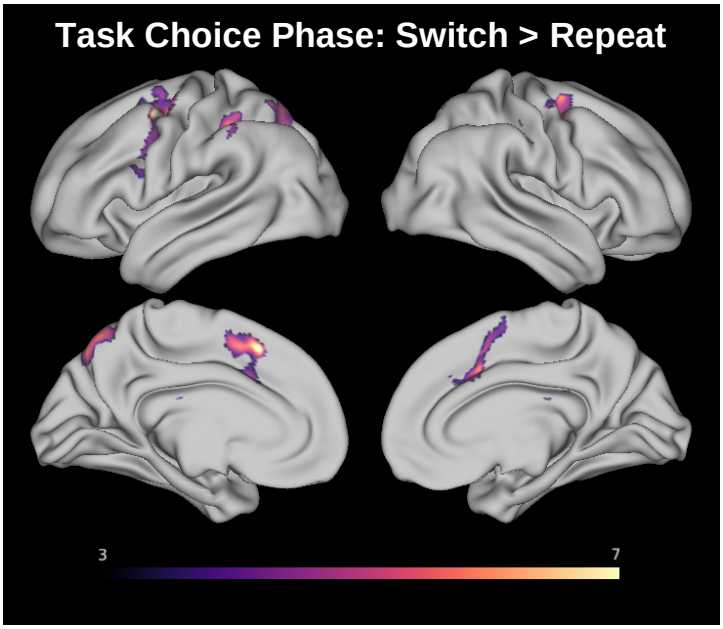

Figure 3. Cortical surface map showing activation of contrast of switch and repeat task choice. Color bar represents t-values with an applied threshold of t > 3.5.

In the critical analysis, activity during the task choice phase was then examined as a function of the previous trial reward feedback (Reward > No Reward). This contrast yielded a number of clusters including a number of posterior occipital/parietal clusters, posterior dorsolateral PFC (FEF, dorsal premotor), the executive subregion of the striatum, anterior dorsomedial prefrontal cortex (area 9), and RLPFC (lateral FP, 9/46V). Clusters are reported in Table 3, and activation maps are shown in Figure 4. As shown in Figure 4B, the striatal activation is primarily in the executive subregion, in contrast to the effect of reward feedback, which was in the limbic subregion (see Figure 2B). Further comparing Figures 2 and 4, there are several noted changes in regions of activation from receiving reward to choosing the next task following a reward. First, and as already noted, there is a

shift from limbic to executive striatum. In the medial PFC, there was a dorsal shift from rostral anterior cingulate/ medial FP to medial area 9. In the lateral prefrontal cortex, there was an anterior shift from area 47/ IFS to the RLPFC (lateral FP/ area 9/46V). In general, this suggests that there was a shift from reward evaluation toward goal processing.

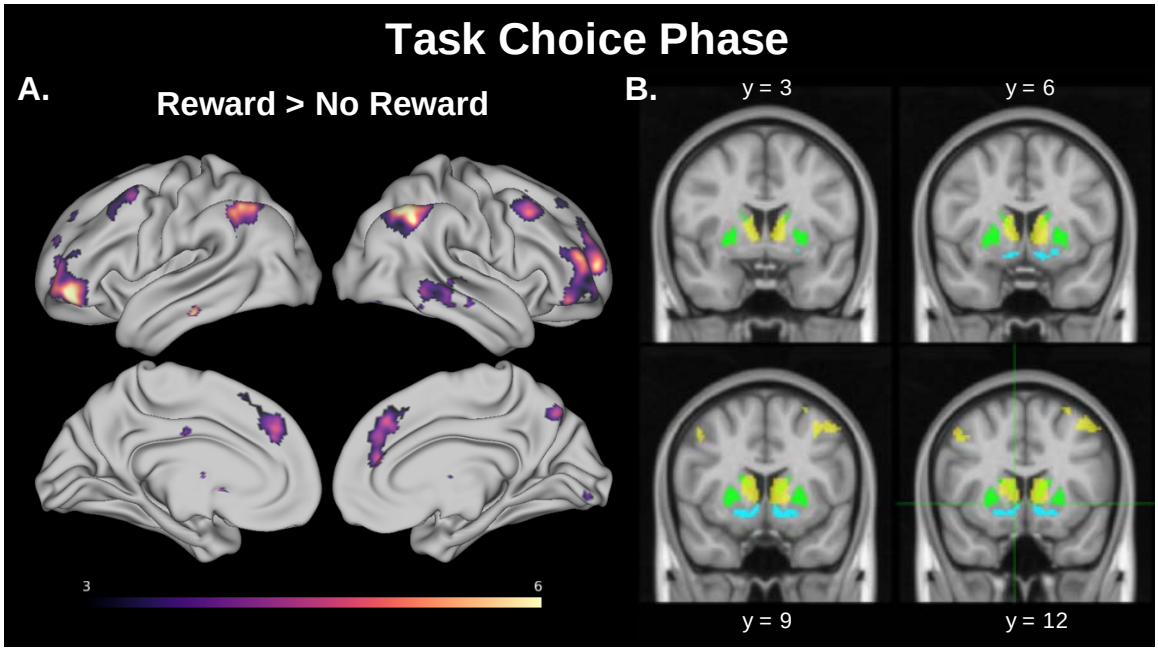

Figure 4. Cortical surface (A) and striatal slices (B) for activation associated with the task choice phase as a function of previous trial reward. Contrast of reward greater than no reward. Color bar represents t-values with a threshold of t > 3.5. B. Striatal slices depict activation (yellow) with the striatal executive subregion mask (60% threshold) shown in green and the striatal limbic subregion mask (70% threshold) shown in cyan.

ROI Analysis

We conducted two separate ROI analyses, one using activation from the reward feedback phase of the trial and another using activation from the task choice phase of the trial. In both cases mean percent signal change (PSC) was extracted from the ROIs. The same four ROIs were used in both: limbic and executive striatal subregions (Tziortzi et al., 2014) and lateral and orbital FP (Orr et al., 2015). The main purpose of the ROI analyses was to test whether reward on the prior trial affected whether to switch vs. repeat tasks on

the current trial. For the analysis of the reward feedback phase, we found a moderate effect of region (F(2.3, 41.0) = 4.5, p = .01, η_p^2 = .20) and a very large effect of reward (F(1,18) = 41.1, p < .001, η_p^2 = .70), as well as a moderately-sized interaction effect of region and reward (F(2.4, 43.8) = 5.0, p = .07, η_p^2 = .22). As shown in Figure 5, the effect was largest in the limbic striatum (Cohen's d = 1.1) and the lateral FP (Cohen's d = 1.1), and smallest in the executive striatum (Cohen's d = .8).

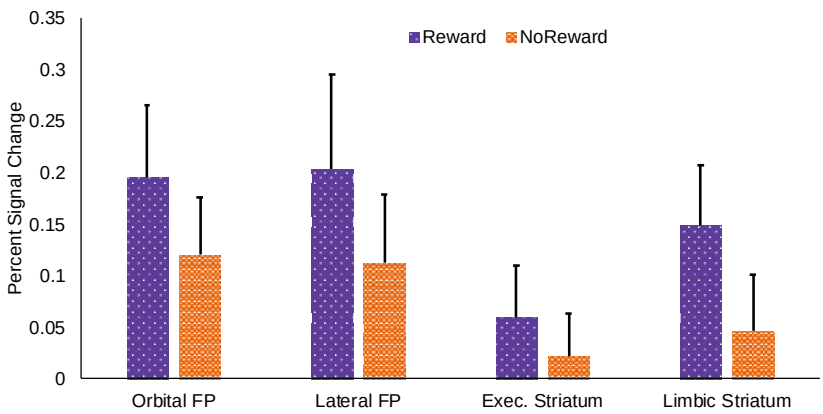

Figure 5. Percent signal change for the reward feedback stimuli in four ROIs. Error bars represent 95% confidence intervals. FP = Frontal Pole.

For the analysis of the task choice phase, there were only significant main effects of region (F(2.1, 37.5) = 6.3, p = .004, η_p^2 = .26) and reward (F(1, 18) = 8.1, p = .01, η_p^2 = .3). As shown in Figure 6, PSC was greater following reward vs. no reward trials, but showed little effect of whether or not the task choice repeated from the prior trial or was switched. While there was no region by previous reward interaction (F(2.2, 39.2) = 1.3, p = .28, η_p^2 = .07), the effect of reward was numerically greater in the lateral FP and executive subregion of the striatum. Nevertheless, there was no apparent trend for an interaction of previous trial reward and current task alternation in any of the four ROIs. Post-hoc repeated

measures ANOVAs for each of the four ROIs confirmed this pattern (all F's < 0.97, all η_p^2 < .05).

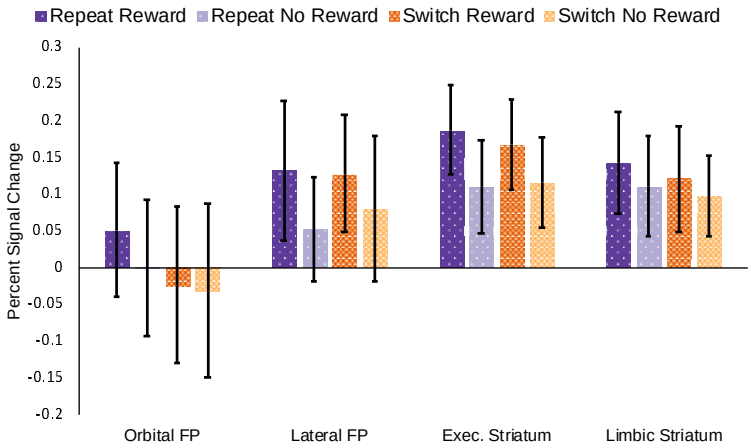

Figure 6. Percent signal change for the task choice period as a function of previous trial reward and current task alternation in four ROIs. Error bars represent 95% confidence intervals. FP = Frontal Pole.

Discussion

The goal of the present study was to investigate the influence of reward on task choice in a voluntary task switching paradigm. Throughout the experiment, participants received occasional small and unexpected rewards after specific trials. To encourage task compliance, they could earn a larger, delayed bonus for producing random task sequences. We hypothesized that the transient rewards would temporarily increase the value of the task that was just performed, biasing participants to choose the task again. As previous VTS studies have shown that salient, bottom-up biases affect task choice despite global instructions to choose the tasks randomly, (e.g., Orr & Weissman, 2011; Weaver & Arrington, 2010; Yeung, 2010), we predicted that the degree to which participants' task choices were guided by the random task choice bonus rather than the transient reward would manifest as individual differences. However, we found no behavioral effect of

reward on task choice on the next trial. While we had hypothesized that reward would bias participants to repeat tasks on the next trial, we also considered whether the reward might be linked not to a specific choice of task, but rather on choice history, that is whether participants coded the reward as linked to repeating a task or switch tasks (regardless of the actual task they performed). However, there was no interaction of task choice sequence (repeat, switch) and reward. Either participants ignored the reward, which seems unlikely given the neuroimaging findings (discussed below) and informal participant debriefing, or participants prioritized other aspects of the task, such as trying to focus on producing random task choices.

The prediction that *random, non-contingent* rewards would influence task choice was based on an influential literature that demonstrates that the brain's reward system is sensitive to unexpected rewards (Schultz et al., 1997). However, a growing literature on the role of reward in executive function suggests that the balance between cognitive flexibility vs. stability depends on reward-behavior contingencies as well as sequential changes in reward magnitude. When rewards are contingent upon behavioral outcomes (i.e., speed cutoffs, accuracy), proactive control appears to be increased, which reinforces stability at the expense of flexibility (Chiew & Braver, 2014; Fröber & Dreisbach, 2016a), while performance non-contingent rewards lead to reduced proactive control (Fröber & Dreisbach, 2016a). Relatedly, work on conflict adaptation (i.e., increased reactive control following a high conflict trial vs. a low conflict trial) have further shown that reward feedback (presented and the end of the trial, as in the current study) has differential effects on conflict adaptation depending on performance contingencies. When reward is presented randomly without performance contingencies, conflict adaptation is reduced following

gains compared to losses or neutral feedback, presumably because the positive affect from gains counteracted the aversive signal for increased control (van Steenbergen, Band, & Hommel, 2009, 2012). However, when reward is only presented infrequently, and is contingent on performance, conflict adaptation is enhanced following gains (Braem, Verguts, Roggeman, & Notebaert, 2012; Stürmer, Nigbur, Schacht, & Sommer, 2011).

Flexibility on the other hand, appears to be sensitive to sequential changes in reward magnitude, such that increases in reward magnitude from the previous trial are associated with reduced switch costs and increased proportion of voluntary task switches (Fröber & Dreisbach, 2016b; Kleinsorge & Rinkenauer, 2012; Shen & Chun, 2011). However, these prior studies have not examined the effects of performance non-contingent reward on voluntary task choice. Furthermore, in these prior studies, the reward magnitude available on each trial was presented at the beginning of the trial in order to influence task preparation or choice, whereas in the current study, reward feedback was only presented at the end of the trial, after participants had already performed the task. It remains to be seen how non-contingent reward presented at the *beginning* of a trial might influences the stability/flexibility trade-off.

The above studies primarily considered the effects of reward locally, that is, task performance on the trial immediately following a reward. Recently, Braem (2017) found that global patterns of reward (i.e., varying the relative proportion of task alternations and repetitions that were rewarded) could reinforce abstract control representations such as the proportion of voluntary task repetitions and alternations across a run. These effects on voluntary switching emerged even though only cued repetitions and alternations were rewarded. This study by Braem raises the possibility that in the current study, participants'

task choice patterns were reinforced by the global reward structure, i.e., the fact that the transient rewards were not performance-contingent and were randomly presented may have reinforced the abstract goal to choose the tasks randomly which was further reinforced by the end-of-task bonus for random task choices. Rather than the transient rewards and the end-of-task bonus having opposing effects on task choice, as we predicted, they may have reinforced each other. Indeed, participants showed a switch bias, which is observed when participants are asked to generate random sequences (Baddeley, 1996; Baddeley, Emslie, Kolodny, & Duncan, 1998; Rapoport & Budescu, 1997), suggesting that participants were motivated to select the tasks randomly. One piece of evidence speaking against the suggestion that the reward structure reinforced abstract control representations that guided task choice, however, is the lack of a benefit of reward on subsequent switch costs; however, the long inter-trial interval may have influenced this, as Braem (2017) did not find a significant switch cost or interaction of reward and alternation in their study. Future work should explore the effects of reward timing (pre- or post-trial) and behavioral contingencies in a principled manner to understand the effects of reward, and motivation in general, on processes underlying voluntary task choice and performance.

While the imaging results did not reveal an interaction of previous reward and task choice, there were three interesting shifts of activation in reward-related brain regions from the phase of the trial in which they experienced receipt of reward to the phase in which they determined their task choice on the subsequent trial. First, in the striatum there was a shift in activation from the ventral limbic subregion to the dorsal executive subregion. One influential theory of the dorsal-ventral gradient in the striatum is the actor-critic model (O'Doherty et al., 2004; Sutton & Barto, 1998). This model proposes that the

ventral striatum uses temporal difference models to predict future reward associated with the current environment, while the dorsal striatum uses this signal to modify action plans to maximize future reward (Haruno, 2004; O'Doherty, 2004; Tricomi, Delgado, & Fiez, 2004). Given this pattern of activation, there is support for our hypothesis that transient rewards influenced task choices. However, we do not have enough evidence to form a model of what policy or action plan participants employed to guide their task choices. This is an issue that might be fruitfully explore in future studies.

The second region in which a shift was observed was in the medial PFC. During the receipt of reward there was activation of rostral medial PFC, while during the task choice period, the dorsal medial PFC was activated. This shift from reward receipt to task choice appears to reflect a shift from reward evaluation and internal monitoring to planning action intentions. Soon and colleagues (2008; 2013) have shown that activity in the rostral medial PFC precedes the conscious awareness of both a voluntary motor choice and a voluntary task choice, suggesting that this region encodes abstract intentions. In an fMRI meta-analysis, Nakao and colleagues (2012) suggested that the rostral medial PFC is associated with internally-guided decision making, that is decision making according to internal preferences rather than external contingencies. The dorsal medial PFC cluster identified in the current study also resembles the region have been linked to voluntary motor and task decisions across a number of studies (Demanet, de Baene, Arrington, & Brass, 2013; Forstmann, Brass, Koch, & von Cramon, 2005, 2006). Brass and Haggard's (2008) "What, When, Whether" model of action posits that dorsal medial PFC regions (anterior to the pre-supplementary motor area) are responsible for representing 'what' response to make, and 'whether' or not to make it. The cluster we identified during the

choice period overlapped with regions ascribed to both of these functions. This shift in the location of activation from reward receipt to task choice is also in line with the idea that task choices were driven by the longer-term reward and goal.

Lastly, in the lateral PFC we observed a shift from activation in the lateral orbitofrontal cortex (area 47/12) during reward receipt to the RLPFC during the selection of the task on the subsequent trial. While the medial orbitofrontal cortex has been fairly well characterized, the function of the lateral portion is less clear. Indeed, when entering the coordinates of the center of gravity for the 47/ Fop clusters (left: -44, 38, -10; right: 41, 36, -10) into the meta-analytic tool *neurosynth.org* (Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011), there are only a handful of significant associations for the right cluster (most of which are anatomical terms followed by vague associations such as "emotional information"), while the left cluster is associated with terms related to language and semantics. One potential reason for the lack of clarity regarding the function of this region is that the lateral orbitofrontal cortex is prone to signal dropout with many BOLD sequences, especially older sequences. For this reason, much of what is known about lateral orbitofrontal function comes from studies of non-human primates or lesion studies in humans.

In that regard, Rushworth and colleagues have demonstrated that in both humans and monkeys, the lateral orbitofrontal cortex is critical for linking stimuli to reward (Noonan et al., 2010; Noonan, Chau, Rushworth, & Fellows, 2017; Noonan, Mars, & Rushworth, 2011; Rudebeck et al., 2008; Rushworth, Noonan, Boorman, Walton, & Behrens, 2011). Lesions to the lateral orbitofrontal cortex impact credit assignment, i.e., the ability to learn the value of stimulus options, but no deficits in comparing the value of different options. Other

evidence regarding this region comes from Neubert and colleagues (2014, 2015) who compared the connectivity patterns of the PFC in humans and macaques. A posterior ventrolateral region they labelled 47 or 47/12 was found to correspond most closely to macaque area 47/12 (Petrides & Pandya, 2002), and was functionally coupled to anterior PFC and anterior temporal cortex. They suggested that this regions connectivity supports its role in credit assignment, allowing it to learn which sensory features in the environment are rewarding.

The role of RLPFC, the region whose activation we observed during task choice has been suggested to play a distinct role with regards to reward processing from these other frontal regions. Boorman and colleagues (2009) had participants freely choose between two possible response options which were associated with random amounts of reward. However, the reward probabilities depended on recent choice history. Using a Bayesian reinforcement learning model, they showed that the RLPFC tracked the advantage of choosing the alternative action choice but did not reflect the value of the chosen option. Conversely, they found that the rostral medial PFC reflected the value of the chosen option but did not encode the alternative action choice. This finding of the rostral medial PFC encoding current value is in line with the current finding that this region was active during the reward feedback phase, but not during the subsequent trial task choice. It should be noted that in Boorman and colleagues' study, the activation was 10-14 mm more lateral that the lateral frontal pole ROI used here and corresponds to area 9/46. Future research is needed to test whether the RLPFC activity observed in the current study during task choice reflects a consideration of choosing the alternative task choice.

Bahlmann and colleagues (2015) recently investigated the influence of reward-based motivation on the rostral-caudal control hierarchy. They varied the level of reward and the level of task complexity (low complexity: stimulus-response mapping task; middle complexity: flexible task switching; high complexity: second-order cue that instructed sustained cue-task associations). Like the current study, the rewards were restricted to correct trials, but were otherwise not performance contingent. As predicted the RLPFC was more activated for high-level complexity than low-level complexity. They further found that reward interacted with complexity in both the RLPFC and middle lateral PFC, but the middle level of complexity showed the strongest influence of reward. In the RLPFC, the interaction between reward and complexity was due to a bigger reward effect at low complexity than high complexity. They suggested that the RLPFC may become involved in low-level complexity with sufficient motivation. Thus, the RLPFC may show interactive effects of cognitive demands and motivation.

The function of the RLPFC has been a topic of much debate (Burgess, 2011; Koechlin, 2011; Tsujimoto & Genovesio, 2011; Tsujimoto, Genovesio, & Wise, 2011). One source of this debate is a lack of consistent naming when referring to regions of the RLPFC. Some authors do not dissociate between area 10 and anterior 9/46 when referring to the frontal pole, and the major cortical atlas packaged in FSL, the Harvard-Oxford Cortical Structural Atlas, labels a very large portion of the RLPFC as 'frontal pole'. Recent work has demonstrated that there are multiple regions of the frontal pole (Bludau et al., 2013; Neubert et al., 2014; Orr et al., 2015; Sallet et al., 2013). In a meta-analysis of fMRI studies that activated the RLPFC, Gilbert and colleagues (2006) found that the most anterior portion was most involved in multitasking, in line with neuropsychology studies of damage

to the frontal pole (Burgess, 2016). Gilbert and colleagues (2006) associated the lateral portions of RLPFC with episodic memory retrieval.

However, most previous studies have focused on medial-lateral functional gradients within the RLPFC, not dorsal-ventral. In our previous parcellation of the RLPFC, we found evidence for a medial-lateral gradient as well as a dorsal-ventral gradient (Orr et al., 2015). We suggested that the medial areas of RLPFC are involved in monitoring and regulation of behavior and emotion while lateral areas maintain abstract cognitive representations; we posited that ventral RLPFC is involved in linking stimuli to values and emotions while dorsal RLPFC is involved in abstract action planning. The ROI analysis in the present study demonstrated that the orbital FP ROI (ventral lateral portion of the RLPFC) was involved during the receipt of reward but was not active during the task choice period. The involvement of the orbital FP during the receipt of reward is in line with the suggestion that ventral portions of the RLPFC are involved with linking stimuli to values. The more dorsal lateral FP ROI however, was active during the task choice period, which is in line with the suggestion that lateral dorsal RLPFC is involved with maintaining abstract cognitive representations and action plans. Future studies should further explore the functional differentiation of the frontal pole subregions.

Limitations and Future Directions

A limitation of the current study is the relatively low number of participants (N=19) that precluded the analysis of individual differences that may have allowed for finer-grained analysis of the trade-off between reward-induced biases and the goal to be random. Individual differences would be of interest in the current context because it is well known that individuals vary in their sensitivity to reward (Braver, 2012; Corr, 2004; Depue

& Collins, 1999; Gray, 1970). Another potential follow-up would be to vary the frequency of reward in a systematic manner to determine whether that might influence behavior and alter the activation across the brain regions noted. It should be noted that the reward feedback phase and task choice phase results came from two different GLM analyses. The ideal approach to examine shifts in brain activation from the feedback phase to the task choice phase would be a Finite Impulse Response model that would have allowed us to model the BOLD timeseries. However, given the variable delay between reward and next trial task choice, such an analysis was not feasible. Finally, when the study was designed, there were no prior VTS neuroimaging paradigms that included reward, so we did not want to greatly alter the task structure from prior behavioral studies. However, since that time Braun and Arrington (2017) have designed a similar task that involves a reward structure that juxtaposes exploration as compared to exploitation of task choice. It would be interesting to see whether the same structures implicated here were involved in mediating between these two strategies. Indeed previous work has implicated the RLPFC in supporting exploration strategies and the striatum and rostral medial PFC for exploitative strategies (Daw, O'Doherty, Dayan, Seymour, & Dolan, 2006b).

Conclusions

While we predicted that participants would show a task choice bias induced by the transient rewards, there was no reliable effect of reward on the next trial's task choice. Nevertheless, these rewards were associated with significant activation of reward-related brain regions. Task choices following the reward showed increased activation of anterior PFC regions thought to be involved in high-level abstract control. Combined with previous work showing that reward can reinforce abstract control representation, these findings

suggest that task choices were guided by abstract goals to choose the tasks randomly as implemented by anterior PFC regions. Overall, this study adds to a growing literature on the role of RLPFC in executive function and decision-making. Moreover, this study represents an initial step towards understanding how reward influences voluntary task selection.

References

Andersson, J. L. R., Jenkinson, M., & Smith, S. (2007a). *Non-linear registration, aka spatial normalisation. FMRIB Technial Report TR07JA2*.

Andersson, J. L. R., Jenkinson, M., & Smith, S. M. (2007b). *Non-linear optimisation. FMRIB technical report TR07JA1*. Retrieved from http://fsl.fmrib.ox.ac.uk/analysis/techrep/tr07ja1/tr07ja1.pdf

Arrington, C. M., & Logan, G. D. (2004). The cost of a voluntary task switch. *Psychological Science*, *15*(9), 610–5. https://doi.org/10.1111/j.0956-7976.2004.00728.x

Arrington, C. M., & Logan, G. D. (2005). Voluntary task switching: chasing the elusive homunculus. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *31*(4), 683–702. https://doi.org/10.1037/0278-7393.31.4.683

Arrington, C. M., Weaver, S. M., & Pauker, R. L. (2010). Stimulus-based priming of task choice during voluntary task switching. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *36*(4), 1060–7. https://doi.org/10.1037/a0019646

Baddeley, A. D. (1996). Exploring the central executive. *Quarterly Journal of Experimental Psychology*, *49A*(1), 5–28. https://doi.org/10.1080/713755608

Baddeley, A. D., Emslie, H., Kolodny, J., & Duncan, J. (1998). Random generation and the

executive control of working memory. *Quarterly Journal of Experimental Psychology*, *51A*(4), 819–852. https://doi.org/10.1080/027249898391413

Badre, D. (2008). Cognitive control, hierarchy, and the rostro-caudal organization of the frontal lobes. *Trends in Cognitive Sciences*, *12*(5), 193–200. https://doi.org/10.1016/j.tics.2008.02.004

Bahlmann, J., Aarts, E., & D'Esposito, M. (2015). Influence of Motivation on Control Hierarchy in the Human Frontal Cortex. *The Journal of Neuroscience*, *35*(7), 3207–3217. https://doi.org/10.1523/JNEUROSCI.2389-14.2015

Bludau, S., Eickhoff, S. B., Mohlberg, H., Caspers, S., Laird, A. R., Fox, P. T., … Amunts, K. (2013). Cytoarchitecture, probability maps and functions of the human frontal pole. *NeuroImage*. https://doi.org/10.1016/j.neuroimage.2013.05.052

Boorman, E. D., Behrens, T. E. J., Woolrich, M. W., & Rushworth, M. F. S. (2009). How green is the grass on the other side? Frontopolar cortex and the evidence in favor of alternative courses of action. *Neuron*, *62*(5), 733–743. https://doi.org/10.1016/j.neuron.2009.05.014

Botvinick, M. M., & Braver, T. S. (2014). Motivation and Cognitive Control: From Behavior to Neural Mechanism. *Annual Review of Psychology*, (September 2014), 1–31. https://doi.org/10.1146/annurev-psych-010814-015044

Braem, S. (2017). Conditioning task switching behavior. *Cognition*, *166*, 272–276. https://doi.org/10.1016/j.cognition.2017.05.037

Braem, S., Verguts, T., Roggeman, C., & Notebaert, W. (2012). Reward modulates adaptations to conflict. *Cognition*, *125*(2), 324–332.

https://doi.org/10.1016/j.cognition.2012.07.015

Brass, M., & Haggard, P. (2008). The what, when, whether model of intentional action. *The Neuroscientist*, *14*(4), 319–25. https://doi.org/10.1177/1073858408317417

Brass, M., & von Cramon, D. Y. (2002). The role of the frontal cortex in task preparation. *Cerebral Cortex*, *12*(9), 908–14. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/12183390

Braun, D. A., & Arrington, C. M. (2017). Assessing the role of reward in task selection using a reward-based voluntary task switching paradigm. *Psychological Research*. https://doi.org/10.1007/s00426-017-0919-x

Braver, T. S. (2012). The variable nature of cognitive control: a dual mechanisms framework. *Trends in Cognitive Sciences*, *16*(2), 106–13. https://doi.org/10.1016/j.tics.2011.12.010

Braver, T. S., Gray, J. R., & Burgess, G. C. (2007). Explaining the many varieties of working memory variation: Dual mechanisms of cognitive control. In C. Jarrold (Ed.), *Variation in Working Memory* (pp. 76–106). Oxford: Oxford University Press. https://doi.org/10.3758/s13423-011-0165-y

Burgess, P. W. (2011). Frontopolar cortex: constraints for theorizing. *Trends in Cognitive Sciences*, *15*(6), 242. https://doi.org/10.1016/j.tics.2011.04.005

Burgess, P. W. (2016). Riddle is to conundrum as the frontal pole is to...? *Brain*, *139*, 1627–1629. https://doi.org/10.1093/brain/awl241

Charron, S., & Koechlin, E. (2010). Divided representation of concurrent goals in the human

frontal lobes. *Science*, *328*(5976), 360–363. https://doi.org/10.1126/science.1183614

Chiew, K. S., & Braver, T. S. (2014). Dissociable influences of reward motivation and positive emotion on cognitive control. *Cognitive, Affective and Behavioral Neuroscience*, *14*(2), 509–529. https://doi.org/10.3758/s13415-014-0280-0

Christoff, K., Prabhakaran, V., Dorfman, J., Zhao, Z., Kroger, J. K., Holyoak, K. J., & Gabrieli, J. D. (2001). Rostrolateral prefrontal cortex involvement in relational integration during reasoning. *NeuroImage*, *14*(5), 1136–1149. https://doi.org/10.1006/nimg.2001.0922

Corr, P. J. (2004). Reinforcement sensitivity theory and personality. *Neuroscience & Biobehavioral Reviews*, *28*(3), 317–332. https://doi.org/10.1016/J.NEUBIOREV.2004.01.005

Daw, N. D., O'Doherty, J. P., Dayan, P., Seymour, B., & Dolan, R. J. (2006a). Cortical substrates for exploratory decisions in humans. *Nature*, *441*(7095), 876–879. https://doi.org/10.1038/nature04766

Daw, N. D., O'Doherty, J. P., Dayan, P., Seymour, B., & Dolan, R. J. (2006b). Cortical substrates for exploratory decisions in humans. *Nature*, *441*(7095), 876–879. https://doi.org/10.1038/nature04766

Demanet, J., de Baene, W., Arrington, C. M., & Brass, M. (2013). Biasing free choices: The role of the rostral cingulate zone in intentional control. *NeuroImage*, *72*, 207–213. https://doi.org/10.1016/j.neuroimage.2013.01.052

Depue, R. A., & Collins, P. F. (1999). Neurobiology of the structure of personality: Dopamine, facilitation of incentive motivation, and extraversion. *Behavioral and Brain Sciences*, *22*(03). https://doi.org/10.1017/S0140525X99002046

Forstmann, B. U., Brass, M., Koch, I., & von Cramon, D. Y. (2005). Internally generated and directly cued task sets: an investigation with fMRI. *Neuropsychologia*, *43*(6), 943–52. https://doi.org/10.1016/j.neuropsychologia.2004.08.008

Forstmann, B. U., Brass, M., Koch, I., & von Cramon, D. Y. (2006). Voluntary selection of task sets revealed by functional magnetic resonance imaging. *Journal of Cognitive Neuroscience*, *18*(3), 388–98. https://doi.org/10.1162/089892906775990589

Fröber, K., & Dreisbach, G. (2014). The differential influences of positive affect, random reward, and performance-contingent reward on cognitive control. *Cognitive, Affective and Behavioral Neuroscience*, *14*(2), 530–547. https://doi.org/10.3758/s13415-014-0259-x

Fröber, K., & Dreisbach, G. (2016a). How performance (non-)contingent reward modulates cognitive control. *Acta Psychologica*, *168*, 65–77. https://doi.org/10.1016/j.actpsy.2016.04.008

Fröber, K., & Dreisbach, G. (2016b). How sequential changes in reward magnitude modulate cognitive flexibility: Evidence from voluntary task switching. *Journal of Experimental Psychology: Learning Memory and Cognition*, *42*(2), 285–295. https://doi.org/10.1037/xlm0000166

Gilbert, S. J., Spengler, S., Simons, J. S., Steele, J. D., Lawrie, S. M., Frith, C. D., & Burgess, P. W. (2006). Functional specialization within rostral prefrontal cortex (area 10): a meta-analysis. *Journal of Cognitive Neuroscience*, *18*(6), 932–48. https://doi.org/10.1162/jocn.2006.18.6.932

Gray, J. A. (1970). The psychophysiological basis of introversion-extraversion. *Behaviour*

Research and Therapy, *8*(3), 249–266. https://doi.org/10.1016/0005-7967(70)90069-0

Haruno, M. (2004). A Neural Correlate of Reward-Based Behavioral Learning in Caudate Nucleus: A Functional Magnetic Resonance Imaging Study of a Stochastic Decision Task. *The Journal of Neuroscience*, *24*(7), 1660–1665. https://doi.org/10.1523/JNEUROSCI.3417-03.2004

Jenkinson, M. (2003). Fast, automated,N-dimensional phase-unwrapping algorithm. *Magnetic Resonance in Medicine*, *49*(1), 193–197. https://doi.org/10.1002/mrm.10354

Jenkinson, M. (2004). Improving the registration of B0-disorted EPI images using calculated cost function weights. *NeuroImage*, *22*, e1544–e1545.

Jenkinson, M., Bannister, P., Brady, M., & Smith, S. M. (2002). Improved Optimization for the Robust and Accurate Linear Registration and Motion Correction of Brain Images. *NeuroImage*, *17*(2), 825–841. https://doi.org/10.1006/nimg.2002.1132

Jenkinson, M., & Smith, S. M. (2001). A global optimisation method for robust affine registration of brain images. *Medical Image Analysis*, *5*(2), 143–156. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11516708

Kim, C., Cilles, S. E., Johnson, N. F., & Gold, B. T. (2012). Domain general and domain preferential brain regions associated with different types of task switching: A Meta-Analysis. *Human Brain Mapping*, *33*(1), 130–142. https://doi.org/10.1002/hbm.21199

Kleinsorge, T., & Rinkenauer, G. (2012). Effects of monetary incentives on task switching. *Experimental Psychology*, *59*(4), 216–226. https://doi.org/10.1027/1618-

3169/a000146

Koechlin, E. (2011). Frontal pole function: what is specifically human? *Trends in Cognitive Sciences*, *15*(6), 241; author reply 243. https://doi.org/10.1016/j.tics.2011.04.005

Koechlin, E., Basso, G., Pietrini, P., Panzer, S., & Grafman, J. (1999). The role of the anterior prefrontal cortex in human cognition. *Nature*, *399*(6732), 148–151. https://doi.org/10.1038/20178

Kool, W., McGuire, J. T., Rosen, Z. B., & Botvinick, M. M. (2010). Decision Making and the Avoidance of Cognitive Demand. *Journal of Experimental Psychology: General*, *139*(4), 665–682. https://doi.org/10.1037/a0020198

Kovach, C. K., Daw, N. D., Rudrauf, D., Tranel, D., O'Doherty, J. P., & Adolphs, R. (2012). Anterior prefrontal cortex contributes to action selection through tracking of recent reward trends. *The Journal of Neuroscience*, *32*(25), 8434–42. https://doi.org/10.1523/JNEUROSCI.5468-11.2012

Liefooghe, B., Demanet, J., & Vandierendonck, A. (2009). Is advance reconfiguration in voluntary task switching affected by the design employed? *Quarterly Journal of Experimental Psychology*, *62*(5), 850–7. https://doi.org/10.1080/17470210802570994

Locke, H. S., & Braver, T. S. (2008). Motivational influences on cognitive control: Behavior, brain activation, and individual differences. *Cognitive, Affective, & Behavioral Neuroscience*, *8*(1), 99–112. https://doi.org/10.3758/CABN.8.1.99

Mayr, U., & Bell, T. (2006). On how to be unpredictable: evidence from the voluntary task-switching paradigm. *Psychological Science*, *17*(9), 774–80.

https://doi.org/10.1111/j.1467-9280.2006.01781.x

McClure, S. M., Laibson, D. I., Loewenstein, G., & Cohen, J. D. (2004). Separate neural systems value immediate and delayed monetary rewards. *Science*, *306*(5695), 503–507. https://doi.org/10.1126/science.1100907

Müller, J., Dreisbach, G., Goschke, T., Hensch, T., Lesch, K. P., & Brocke, B. (2007). Dopamine and cognitive control: The prospect of monetary gains influences the balance between flexibility and stability in a set-shifting paradigm. *European Journal of Neuroscience*, *26*(12), 3661–3668. https://doi.org/10.1111/j.1460-9568.2007.05949.x

Nakao, T., Ohira, H., & Northoff, G. (2012). Distinction between externally vs. Internally guided decision-making: Operational differences, meta-analytical comparisons and their theoretical implications. *Frontiers in Neuroscience*, *6*(MAR), 1–26. https://doi.org/10.3389/fnins.2012.00031

Nee, D. E., & D'Esposito, M. (2016). The hierarchical organization of the lateral prefrontal cortex. *ELife*, *5*, 1–26. https://doi.org/10.7554/eLife.12112

Nee, D. E., & D'Esposito, M. (2017). Causal evidence for lateral prefrontal cortex dynamics supporting cognitive control. *ELife*, *6*. https://doi.org/10.7554/eLife.28040

Neubert, F.-X., Mars, R. B., Sallet, J., & Rushworth, M. F. S. (2015). Connectivity reveals relationship of brain areas for reward-guided learning and decision making in human and monkey frontal cortex. *Proceedings of the National Academy of Sciences*, *112*(20), E2695–E2704. https://doi.org/10.1073/pnas.1410767112

Neubert, F.-X., Mars, R. B., Thomas, A. G., Sallet, J., & Rushworth, M. F. S. (2014). Comparison of human ventral frontal cortex areas for cognitive control and language with areas in

monkey frontal cortex. *Neuron*, *81*(3), 700–13. https://doi.org/10.1016/j.neuron.2013.11.012

Noonan, M. P., Chau, B. K. H., Rushworth, M. F. S., & Fellows, L. K. (2017). Contrasting Effects of Medial and Lateral Orbitofrontal Cortex Lesions on Credit Assignment and Decision-Making in Humans. *The Journal of Neuroscience*, *37*(29), 7023–7035. https://doi.org/10.1523/JNEUROSCI.0692-17.2017

Noonan, M. P., Mars, R. B., & Rushworth, M. F. S. (2011). Distinct Roles of Three Frontal Cortical Areas in Reward-Guided Behavior. *The Journal of Neuroscience*, *31*(40), 14399–14412. https://doi.org/10.1523/JNEUROSCI.6456-10.2011

Noonan, M. P., Walton, M. E., Behrens, T. E. J., Sallet, J., Buckley, M. J., & Rushworth, M. F. S. (2010). Separate value comparison and learning mechanisms in macaque medial and lateral orbitofrontal cortex. *Proceedings of the National Academy of Sciences*, *107*(47), 20547–20552. https://doi.org/10.1073/pnas.1012246107

O'Doherty, J. P. (2004). Reward representations and reward-related learning in the human brain: Insights from neuroimaging. *Current Opinion in Neurobiology*, *14*(6), 769–776. https://doi.org/10.1016/j.conb.2004.10.016

O'Doherty, J. P., Dayan, P., Schultz, J., Deichmann, R., Friston, K. J., & Dolan, R. J. (2004). Dissociable Role of Ventral and Dorsal Striatum in Instrumental Conditioning. *Science*, *304*(5669), 452–454. https://doi.org/10.1126/science.1094285

O'Reilly, R. C. (2010). The What and How of prefrontal cortical organization. *Trends in Neurosciences*, *33*(8), 355–361. https://doi.org/10.1016/j.tins.2010.05.002

Orr, J. M., & Banich, M. T. (2014). The neural mechanisms underlying internally and

externally guided task selection. *NeuroImage*, *84*, 191–205. https://doi.org/10.1016/j.neuroimage.2013.08.047

Orr, J. M., Carp, J., & Weissman, D. H. (2012). The influence of response conflict on voluntary task switching: a novel test of the conflict monitoring model. *Psychological Research*, *76*(1), 60–73. https://doi.org/10.1007/s00426-011-0324-9

Orr, J. M., Smolker, H. R., & Banich, M. T. (2015). Organization of the human frontal pole revealed by large-scale DTI-based connectivity: Implications for control of behavior. *PLoS One*, *10*(5). https://doi.org/10.1371/journal.pone.0124797

Orr, J. M., & Weissman, D. H. (2011). Succumbing to bottom-up biases on task choice predicts increased switch costs in the voluntary task switching paradigm. *Frontiers in Psychology*, *2*(February), 31. https://doi.org/10.3389/fpsyg.2011.00031

Petrides, M., & Pandya, D. N. (2002). Comparitive cytoarchitectonic analysis of the human and the macaque ventrolateral prefrontal cortex and the corticocortical connection patterns in the monkey. *European Journal of Neuroscience*, *16*, 291–310. https://doi.org/10.1046/j.1460-9568.2002.02090.x

Pruim, R. H. R., Mennes, M., Buitelaar, J. K., & Beckmann, C. F. (2015). Evaluation of ICA-AROMA and alternative strategies for motion artifact removal in resting state fMRI. *NeuroImage*, *112*, 278–287. https://doi.org/10.1016/j.neuroimage.2015.02.063

Pruim, R. H. R., Mennes, M., van Rooij, D., Llera, A., Buitelaar, J. K., & Beckmann, C. F. (2015). ICA-AROMA: A robust ICA-based strategy for removing motion artifacts from fMRI data. *NeuroImage*, *112*, 267–277. https://doi.org/10.1016/j.neuroimage.2015.02.064

Rapoport, A., & Budescu, D. V. (1997). Randomization in individual choice behavior.

Psychological Review, *104*(3), 603–617. https://doi.org/10.1037//0033-295X.104.3.603

Reineberg, A. E., Andrews-Hanna, J. R., Depue, B. E., Friedman, N. P., & Banich, M. T. (2015). Resting-state Networks Predict Individual Differences in Common and Specific Aspects of Executive Function. *NeuroImage*, *104*, 69–78. https://doi.org/10.1016/j.neuroimage.2014.09.045

Reineberg, A. E., & Banich, M. T. (2016). Functional connectivity at rest is sensitive to individual differences in executive function: A network analysis. *Human Brain Mapping*, *37*(8), 2959–2975. https://doi.org/10.1002/hbm.23219

Rouder, J. N., Speckman, P. L., Sun, D., Morey, R. D., & Iverson, G. (2009). Bayesian t tests for accepting and rejecting the null hypothesis. *Psychonomic Bulletin and Review*, *16*(2), 225–237. https://doi.org/10.3758/PBR.16.2.225

Rudebeck, P. H., Behrens, T. E. J., Kennerley, S. W., Baxter, M. G., Buckley, M. J., Walton, M. E., & Rushworth, M. F. S. (2008). Frontal Cortex Subregions Play Distinct Roles in Choices between Actions and Stimuli. *The Journal of Neuroscience*, *28*(51), 13775–13785. https://doi.org/10.1523/JNEUROSCI.3541-08.2008

Rushworth, M. F. S., Noonan, M. P., Boorman, E. D., Walton, M. E., & Behrens, T. E. J. (2011). Frontal Cortex and Reward-Guided Learning and Decision-Making. *Neuron*, *70*(6), 1054–1069. https://doi.org/10.1016/j.neuron.2011.05.014

Sallet, J., Mars, R. B., Noonan, M. P., Neubert, F.-X., Jbabdi, S., O'Reilly, J. X., … Rushworth, M. F. S. (2013). The organization of dorsal frontal cortex in humans and macaques. *The Journal of Neuroscience*, *33*(30), 12255–12574.

https://doi.org/10.1523/JNEUROSCI.5108-12.2013

Schultz, W. (2006). Behavioral Theories and the Neurophysiology of Reward. *Annual Review of Psychology*, *57*(1), 87–115. https://doi.org/10.1146/annurev.psych.56.091103.070229

Schultz, W., Dayan, P., & Montague, P. R. (1997). A Neural Substrate of Prediction and Reward. *Science*, *275*(5306), 1593–1599. https://doi.org/10.1126/science.275.5306.1593

Shen, Y. J., & Chun, M. M. (2011). Increases in rewards promote flexible behavior. *Attention, Perception, and Psychophysics*, *73*(3), 938–952. https://doi.org/10.3758/s13414-010-0065-7

Smith, S. M. (2002). Fast robust automated brain extraction. *Human Brain Mapping*, *17*(3), 143–155. https://doi.org/10.1002/hbm.10062

Smith, S. M., & Nichols, T. E. (2009). Threshold-free cluster enhancement: addressing problems of smoothing, threshold dependence and localisation in cluster inference. *NeuroImage*, *44*(1), 83–98. https://doi.org/10.1016/j.neuroimage.2008.03.061

Smolker, H. R., Depue, B. E., Reineberg, A. E., Orr, J. M., & Banich, M. T. (2015). Individual differences in regional prefrontal grey matter morphometry and fractional anisotropy are associated with different constructs of executive function. *Brain Structure & Function*, *220*(3), 1291–1306. https://doi.org/10.1007/s00429-014-0723-y

Soon, C. S., Brass, M., Heinze, H.-J., & Haynes, J.-D. (2008). Unconscious determinants of free decisions in the human brain. *Nature Neuroscience*, *11*(5), 543–545. https://doi.org/10.1038/nn.2112

Soon, C. S., He, H. H., Bode, S., & Haynes, J.-D. (2013). Predicting free choices for abstract intentions. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(15), 6217–6222. https://doi.org/10.1073/pnas.1212218110

Stürmer, B., Nigbur, R., Schacht, A., & Sommer, W. (2011). Reward and punishment effects on error processing and conflict control. *Frontiers in Psychology*, *2*(November), 335. https://doi.org/10.3389/fpsyg.2011.00335

Sutton, R. S., & Barto, A. C. (1998). *Reinforcement Learning: An Introduction*. Cambridge, MA: The MIT Press.

Tricomi, E. M., Delgado, M. R., & Fiez, J. A. (2004). Modulation of Caudate Activity by Action Contingency. *Neuron*, *41*(2), 281–292. https://doi.org/10.1016/S0896-6273(03)00848-1

Tsujimoto, S., & Genovesio, A. (2011). Appreciating the differences: response to Burgess. *Trends in Cognitive Sciences*, *15*(6), 6613. https://doi.org/10.1016/j.tics.2011.04.005

Tsujimoto, S., Genovesio, A., & Wise, S. P. (2011). Frontal pole cortex: encoding ends at the end of the endbrain. *Trends in Cognitive Sciences*, *15*(4), 169–76. https://doi.org/10.1016/j.tics.2011.02.001

Tziortzi, A. C., Haber, S. N., Searle, G. E., Tsoumpas, C., Long, C. J., Shotbolt, P., … Gunn, R. N. (2014). Connectivity-Based Functional Analysis of Dopamine Release in the Striatum Using Diffusion-Weighted MRI and Positron Emission Tomography. *Cerebral Cortex*, *24*(5), 1165–1177. https://doi.org/10.1093/cercor/bhs397

Van Essen, D. C., Smith, J., Glasser, M. F., Elam, J., Donahue, C. J., Dierker, D. L., … Harwell, J. (2017). The Brain Analysis Library of Spatial maps and Atlases (BALSA) database.

NeuroImage, *144*, 270–274. https://doi.org/10.1016/j.neuroimage.2016.04.002

van Steenbergen, H., Band, G. P. H., & Hommel, B. (2009). Reward counteracts conflict adaptation. Evidence for a role of affect in executive control. *Psychological Science*, *20*(12), 1473–7. https://doi.org/10.1111/j.1467-9280.2009.02470.x

van Steenbergen, H., Band, G. P. H., & Hommel, B. (2012). Reward valence modulates conflict-driven attentional adaptation: Electrophysiological evidence. *Biological Psychology*, *90*(3), 234–241. https://doi.org/10.1016/j.biopsycho.2012.03.018

Weaver, S. M., & Arrington, C. M. (2010). What's on your mind: the influence of the contents of working memory on choice. *Quarterly Journal of Experimental Psychology*, *63*(4), 726–37. https://doi.org/10.1080/17470210903137180

Winkler, A. M., Ridgway, G. R., Webster, M. a, Smith, S. M., & Nichols, T. E. (2014). Permutation Inference for the General Linear Model. *NeuroImage*, *92*, 381–97. https://doi.org/10.1016/j.neuroimage.2014.01.060

Woolrich, M. W., Ripley, B. D., Brady, M., & Smith, S. M. (2001). Temporal Autocorrelation in Univariate Linear Modeling of FMRI Data. *NeuroImage*, *14*(6), 1370–1386. https://doi.org/10.1006/nimg.2001.0931

Yarkoni, T., Poldrack, R. A., Nichols, T. E., Van Essen, D. C., & Wager, T. D. (2011). Large-scale automated synthesis of human functional neuroimaging data. *Nature Methods*, *8*(8), 665–675. https://doi.org/10.1038/NMETH.1635

Yeung, N. (2010). Bottom-up influences on voluntary task switching: the elusive homunculus escapes. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *36*(2), 348–62. https://doi.org/10.1037/a0017894

Table 1

Choice reaction time as a function of task alternation and previous trial reward.

Task Alternation	**Previous Trial Reward**	**Mean**	**SEM**
Repeat	No Reward	404	23
	Reward	426	28
Switch	No Reward	381	19
	Reward	392	24

Table 2

Target reaction time and accuracy as a function of task alternation, target congruency, and previous trial reward.

			Reaction Time		Accuracy	
Previous Trial Reward	**Task Alternation**	**Target Congruency**	**Mean**	**SEM**	**Mean**	**SEM**
No Reward	Repeat	Congruent	465	20	95.7%	1.67%
		Incongruent	550	26	81.6%	2.84%
	Switch	Congruent	469	19	96.0%	0.99%
		Incongruent	558	25	77.6%	2.64%
Reward	Repeat	Congruent	451	16	98.8%	0.69%
		Incongruent	534	28	79.7%	2.59%
	Switch	Congruent	463	16	98.1%	0.94%
		Incongruent	569	40	76.2%	3.33%

Table 3

Cluster report from contrast of Reward and No Reward Feedback Stimuli. Additional threshold of t > 5.0 was applied to separate large clusters

ClusterIndex	Voxels	MAX	MAX X (mm)	MAX Y (mm)	MAX Z (mm)	COG X (mm)	COG Y (mm)	COG Z (mm)	Laterality	Structure label for center of mass
26	5535	12.6	-26	-82	-2	1.35	-84.1	2.14	Bilateral	37% Intracalcarine Cortex
25	1771	8.93	4	66	4	-4.95	48.5	18.4	Medial	77% Paracingulate Gyrus
24	493	8.31	8	10	-4	17.2	8.97	-5.41	Bilateral	58% Striatum Limbic Subregion
23	354	10.5	22	-28	0	25.7	-30.8	-6.35	Right	49% Hippocampus
22	277	7.6	-58	-64	34	-53.9	-61.1	38	Left	58% Lateral Occipital Cortex
21	246	8.22	-20	14	-18	-25.2	16.3	-13.9	Left	32% Frontal Orbital Cortex
20	173	6.5	-4	-34	36	0.827	-37.3	37.5	Medial	77% Cingulate Gyrus, posterior division
19	147	7.02	18	46	50	16.6	44.4	44.9	Right	76% Frontal Pole (medial)
18	143	7.56	-22	-36	-2	-20.9	-32.4	-2.09	Left	76% Thalamus
17	132	7.09	4	-2	34	1.71	-5.46	32.8	Medial	79% Cingulate Gyrus, anterior division
16	101	7.15	42	36	-8	40.9	35.8	-9.61	Right	52% Neubert Area 47, 44% Neubert Frontal Operculum
15	86	8.32	62	-38	-4	63	-35.8	-4.12	Right	35% Middle Temporal Gyrus, posterior division
14	59	6.34	-46	38	-10	-43.4	37.7	-11	Left	60% Neubert Area 47
13	52	5.96	16	30	52	19.3	30.9	55.2	Right	64% Superior Frontal Gyrus
12	49	6.67	-34	12	-8	-32.8	13.6	-7.12	Left	42% Insular Cortex
11	48	6.84	68	-12	-14	66.1	-11.3	-13.6	Right	64% Middle Temporal Gyrus, posterior division
10	38	6.7	46	20	16	46.8	21.2	17.6	Right	12% Inferior Frontal Gyrus, pars triangularis
9	35	5.97	-4	-52	18	-4.28	-53.2	17.9	Left	49% Precuneous Cortex
8	32	6.1	6	-54	18	5.42	-54.1	22.6	Right	40% Precuneous Cortex
7	29	6.3	0	60	38	-1.67	58.6	37.4	Medial	Sallet Area 9
6	26	5.63	44	-60	38	44.6	-60.7	40.7	Right	41% Lateral Occipital Cortex, superior division
5	26	6.12	-6	-66	28	-5.34	-66.4	29.7	Left	55% Precuneous Cortex
4	25	7.2	-44	-46	-14	-43.9	-46.6	-13.7	Left	23% Inferior Temporal Gyrus, temporooccipital part
3	25	6.07	44	-46	-14	44.7	-46.1	-11.8	Right	24% Temporal Occipital Fusiform Cortex
2	19	5.38	4	-70	8	3.38	-69.2	10.1	Medial	53% Intracalcarine Cortex
1	17	5.49	-40	-62	46	-39.5	-63.2	47.1	Left	55% Lateral Occipital Cortex, superior division

Structures to which each cluster belongs to

Cluster 26	Average Atlas Probability
Occipital Pole	21.0
Occipital Fusiform Gyrus	10.4
Lateral Occipital Cortex, superior division	6.7
Lingual Gyrus	5.7
Lateral Occipital Cortex, inferior division	3.8
Temporal Occipital Fusiform Cortex	2.9
Intracalcarine Cortex	2.3

Cluster 25	Average Atlas Probability
Paracingulate Gyrus	28.3
Medial Frontal Pole	22.6
Superior Frontal Gyrus	8.8
Cingulate Gyrus, anterior division	5.4

Cluster 22	Average Atlas Probability
Lateral Occipital Cortex, superior division	32.7
Angular Gyrus	24.6

Cluster 21	Average Atlas Probability
Neubert Area Frontal Operculum	44.4
Striatum: Limbic Subregion	9.7

Table 4

Cluster report from contrast of Switch and Repeat task choices. Additional threshold of t > 3.5 was applied to separate large clusters

ClusterIndex	Voxels	MAX	MAX X (mm)	MAX Y (mm)	MAX Z (mm)	COG X (mm)	COG Y (mm)	COG Z (mm)	Laterality	Structure label for center of mass
10	2550	7.55	-38	-42	38	-28.8	-53.6	45.9	Left	38% Superior Parietal Lobule
9	1801	10.1	-34	-4	54	-36.3	-0.763	46.5	Left	80% Neubert Area 6v
8	1513	7.8	-6	20	48	10.3	6.38	49.4	Medial	44% Juxtapositional Lobule Cortex
7	580	5.91	8	-30	24	-1.61	-25.4	15.9	Medial	70% Left Cerebral White Matter
6	330	6.32	16	-66	56	18.8	-64.4	53.7	Right	36% Lateral Occipital Cortex
5	197	5	52	-26	42	51.1	-22.8	43	Right	55% Postcentral Gyrus
4	121	4.98	36	-36	40	38.4	-37.3	45.6	Right	29% Supramarginal Gyrus
3	104	4.75	44	2	26	47.9	3.54	31.7	Right	54% Precentral Gyrus
2	70	4.46	-26	10	14	-29.1	18	10.3	Left	100% Neubert 45A, 100% Neubert 44v
1	16	4.21	-16	4	22	-17.6	4.24	21.8	Left	Striatum: 23% Executive Subregion

Structures to which each cluster belongs to:

Cluster 10	Average Atlas Probability
Lateral Occipital Cortex, superior division	18.9
Precuneous Cortex	8.1
Superior Parietal Lobule	7.9
Supramarginal Gyrus, anterior division	7.7

Cluster 9	Average Atlas Probability
Sallet Anterior Premotor Dorsal	16.0
Neubert 6v	10.8
Neubert IFJ	8.1
Sallet Area 8A (Frontal Eye Fields)	5.4

Cluster 8	Average Atlas Probability
Paracingulate Gyrus	14.7
Juxtapositional Lobule Cortex	12.4
Cingulate Gyrus, anterior division	8.9

Cluster 7	Average Atlas Probability
Left Thalamus	26.0
Left Cerebral White Matter	25.3
Right Cerebral White Matter	24.4

Table 5

Cluster report from contrast of task choices following Reward vs No Reward. Additional threshold of t > 3.5 was applied to separate large clusters

ClusterIndex	Voxels	MAX	MAX X (mm)	MAX Y (mm)	MAX Z (mm)	COG X (mm)	COG Y (mm)	COG Z (mm)	Laterality	Structure label for center of mass
22	1810	7.67	44	-56	44	49.2	-57.3	44	Right	43% Lateral Occipital Cortex, superior division
21	1355	6.4	22	56	8	35.4	50.7	8.26	Right	100% Neubert Area 46
20	1155	8.06	8	6	4	2.04	9.95	5.77	Right	58% Striatum Executive Subregion
19	1130	6.33	-38	-60	38	-46.3	-59	46	Left	43% Angular Gyrus
18	971	7.52	-40	44	-10	-37.6	49.3	-2.1	Left	100% Neubert Inferior Frontal Sulcus
17	777	5.69	4	32	38	2.68	37.8	33.3	Medial	63% Paracingulate Gyrus
16	593	5.65	70	-34	-14	61.2	-37.4	-10.1	Right	26% Middle Temporal Gyrus, posterior division
15	530	5.24	-34	18	60	-37.7	16.3	53.2	Left	29% Sallet Area 8A (Frontal Eye Fields)
14	404	6.4	40	26	52	42	19.3	45.9	Right	25% Neubert Area 9/46V
13	156	6.83	28	-16	-4	29.8	-14.3	-6.1	Right	50% Striatum Occipital Subregion
12	126	4.84	8	-66	44	7.65	-68.1	42.7	Right	58% Precuneous Cortex
11	70	4.65	38	-76	-14	35.9	-76.8	-15.1	Right	45% Occipital Fusiform Gyrus
10	38	5.48	0	-96	0	-1.07	-97.7	-0.619	Medial	59% Occipital Pole
9	35	4.07	2	-14	32	0.308	-13	32.3	Medial	60% Cingulate Gyrus, anterior division
8	35	6.32	-60	-28	-18	-59.5	-26.6	-17.9	Left	45% Middle Temporal Gyrus, posterior division
7	32	4.52	-58	-56	26	-58.5	-55.5	26.7	Left	59% Angular Gyrus
6	29	4.03	4	36	58	3.54	38.5	57.5	Medial	13% Superior Frontal Gyrus/ Pre-SMA
5	28	4.23	2	-88	30	2.39	-88.5	30.2	Medial	45% Cuneal Cortex
4	21	5.03	46	-28	2	46.6	-29.2	0.904	Right	46% Superior Temporal Gyrus, posterior division
3	21	4.53	4	-42	38	4.68	-42.7	38.2	Medial	57% Cingulate Gyrus, posterior division
2	21	4.55	2	58	38	2.46	57.8	38.2	Medial	7% Frontal Pole
1	19	4.62	62	16	14	60.9	17.5	12.9	Right	53% Inferior Frontal Gyrus, pars opercularis

Structures to which each cluster belongs to:

Cluster 22	Average Atlas Probability
Angular Gyrus	23.0
Lateral Occipital Cortex, superior division	20.9

Cluster 21	Average Atlas Probability
Neubert Area 46	27.0
Neubert Inferior Frontal Sulcus	12.3
Neubert Frontal Pole, Lateral	9.9

Cluster 18	Average Atlas Probability
Neubert/Sallet Area 46	38
Neubert Lateral Frontal Pole	12.1
Neubert Area IFS	7.7