Reward motivation modulates representation of behaviorally-relevant information across the frontoparietal cortex

Sneha Shashidhara[1]

Yaara Erez[1]

[1]MRC Cognition and Brain Sciences Unit, 15 Chaucer Road, Cambridge CB2 7EF, UK

Abbreviated title: Reward sharpens task-relavent representations

Correspondence: Sneha Shashidhara, MRC Cognition and Brain Sciences Unit, 15 Chaucer Road, Cambridge CB2 7EF, UK. Email: sneha.shashidhara@mrc-cbu.cam.ac.uk, +44 1223 355592

Abstract

Motivation has been shown to improve behavioral performance across multiple cognitive tasks, yet the underlying neural mechanisms that link motivation and control processes remain unclear. Here, we used functional magnetic resonance imaging (fMRI) in 24 human volunteers (13 females) to test whether reward motivation enhances the representation of task-relevant content across the cognitive control frontoparietal network. In a cued-detection categorization task, participants detected whether an object from a cued visual category was present in a subsequent display. Some of the objects could serve as targets depending on the cued category, therefore highly competed for attention, while others were never cued. Half of all trials offered the possibility of a substantial reward. Multivariate pattern analysis (MVPA) showed a competition-contingent enhancement effect of reward across the MD network. Reward increased the discrimination between highly competing task-relevant categories, but not between less conflicting distinctions. This selective effect was not driven by visual differences. In contrast, Reward did not modulate task-related category distinctions in the high visual region, the lateral occipital complex (LOC). These findings provide evidence that reward leads to selective enhancement of task-relevant information representation across the MD network, suggesting a facilitative effect of reward motivation on efficient allocation of attentional resources.

Significance Statement

Motivation is essential in daily life, yet its effect on goal-directed behaviour at the neural level is unclear. In this fMRI study, we tested for effects of reward motivation on the neural representation of the task-relevant information that is required to successfully complete the current task. Across the frontoparietal cognitive control network, reward selectively enhanced representation of task-relevant information only when items highly competed for attention. We propose that this enhancement reflects efficient allocation of resources, in which reward influences neural representation of items from the external world only when it is most needed.

Introduction

Motivation is integral to task processing and plays a key role in goal-directed behaviour. It has been proposed that motivation enhances control processes by sharpening representation of task goals and prioritising task-relevant information across the frontoparietal network and other regions associated with cognitive control (Simon, 1967; Kruglanski et al., 2002; Botvinick and Braver, 2015; Etzel et al., 2016). In line with this idea, it has been shown that motivation, usually manipulated as monetary reward, increases task performance (Padmala and Pessoa, 2010, 2011). Neuroimaging studies in humans linked increased activity with reward in frontoparietal regions across a range of tasks, including working memory (Pochon et al., 2002; Taylor et al., 2004), selective attention (Mohanty et al., 2008; Krebs et al., 2012), response inhibition (Padmala and Pessoa, 2011), and problem solving (Shashidhara et al., submitted).

These frontoparietal regions align well with the multiple-demand (MD) network that has been associated with cognitive control (Norman and Shallice 1980; Desimone and Duncan 1995; Miller and Cohen 2001; Duncan 2013). This network spans the anterior-posterior axis of the middle frontal gyrus (MFG); posterior dorso-lateral frontal cortex (pdLFC); the anterior insula and frontal operculum (AI/FO); the pre-supplementary motor area and the adjacent dorsal anterior cingulate (preSMA/ACC); and intraparietal sulcus (IPS) (Duncan, 2010). Activity in this network increases with increased cognitive demand, as was demonstrated across multiple cognitive domains, including spatial and verbal working memory, math, conflict monitoring, rule-guided categorisation and task switching (Fedorenko et al., 2013; Vergauwe and Cowan, 2015; Cole et al., 2016).

Although accumulating evidence at the behavioural and neural level in humans are consistent with the sharpening and prioritizing account (Wallace 1960; Simon 1967; Kruglanski et al. 2002; Pessoa 2009; Braver 2012; Chiew and Braver 2014), they do not directly address the effect of motivation on the representation of task-relevant information. Some support for this idea comes from single-neuron data recorded from the prefrontal cortex of non-human primates: reward was associated with greater spatial selectivity, enhanced working-memory related activity and modulated task-related activity based on type of reward (Watanabe, 1996; Leon and Shadlen, 1999; Kennerley and Wallis, 2009).

Recently, Etzel et al. (2016) showed that reward enhances representation of task cues across the frontoparietal cortex as measured by fMRI in humans, and suggested that task-set efficacy increases with reward. It remains unclear, however, if this facilitative effect is limited to preparatory cues, or whether reward also enhances the representation of task-related information in the task execution phase. Furthermore, reward has been associated with decreasing conflict in interference tasks (Padmala and Pessoa, 2011; Stürmer et al., 2011; Krebs et al., 2013), suggesting that any effects of reward may be particularly important for high-conflict items, but the evidence for that are limited.

In this study, we used multivariate pattern analysis (MVPA) for fMRI data to directly test for the effect of reward motivation on the representation of task-related information, and whether such effect is selective for highly-competing items. We particularly designed the study to test for this effect in the task execution phase, rather than the cue phase. In a cued categorisation task, participants detected whether an object from a cued visual category (target category) was present or absent. On each trial, one of two categories was cued, and objects from those two categories could be either Targets (T), or Nontarget-Inconsistent (NI) as they could be targets on other trials. An additional category was never cued, serving as Nontarget-Consistent (NC), thus creating three behavioural categories (T, NI, NC). To manipulate motivation, on half of all trials a substantial monetary reward was offered.

Following the sharpening hypothesis, we tested whether reward enhances the discrimination between pairs of behavioural categories across the frontoparietal network and in the high-level visual region, the lateral occipital complex (LOC).

Materials and Methods

Participants

24 participants (13 females), between the ages of 18-40 years (mean age: 25) took part in the study. Four additional participants were excluded due to large head movements during the scan (greater than 5 mm). The sample size was determined prior to data collection, as typical for neuroimaging studies and in accordance with counter-balancing (across participants) requirements of the experimental design. All participants were right handed with normal or corrected-to-normal vision and had no history of neurological or psychiatric illness. The study was conducted with approval by the Cambridge Psychology Research Ethics Committee. All participants gave written informed consent and were reimbursed for their time.

Task Design

Participants performed a cued categorisation task in the MRI scanner (Figure 1A). At the beginning of each trial, one of three visual categories (sofas, shoes, cars) was cued to determine the target category for that trial. Participants had to indicate whether the subsequent object matched this category or not, by pressing a button. For each participant, only two of the categories could be cued as targets throughout the experiment. Depending on the cue on a given trial, objects from these categories could be Targets (T) or Nontargets-Inconsistent (NI, as they could serve as targets on other trials). The third category was never cued, therefore objects from this category served as consistent nontargets (NC – Nontarget-Consistent). This design yielded three behavioural categories: T, NI and NC (Figure 1B). The assignment of the categories to be cued (and therefore serve as either T or NI) or not (and serve as NC) was counter-balanced across participants.

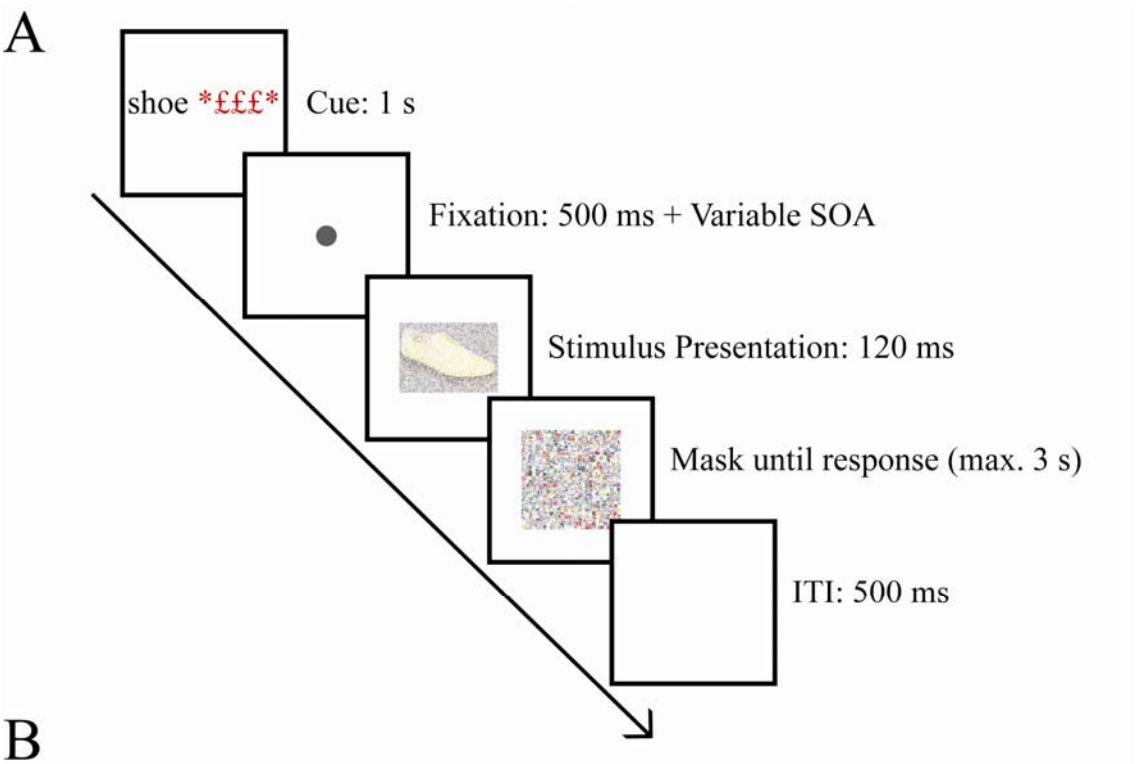
To manipulate motivation, half of the trials were cued as reward trials, in which participants had the chance of earning £1 if they completed the trial correctly and within a time threshold. To assure the incentive on each reward trial, four random reward trials out of 40 in each run were assigned the £1 reward. The response time threshold was set separately for each participant, was based on their

performance in a pre-scan training session. The participants were told that the maximum reward they could earn is £24 in the entire session (£4 per run), and were not told what the time threshold was. Therefore, to maximize their gain, they had to treat every reward trial as a £1 trial and respond as quickly and as accurately as possible, just as to no-reward trials.

Each trial started with a 1 s cue, which was the name of a visual category that served as the target category for this trial. On reward trials, the cue included three red pound signs presented next to the category name. The cue was followed by a fixation dot in the centre of the screen presented for 0.5 s and an additional stimulus onset asynchrony (SOA) of either 0.1, 0.4, 0.7 or 1 s, selected randomly, in order to make the stimulus onset time less predictable. Stimulus was presented for 120 ms followed by a mask and participants indicated by a button press whether this object belonged to the cued target category (present) or not (absent). Following response, a 1 s blank inter-trial interval (ITI) separated two trials. Response time was limited to a maximum of 3 s.

We used catch trials to decorrelate the BOLD signals of the cue and stimulus phases. 33% of all trials included only cue, followed by fixation dot for 500 ms, which then turned red for another 500 ms, indicating the absence of the stimulus and ITI.

A



B

	Target (T)	Non-target Inconsistent (NI)	Non-target Consistent (NC)
Cue: shoe	shoe 	sofa 	car 
Cue: sofa	sofa 	shoe 	car 

Figure 1: Experimental paradigm. A. An example of a reward trial. A trial began with a cue (1 s) indicating the target category, followed by 500 ms fixation period. Reward trials were cued with three red £ symbols next to the target category. After an additional variable SOA (0.4, 0.7, 1.0 or 1.3 s), an

object was presented for 120 ms. The object was then masked (a scramble of the all the stimuli used), and the mask was displayed until response or for a maximum of 3 s. The participants pressed a button to indicate whether the object was from the cued category (Target trials) or not (Nontarget trials). **B. Experimental conditions.** For each participant, two categories served as potential targets depending on the cue, and a third category never served as target. Here as an example, shoes and sofas are taken as the cued categories and cars as the uncued category. In the Target (T) trials, the presented object matched the cued category. In the Nontarget-Inconsistent (NI) trials, the object did not match the cued category for this trial, but was from the other cued category, therefore could serve as a target on other trials. In the Nontarget-Consistent (NC) trials, the presented object was from the category that was never cued. This design was used for both no-reward and reward conditions.

Stimuli

Objects were presented at the centre of the screen on a grey background. The objects were 2.95° visual angle along the width and 2.98° visual angle along the height. Four exemplars from each visual category were used. Exemplars were chosen with similar colors, similar dimensions, and similar orientation across the categories. All exemplars were used an equal number of times in each condition in each run. To increase the task demand, based on pilot data, we added Gaussian white noise to the stimuli. The post-stimulus mask was generated by randomly combining pieces of the stimuli that were used in the experiment. The mask was the same size as the stimuli and was presented until a response was made or the response time expired.

Structure and Design

Each participant completed 6 functional runs of the task in the scanner (mean duration ± SD: 6.2 ± 0.13 min). Each run started with a response-mapping instructions screen (.e.g. left = target present, right = target absent), displayed until the participants pressed a button to continue. Halfway through the run, the instructions screen was presented again with the reversed response mapping. All trials required a button response (target present or absent) depending on the response mapping, and the change of response-mapping ensured that conditions were not confounded by the side of button press.

Each run included 104 trials. Out of these, 8 were dummy trials following the response mapping instructions (4 after each instructions screen), and were excluded from the analysis. Of the remaining 96 trials, one-third (32 trials) were cue-only trials (catch trials), which were of no interest for our main question and were not included in the analysis. Of the remaining 64 trials, 32 were no-reward trials and 32 were reward trials. Of the 32 no-reward trials, half (16) were cued with one visual category, and half (16) with the other. For each cued category, half of the trials (8) were T trials, and half of the trials (8) were nontarget trials, to assure an equal number of target (present) and non-target (absent) trials. Of the nontarget trials, half (4) were NIs, and half (4) were NCs. Therefore, the T trials included two repetitions of each combination of cue, visual category and exemplar. A similar split was used for reward trials. An event-related design was used and the order of the trials was randomized in each run. At the end of each run, the money earned in the reward trials and the number of correct trials (across both reward and no-reward trials) were presented on the screen.

Functional Localisers

In addition to the main task, we used two other tasks in order to functionally localise MD regions and LOC in individual participants using independent data. These were used in conjunction with ROI templates and a double-masking procedure to extract voxel data for MVPA (See ROI definition for more details).

To localise MD regions, we used a spatial working memory task (Fedorenko et al., 2013). On each trial, participants remembered 4 locations (in the Easy condition) or 8 locations (in the Hard condition) in a 3X4 grid. Each trial started with fixation for 500 ms. Locations on the grid were then highlighted consecutively for 1 s (1 or 2 locations at a time, for the Easy and Hard conditions, respectively). In a subsequent two-alternative forced-choice display (3 s), participants had to choose the grid with the correct highlighted locations by pressing left or right button. Feedback was given after every trial for 250 ms. Each trial was 8 s long, and each block included 4 trials (32 s). There was an equal number of correct grids on the right and left in the choice display. Participants completed 2

functional runs of 5 min 20 sec each, with 5 Easy blocks alternated with 5 Hard blocks in each run. We used the contrast of Hard vs. Easy blocks to localise MD regions.

As a localiser for LOC we used a one-back task with blocks of objects interleaved with blocks of scrambled objects. Participants had to press a button when the same image was presented twice in a row. Images were presented for 300 ms followed by a 500 ms fixation. Each block included 15 images with two image repetitions and was 12 s long. Participants completed two runs of this task, with 8 object blocks, 8 scrambled object blocks, and 5 fixation blocks. The contrast that was used to localise LOC was objects vs. scrambled objects conditions.

Scanning Session

The scanning session included a structural scan, 6 functional runs of the main task, and 4 functional localiser runs – 2 for MD regions and 2 for LOC. The tasks were introduced to the participants in a pre-scan training session. The average reaction time of 32 no-reward trials of the main task completed in this practice session was set as the time threshold for the reward trials to be used in the scanner session. All tasks were written and presented using Psychtoolbox3 (Brainard, 1997) and MatLab (The MathWorks, Inc).

Data Acquisition

fMRI data were acquired using a Siemens 3T Prisma scanner with a 32-channel head coil. We used a multi-band imaging sequence (CMRR, release 016a) with a multi-band factor of 3, acquiring 2 mm isotropic voxels (Feinberg et al., 2010). Other acquisition parameters were: TR = 1.1 s, TE = 30 ms, 48 slices per volume with a slice thickness of 2 mm and no gap between slices, in plane resolution 2 × 2 mm, field of view 205 mm, and flip angle 62°. No iPAT or in-plane acceleration were used. T1-weighted multiecho MPRAGE (van der Kouwe et al., 2008) high-resolution images were also acquired for all participants (voxel size 1 mm isotropic, field of view of 256 × 256 × 192 mm, TR = 2530 ms, TE = 1.64, 3.5, 5.36, and 7.22ms). The voxelwise root mean square across the four MPRAGE images was computed to obtain a single structural image.

Data and Statistical Analysis

The primary analysis approach was multi-voxel pattern analysis (MVPA), to assess task information representation with and without reward. An additional whole-brain and ROI-based univariate analysis was conducted to confirm the recruitment of the MD network. Preprocessing, GLM and univariate analysis of the fMRI data were performed using SPM12 (Wellcome Department of Imaging Neuroscience, London, England; www.fil.ion. ucl.ac.uk), and the Automatic Analysis (aa) toolbox (Cusack et al., 2014).

We used an alpha level of .05 for all statistical tests. Bonferroni correction for multiple comparisons was used when required, and the corrected p-values and uncorrected t-values are reported. All t tests that were used to compare two conditions were paired. A one-tailed t test was used when the prediction was directional or when classification accuracies were compared to chance level. All other t tests were two-tailed. Additionally, effect size (Cohen's d_z) was computed for one-sample (compared to chance) or paired samples. All analyses were conducted using custom-made MATLAB (The Mathworks, Inc) scripts, unless otherwise stated.

All raw data and code used in this study will be publicly available upon publication.

Pre-processing

Initial processing included motion correction and slice time correction. The structural image was coregistered to the Montreal Neurological Institute (MNI) template, and then the mean EPI was coregistered to the structural. The structural was then normalised to the MNI template via a nonlinear deformation, and the resulting transformation was applied on the EPI volumes. Spatial smoothing of FWHM = 5 mm was performed for the whole-brain univariate analysis of the main task and on the functional localisers data only.

General Linear Model (GLM) for the Main Task

We used GLM to model the main task and localisers' data. Regressors for the main task included 12 task conditions during the stimulus epoch, split according to reward level (no-reward, reward), cued

category (category 1, category 2), and behavioural category (T, NI, NC). To assure an equal number of T and N trials, the number of T trials in our design was twice the number of NI and NC trials. The T trials included two repetitions of each combination of cue, visual category and exemplar, with a similar split for reward trials. These two T repetitions were modelled as separate T1 and T2 regressors in the GLM to keep the balanced, thus resulting in 16 regressors of interest for the 12 task conditions. To account for possible effects of RT on the beta estimates because of the varying duration of the stimulus epoch, and as a consequence their potential effect on decoding results, these regressors were modelled with durations from stimulus onset to response (Woolgar et al., 2014). Additional regressors included the cue epoch, split according to the reward level and the cued category, modelled with duration of 1 s. The analysis focused on the stimulus epoch to address our research question, therefore the cue epoch regressors were not further analysed. Regressors were convolved with the canonical hemodynamic response function (HRF). As one-third of all trials were catch trials (cue-only trials), the cue and stimulus epoch regressors were decorrelated and separable in the GLM. The 6 movement parameters and run means were included as covariates of no interest.

GLM for the Functional Localisers

For the MD localiser, regressors included Easy and Hard blocks. For LOC, regressors included objects and scrambled objects blocks. Each block was modelled with its duration. The regressors were convolved with the canonical hemodynamic response function (HRF). The 6 movement parameters and run means were included as covariates of no interest.

Univariate Analysis

A random effects whole-brain analysis and an ROI analysis were conducted to test for the recruitment of the frontoparietal control system with reward. For the whole-brain analysis, we contrasted all reward with all no-reward conditions, across behavioural category conditions (T, NI, NC) and cued category, during the stimulus display epoch. The t-statistic from a second level group analysis was thresholded at the voxel level using FDR correction ($p < 0.05$). For regions of interest (ROI) analysis, we used templates for the MD network and for LOC as defined below (see ROI definition). Using the

MarsBaR toolbox (http://marsbar.sourceforge.net; Brett et al. 2002) for SPM 12, beta estimates for each regressor of interest were extracted and averaged across runs and across voxels within each ROI, separately for each participant and condition. Second-level analysis was done on beta estimates across participants using repeated measures ANOVA. For the univariate analysis, all data for the T condition were averaged across the two T1 and T2 regressors, separately for no-reward and reward.

ROI Definition

MD network template. ROIs of the MD network were defined using an independent data set (Fedorenko et al. 2013; see t-map at http://imaging.mrc-cbu.cam.ac.uk/imaging/MDsystem). These included the anterior, middle, and posterior parts of the middle frontal gyrus (aMFG, mMFG, and pMFG, respectively), a posterior dorsal region of the LFC (pdLFC), AI-FO, pre-SMA/ACC, and IPS, defined in the left and right hemispheres. The visual component in this template was not included in this analysis as it is not normally considered as part of the frontoparietal MD network.

LOC template. LOC was defined using data from a functional localizer in an independent study with 15 participants (Lorina Naci, PhD dissertation, University of Cambridge). In this localiser, forward- and backward-masked objects were presented, as well as masks alone. Masked objects were contrasted with masks alone to identify object-selective cortex (Malach et al., 1995). Division to the anterior part of LOC, the posterior fusiform region (pFs) of the inferior temporal cortex, and its posterior part, the lateral occipital region (LO) was done using a cut-off MNI coordinate of Y=-62, as previous studies have shown differences in processing for these two regions (MacEvoy and Epstein, 2011; Erez and Yovel, 2014).

Voxels selection for MVPA

To compare between regions within the MD network and between sub-regions in LOC, we controlled for the ROI size and used the same number of voxels for all regions. We used a double-masking approach that allowed the use of both a template, consistent across participants, as well as subject-specific data as derived from the functional localisers (Erez and Duncan, 2015). For each participant,

beta estimates of each condition and run were extracted for each ROI based on the MD network and LOC templates. For each MD ROI, we then selected the 200 voxels with the largest t-value for the Hard vs. Easy contrast as derived from the independent subject-specific functional localiser data. This number of voxels was chosen prior to any data analysis, similarly to our previous work (Erez and Duncan, 2015). For each LOC sub-region, we selected 180 voxels with the largest t-values of the object vs. scrambled contrast from the independent subject-specific functional localiser data. The selected voxels were used for the voxelwise patterns in the MVPA for the main task. The number of voxels that was used for LOC was smaller than for MD regions because of the size of the pFs and LO masks. For the analysis that compared MD regions with the visual regions, we used 180 voxels from all regions to keep the ROI size the same. To ensure the robustness of the results, we repeated the analysis across a range of ROI sizes (100, 150, 250 and 300 voxels).

Multivoxel pattern analysis (MVPA)

We used MVPA to test for the effect of reward motivation on the discrimination between task-related behavioural categories. Voxelwise patterns using the selected voxels within each template were computed for all the task conditions in the main task. We applied our classification procedure on all possible pairs of conditions as defined by the GLM regressors of interest during the stimulus presentation epoch, for the no-reward and reward conditions separately (Figure 1B). For each pair of conditions, MVPA was performed using a support vector machine classifier (LIBSVM library for MATLAB, c=1) implemented in the Decoding Toolbox (Hebart et al., 2015). We used leave-one-run-out cross-validation in which the classifier was trained on the data of five runs (training set) and tested on the sixth run (test set). This was repeated 6 times, leaving a different run to test each time, and classification accuracies were averaged across these 6 folds. Classification accuracies were then averaged across pairs of different cued categories, yielding discrimination measures for three pairs of behavioural categories (T vs. NI, T vs. NC, and NI vs. NC), for the two reward conditions (no-reward, reward). Classification accuracies were tested against chance (50%) using a second level group analysis (one-tailed t-test). Because the number of T trials in our design was twice the number of NI

and NC trials, each discrimination that involved a T condition was computed separately for each half of the T trials (T1 and T2 regressors) and classification accuracies were averaged across them.

The T and NI pairs of conditions included cases when both conditions had an item from the same visual category as the stimulus (following different cues), as well as cases in which items from two different visual categories were displayed as stimuli (following the same cue). To test for the contribution of the visual category to the discrimination, we split the T vs. NI pairs of conditions into these two cases and the applied statistical tests according to the required contrasts.

To ensure that our results are robust across different pattern analysis techniques, we tested for the modulation of task-related information by reward using a linear discriminant contrast (LDC) (Nili et al., 2014; Carlin and Kriegeskorte, 2017), in addition to SVM. All of the MVPA analysis as described above was repeated with the LDC measure and using the same voxel selection procedure. Cross-validated Malanobis distances were computed for each pair of behavioural categories, with a larger LDC indicating greater pattern dissimilarity, i.e., greater discriminability. LDCs for no-reward and reward conditions were then compared.

Whole-brain searchlight pattern analysis

To test whether additional regions outside the MD network show change in discriminability between voxelwise patterns of activity of task-related information when reward is introduced, we conducted a whole-brain searchlight pattern analysis (Kriegeskorte et al., 2006). This analysis enables the identification of focal regions that carry relevant information, unlike the decoding based on larger ROIs, which tests for a more widely distributed representation of information. For each participant, data was extracted from spherical ROIs with an 8 mm radius, centred on each voxel in the brain. These voxels were used to perform the same MVPA analysis as described above. Thus, for each voxel, we computed the classification accuracies for the relevant behavioural distinctions, separately for the reward and no-reward conditions. These whole-brain maps were smoothed using a 5 mm

FWHM Gaussian kernel. A second-level random-effects analysis similar to the univariate one was run on the smoothed maps.

Results

Behaviour

Reaction times (RT) for T, NI and NC conditions in the no-reward trials were 589 ± 98 ms, 662 ± 103 ms, and 626 ± 107 ms, respectively (mean ± SD); RTs for these conditions in the reward trials were 541 ± 99 ms, 614 ± 99 ms, 585 ± 97 ms, respectively (mean ± SD). A two-way repeated measure ANOVA with motivation (no-reward, reward) and behavioural categories (T, NI, NC) as within-subject factors showed a main effect of motivation ($F_{1, 23}$ = 40.07, p < 0.001), a main effect of behavioural category ($F_{2, 23}$ = 50.97, p < 0.001), and no interaction ($F_{2, 23}$ = 0.63, p = 0.54). RTs in reward trials were shorter, as expected from the experimental design in which response was required within a time threshold to receive the reward. RTs for T trials were faster than NI and NC (t_{23} = 10.03, p < 0.001, d_z = 2.05; t_{23} = 5.17, p < 0.001, d_z = 1.06 respectively), and NC trials were faster than NI (t_{23} = 4.96, p < 0.001, d_z = 1.01), as expected from a cued target detection task.

Overall accuracy levels were high (mean ± SD: 92.51% ± 0.08%). Mean and SD accuracy rates for T, NI and NC conditions in the no-reward trials were 91.2% ± 5.8%, 89.1% ± 8.8%, and 96.6% ± 3.8%, respectively; and for the reward trials they were 94.2% ± 5.0%, 87.8%± 8.7%, 96.1% ± 4.4%, respectively. A two-way repeated measure ANOVA with motivation and behavioural categories as within-subject factors showed a main effect of behavioural category ($F_{2, 23}$ = 29.64, p < 0.001) and no main effect of motivation ($F_{1, 23}$ = 0.49, p = 0.49), confirming that the added time constraint for reward trials did not lead to drop in performance. There was a significant interaction between motivation and behavioural categories ($F_{2, 23}$ = 5.81, p < 0.01). Post hoc tests with Bonferroni correction for multiple comparisons showed larger accuracies for NC compared to T and NI (Two-tailed t-test: t_{23} = 5.64, p < 0.001, d_z = 1.15; t_{23} = 5.50, p < 0.001, d_z = 1.12 respectively) in the no-reward trials, as expected given that the NC category was fixed throughout the experiment. In the reward trials, performance accuracies were larger for T compared to NI (t_{23} = 4.45, p < 0.001, d_z = 0.91) and NC compared to NI (t_{23} = 5.92, p < 0.001, d_z = 1.2) and similar between T and NC (t_{23} =

2.49, $p > 0.05$). Accuracies were larger for the reward trials compared to no-reward for T trials only ($t_{23} = 2.92$, $p = 0.008$, $d_z = 0.61$), but not for NI and NC ($t_{23} < 1.1$, $p > 0.1$, for both).

Univariate activity in the MD network

To examine the effect of reward motivation on the overall activity of MD regions during task performance, we contrasted reward and no-reward trials across all three behavioural category conditions. Whole brain analysis corrected with FDR ($p < 0.05$) showed MD-like pattern of activity, confirming the recruitment of the MD network when reward is introduced (Figure 2). Regions of increased activity with reward included the middle frontal gyrus, anterior insula, pdLFC and a large area around the IPS on the lateral surface. Activity on the medial surface was widespread, including the preSMA and the IPS. In a further ROI analysis, we used average β estimates for each behavioural category (T, NI, NC) and reward level (no-reward, reward) in each of the MD ROIs. A four-way repeated measures ANOVA with reward (2), behavioural categories (3), ROIs (7) and hemispheres (2) as within-subject factors showed a main effect of reward ($F_{1, 23} = 4.65$, $p = 0.042$), with increased activity for reward conditions, in line with the whole-brain results. There was an interaction of reward level and ROI ($F_{6, 138} = 3.99$, $p = 0.001$), but all ROIs showed either a significant increase of activity with reward or a trend towards that. Importantly, there was no main effect for behavioural category ($F_{2, 46} = 0.56$, $p = 0.57$), indicating similar levels of activity for the three behavioural categories, and no interaction of reward and behavioural category ($F_{2, 46} = 0.16$, $p = 0.85$). Overall, the univariate results indicated an increase in activity across the MD network when reward is introduced.

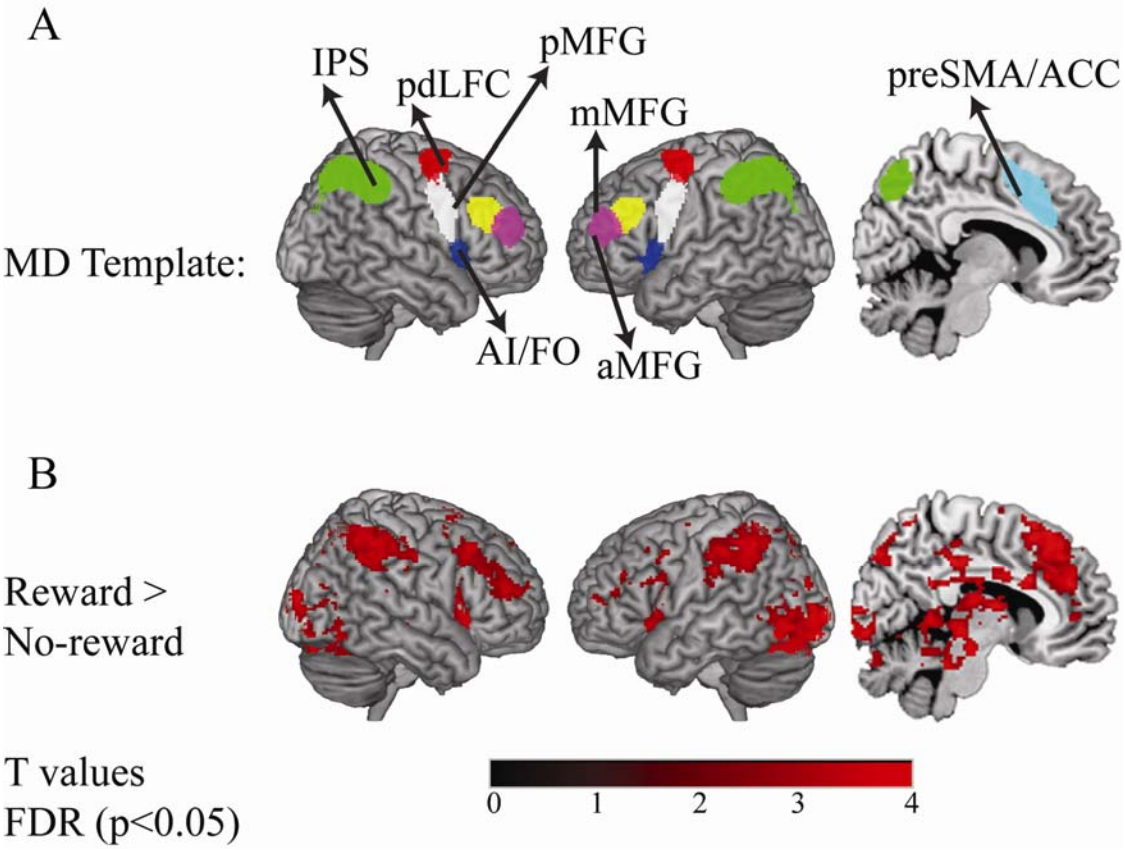


Figure 2: A. The MD template used for the ROI analysis (Fedorenko et al., 2013). **B. Second level t-maps** of the contrast of all reward conditions minus all no-reward conditions, across behavioural categories, showing a pattern similar to the MD template. The contrast is corrected for multiple comparisons using FDR ($p<0.05$).

Effect of reward motivation on discrimination of behavioural categories in the MD network

We used MVPA to test for the effect of reward motivation on the representation of task-related information. For each participant and ROI we computed the classification accuracy above chance (50%) for the behavioural distinctions T vs. NI, T vs. NC and NI vs. NC, separately for no-reward and reward conditions (Figure 3). A four-way repeated-measures ANOVA with reward (2), behavioural distinction (3), ROIs (7), and hemispheres (2) as within-subject factors showed no main effect of ROI or hemisphere ($F_{6, 138} = 1.41$, $p = 0.21$; $F_{1, 23} = 1.16$, $p = 0.29$, respectively) or any interaction of ROI

or hemisphere with reward and behavioural distinction ($F < 1.78$, $p > 0.11$). Therefore, the classification accuracies for the behavioural distinctions in each of the reward levels were averaged across hemispheres and ROIs for further analysis (Figure 3A). We first looked at whether individual pairs of conditions were decoded above chance and used correction for multiple (6) comparisons. The distinction of T vs. NI was above chance for reward trials (One-tailed t-test: $t_{23} = 4.40$, $p < 0.001$, $d_z = 0.90$), accuracy levels above for the no-reward trials did not survive the correction for multiple comparisons (One-tailed t-test: $t_{23} = 1.89$, $p = 0.21$, $d_z = 0.38$). The distinction of T vs. NC was significantly above chance for both reward and no-reward trials (One-tailed t-test: $t_{23} = 2.66$, $p = 0.0419$, $d_z = 0.54$; $t_{23} = 3.05$, $p = 0.017$, $d_z = 0.62$, respectively), and the distinction between the two non-target behavioural categories, NI vs. NC, was not above chance in either (One-tailed t-test: $t_{23} = 0.55$, $p > 0.1$; $t_{23} = 1.41$, $p > 0.1$, respectively). A two-way repeated measures ANOVA with reward (2) and behavioural distinction (3) as within-subject factors showed no main effects of reward or behavioural distinction ($F_{1, 23} = 0.74$, $p = 0.40$; $F_{2, 46} = 1.43$, $p = 0.25$, respectively), but revealed an interaction of the two ($F_{2, 46} = 4.61$, $p = 0.015$). To test for the increase of behavioural distinction by reward in individual pairs of behavioural categories, we used post-hoc tests with correction for multiple (3) comparisons. For the T vs. NI distinction, classification accuracy was larger in the reward trials compared to the no-reward trials (One-tailed t-test: $t_{23} = 2.61$, $p = 0.047$, $d_z = 0.53$). There was no difference in classification accuracy between the reward and no-reward trials for the T vs. NC and NI vs. NC distinctions (One-tailed t-tests: $t_{23} = 0.28$, $p > 0.1$, $d_z = 0.06$; $t_{23} = 0.73$, $p > 0.1$, $d_z = 0.15$, respectively). These results are in line with the competition-contingent hypothesis and demonstrate that reward motivation increases the representation across the MD network selectively for the most conflicting information, namely T vs. NI.

We conducted several control analyses to confirm the robustness and specificity of the results. First, a similar pattern of results was evident across a range of ROI sizes (100, 150, 250 and 300 voxels), confirming the robustness of this effect. In particular, classification accuracy for the T vs. NI distinction was larger in the reward trials compared to the no-reward trials in all the ROI sizes (One-tailed t-test: $t_{23} > 2.07$, $p < 0.025$, $d_z > 0.42$). For the T vs. NC and NI vs. NC pairs of behavioural

categories, classification accuracy was not larger in the reward trials compared to the no-reward trials in any of the ROI sizes (One tailed t-test: $t_{23} < 0.6$, $p > 0.23$, $d_z < 0.14$).

Second, we used another measure of multivariate discriminability, linear discriminant contrast (LDC), to assess the difference in dissimilarity of distributed patterns of activity of the three behavioural categories, with and without reward. A larger LDC value between two conditions indicates greater dissimilarity, therefore we tested whether LDC was larger for reward versus no-reward trials for the three pairs of behavioural distinctions. Overall, the LDC analysis revealed similar results to those obtained using the decoding analysis. A three-way repeated-measures ANOVA with behavioural distinctions (3), ROIs (7) and Hemispheres (2) as within subject factors and ΔLDC (reward minus no-reward) as the dependent variable showed a main effect of behavioural distinction ($F_{2, 46} = 3.96$, $p = 0.026$), and no main effects of ROIs or hemispheres ($F_{6, 138} = 0.60$, $p = 0.73$; $F_{1, 23} = 0.02$, $p = 0.9$, respectively), nor any interaction ($F < 1.19$, $p > 0.29$). ΔLDC values were therefore averaged across ROIs and hemispheres. Post-hoc tests with correction for multiple (3) comparisons showed that ΔLDC was larger for T vs. NI compared to NI vs. NC (two tailed t-test: $t_{23} = 2.89$, $p = 0.025$, $d_z = 0.59$), while ΔLDC for the T vs. NI distinction was not larger than for the T vs. NC distinction, and the T vs. NC was not larger than the NI vs. NC distinction (Two-tailed t-tests: $t_{23} = 1.43$, $p = 0.17$, $d_z = 0.29$; $t_{23} = 1.35$, $p = 0.19$, $d_z = 0.28$, respectively).

Lastly, we used a whole-brain searchlight analysis to test for increased discrimination for highly competing behavioural categories following reward across the brain. A second level random-effects analysis of T vs. NI classification maps was conducted, and while none of the voxels survived an FDR threshold of $p < 0.05$, using a more lenient threshold of $p < 0.05$ without correction for multiple-comparisons showed an overall MD-like pattern. Increased distinctions of T vs. NI with reward were observed along the MFG (posterior, middle and anterior), IPS, AI and pre-SMA on both hemispheres.

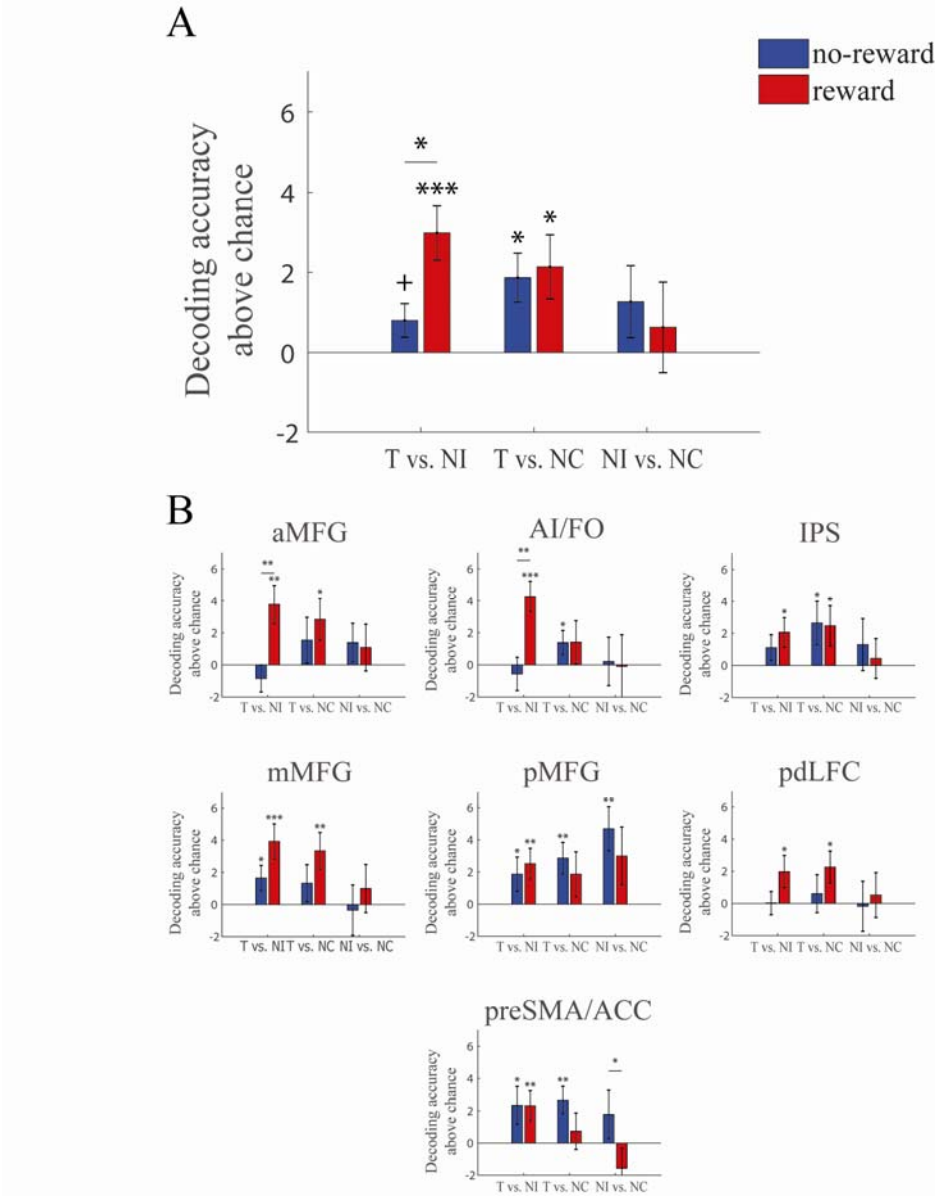


Figure 3: Reward motivation selectively increases distinction between highly competing behavioural categories across the MD network. A. reward leads to increased discrimination between behavioural categories that are highly competing (T vs. NI), but not between behavioural categories that are less competing (T vs. NC, NI vs. NC), demonstrating a competition-contingent effect of reward motivation. Classification accuracy is presented as percentage above chance (50%), averaged across all MD regions, for no-reward (blue bars) and reward (red bars) trials. Asterisks above bars show significant discrimination between behavioural categories above chance (One-tailed t-test against zero, corrected for multiple comparisons (6)). Asterisks above black horizontal lines

show significance of difference between reward and no-reward conditions for a given distinction between behavioural categories (One-tailed t-test, corrected for multiple comparisons (3)). **B.** Classification results shown for the individual MD regions. Plots conventions are the same as in A. Errors bars indicate S.E.M. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, + $p < 0.05$ uncorrected.

Effects of reward motivation on behavioural category distinctions in LOC

A common view posits that top-down signals from the frontoparietal MD network to the visual cortex play an important role in the processing of task-related information. To test for the effect of reward motivation on the processing of task-relevant categories in the visual cortex, we conducted similar univariate and MVPA analyses in the object-selective high-level visual region, the lateral occipital complex (LOC), separately for its two sub-regions, LO and pFs. A whole-brain univariate analysis of reward vs. no-reward trials showed some scattered activity in the visual cortex, and particularly on the left hemisphere. An ROI univariate analysis did not show increase in BOLD response with reward in LOC. A four-way repeated-measures ANOVA with reward (2), behavioural categories (3), ROIs (2), and hemispheres (2) as within subject factors showed no main effect of reward ($F_{1, 23} = 1.12$, $p = 0.30$), but there was an interaction of reward and ROIs ($F_{1, 23} = 7.78$, $p = 0.011$). Post-hoc tests with correction for multiple (2) comparisons showed that for no-reward conditions, activation was higher in pFs compared to LO (Two-tailed t-test: $t_{23} = 3.13$, $p = 0.01$, $d_z = 0.64$). However, more importantly, activation was not larger for reward compared to no-reward trials in both LO and pFs (Two-tailed t-test: $t_{23} = 1.9$, $p = 0.07$, $d_z = 0.39$; $t_{23} = 0.29$, $p = 0.77$, $d_z = 0.06$; for LO and pFs, respectively). There was a main effect of behavioural category ($F_{2, 23} = 9.64$, $p < 0.001$), but no interaction of behavioural category and reward ($F_{2, 46} = 0.17$, $p = 0.85$). Altogether, the univariate results show that reward motivation did not lead to increased activity in LOC.

We then tested for the effect of reward on the representation of task-relevant information. MVPA results showed significant decoding of behavioural category (above chance) for all pairs of behavioural categories, for both reward and no-reward conditions for the average of LO and pFs (One-tailed t-test, corrected for multiple (6) comparisons: $t_{23} > 2.92$, $p < 0.015$, $d_z > 0.6$, for all)

(Figure 4). However, classification accuracies were not larger for the reward conditions compared to the no-reward conditions in any of the behavioural category pairs. A four-way repeated-measures ANOVA with reward (2), behavioural distinction (3), ROIs (2) and hemispheres (2) as within subject factors showed no main effects or interactions ($F < 3.06$, $p > 0.093$). These results demonstrate that, in LOC, in contrast to the MD network, reward motivation did not modulate the representation of task-related information.

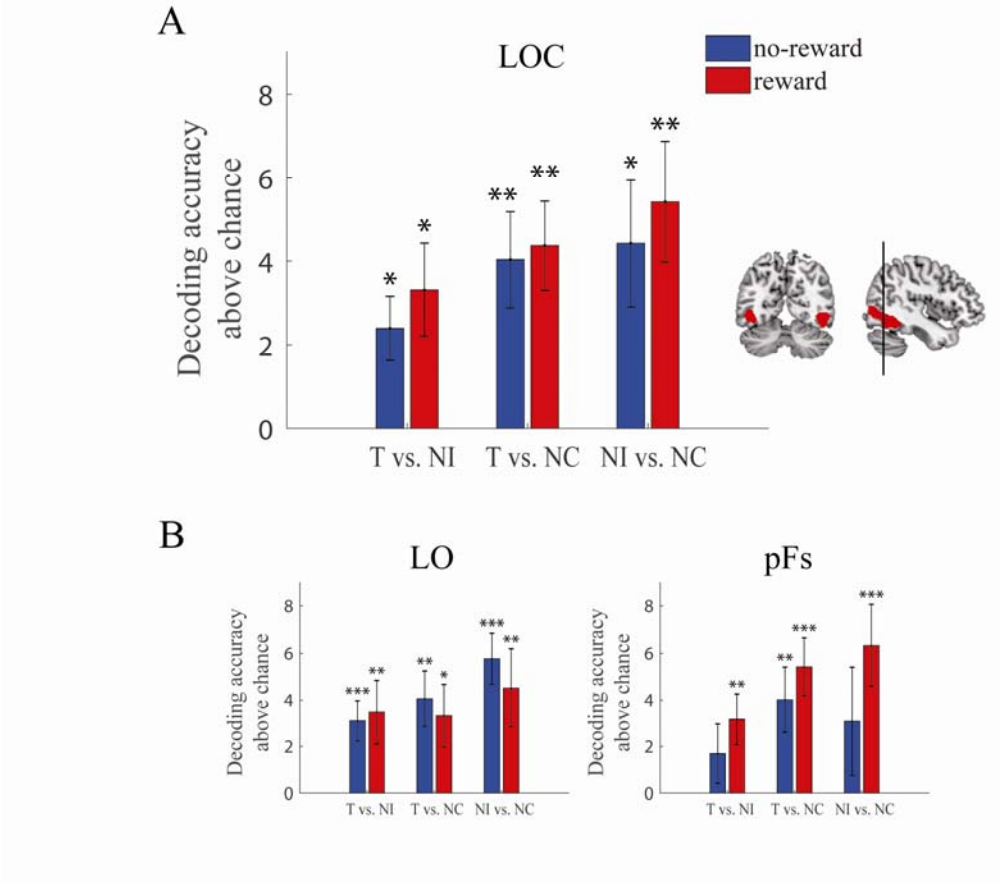


Figure 4: Reward motivation does not increase task-related information representation in LOC. Classification accuracies for no-reward (blue bars) and reward (red bars) conditions are similar for all three pairs of behavioural categories. Classification accuracy is presented as percentage above chance (50%). **A.** Averaged classification accuracies across LO and pFs are presented. **B.** Classification accuracies for LO and pFs presented separately for each ROI. LOC template is shown on sagittal and coronal planes, with a vertical line dividing it into posterior (LO) and anterior (pFs) regions. Asterisks above bars show significant discrimination between behavioural categories above chance (One-tailed

t-test against zero, corrected for multiple comparisons (6)). Errors bars indicate S.E.M. * $p<0.05$, ** $p<0.01$.

Competition-contingent vs. visual category effects

An important aspect of the T and NI conditions in this experiment was that they both contained the same visual categories, which could be either a target on a T trial, or a distractor on an NI trial (Figure 1B). Therefore, the T vs. NI pairs of conditions in our decoding analysis included cases where the T and NI stimuli were items from different visual categories (e.g. shoe and sofa following a 'shoe' cue), as well as cases where the T and NI stimuli were items from the same visual category (e.g. shoe following a 'shoe' cue and a 'sofa' cue). We further investigated whether the increase in decoding of T vs. NI with reward in the MD network was driven by the task-related high competition nature of the two conditions (competition-contingent), or by the different visual categories of the stimuli. For each participant, the decoding accuracy for T vs. NI was separately computed for pairs of conditions in which the stimuli belonged to the same visual category (different cue trials), and for pairs in which the stimuli belonged to different visual categories (same cue trials). A similar analysis was conducted for LOC regions, to test for an effect driven by the visual categorisation in the visual system. This analysis was conducted by selecting 180 voxels for both MD and LOC ROIs, to keep the ROI size the same. For both MD and LOC regions, there was no interaction with ROI or hemisphere, therefore accuracy levels were averaged across hemispheres and ROIs for the MD network and LOC separately (repeated measures ANOVA with reward (2), distinction type (2, same or different visual category), ROIs (7 for MD, 2 for LOC) and hemispheres (2) as within subject factors: $F < 1.1$, $p > 0.05$ for all interactions with ROI and hemisphere). Figure 5 shows T vs. NI distinctions separately for same and different visual categories for no-reward and reward conditions, for both the MD and LOC. A three-way repeated measures ANOVA with reward (2), distinction type (2, same or different visual category) and brain system (2, MD or LOC) as within subject factors revealed a no main effect of brain system ($F_{1, 23} = 1.59$, $p = 0.22$), allowing us to compare between the two systems. Importantly, there was a main effect of reward and distinction type ($F_{1, 23} = 5.18$, $p = 0.032$; $F_{1, 23} = 7.79$, $p = 0.01$, respectively) and an interaction between distinction type and system ($F_{1, 23} = 7.89$, $p = 0.01$). There

was no interaction of reward and system ($F_{1, 23}$ = 1.36, p = 0.26). Post-hoc tests with correction for multiple (2) comparisons showed higher classification accuracy across reward conditions for different visual category than same visual category in LOC but not in the MD system (Two-tailed t test: t_{23} = 3.06, p = 0.012, d_z = 0.63; t_{23} = 0.39, p > 0.1, d_z = 0.08, respectively). Additionally, in the MD network, T vs. NI decoding accuracy was not different for same and different visual categories, in neither reward nor no-reward conditions (Two-tailed t test: t_{23} = 0.67, p = 0.51, d_z = 0.14; t_{23} = 0.38, p = 0.71, d_z = 0.07, respectively). Across reward conditions, the difference in classification accuracy between different-visual category and same-visual category was larger in LOC than in the MD system (Two-tailed t test: t_{23} = 2.81, p = 0.01, d_z = 0.57).

To further investigate the effects of distinction type in each system, we conducted separate ANOVAs for MD and LOC. In the MD network, A two-way repeated measures ANOVA with reward (2) and distinction type (2, same or different visual category) as factors showed a main effect of reward ($F_{1, 23}$ = 7.06, p = 0.014) and no effect of visual category distinction or their interaction ($F_{1, 23}$ = 0.15, p = 0.7; $F_{1, 23}$ = 0.49, p = 0.49, respectively). In contrast, in LOC, a two-way repeated measures ANOVA with reward (2) and distinction type (2, same or different visual category) as factors showed a main effect of visual category distinction type ($F_{1, 23}$ = 9.38, p = 0.006) and no effect of reward or their interaction ($F_{1, 23}$ = 0.79, p = 0.38; $F_{1, 23}$ < 0.1, p = 0.99, respectively). Overall, these results demonstrate that the increase in decoding with reward motivation in the MD network was demand-contingent rather than driven by the visual categorisation, while decoding accuracies in the LOC were primarily driven by the visual categories.

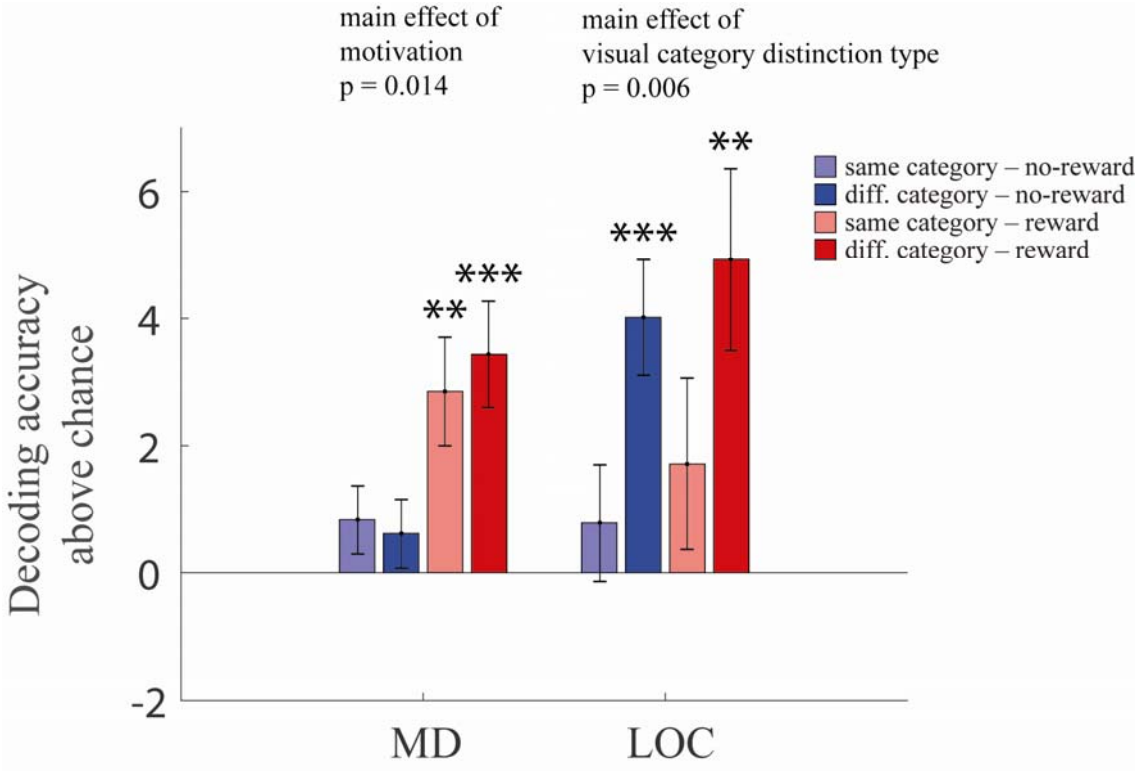


Figure 5: Modulation of decoding of highly competing behavioural categories (T vs. NI) in the MD network and LOC. Classification accuracies above chance (50%) for no-reward same-visual-category distinctions (light blue), no-reward different-visual-category distinctions (dark blue bars), reward same-visual-category distinctions (light red bars) and reward different-visual-category distinctions (dark red bars) are shown separately for the MD network and the LOC, averaged across regions in each system. In the MD network, discrimination increases when reward is introduced, and this effect is not driven by the visual category of the presented object. In contrast, LOC classification accuracies are larger when the displayed objects are from two different visual categories compared to when they belong to the same visual category, irrespective of the reward level. Asterisks above bars show significant discrimination above chance (One-tailed t-test against zero, corrected for multiple (4) comparisons within each system). Significant main effects in a two-way repeated measures ANOVA with reward and visual category distinctions as factors, computed separately for each system, are shown above the bars of each system. Errors bars indicate S.E.M. ** $p<0.01$, *** $p<0.001$.

Discussion

In this study we used a cued target detection task to test for the effect of reward motivation on the task-related representational space in the frontoparietal network as reflected in distributed patterns of fMRI data. Using MVPA, we showed that motivation, in the form of monetary reward, selectively enhances the representation of task-related information across the MD network. This selective effect is competition-contingent: the distinction between behavioural categories increased only for the highly competing ones.

Previous reports showed an enhancement effect of motivation on overall activity in the frontoparietal control network (Padmala and Pessoa, 2011; Dixon and Christoff, 2012; Botvinick and Braver, 2015). Recently, Etzel et al. (2016) demonstrated that task-set representation, as measured by cue decoding, increased with motivation. However, it remained unclear, whether this effect of reward motivation is limited to the preparatory activity or whether reward also modulates the representation of task-related information that is processed based on the cue. Here we showed that when monetary reward is introduced, the representation of task-related information following the cue is enhanced. We used an experimental design with three levels of task-relevant behavioural categories, and showed that this effect of reward does not affect all the distinctions between the behavioural categories similarly. The effect instead is competition-contingent – reward enhances the distinction between behavioural categories that are highly competing, i.e., the more demanding distinction. This is consistent with previous studies which suggested that motivation particularly affects conditions of high conflict. Padmala and Pessoa (2011) reported a decrease in interference with reward in response inhibition tasks. Reward also reduced incongruency effect in the Stroop task compared to non-rewarded trials (Krebs et al., 2013) and enhanced error related negativity (Stürmer et al., 2011). Our results directly demonstrate this selective competition-contingent effect on information representation.

Our findings provide support to the sharpening and prioritisation account which postulates that motivation leads to a sharpened neural representation of relevant information while relevant information is prioritised depending on the current task and needs. The sharpening aspect is reflected in the higher classification accuracies with reward in our data, and previous neurophysiological

evidence provide support for this aspect: reward has been associated with firing of dopaminergic neurons (Schultz et al., 1997; Bayer and Glimcher, 2005), and dopamine has been shown to modulate tuning of prefrontal neurons and to sharpen their representations (Vijayraghavan et al., 2007; Thurley et al., 2008; Ott and Nieder, 2016). The prioritization aspect can be related to the expected value of control (EVC) theory (Shenhav et al., 2013) and reward-based models for the interaction of reward and cognitive control, essentially a cost-benefit trade-off (Botvinick and Braver, 2015). Cognitive control is effortful and hence an ideal system would allocate it efficiently, with a general aim of maximizing expected utility. In the current study, only the highly competing conditions showed a reward motivation modulation effect. This could be interpreted as efficient prioritization of information processing, in which reward only affects the most effortful distinction between conditions, and no additional resources are invested when the cognitive effort required is lower.

Our results show a non-uniform effect of reward on the representation of task-related information. The exact neural mechanisms that underlie such an effect are still unclear, and electrophysiology studies in non-human primates might provide some potential insights. A similar task with behavioural distinctions of T, NI and NC has been used to show predominantly two opponent types of coding in LPFC neurons (Kusunoki et al., 2010). Patterns of activity showed highest firing rate for T and lowest for NC and a medium firing rate level for NI, or the exact opposite with highest firing for NC and lowest for T. These results imply that the level of targetness is reflected in the tuning curves of individual neurons. A speculative mechanism for the effect of reward on representation could be that the tuning is selectively sharpened when reward is introduced, making T and NI more distinct, with a smaller, or no effect, on activity related to T vs. NC.

The competition contingent effect of reward motivation observed in our data was similar across the MD network. This is in line with previous studies that reported similar representation of task information across the frontoparietal cognitive control network (Erez and Duncan, 2015; Woolgar et al., 2015; Wisniewski et al., 2016). Effects of reward have been previously demonstrated across this network (Padmala and Pessoa 2011; Dixon and Christoff 2012; Botvinick and Braver 2015; Shashidhara et al., submitted), as well as in particular regions (Rushworth et al., 2004; Knutson et al.,

2005; Hampton and O'doherty, 2007; Shenhav et al., 2013). It is not unlikely, however, that the different MD regions have, at least in part, different functions (Dosenbach et al., 2006, 2007; Koechlin and Summerfield, 2007; Nomura et al., 2010; Crittenden et al., 2016; Badre and Nee, 2018). This differential functionality was not observed in our data, and one possible explanation for that could be the slow time course of the fMRI BOLD signal. Along the same lines, the reward effect seen in the different regions could reflect different processes including, but not limited to, increased attention, motor preparation etc.

To ensure that our results are not affected by confounds related to the experimental design, we used a balanced task in respect to the visual and behavioural category of the stimuli, cues, reward level, and stimulus-response mapping. The use of catch trials ensured that the cue and stimulus GLM regressors were appropriately decorrelated. The overall classification accuracies in our data were low, similarly to previous studies that used MVPA for fMRI data across the frontoparietal cortex (Soon et al., 2008; Woolgar et al., 2011; Nelissen et al., 2013; Erez and Duncan, 2015), and possibly related to the functional organization at the neuronal population level (Dubois et al., 2015; Bhandari et al., 2018). Importantly, we emphasize the change in representation when reward is introduced: the classification accuracy for the highly-competing behavioural distinctions was larger for the reward than for the no-reward trials, and this effect was robust and consistent.

We ensured the robustness of our results by using several control analyses. First, the effect is not driven by mere increases in univariate activity due to reward. While univariate activity was larger in reward trials than no-reward trials, it was similar for the behavioural categories T, NI and NC, and could not have driven the selective increase in the distinction between T and NI. Second, the effect was consistent across a range of ROI sizes used for voxel selection. Third, a searchlight analysis (Kriegeskorte et al., 2006) demonstrated that the increase in classification for the high competition distinction following reward was limited to the MD network, thus confirming the validity of the ROIs we used. Lastly, we repeated the analyses using a different discriminability measure, LDC (Nili et al., 2014), which yielded similar results. Therefore, the results are not limited by the choice of analysis method either.

The visual categorisation aspect of our task allowed us to investigate effects of reward on representation in LOC compared to the MD network, which showed overall similar levels of classification accuracies but different profiles of activity. In particular, reward led to an increase in T vs. NI distinction in the MD regions but not in LOC. While all behavioural categories were represented in LOC, there was no change in representation with reward. A subsequent analysis showed that, in the MD network, discrimination between the behavioural categories was driven by reward and not by visual differences between the stimuli. This does not mean that there is no visual information in the MD network (Stokes et al., 2013), but rather that the increased representation with reward was not driven by it. In contrast, the discrimination in LOC was driven by the visual categories, with T and NI behavioural categories being discriminable only when they belonged to two different visual categories. While it is widely agreed that the frontoparietal cortex exerts top-down effects on visual areas, there is no clear prediction as to whether any effects of reward should be observed in the visual cortex. Our results provide evidence that the effects of reward on the task representational space are limited to the MD network and do not extend to LOC. Although previous studies have shown differences in representations between pFs and LO (Jiang et al., 2007; Li et al., 2007; Harel et al., 2014), our results were similar for both regions .

In summary, our results show that reward motivation enhances the representation of task-related information across the frontoparietal network. This facilitative effect is competition-contingent – only the representation of highly competing behavioural categories was modulated by reward. Our findings provide another tier of evidence regarding the interaction of motivation and cognitive control, and support the idea of sharpening representation of task information by motivation. We propose that this selective enhancement of representation reflects an efficient allocation of resources, in which reward signals modulate internal cognitive states only when it is most needed in order to successfully complete a task.

References

Badre D, Nee DE (2018) Frontal Cortex and the Hierarchical Control of Behavior. Trends Cogn Sci 22:170–188.

Bayer HM, Glimcher PW (2005) Midbrain Dopamine Neurons Encode a Quantitative Reward Prediction Error Signal. Neuron 47:129–141.

Bhandari A, Gagne C, Badre D (2018) Just above Chance: Is It Harder to Decode Information from Prefrontal Cortex Hemodynamic Activity Patterns? J Cogn Neurosci 30:1473–1498.

Botvinick M, Braver T (2015) Motivation and Cognitive Control: From Behavior to Neural Mechanism. Annu Rev Psychol 66:80–113.

Brainard DH (1997) The Psychophysics Toolbox. Spat Vis 10:433–436.

Braver TS (2012) The variable nature of cognitive control: a dual mechanisms framework. Trends Cogn Sci 16:106–113.

Brett M, Anton J-LL, Valabregue R, Poline J-B (2002) Region of interest analysis using an SPM toolbox - Abstract Presented at the 8th International Conference on Functional Mapping of the Human Brain, June 2-6, 2002, Sendai, Japan. Neuroimage.

Carlin JD, Kriegeskorte N (2017) Adjudicating between face-coding models with individual-face fMRI responses. PLoS Comput Biol 13:e1005604.

Chiew KS, Braver TS (2014) Dissociable influences of reward motivation and positive emotion on cognitive control. Cogn Affect Behav Neurosci 14:509–529.

Cole MW, Ito T, Braver TS (2016) The Behavioral Relevance of Task Information in Human Prefrontal Cortex. Cereb Cortex 26:2497–2505.

Crittenden BM, Mitchell DJ, Duncan J (2016) Task Encoding across the Multiple Demand Cortex Is Consistent with a Frontoparietal and Cingulo-Opercular Dual Networks Distinction. J Neurosci

36:6147–6155.

Cusack R, Vicente-Grabovetsky A, Mitchell DJ, Wild CJ, Auer T, Linke AC, Peelle JE (2014) Automatic analysis (aa): efficient neuroimaging workflows and parallel processing using Matlab and XML. Front Neuroinform 8:90.

Desimone R, Duncan J (1995) Neural Mechanisms of Selective Visual Attention. Annu Rev Neurosci 18:193–222.

Dixon ML, Christoff K (2012) The Decision to Engage Cognitive Control Is Driven by Expected Reward-Value: Neural and Behavioral Evidence. PLoS One 7:e51637.

Dosenbach NUF, Fair DA, Miezin FM, Cohen AL, Wenger KK, Dosenbach RAT, Fox MD, Snyder AZ, Vincent JL, Raichle ME, Schlaggar BL, Petersen SE (2007) Distinct brain networks for adaptive and stable task control in humans. Proc Natl Acad Sci 104:11073–11078.

Dosenbach NUF, Visscher KM, Palmer ED, Miezin FM, Wenger KK, Kang HC, Burgund ED, Grimes AL, Schlaggar BL, Petersen SE (2006) A Core System for the Implementation of Task Sets. Neuron 50:799–812.

Dubois J, de Berker AO, Tsao DY (2015) Single-unit recordings in the macaque face patch system reveal limitations of fMRI MVPA. J Neurosci 35:2791–2802.

Duncan J (2010) The multiple-demand (MD) system of the primate brain: mental programs for intelligent behaviour. Trends Cogn Sci 14:172–179.

Duncan J (2013) The Structure of Cognition: Attentional Episodes in Mind and Brain. Neuron 80:35–50.

Erez Y, Duncan J (2015) Discrimination of Visual Categories Based on Behavioral Relevance in Widespread Regions of Frontoparietal Cortex. J Neurosci 35:12383–12393.

Erez Y, Yovel G (2014) Clutter Modulates the Representation of Target Objects in the Human Occipitotemporal Cortex. J Cogn Neurosci 26:490–500.

Etzel JA, Cole MW, Zacks JM, Kay KN, Braver TS (2016) Reward Motivation Enhances Task Coding in Frontoparietal Cortex. Cereb Cortex 26:1647–1659.

Fedorenko E, Duncan J, Kanwisher N (2013) Broad domain generality in focal regions of frontal and parietal cortex. Proc Natl Acad Sci 110:16616–16621.

Feinberg DA, Moeller S, Smith SM, Auerbach E, Ramanna S, Gunther M, Glasser MF, Miller KL, Ugurbil K, Yacoub E (2010) Multiplexed echo planar imaging for sub-second whole brain FMRI and fast diffusion imaging. PLoS One 5:e15710.

Hampton AN, O'doherty JP (2007) Decoding the neural substrates of reward-related decision making with functional MRI. Proc Natl Acad Sci U S A 104:1377–1382.

Harel A, Kravitz DJ, Baker CI (2014) Task context impacts visual object processing differentially across the cortex. Proc Natl Acad Sci 111:E962–E971.

Hebart MN, Görgen K, Haynes J-D (2015) The Decoding Toolbox (TDT): a versatile software package for multivariate analyses of functional imaging data. Front Neuroinform 8:88.

Jiang X, Bradley E, Rini RA, Zeffiro T, Vanmeter J, Riesenhuber M (2007) Categorization training results in shape- and category-selective human neural plasticity. Neuron 53:891–903.

Kennerley SW, Wallis JD (2009) Reward-dependent modulation of working memory in lateral prefrontal cortex. J Neurosci 29:3259–3270.

Knutson B, Taylor J, Kaufman M, Peterson R, Glover G (2005) Distributed Neural Representation of Expected Value. J Neurosci 25:4806–4812.

Koechlin E, Summerfield C (2007) An information theoretical approach to prefrontal executive function. Trends Cogn Sci 11:229–235.

Krebs RM, Boehler CN, Appelbaum LG, Woldorff MG (2013) Reward Associations Reduce Behavioral Interference by Changing the Temporal Dynamics of Conflict Processing Geng JJ, ed. PLoS One 8:e53894.

Krebs RM, Boehler CN, Roberts KC, Song AW, Woldorff MG (2012) The involvement of the dopaminergic midbrain and cortico-striatal-thalamic circuits in the integration of reward prospect and attentional task demands. Cereb Cortex 22:607–615.

Kriegeskorte N, Goebel R, Bandettini P (2006) Information-based functional brain mapping. Proc Natl Acad Sci 103:3863–3868.

Kruglanski AW, Shah JY, Fishbach A, Friedman R, Woo Young Chun, Sleeth-Keppler D (2002) A theory of goal systems. Adv Exp Soc Psychol 34:331–378.

Kusunoki M, Sigala N, Nili H, Gaffan D, Duncan J (2010) Target Detection by Opponent Coding in Monkey Prefrontal Cortex. J Cogn Neurosci 22:751–760.

Leon MI, Shadlen MN (1999) Effect of Expected Reward Magnitude on the Response of Neurons in the Dorsolateral Prefrontal Cortex of the Macaque. Neuron 24:415–425.

Li S, Ostwald D, Giese M, Kourtzi Z (2007) Flexible Coding for Categorical Decisions in the Human Brain. J Neurosci 27:12321–12330.

MacEvoy SP, Epstein RA (2011) Constructing scenes from objects in human occipitotemporal cortex. Nat Neurosci 14:1323–1329.

Malach R, Reppas JB, Benson RR, Kwong KK, Jiang H, Kennedy WA, Ledden PJ, Brady TJ, Rosen BR, Tootell RB (1995) Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. Proc Natl Acad Sci U S A 92:8135–8139.

Miller EK, Cohen JD (2001) An Integrative Theory of Prefrontal Cortex Function. Annu Rev Neurosci 24:167–202.

Miller GA, Galanter E, Pribram K. H (1960) Plans and the structure of behavior. Holt, Rinehart and Winston, Inc.

Mohanty A, Gitelman DR, Small DM, Mesulam MM (2008) The Spatial Attention Network Interacts with Limbic and Monoaminergic Systems to Modulate Motivation-Induced Attention Shifts.

Cereb Cortex 18:2604–2613.

Nelissen N, Stokes M, Nobre AC, Rushworth MFS (2013) Frontal and Parietal Cortical Interactions with Distributed Visual Representations during Selective Attention and Action Selection. J Neurosci 33:16443–16458.

Nili H, Wingfield C, Walther A, Su L, Marslen-Wilson W, Kriegeskorte N (2014) A Toolbox for Representational Similarity Analysis Prlic A, ed. PLoS Comput Biol 10:e1003553.

Nomura EM, Gratton C, Visser RM, Kayser A, Perez F, D'Esposito M (2010) Double dissociation of two cognitive control networks in patients with focal brain lesions. Proc Natl Acad Sci 107:12017–12022.

Norman DA, Shallice T (1980) Attention to action: willed and automatic control of behavior. San Diego: University of California Center for Human Information Processing.

Ott T, Nieder A (2016) Dopamine D2 Receptors Enhance Population Dynamics in Primate Prefrontal Working Memory Circuits. Cereb Cortex 27:4423–4435.

Padmala S, Pessoa L (2010) Interactions between cognition and motivation during response inhibition. Neuropsychologia 48:558–565.

Padmala S, Pessoa L (2011) Reward Reduces Conflict by Enhancing Attentional Control and Biasing Visual Cortical Processing. J Cogn Neurosci 23:3419–3432.

Pessoa L (2009) How do emotion and motivation direct executive control? Trends Cogn Sci 13:160–166.

Pochon JB, Levy R, Fossati P, Lehericy S, Poline JB, Pillon B, Le Bihan D, Dubois B (2002) The neural system that bridges reward and cognition in humans: An fMRI study. Proc Natl Acad Sci 99:5669–5674.

Rushworth MFS, Walton ME, Kennerley SW, Bannerman DM (2004) Action sets and decisions in the medial frontal cortex. Trends Cogn Sci 8:410–417.

Schultz W, Dayan P, Montague PR (1997) A neural substrate of prediction and reward. Science (80-) 275:1593–1599.

Shenhav A, Botvinick MM, Cohen JD (2013) The expected value of control: An integrative theory of anterior cingulate cortex function. Neuron 79:217–240.

Simon HA (1967) Motivational and emotional controls of cognition. Psychol Rev 74:29–39.

Soon CS, Brass M, Heinze H-J, Haynes J-D (2008) Unconscious determinants of free decisions in the human brain. Nat Neurosci 11:543–545.

Stokes MG, Kusunoki M, Sigala N, Nili H, Gaffan D, Duncan J (2013) Dynamic coding for cognitive control in prefrontal cortex. Neuron 78:364–375.

Stürmer B, Nigbur R, Schacht A, Sommer W (2011) Reward and punishment effects on error processing and conflict control. Front Psychol 2:335.

Taylor SF, Welsh RC, Wager TD, Luan Phan K, Fitzgerald KD, Gehring WJ (2004) A functional neuroimaging study of motivation and executive function. Neuroimage 21:1045–1054.

Thurley K, Senn W, Lüscher H-R (2008) Dopamine Increases the Gain of the Input-Output Response of Rat Prefrontal Pyramidal Neurons. J Neurophysiol 99:2985–2997.

van der Kouwe AJW, Benner T, Salat DH, Fischl B (2008) Brain morphometry with multiecho MPRAGE. Neuroimage 40:559–569.

Vergauwe E, Cowan N (2015) Attending to items in working memory: evidence that refreshing and memory search are closely related. Psychon Bull Rev 22:1001–1006.

Vijayraghavan S, Wang M, Birnbaum SG, Williams G V, Arnsten AFT (2007) Inverted-U dopamine D1 receptor actions on prefrontal neurons engaged in working memory. Nat Neurosci 10:376–384.

Wallace AFC (1960) : Plans and the Structure of Behavior . George A. Miller, Eugene Galanter, Karl H. Pribram. Am Anthropol 62:1065–1067.

Watanabe M (1996) Reward expectancy in primate prefrental neurons. Nature 382:629–632.

Wisniewski D, Goschke T, Haynes J-D (2016) Similar coding of freely chosen and externally cued intentions in a fronto-parietal network. Neuroimage 134:450–458.

Woolgar A, Golland P, Bode S (2014) Coping with confounds in multivoxel pattern analysis: What should we do about reaction time differences? A comment on Todd, Nystrom & Cohen 2013. Neuroimage 98:506–512.

Woolgar A, Thompson R, Bor D, Duncan J (2011) Multi-voxel coding of stimuli, rules, and responses in human frontoparietal cortex. Neuroimage 56:744–752.

Woolgar A, Williams MA, Rich AN (2015) Attention enhances multi-voxel representation of novel objects in frontal, parietal and visual cortices. Neuroimage 109:429–437.

Acknowledgements:

This work was funded by a Royal Society Dorothy Hodgkin Research Fellowship (UK) to Yaara Erez (DH130100). Sneha Shashidhara was supported by a scholarship from the Gates Cambridge Trust, Cambridge, UK. We thank John Duncan and Daniel Mitchell for fruitful discussions and advice throughout the study.

The authors declare no competing financial interests.