Reward motivation modulates coding of behaviorally relevant category distinctions 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 modulates task-related information coding

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

Selection and integration of information based on current goals is a fundamental aspect of flexible goal-directed behavior. Motivation has been shown to improve behavioral performance across multiple cognitive tasks, yet the underlying neural mechanisms that link motivation and control processes, and in particular its effect on context-dependent information processing, remain unclear. Here, we used functional magnetic resonance imaging (fMRI) in 24 human volunteers to test whether reward motivation enhances the coding of behaviorally relevant category distinctions across the frontoparietal cortex. In a cued-detection categorization task, participants detected whether an object from a cued visual category was present in a subsequent display. Objects from one of two cued categories could serve as either Targets or High-conflict nontargets, depending on the cue on a given trial. Objects from a third category were never cued and served as Low-conflict nontargets, thus yielding three levels of behavioral status for the displayed categories (Targets, High-conflict nontargets, and Low-conflict nontargets). Half of all trials offered the possibility of a substantial reward. Multivariate pattern analysis (MVPA) showed a conflict-contingent enhancement effect of reward across the frontoparietal cortex. Reward increased the discrimination between highly conflicting behavioral status conditions, but not between less conflicting distinctions, and this selective effect was not driven by visual differences. In contrast, reward did not modulate these task-related distinctions in the high-level general object visual region, the lateral occipital complex. These findings suggest that reward modulates the representation of behaviorally relevant information only when it is most needed to successfully complete a task, and therefore facilitates an efficient allocation of attentional resources.

Introduction

A fundamental aspect of flexible goal-directed behavior is the selection and integration of information depending on a current goal to determine its relevance to behavior and lead to a decision. In non-human primates, single-cell data from the lateral prefrontal cortex, as well as parietal cortex, provide detailed evidence for the coding of task-relevant information. It has been shown that neural activity contains information about the context, also referred to as cue or task-set, as well as the integrated information of cue and a subsequent input stimulus, such as task-related categorical and behavioral decision (Freedman, Riesenhuber, Poggio, & Miller, 2001; Kadohisa et al., 2013; Kusunoki, Sigala, Nili, Gaffan, & Duncan, 2010; Mante, Sussillo, Shenoy, & Newsome, 2013; Stokes et al., 2013; Wallis, Anderson, & Miller, 2001). In the human brain, a network of frontal and parietal cortical regions, the 'multiple-demand' (MD) network (Fedorenko, Duncan, & Kanwisher, 2013; Mitchell et al., 2016), has been shown to be involved in information selection and integration, and more generally in control processes. This network is associated with multiple aspects of cognitive control, such as spatial and verbal working memory, math, conflict monitoring, rule-guided categorization and task switching, (Cole, Ito, & Braver, 2016; Fedorenko et al., 2013; Vergauwe & Cowan, 2015). The MD 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 cortex (preSMA/ACC); and intraparietal sulcus (IPS) (Duncan, 2010). Multiple neuroimaging studies demonstrated that distributed patterns of activity across the MD network and similar areas across frontoparietal cortex as measured by functional magnetic resonance imaging (fMRI) reflected a variety of task-related information. These include task sets, behavioral relevance and task-dependent categorical decisions (Erez & Duncan, 2015; Li, Ostwald, Giese, & Kourtzi, 2007; Muhle-Karbe, Duncan, De Baene, Mitchell, & Brass, 2017; Wisniewski, Goschke, & Haynes, 2016; Woolgar, Hampshire, Thompson, & Duncan, 2011; Woolgar, Thompson, Bor, & Duncan, 2011; Woolgar, Williams, & Rich, 2015). In contrast, sensory areas such as the high-level general object visual region, the lateral occipital complex (LOC), as well as the primary visual cortex, contained information about the visual properties and categorization of

stimuli, with weaker, or non-existing, task effects (Bugatus, Weiner, & Grill-Spector, 2017; Harel, Kravitz, & Baker, 2014; Hebart, Bankson, Harel, Baker, & Cichy, 2018).

With growing interest in recent years in the link between cognitive control and motivation, it has been proposed that motivation enhances control processes by sharpening representation of task goals and prioritizing task-relevant information across the frontoparietal network and other regions associated with cognitive control (Botvinick & Braver, 2015; Etzel, Cole, Zacks, Kay, & Braver, 2016; Kruglanski et al., 2002; Simon, 1967). In line with this idea, it has been shown that motivation, usually manipulated as monetary reward, increases task performance (Padmala & Pessoa, 2010, 2011). Neuroimaging studies 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 (Krebs, Boehler, Roberts, Song, & Woldorff, 2012; Mohanty, Gitelman, Small, & Mesulam, 2008), response inhibition (Padmala & Pessoa, 2011), and problem solving (Shashidhara et al., in press).

Although the accumulating evidence at the behavioral and neural level in humans are consistent with this sharpening and prioritizing account (Braver, 2012; Chiew & Braver, 2014; Kruglanski et al., 2002; Pessoa, 2009; Simon, 1967; Wallace, 1960), they do not directly address the effect of motivation on the coding of task-related information and selection and integration processes. 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 activity related to working memory and modulated task-related activity based on the type of reward (Kennerley & Wallis, 2009; Leon & Shadlen, 1999; Watanabe, 1996). A more direct evidence in humans was recently demonstrated by Etzel et al. (2016). They showed that reward enhances coding of task cues across the frontoparietal cortex, and suggested that task-set efficacy increases with reward. It remains unclear, however, if this facilitative effect of reward is limited to preparatory cues, or whether reward also enhances the coding of behaviorally relevant information, when the cue and a subsequent stimulus are integrated, leading to the behavioral decision.

Following the sharpening hypothesis, in this study we asked whether reward motivation enhances the representation of behaviorally relevant information, as determined by the integration of cue and stimulus input. Furthermore, previous studies have associated reward with decreased conflict in interference tasks (Krebs, Boehler, Appelbaum, & Woldorff, 2013; Padmala & Pessoa, 2011; Stürmer, Nigbur, Schacht, & Sommer, 2011), suggesting that any effect of reward may be particularly important for high-conflict items, or in other words, a conflict-contingent effect. We therefore also asked whether such facilitative effect of reward is selective for highly conflicting items. We recently showed that behaviorally relevant, but not irrelevant, category distinctions of objects were coded across the MD network (Erez & Duncan, 2015). In LOC, in contrast, such differences were not observed. Here, we used a similar cued detection categorization task while participants' brain activity was measured using fMRI. 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, or nontargets with high behavioral conflict, as they could be targets on other trials (High-conflict nontarget). An additional category was never cued, serving as nontarget with low behavioral conflict (Low-conflict nontarget). This design created three levels of behavioral status (Targets, High-conflict nontargets, Low-conflict nontargets). Importantly, following this integration process, the critical relevant information that is expected to be represented across the MD network is the behavioral status of a given category, rather than the visual category itself. Therefore, the behaviorally relevant category distinctions were pairs of categories with different behavioral status. We used multivariate pattern analysis (MVPA) to measure representation of the behaviorally relevant category distinctions as reflected in distributed patterns of response in the *a priori* defined MD network and in LOC. To manipulate motivation, on half of all trials a substantial monetary reward was offered. We tested whether the neural pattern discriminability between the behaviorally relevant category distinctions increased with reward, and whether this effect was selective for the distinction between Targets and High-conflict nontargets.

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 requirements of the experimental design across participants. 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 monetarily reimbursed for their time.

Task Design

Participants performed a cued categorization 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 High-conflict nontargets, as they could serve as targets on other trials. The third category was never cued, therefore objects from this category served as Low-conflict nontargets. This design yielded three behavioral status conditions: Targets, High-conflict nontargets and Low-conflict nontargets (Figure 1B). The assignment of the categories to be cued (and therefore serve as either Targets or High-conflict nontargets) or not (and serve as Low-conflict nontargets) was counter-balanced across participants.

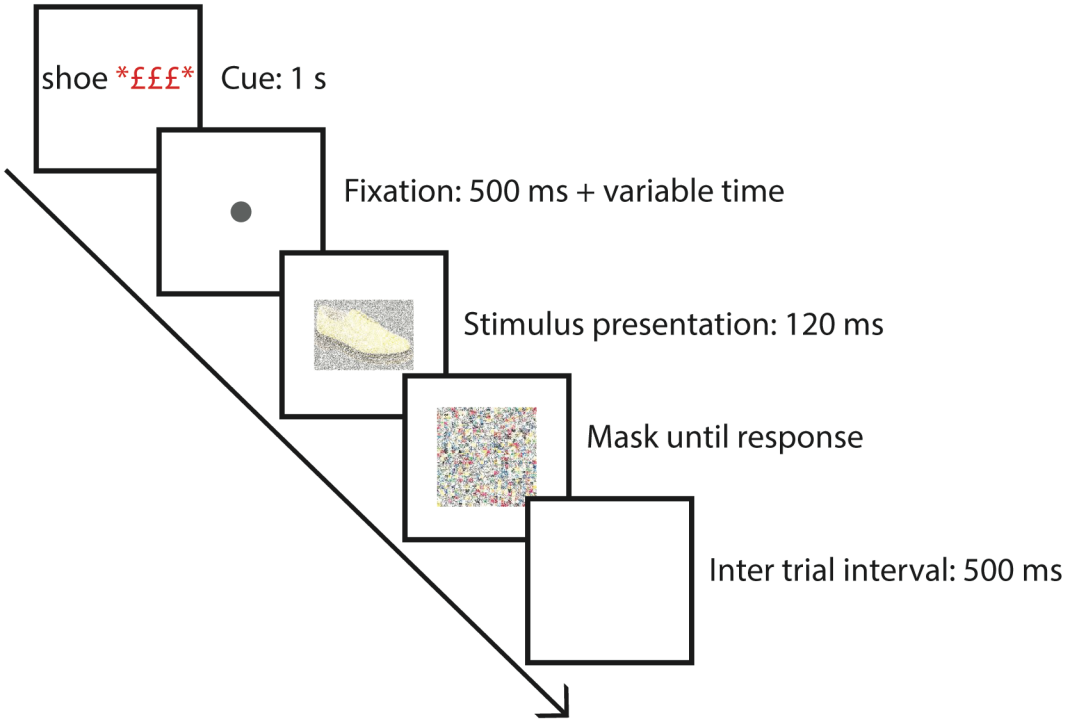
To manipulate motivation, half of the trials were cued as reward trials, in which participants had the chance of earning £1 if they completed the trial correctly and within a time limit. To assure the incentive on each reward trial, four random reward trials out of 40 in each run were assigned the £1

reward. To avoid longer reaction times as a trade-off of increased accuracy when participants try to maximize their reward, a response time threshold was used, set separately for each participant as the average of 32 trials in a pre-scan 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, participants had to treat every reward trial as a £1 trial and respond as quickly and as accurately as possible, just as in 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 center of the screen presented for 0.5 s and an additional variable time of either 0.1, 0.4, 0.7 or 1 s, selected randomly, in order to make the stimulus onset time less predictable. The stimulus was then presented for 120 ms and was followed by a mask. 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 separated two trials. For both reward and no-reward trials, response time was limited to a maximum of 3 s, after which the 1 s blank inter-trial interval started even when no response was made. For reward trials, an additional subject-specific response time threshold was used as mentioned above to determine whether the participants earned the reward or not, but this time threshold did not affect the task structure and was invisible to the participants.

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, followed by the inter-trial interval.

A



B

	Target	High-conflict nontarget	Low-conflict nontarget
Cue: shoe	shoe	sofa	car
Cue: sofa	sofa	shoe	car

Figure 1: Experimental paradigm. A. An example of a 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 time (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), 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 serve as the cued categories and cars as the uncued category. In the Target trials, the presented object matched the cued category. In the High-conflict nontarget trials, the object did not match the cued category, but was from the other cued category, therefore could serve as a target on other trials. In the Low-conflict nontarget trials, the presented object was from the category that was never cued. Overall, this design yielded three levels of behavioral status: Targets, High-conflict nontargets, and Low-conflict nontargets. The design was used for both no-reward and reward conditions.

Stimuli

Objects were presented at the center 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, dimensions, and orientation across the categories. All exemplars were used an equal number of times in each condition and in each run. To increase the task demand, and 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 the 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 Target trials, and half of the trials (8) were nontarget trials, to assure an equal number of target (present) and nontarget (absent) trials. Of the nontarget trials, half (4) were High-conflict nontargets, and half (4) were Low-conflict nontargets. There were 4 trials per cue and reward level for the High- and Low-conflict nontarget conditions, and 8 for the Target condition, with the latter split into two regressors (see General Linear Model (GLM) for the Main Task section below). 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 Localizers

In addition to the main task, we used two other tasks in order to functionally localize 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 localize 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 localize MD regions.

As a localizer for LOC we used a one-back task with blocks of objects interleaved with blocks of scrambled objects. The objects were in grey scale and taken from a set of 61 everyday objects (e.g. camera, coffee cup, etc.). 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 objects vs. scrambled objects contrast was used to localize LOC.

Scanning Session

The scanning session included a structural scan, 6 functional runs of the main task, and 4 functional localizer runs – 2 for MD regions and 2 for LOC. The scanning session lasted up to 100 minutes, with an average 65 minutes of EPI time. 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, flip angle 62°, and interleaved slice acquisition order. No iPAT or in-plane acceleration were used. T1-weighted multiecho MPRAGE (van der Kouwe, Benner, Salat, & Fischl, 2008) high-resolution images were also acquired for all participants, in which four different TEs were used to generate four images (voxel size 1 mm isotropic, field of view of 256 × 256 × 192

mm, TR = 2530 ms, TE = 1.64, 3.5, 5.36, and 7.22 ms). 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 representation of behaviorally relevant category distinctions with and without reward. An additional 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 due to the within-subject design. A one-tailed t test was used when the prediction was directional, including for testing for classification accuracy above chance level. All other t tests in which the *a priori* hypothesis was not directional 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 image was then normalized 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 functional localizers data only.

General Linear Model (GLM) for the Main Task

We used GLM to model the main task and localizers' data. Regressors for the main task included 12 task conditions during the stimulus epoch, split according to reward level (no-reward, reward), cued visual category (category 1, category 2), and behavioral status (Target, High-conflict nontarget, Low-conflict nontarget). To assure an equal number of target present and target absent trials, the number of Target trials in our design was twice the number of High-conflict and Low-conflict nontarget trials. The Target trials included two repetitions of each combination of cue, visual category and exemplar, with a similar split for reward trials. These two Target repetitions were modelled as separate Target1 and Target2 regressors in the GLM to make sure that all the regressors were based on an equal number of trials, but were invisible to the participants. All the univariate and multivariate analyses were carried out while keeping the two Target regressors separate to avoid any bias of the results, and they were averaged at the final stage of the results (i.e., decoding accuracies). Overall, the GLM included 16 regressors of interest for the 12 task conditions. Each regressor was based on data from 4 trials in each run using the 4 exemplars from the relevant visual category. Together with the counter-balancing of the cued visual categories (Targets, High-conflict nontargets) and non-cued visual categories (Low-conflict nontargets) across participants, this ensured that the variability of exemplars would not account for any differences between the experimental conditions. To account for possible effects of reaction time (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, Golland, & Bode, 2014). This model scales the regressors based on the reaction time, thus the beta estimates reflect activation per unit time and are comparable across conditions with different durations. 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 Localizers

For the MD localizer, 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

We conducted an ROI analysis to test for the effect of reward on overall activity for the different behavioral status conditions. 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. For the MD network, beta estimates were also averaged across hemispheres (see ROI definition below). Second-level analysis was done on beta estimates across participants using repeated measures ANOVA. The data for the Target condition was averaged across the two Target1 and Target2 regressors, separately for the no-reward and reward conditions.

ROI Definition

MD network template. ROIs of the MD network were defined *a priori* 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 lateral frontal cortex (pdLFC), AI-FO, pre-SMA/ACC, and IPS, defined in the left and right hemispheres. The visual component in this template is widely accepted as a by-product of using largely visual tasks, and is not normally considered as part of the MD network. Therefore, it was not included in the analysis. The MD network is highly

bilateral, with similar responses in both hemispheres (Erez & Duncan, 2015; Fedorenko et al., 2013). We therefore averaged the results across hemispheres in all the analyses.

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 localizer, 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 (Erez & Yovel, 2014; MacEvoy & Epstein, 2011).

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 localizers (Erez & Duncan, 2015; Shashidhara, Spronkers, & Erez, 2019). 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 localizer data. This number of voxels was chosen prior to any data analysis, similar 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 localizer 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 the task-related behavioral status pairs. 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, Görgen, & Haynes, 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 behavioral status (Targets vs. High-conflict nontargets, Targets vs. Low-conflict nontargets, and High-conflict vs. Low-conflict nontargets) within each reward level (no-reward, reward). Classification accuracies above chance (50%) were tested using a second level group analysis (one-tailed t-test). Because the number of Target trials in our design was twice the number of High-conflict and Low-conflict nontarget trials, each discrimination that involved a Target condition was computed separately for the two Target regressors (Target1 and Target2) and classification accuracies were averaged across them.

The Target and High-conflict nontarget 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 Target vs. High-conflict nontarget pairs of conditions into these two cases and the applied statistical tests accordingly.

To ensure that our results are robust across different pattern analysis techniques, we tested for the modulation of behavioral status coding by reward using a linear discriminant contrast (LDC) (Carlin & Kriegeskorte, 2017; Nili et al., 2014), in addition to SVM. All of the MVPA 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 behavioral status conditions, 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 behavioral status conditions when reward is introduced, we conducted a whole-brain searchlight pattern analysis (Kriegeskorte, Goebel, & Bandettini, 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, centered 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 distinctions, separately for the reward and no-reward conditions. These whole-brain maps were smoothed using a 5 mm FWHM Gaussian kernel. The t-statistic from a second level random-effects analysis on the smoothed maps was thresholded at the voxel level using FDR correction ($p < 0.05$).

Results

Behavior

RT for three behavioral status conditions, Target, High-conflict nontarget and Low-conflict nontarget, 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 behavioral status as within-subject factors showed a main effect of motivation ($F_{1, 23}$ = 40.07, p < 0.001), with reward trials being shorter than no-reward trials, as expected from the experimental design in which response was required within a time limit to receive the reward. An additional main effect of behavioral status ($F_{2, 23}$ = 50.97, p < 0.001) was observed, with no interaction between reward and behavioral status ($F_{2, 23}$ = 0.63, p = 0.54). Subsequent post-hoc tests with Bonferroni correction for multiple comparisons showed that RTs for Target trials were faster than High-conflict and Low-conflict nontarget trials (t_{23} = 10.03, p < 0.001, d_z = 2.05; t_{23} = 5.17, p < 0.001, d_z = 1.06 respectively), and Low-conflict nontarget trials were faster than the High-conflict ones (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 the Target, High-conflict nontarget and Low-conflict nontarget 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 behavioral status as within-subject factors showed 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 main effect of behavioral status ($F_{2, 23}$ = 29.64, p < 0.001) and an interaction between motivation and behavioral status ($F_{2, 23}$ = 5.81, p < 0.01). Post-hoc tests with Bonferroni correction for multiple comparisons showed larger accuracies for Low-conflict nontargets compared to Targets and High-conflict nontargets (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 Low-conflict nontarget category was fixed throughout the experiment. In the reward trials, performance

accuracies were larger for Target compared to High-conflict nontarget (t_{23} = 4.45, p < 0.001, d_z = 0.91) and Low-conflict nontarget compared to High-conflict ones (t_{23} = 5.92, p < 0.001, d_z = 1.2) and similar between Targets and Low-conflict nontargets (t_{23} = 2.49, p = 0.06). Accuracies for Target trials were larger for the reward trials compared to no-reward (t_{23} = 2.92, p = 0.008, d_z = 0.61), indicating a possible behavioral benefit of reward. There was no difference between reward and no-reward trials for High-conflict and Low-conflict nontargets (t_{23} < 1.1, p > 0.1, for both).

Univariate activity in the MD network

We first tested for the effect of reward motivation on the overall activity in MD regions, and whether such effect is different for the three behavioral status conditions. We used averaged β estimates for each behavioral status (Target, High-conflict nontarget, Low-conflict nontarget) and reward level (no-reward, reward) in each of the MD ROIs (Figure 2). A three-way repeated measures ANOVA with reward (2), behavioral status (3) and ROI (7) as within-subject factors showed a main effect of reward ($F_{1,\ 23}$ = 4.65, p = 0.042) with increased activity for reward conditions compared to no-reward conditions, demonstrating that overall activity across the MD network increased with reward. 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, demonstrating that reward led to increased activity in all the MD ROIs. Importantly, there was no main effect of behavioral status ($F_{2,\ 46}$ = 0.56, p = 0.57) and no interaction of reward and behavioral status ($F_{2,\ 46}$ = 0.16, p = 0.85). Overall, the univariate results indicated similar levels of activity for the three behavioral status conditions, an increase in activity across the MD network when reward is introduced, and similar increases for all the behavioral status conditions.

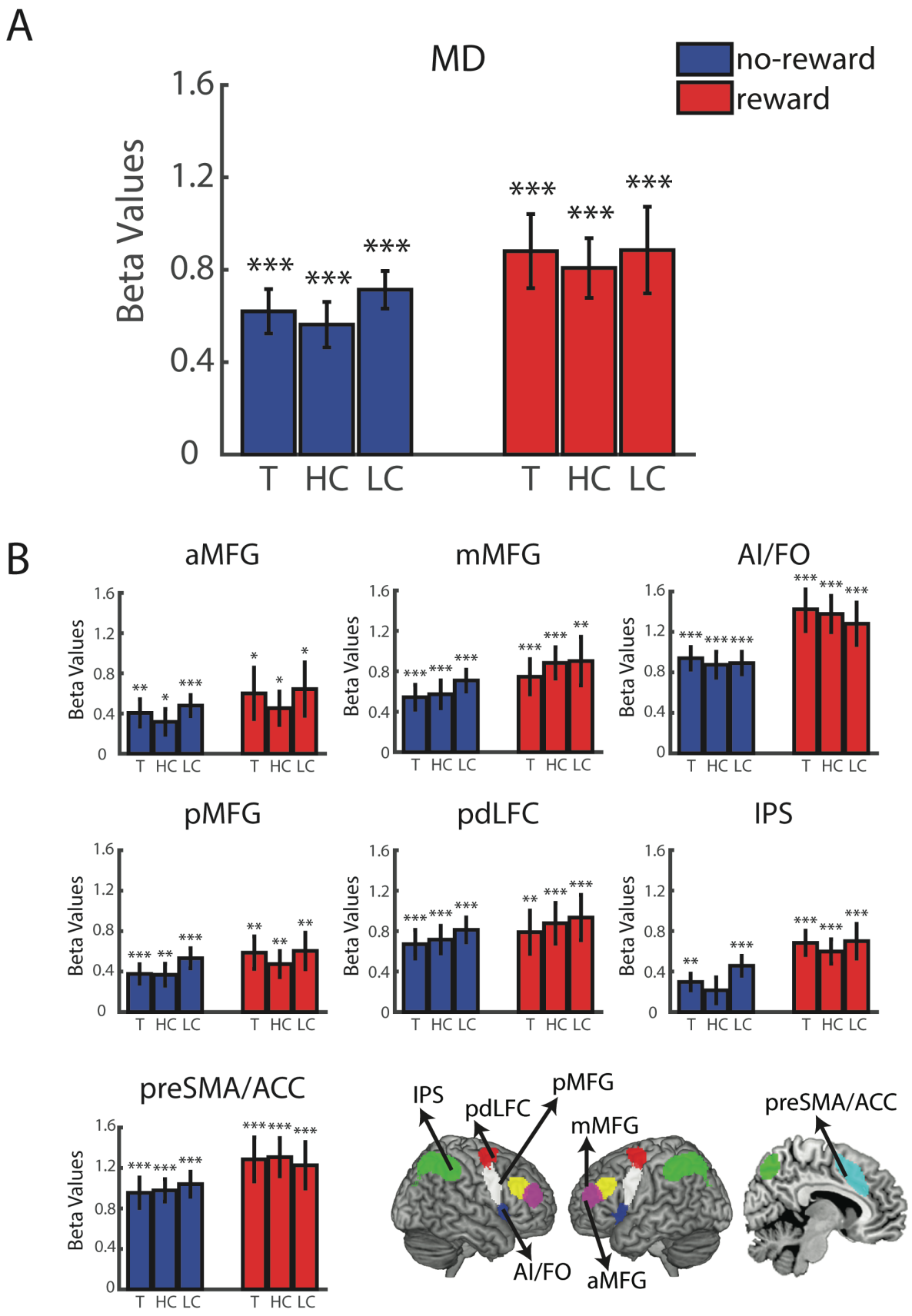


Figure 2: Univariate activity across the MD network increases with reward. A. Univariate results averaged across all MD regions. Activity increases with reward and is similar for the three behavioral

status conditions. Data is averaged across hemispheres and is shown for the three behavioral status conditions (T: Target, HC: High-conflict nontarget, LC: Low-conflict nontarget), for both no-reward (blue bars) and reward (red bars) conditions. **B.** Univariate results for the individual MD regions, averaged across hemispheres. Plot conventions are the same as in A. The MD network template is shown for reference. pdLFC: posterior/dorsal lateral prefrontal cortex, IPS: intraparietal sulcus, preSMA: pre-supplementary motor area, ACC: anterior cingulate cortex, AI: anterior insula, FO: frontal operculum, aMFG, mMFG, pMFG: anterior, middle and posterior middle frontal gyrus, respectively. Errors bars indicate S.E.M. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Effect of reward motivation on discrimination of behaviorally relevant category distinctions in the MD network

We used MVPA to test for the effect of reward motivation on the representation of the task-related behavioral status. For each participant and ROI we computed the classification accuracy above chance (50%) for the distinctions between Target vs. High-conflict nontarget, Target vs. Low-conflict nontarget and High-conflict vs. Low-conflict nontargets, separately for no-reward and reward conditions (Figure 3). The analysis was set to test for discrimination between behavioral status conditions within each reward level, and whether these discriminations are larger when reward is introduced compared to the no-reward condition. A three-way repeated-measures ANOVA with reward (2), behavioral distinction (3) and ROI (7) as within-subject factors showed no main effect of ROI ($F_{6, 138} = 1.41$, $p = 0.21$) or any interaction of ROI with reward and behavioral distinction ($F < 1.78$, $p > 0.06$). Therefore, the classification accuracies were averaged across 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. Decoding accuracies above chance for the pairs of behavioral status were mixed. The distinction of Target vs. High-conflict nontarget was above chance for reward trials (One-tailed t-test: $t_{23} = 4.40$, $p < 0.001$, $d_z = 0.90$), but decoding accuracy above chance 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 Target vs. Low-conflict nontarget was above chance for both reward and no-reward trials (One-tailed t-test: t_{23} = 2.66, p = 0.042, d_z = 0.54; t_{23} = 3.05, p = 0.017, d_z = 0.62, respectively), and the distinction between the two nontarget behavioral status conditions, High-conflict vs. Low-conflict nontargets, was not above chance in either (One-tailed t-test: t_{23} = 0.55, p = 0.26, d_z = 0.29; t_{23} = 1.41, p = 0.88, d_z = 0.11, for no-reward and reward conditions, respectively).

Next, to address the main question in our study, we tested for the effect of reward on the discriminability between pairs of behavioral status. A two-way repeated measures ANOVA with reward (2) and behavioral distinction (3) as within-subject factors showed no main effects of reward or behavioral 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). Following this interaction, to further test for the increase in discriminability between the pairs of behavioral status when reward is introduced, we conducted post-hoc tests with Bonferroni correction for multiple (3) comparisons. Classification accuracy was larger in the reward trials compared to the no-reward trials for the Target vs. High-conflict nontarget distinction only (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 Target vs. Low-conflict nontarget and High-conflict vs. Low-conflict nontarget distinctions (One-tailed t-tests: t_{23} = 0.28, p > 0.9 d_z = 0.06; t_{23} = 0.73, p > 0.9 d_z = 0.15, respectively). To further test whether the observed increase in decoding with reward for the Target vs. High-conflict nontarget distinction was different from the other two distinctions, we conducted additional post-hoc t-tests with the difference in classification accuracy between reward and no-reward conditions (Δaccuracy) as the dependent measure and Bonferroni correction for multiple comparisons (3). The difference in accuracy for the Target vs. High-conflict nontarget distinction was larger than the difference for the High-conflict and Low-conflict nontarget distinction (two-tailed t-test: t_{23} = 2.89, p = 0.022, d_z = 0.51), and no other differences in accuracy were significantly different from each other (two-tailed t-test: t_{23} < 1.9, p > 0.21, d_z < 0.039). Overall, these results are in line with the conflict-contingent hypothesis and

demonstrate that, across the MD network, reward motivation increases the coding of the most conflicting information only, namely Targets vs. High-conflict nontargets.

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, we tested for the increase in classification in the reward compared to the no-reward conditions for the three distinctions between behavioral status levels. Classification accuracy for the Target vs. High-conflict nontarget 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 Target vs. Low-conflict nontarget and the High-conflict vs. Low-conflict nontarget pairs of behavioral status, 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 behavioral status conditions, with and without reward. A larger LDC value between two conditions indicates greater dissimilarity, or greater discriminability, therefore we tested whether LDC was larger for reward versus no-reward trials for the three distinctions. Overall, the LDC analysis revealed similar results to those obtained using the decoding analysis, with a differential effect of reward on the discriminability between behavioral status distinctions and an increase in discriminability for the Targets vs. High-conflict nontargets distinction only. Effects of reward were similar for all ROIs, therefore LDC values were averaged across ROIs (Three-way repeated-measures ANOVA with reward (2), behavioral distinction (3), and ROI (7) as within-subject factors: main effect of ROI ($F_{6, 138} = 4.1$, $p < 0.001$), but no interaction with ROI, $F < 1$, $p > 0.6$). Across MD regions, the effect of reward was different for the three behavioral status distinctions (Two-way repeated-measures ANOVA with reward (2) and behavioral distinction (3): no main effect of reward ($F_{1, 23} = 0.6$, $p = 0.7$) or behavioral distinction ($F_{2, 46} = 1.2$, $p = 0.3$), but a significant interaction of the two ($F_{2, 46} = 3.96$, $p = 0.026$). Post-hoc tests showed that LDC was numerically larger in reward trials compared to no-reward trials for the High-

conflict distinction (marginally significant effect after correction for multiple (3) comparisons in a one tailed t-test: $t_{23} = 2.13$, $p = 0.066$, $d_z = 0.59$), but not for the other two behavioral status distinctions ($t_{23} < 0.9$, $p > 0.6$). Furthermore, similar to the SVM analysis, we used additional post-hoc tests and asked whether the difference in LDC between reward and no-reward conditions (ΔLDC) was different for the three behavioral status distinctions. ΔLDC was larger for the Target vs. High-conflict nontarget distinction than for the High- vs. Low-conflict nontarget distinction (two-tailed t-test: $t_{23} = 2.89$, $p = 0.025$, corrected for multiple (3) comparisons), and no other differences in ΔLDC were different from one another (two-tailed t-test: $t_{23} < 1.4$, $p > 0.5$).

Lastly, we used a whole-brain searchlight analysis to test for additional focal regions beyond the MD network that show increased discrimination with reward for the highly conflicting behavioral distinction. In a second level random-effects analysis of Target vs. High-conflict nontarget classification maps, none of the voxels survived an FDR threshold of $p < 0.05$, therefore no such additional regions were revealed. When we used a more lenient threshold of $p < 0.05$ without correction for multiple-comparisons, an overall MD-like pattern emerged. Increased distinctions of Target vs. High-conflict nontarget with reward were observed along the MFG (posterior, middle and anterior), IPS, AI and pre-SMA on both hemispheres. While these uncorrected results should be interpreted cautiously, we note that the emerging pattern of activity resembled an MD-like network rather than being scattered and randomly distributed across the brain.

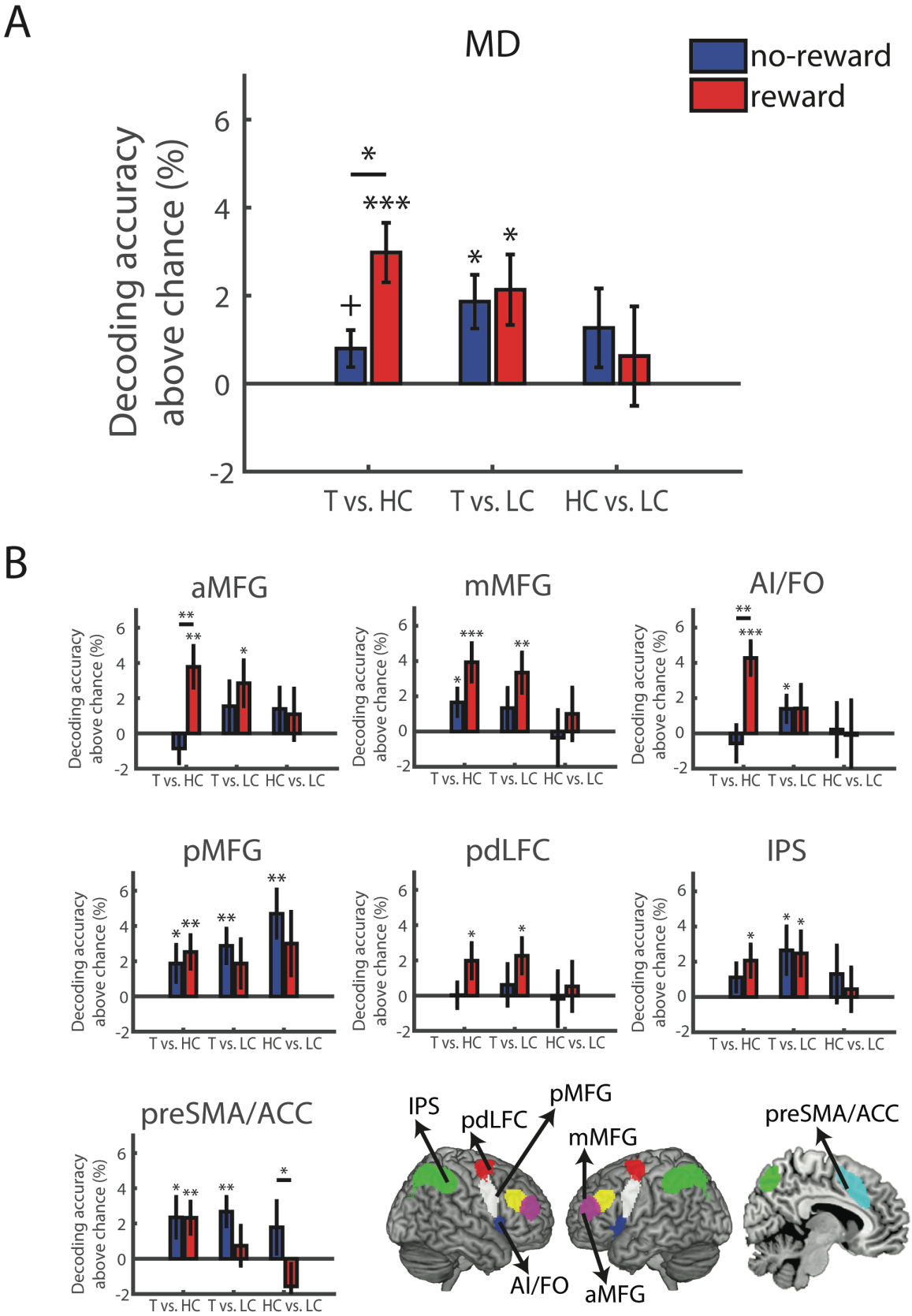


Figure 3: Reward motivation selectively increases the coding of highly conflicting behavioral status distinctions across the MD network. A. Reward leads to increased discrimination between

behavioral status pairs of conditions that are highly conflicting (Target vs. High-conflict nontarget), but not between behavioral categories that are less conflicting (Target vs. Low-conflict nontarget, High- vs. Low-conflict nontargets), demonstrating a conflict-contingent effect of reward. Classification accuracy is presented as percentage above chance (50%), averaged across all MD regions and both hemispheres, for no-reward (blue bars) and reward (red bars) trials. T: Target, HC: High-conflict nontarget, LC: Low-conflict nontarget Asterisks above bars show significant discrimination between behavioral 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 behavioral status conditions (One-tailed t-test, corrected for multiple comparisons (3)). **B.** Decoding results are shown for the individual MD regions, averaged across hemispheres. Plot conventions are the same as in A. The MD network template is shown for reference. pdLFC: posterior/dorsal lateral prefrontal cortex, IPS: intraparietal sulcus, preSMA: pre-supplementary motor area, ACC: anterior cingulate cortex, AI: anterior insula, FO: frontal operculum, aMFG, mMFG, pMFG: anterior, middle and posterior middle frontal gyrus, respectively. Errors bars indicate S.E.M. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, + $p < 0.05$ uncorrected.

Effects of reward motivation on behaviorally relevant 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 representation of the behavioral status distinctions in the visual cortex, we conducted similar univariate and MVPA analyses in the high-level general object visual region, the lateral occipital complex (LOC), separately for its two sub-regions, LO and pFs. We first conducted univariate analysis to test for an effect of reward and behavioral status on overall activity in LOC. An ROI univariate analysis did not show a change in BOLD response with reward in LOC. A four-way

repeated-measures ANOVA with reward (2), behavioral status (3), ROI (2), and hemisphere (2) as within-subject factors showed no main effect of reward ($F_{1,\ 23}$ = 1.12, p = 0.30). There was an interaction of reward and ROI ($F_{1,\ 23}$ = 7.78, p = 0.011), but post-hoc tests with correction for multiple (2) comparisons showed that activity 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 behavioral status ($F_{2,\ 23}$ = 9.64, p < 0.001), but no interaction of behavioral status and reward ($F_{2,\ 46}$ = 0.17, p = 0.85). Altogether, the univariate results show that reward did not lead to increased activity in LOC for any of the behavioral status conditions.

We then tested for the effect of reward on the representation of the task-related behavioral status conditions (Figure 4). MVPA results showed that classification accuracies were not larger for the reward conditions compared to the no-reward conditions for any of the behavioral status distinctions, with similar results for both LO and pFs [Four-way repeated-measures ANOVA with reward (2), behavioral distinction (3), ROIs (2) and hemispheres (2) as within-subject factors: no main effects or interactions (F < 3.06, p > 0.093)]. Averaged across LO and pFs, there was significant decoding of behavioral status above chance for all pairs of behavioral status levels, for both reward and no-reward conditions (One-tailed t-test, corrected for multiple (6) comparisons: t_{23} > 2.92, p < 0.015, d_z > 0.6, for all). Overall, these results demonstrate that, in contrast to the MD network, reward motivation did not modulate the coding of the task-related behavioral status distinctions in LOC.

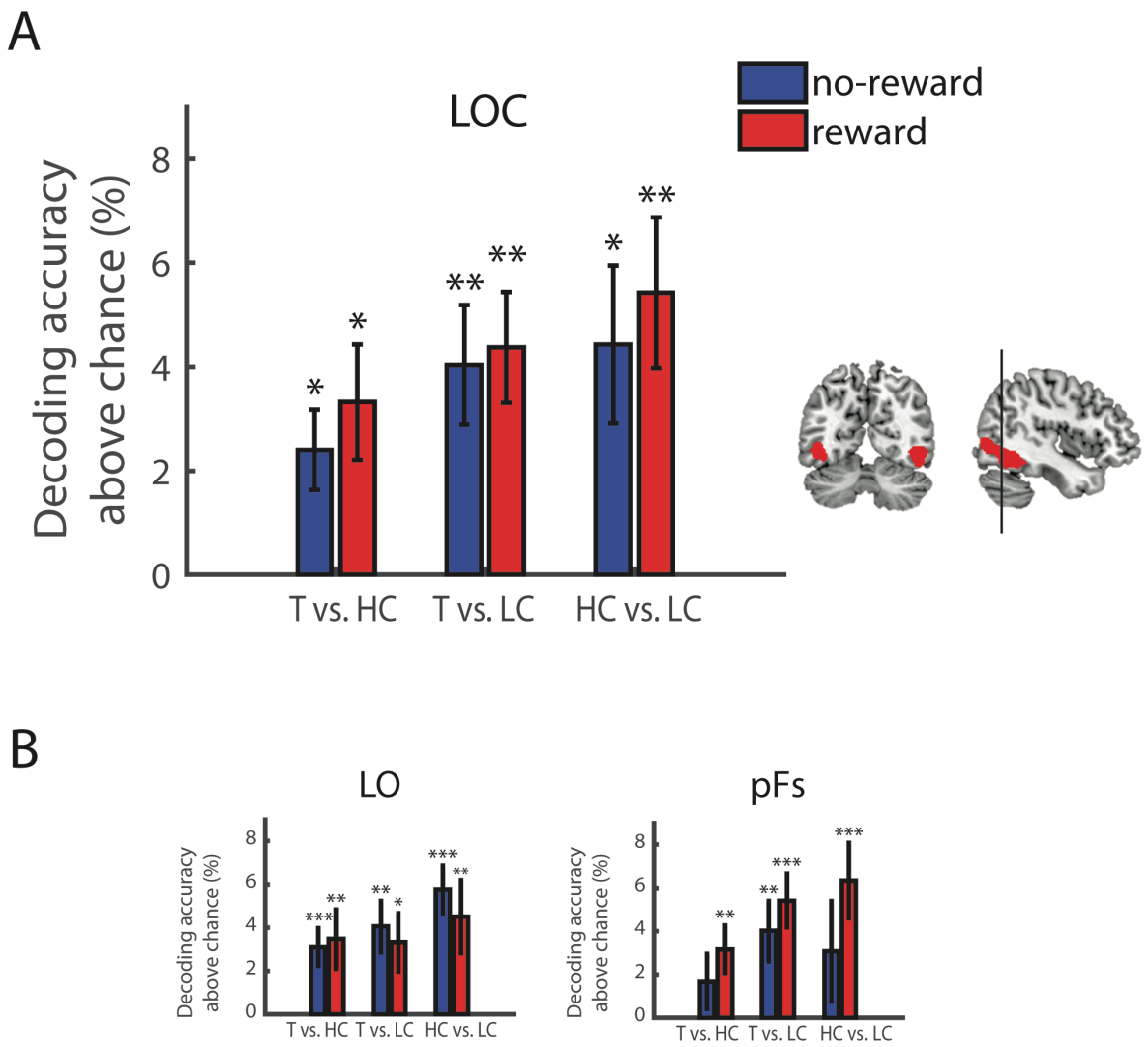


Figure 4: Reward motivation does not increase coding of behavioral status in LOC. A. Classification accuracies in LOC. Classification accuracies for no-reward (blue bars) and reward (red bars) conditions are similar for all three behavioral status distinctions. T: Target, HC: High-conflict nontarget, LC: Low-conflict nontarget. Classification accuracy is presented as percentage above chance (50%), averaged across LO and pFS and both hemispheres. Asterisks above bars show significant discrimination between behavioral status pairs above chance (One-tailed t-test against zero, corrected for multiple comparisons (6)). The LOC template is shown on sagittal and coronal planes, with a vertical line dividing it into posterior (LO) and anterior (pFs) regions. **B.** Classification accuracies for LO and pFs presented separately for each ROI, averaged across hemispheres. Plot conventions are the same as in A. Errors bars indicate S.E.M. * $p<0.05$, ** $p<0.01$, *** $p < 0.001$.

Conflict-contingent vs. visual category effects

An important aspect of the Target and High-conflict nontarget conditions in this experiment was that they both contained the same visual categories, which could be either a target or a nontarget (Figure 1B). Therefore, the Target vs. High-conflict nontarget pairs of conditions in our decoding analysis included cases where the stimuli in the two conditions were items from different visual categories (e.g. shoe and sofa following a 'shoe' cue), as well as cases where the two 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 Targets vs. High-conflict nontargets with reward in the MD network was driven by the task-related high conflict nature of the two conditions (conflict-contingent), or by the different visual categories of the stimuli. For each participant, the decoding accuracy for this behavioral status distinction was computed separately 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 the LOC regions, to test for an effect driven by the visual categorization 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 (repeated measures ANOVA with reward (2), distinction type (2, same or different visual category), ROIs (7 for MD, 2 for LOC) and hemispheres (2, just for LOC) as within-subject factors: $F < 3.1$, $p > 0.05$ for all interactions with ROI and hemisphere). Figure 5 shows Target vs. High-conflict nontarget distinctions separately for same and different visual categories for no-reward and reward conditions, for both the MD and LOC.

We first investigated the effects of the visual category distinction type and reward separately in each system. 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 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 similar ANOVA showed a main effect of 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).

We then tested for differential effects of distinction type and reward in the two systems. 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 no main effect of brain system ($F_{1, 23}$ = 1.59, p = 0.22), allowing us to compare between the two systems. Interestingly, an interaction between distinction type and system ($F_{1, 23}$ = 7.89, p = 0.01) suggested that decoding levels in the two systems might be affected differently by the visual category. We therefore conducted additional post-hoc tests (corrected for multiple comparisons) to unravel the simple effects that drive this dissociation. Classification accuracy across reward conditions was higher for different visual category pairs than same visual category pairs 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 = 0.7, d_z = 0.08, respectively). Additionally, in the MD network, decoding accuracy was not different for same and different visual category pairs, 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 pairs was larger in LOC than in the MD system (Two-tailed t test: t_{23} = 2.81, p = 0.01, d_z = 0.57). The ANOVA did not show an interaction of reward and system ($F_{1, 23}$ = 1.36, p = 0.26). Overall, these results demonstrate that the increase in decoding with reward motivation in the MD network was conflict-contingent rather than driven by the visual categories, while decoding accuracies in the LOC were primarily driven by the visual categories.

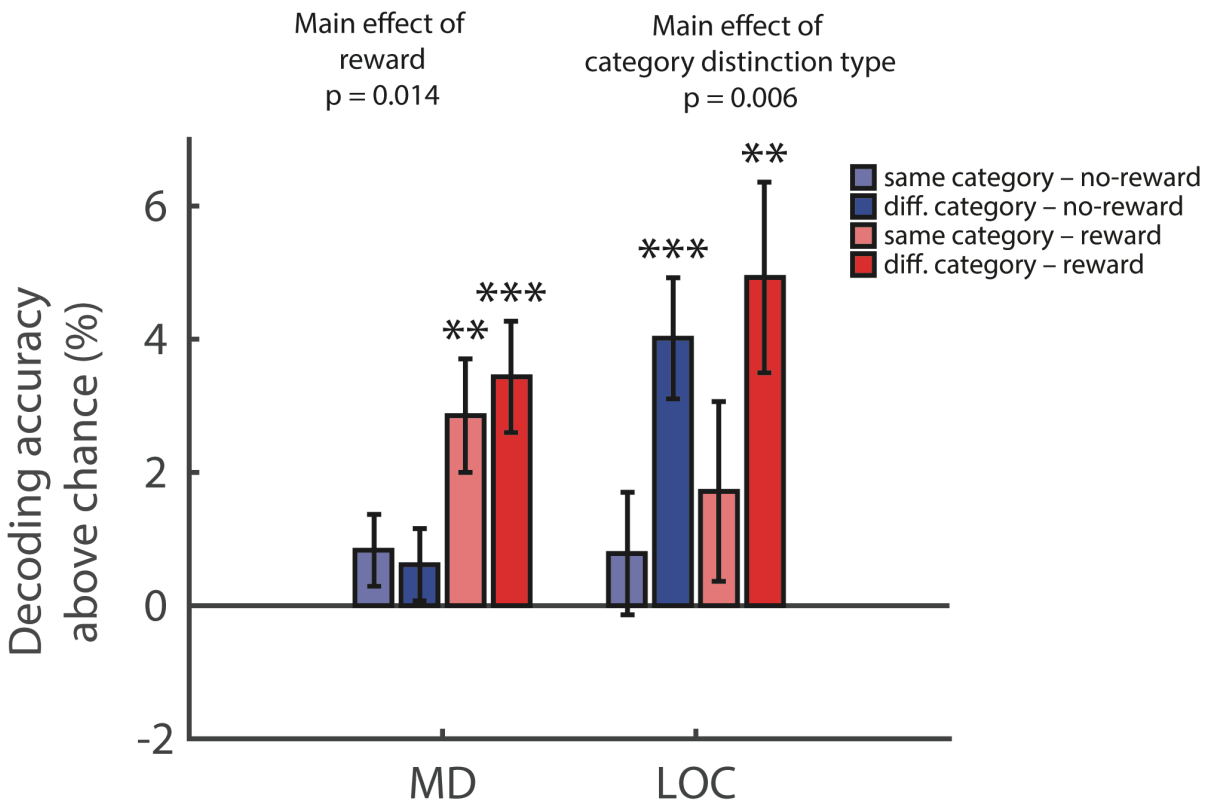


Figure 5: Reward modulation of decoding of highly conflicting behavioral status distinctions in the MD network and LOC. Classification accuracies above chance (50%) are presented for no-reward and same-visual-category distinctions (light blue), no-reward and different-visual-category distinctions (dark blue), reward and same-visual-category distinctions (light red), and reward and different-visual-category distinctions (dark red), separately for the MD network and the LOC, averaged across regions and hemispheres 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 coding of task-related behaviorally-relevant category distinctions in the frontoparietal MD network as reflected in distributed patterns of fMRI data. Participants detected whether an item belonged to a cued visual category. Two visual categories served as either targets or nontargets, depending on the cue. A third category was never cued and therefore was never a target. This design created three levels of behavioral status: Targets, High-conflict nontargets (that could be targets on other trials depending on the cue), and Low-conflict nontargets (never targets). Using MVPA, we showed that motivation, in the form of monetary reward, selectively enhances the distinctions between the three behavioral status conditions across the MD network. This selective effect was conflict-contingent: the distinction between behavioral status conditions increased with reward only for the highly conflicting ones, namely Targets and High-conflict nontargets, suggesting a facilitative effect of reward on conflict resolution only when it is most needed.

Previous reports showed an enhancement effect of motivation on overall activity in the frontoparietal control network (Botvinick & Braver, 2015; Dixon & Christoff, 2012; Padmala & Pessoa, 2011). 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 while cue and stimulus information are integrated. Importantly, these two effects of reward are complementary to one another, and both are key aspects of cognitive control and essential when reaching a decision. If reward enhances cue coding, then it would be reasonable to hypothesize that it may also facilitate the integration process of the cue and the subsequent stimulus that leads to a behavioral decision. Here, we showed that when monetary reward is introduced, the discrimination between task-related behavioral status distinctions following the cue is enhanced. This effect of reward does not affect all the distinctions between the behavioral status conditions similarly. The effect instead is conflict-contingent – reward enhances the distinction between conditions that are highly conflicting, 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 monitoring (Stürmer et al., 2011). Our results directly demonstrate this selective conflict-contingent effect on information representation. While our study included a cue phase during the trials, the cues (category names words) were chosen to allow high performance on the task rather than maximizing their decodability. The way the facilitative effect of reward on cue coding and the facilitative effect on the integrated cue and stimulus information interact with one another remains an open question.

Our findings provide support to the sharpening and prioritization account, which postulates that motivation leads to a sharpened neural representation of relevant information depending on the current task and needs. The sharpening aspect is reflected in the higher classification accuracies with reward in our data. Previous neurophysiological evidence provide support for this aspect: reward has been associated with firing of dopaminergic neurons (Bayer & Glimcher, 2005; Schultz, Dayan, & Montague, 1997), and dopamine has been shown to modulate tuning of prefrontal neurons and to sharpen their representations (Ott & Nieder, 2016; Thurley, Senn, & Lüscher, 2008; Vijayraghavan, Wang, Birnbaum, Williams, & Arnsten, 2007). The prioritization aspect can be related to the expected value of control (EVC) theory (Shenhav, Botvinick, & Cohen, 2013) and reward-based models for the interaction of reward and cognitive control, essentially a cost-benefit trade-off (Botvinick & 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 conflicting conditions showed a reward motivation modulatory effect. This could be interpreted as efficient prioritization of information processing, in which attentional resources are directed at increasing the discrimination between highly conflicting items only, which is the most effortful distinction between conditions, without investing resources in low-conflict distinctions where the required cognitive effort is lower. At the behavioral level, we observed some evidence for such a benefit of reward. Accuracy levels of performance in the task for Target trials were higher in the reward compared to the no-

reward condition. Additionally, while in the no-reward condition Target trials were less accurate than Low-conflict nontargets, in the reward condition there were no differences between them. We did not observe a similar benefit in reaction times. This could be due to the time threshold that we used for reward trials, which reduced the reaction time on all the reward trials, and may have masked an interaction with reward.

The neural mechanisms that underlie the selective effect of reward observed in our study are still unclear, and electrophysiology studies in non-human primates might provide some potential insights. A similar task with behavioral status distinctions of Targets, High-conflict nontargets and Low-conflict nontargets has been used to show predominantly two opponent types of coding in lateral prefrontal cortex neurons (Kusunoki et al., 2010). Patterns of activity showed highest firing rate for Targets, lowest for Low-conflict nontargets, and a medium firing rate level for the High-conflict nontargets, or the exact opposite with highest firing for Low-conflict nontargets and lowest for Targets. These results imply that the level of 'targetness' may be 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 Targets and High-conflict nontargets more distinct, with a smaller, or no effect, on activity related to the low-conflict distinction.

The conflict-contingent effect of reward motivation observed in our data was similar across the MD network, with no statistically significant differences between the regions within this *a priori* defined network. This is in line with previous studies that reported similar coding of task information across the MD network and equivalent frontoparietal areas associated with cognitive control (Erez & Duncan, 2015; Wisniewski et al., 2016; Woolgar et al., 2015). Effects of reward have been previously demonstrated across the frontoparietal cortex (Padmala and Pessoa 2011; Dixon and Christoff 2012; Botvinick and Braver 2015; Shashidhara et al., in press), as well as in particular regions (Hampton & O'doherty, 2007; Knutson, Taylor, Kaufman, Peterson, & Glover, 2005; Rushworth, Walton, Kennerley, & Bannerman, 2004; Shenhav et al., 2013). It is not unlikely, however, that the different MD regions have, at least in part, different functions (Badre & Nee, 2018; Crittenden, Mitchell, & Duncan, 2016; N. U. F. Dosenbach et al., 2007; Nico U F Dosenbach et al., 2006; Koechlin &

Summerfield, 2007; Nomura et al., 2010). Some evidence in this direction can be seen in our data. Increased decoding for the high-conflict distinction with reward was observed in some MD regions more than in others, and particularly in the anterior middle-frontal gyrus and the anterior insula and frontal operculum. This differential functionally did not reach statistical significance though, possibly because of the slow time course of the 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. Further studies are required to tease apart the different roles and functions of regions within MD network, and linking the evidence across studies is essential. The double-masking approach that we used in our study to localize the MD network in individual subjects ensures that the targeted areas are similar for all subjects (i.e., within the MD template) and therefore allows for comparability across participants and studies (Shashidhara et al., 2019).

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 category and behavioral status 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 (Erez & Duncan, 2015; Nelissen, Stokes, Nobre, & Rushworth, 2013; Soon, Brass, Heinze, & Haynes, 2008; Woolgar, Thompson, et al., 2011), and this may be possibly related to the functional organization at the neuronal population level (Bhandari, Gagne, & Badre, 2018; Dubois, de Berker, & Tsao, 2015). Importantly, we emphasize the change in coding when reward is introduced: the classification accuracy for the highly conflicting distinctions was larger for the reward than for the no-reward trials.

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 in the MD network, it was similar for all the behavioral status conditions. Importantly, the discrimination between the behavioral status pairs of conditions using MVPA was measured within each reward level, and not across. Therefore, univariate effects could not have driven the selective increase in the distinction between Targets and High-conflict nontargets that

we observed. Second, the effect was consistent across a range of ROI sizes used for voxel selection. Lastly, a different discriminability measure, LDC (Nili et al., 2014), yielded similar results to the ones obtained using the SVM analysis, with only negligible numerical differences which are reasonable given some level of noise in the data. We also note that that while overall reward trials were shorter than no-reward trials, the multivariate results that we observed are unlikely to be driven by these differences in reaction times. The GLM regressors were modelled for each trial from stimulus onset to response, thus removing the effect of time (Woolgar et al., 2014). Additionally, the reward showing higher univariate activity as well as increased multivariate discrimination would suggest that the shorter reaction times of the reward trials were not able to mask the effect of reward on neural activity.

The visual categorization 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 Target vs. High-conflict nontarget distinction in the MD regions but not in LOC. While all behavioral status distinctions were decodable in LOC, there was no change in decoding levels with reward. A subsequent analysis showed that, in the MD network, discrimination between the behavioral status pairs 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 decoding with reward observed in this study was not driven by it. In contrast, the discrimination in LOC was driven by the visual categories, with Targets and High-conflict nontargets being discriminable only when items 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 tested here are limited to the MD network and do not extend to LOC. Although previous studies have shown differences in representations between pFs and LO (Harel et al., 2014; Jiang et al., 2007; Li et al., 2007), our results were similar for both regions.

In summary, our results show that reward motivation enhances the representation of behaviorally relevant category distinctions across the MD network. This facilitative effect is conflict-contingent – reward modulated only the representation of highly conflicting behavioral status distinctions. Our findings provide another tier of evidence for the interaction between motivation and cognitive control, and support the idea of sharpening the 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, D. E. (2018). Frontal Cortex and the Hierarchical Control of Behavior. *Trends in Cognitive Sciences*, *22*(2), 170–188. https://doi.org/10.1016/j.tics.2017.11.005

Bayer, H. M., & Glimcher, P. W. (2005). Midbrain Dopamine Neurons Encode a Quantitative Reward Prediction Error Signal. *Neuron*, *47*(1), 129–141. https://doi.org/10.1016/J.NEURON.2005.05.020

Bhandari, A., Gagne, C., & Badre, D. (2018). Just above Chance: Is It Harder to Decode Information from Prefrontal Cortex Hemodynamic Activity Patterns? *Journal of Cognitive Neuroscience*, *30*(10), 1473–1498. https://doi.org/10.1162/jocn_a_01291

Botvinick, M., & Braver, T. (2015). Motivation and Cognitive Control: From Behavior to Neural Mechanism. *Annual Review of Psychology*, *66*, 80–113. https://doi.org/10.1146/annurev-psych-010814-015044

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/9176952

Braver, T. S. (2012). The variable nature of cognitive control: a dual mechanisms framework. *Trends in Cognitive Sciences*, *16*(2), 106–113. https://doi.org/10.1016/j.tics.2011.12.010

Brett, M., Anton, J.-L. L., 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*. https://doi.org/10.1016/S1053-8119(02)90010-8

Bugatus, L., Weiner, K. S., & Grill-Spector, K. (2017). Task alters category representations in prefrontal but not high-level visual cortex. *NeuroImage*, *155*, 437–449. https://doi.org/10.1016/J.NEUROIMAGE.2017.03.062

Carlin, J. D., & Kriegeskorte, N. (2017). Adjudicating between face-coding models with individual-face fMRI responses. *PLoS Computational Biology*, *13*(7), e1005604.

https://doi.org/10.1371/journal.pcbi.1005604

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

Cole, M. W., Ito, T., & Braver, T. S. (2016). The Behavioral Relevance of Task Information in Human Prefrontal Cortex. *Cerebral Cortex*, *26*(6), 2497–2505. https://doi.org/10.1093/cercor/bhv072

Crittenden, B. M., Mitchell, D. J., & Duncan, J. (2016). Task Encoding across the Multiple Demand Cortex Is Consistent with a Frontoparietal and Cingulo-Opercular Dual Networks Distinction. *Journal of Neuroscience*, *36*(23), 6147–6155. https://doi.org/10.1523/JNEUROSCI.4590-15.2016

Cusack, R., Vicente-Grabovetsky, A., Mitchell, D. J., Wild, C. J., Auer, T., Linke, A. C., & Peelle, J. E. (2014). Automatic analysis (aa): efficient neuroimaging workflows and parallel processing using Matlab and XML. *Frontiers in Neuroinformatics*, *8*, 90. https://doi.org/10.3389/fninf.2014.00090

Dixon, M. L., & Christoff, K. (2012). The Decision to Engage Cognitive Control Is Driven by Expected Reward-Value: Neural and Behavioral Evidence. *PLoS ONE*, *7*(12), e51637. https://doi.org/10.1371/journal.pone.0051637

Dosenbach, N. U. F., Fair, D. A., Miezin, F. M., Cohen, A. L., Wenger, K. K., Dosenbach, R. A. T., … Petersen, S. E. (2007). Distinct brain networks for adaptive and stable task control in humans. *Proceedings of the National Academy of Sciences*, *104*(26), 11073–11078. https://doi.org/10.1073/pnas.0704320104

Dosenbach, N. U. F., Visscher, K. M., Palmer, E. D., Miezin, F. M., Wenger, K. K., Kang, H. C., … Petersen, S. E. (2006). A Core System for the Implementation of Task Sets. *Neuron*, *50*(5), 799–812. https://doi.org/10.1016/j.neuron.2006.04.031

Dubois, J., de Berker, A. O., & Tsao, D. Y. (2015). Single-unit recordings in the macaque face patch

system reveal limitations of fMRI MVPA. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *35*(6), 2791–2802. https://doi.org/10.1523/JNEUROSCI.4037-14.2015

Duncan, J. (2010). The multiple-demand (MD) system of the primate brain: mental programs for intelligent behaviour. *Trends in Cognitive Sciences*, *14*(4), 172–179. https://doi.org/10.1016/j.tics.2010.01.004

Erez, Y., & Duncan, J. (2015). Discrimination of Visual Categories Based on Behavioral Relevance in Widespread Regions of Frontoparietal Cortex. *Journal of Neuroscience*, *35*(36), 12383–12393. https://doi.org/10.1523/JNEUROSCI.1134-15.2015

Erez, Y., & Yovel, G. (2014). Clutter Modulates the Representation of Target Objects in the Human Occipitotemporal Cortex. *Journal of Cognitive Neuroscience*, *26*(3), 490–500. https://doi.org/10.1162/jocn_a_00505

Etzel, J. A., Cole, M. W., Zacks, J. M., Kay, K. N., & Braver, T. S. (2016). Reward Motivation Enhances Task Coding in Frontoparietal Cortex. *Cerebral Cortex*, *26*(4), 1647–1659. https://doi.org/10.1093/cercor/bhu327

Fedorenko, E., Duncan, J., & Kanwisher, N. (2013). Broad domain generality in focal regions of frontal and parietal cortex. *Proceedings of the National Academy of Sciences*, *110*(41), 16616–16621. https://doi.org/10.1073/pnas.1315235110

Feinberg, D. A., Moeller, S., Smith, S. M., Auerbach, E., Ramanna, S., Gunther, M., … Yacoub, E. (2010). Multiplexed echo planar imaging for sub-second whole brain FMRI and fast diffusion imaging. *PloS One*, *5*(12), e15710. https://doi.org/10.1371/journal.pone.0015710

Freedman, D. J., Riesenhuber, M., Poggio, T., & Miller, E. K. (2001). Categorical Representation of Visual Stimuli in the Primate Prefrontal Cortex. *Science*, *291*(5502), 312–316. https://doi.org/10.1126/science.291.5502.312

Hampton, A. N., & O'doherty, J. P. (2007). Decoding the neural substrates of reward-related decision making with functional MRI. *Proceedings of the National Academy of Sciences of the United*

States of America, *104*(4), 1377–1382. https://doi.org/10.1073/pnas.0606297104

Harel, A., Kravitz, D. J., & Baker, C. I. (2014). Task context impacts visual object processing differentially across the cortex. *Proceedings of the National Academy of Sciences*, *111*(10), E962–E971. https://doi.org/10.1073/pnas.1312567111

Hebart, M. N., Bankson, B. B., Harel, A., Baker, C. I., & Cichy, R. M. (2018). The representational dynamics of task and object processing in humans. *ELife*, *7*. https://doi.org/10.7554/eLife.32816

Hebart, M. N., Görgen, K., & Haynes, J.-D. (2015). The Decoding Toolbox (TDT): a versatile software package for multivariate analyses of functional imaging data. *Frontiers in Neuroinformatics*, *8*, 88. https://doi.org/10.3389/fninf.2014.00088

Jiang, X., Bradley, E., Rini, R. A., Zeffiro, T., Vanmeter, J., & Riesenhuber, M. (2007). Categorization training results in shape- and category-selective human neural plasticity. *Neuron*, *53*(6), 891–903. https://doi.org/10.1016/j.neuron.2007.02.015

Kadohisa, M., Petrov, P., Stokes, M., Sigala, N., Buckley, M., Gaffan, D., … Duncan, J. (2013). Dynamic Construction of a Coherent Attentional State in a Prefrontal Cell Population. *Neuron*, *80*(1), 235–246. https://doi.org/10.1016/j.neuron.2013.07.041

Kennerley, S. W., & Wallis, J. D. (2009). Reward-dependent modulation of working memory in lateral prefrontal cortex. *Journal of Neuroscience*, *29*(10), 3259–3270. https://doi.org/10.1523/JNEUROSCI.5353-08.2009

Knutson, B., Taylor, J., Kaufman, M., Peterson, R., & Glover, G. (2005). Distributed Neural Representation of Expected Value. *Journal of Neuroscience*, *25*(19), 4806–4812. https://doi.org/10.1523/JNEUROSCI.0642-05.2005

Koechlin, E., & Summerfield, C. (2007). An information theoretical approach to prefrontal executive function. *Trends in Cognitive Sciences*, *11*(6), 229–235. https://doi.org/10.1016/j.tics.2007.04.005

Krebs, R. M., Boehler, C. N., Appelbaum, L. G., & Woldorff, M. G. (2013). Reward Associations

Reduce Behavioral Interference by Changing the Temporal Dynamics of Conflict Processing. *PLoS ONE*, *8*(1), e53894. https://doi.org/10.1371/journal.pone.0053894

Krebs, R. M., Boehler, C. N., Roberts, K. C., Song, A. W., & Woldorff, M. G. (2012). The involvement of the dopaminergic midbrain and cortico-striatal-thalamic circuits in the integration of reward prospect and attentional task demands. *Cerebral Cortex (New York, N.Y. : 1991)*, *22*(3), 607–615. https://doi.org/10.1093/cercor/bhr134

Kriegeskorte, N., Goebel, R., & Bandettini, P. (2006). Information-based functional brain mapping. *Proceedings of the National Academy of Sciences*, *103*(10), 3863–3868. https://doi.org/10.1073/pnas.0600244103

Kruglanski, A. W., Shah, J. Y., Fishbach, A., Friedman, R., Woo Young Chun, & Sleeth-Keppler, D. (2002). A theory of goal systems. *Advances in Experimental Social Psychology*, *34*, 331–378. https://doi.org/10.1016/S0065-2601(02)80008-9

Kusunoki, M., Sigala, N., Nili, H., Gaffan, D., & Duncan, J. (2010). Target Detection by Opponent Coding in Monkey Prefrontal Cortex. *Journal of Cognitive Neuroscience*, *22*(4), 751–760. https://doi.org/10.1162/jocn.2009.21216

Leon, M. I., & Shadlen, M. N. (1999). Effect of Expected Reward Magnitude on the Response of Neurons in the Dorsolateral Prefrontal Cortex of the Macaque. *Neuron*, *24*(2), 415–425. https://doi.org/10.1016/S0896-6273(00)80854-5

Li, S., Ostwald, D., Giese, M., & Kourtzi, Z. (2007). Flexible Coding for Categorical Decisions in the Human Brain. *Journal of Neuroscience*, *27*(45), 12321–12330. https://doi.org/10.1523/JNEUROSCI.3795-07.2007

MacEvoy, S. P., & Epstein, R. A. (2011). Constructing scenes from objects in human occipitotemporal cortex. *Nature Neuroscience*, *14*(10), 1323–1329. https://doi.org/10.1038/nn.2903

Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W. A., … Tootell, R. B. (1995). Object-related activity revealed by functional magnetic resonance imaging in human

occipital cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *92*(18), 8135–8139. https://doi.org/10.1073/PNAS.92.18.8135

Mante, V., Sussillo, D., Shenoy, K. V., & Newsome, W. T. (2013). Context-dependent computation by recurrent dynamics in prefrontal cortex. *Nature*, *503*(7474), 78–84. https://doi.org/10.1038/nature12742

Mitchell, D. J., Bell, A. H., Buckley, M. J., Mitchell, A. S., Sallet, J., & Duncan, J. (2016). A Putative Multiple-Demand System in the Macaque Brain. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *36*(33), 8574–8585. https://doi.org/10.1523/JNEUROSCI.0810-16.2016

Mohanty, A., Gitelman, D. R., Small, D. M., & Mesulam, M. M. (2008). The Spatial Attention Network Interacts with Limbic and Monoaminergic Systems to Modulate Motivation-Induced Attention Shifts. *Cerebral Cortex*, *18*(11), 2604–2613. https://doi.org/10.1093/cercor/bhn021

Muhle-Karbe, P. S., Duncan, J., De Baene, W., Mitchell, D. J., & Brass, M. (2017). Neural Coding for Instruction-Based Task Sets in Human Frontoparietal and Visual Cortex. *Cerebral Cortex*, *27*(3), 1891–1905. https://doi.org/10.1093/cercor/bhw032

Nelissen, N., Stokes, M., Nobre, A. C., & Rushworth, M. F. S. (2013). Frontal and parietal cortical interactions with distributed visual representations during selective attention and action selection. *Journal of Neuroscience*, *33*(42), 16443–16458. https://doi.org/10.1523/JNEUROSCI.2625-13.2013

Nili, H., Wingfield, C., Walther, A., Su, L., Marslen-Wilson, W., & Kriegeskorte, N. (2014). A Toolbox for Representational Similarity Analysis. *PLoS Computational Biology*, *10*(4), e1003553. https://doi.org/10.1371/journal.pcbi.1003553

Nomura, E. M., Gratton, C., Visser, R. M., Kayser, A., Perez, F., & D'Esposito, M. (2010). Double dissociation of two cognitive control networks in patients with focal brain lesions. *Proceedings of the National Academy of Sciences*, *107*(26), 12017–12022. https://doi.org/10.1073/pnas.1002431107

Ott, T., & Nieder, A. (2016). Dopamine D2 Receptors Enhance Population Dynamics in Primate Prefrontal Working Memory Circuits. *Cerebral Cortex*, *27*(9), 4423–4435. https://doi.org/10.1093/cercor/bhw244

Padmala, S., & Pessoa, L. (2010). Interactions between cognition and motivation during response inhibition. *Neuropsychologia*, *48*(2), 558–565. https://doi.org/10.1016/j.neuropsychologia.2009.10.017

Padmala, S., & Pessoa, L. (2011). Reward Reduces Conflict by Enhancing Attentional Control and Biasing Visual Cortical Processing. *Journal of Cognitive Neuroscience*, *23*(11), 3419–3432. https://doi.org/10.1162/jocn_a_00011

Pessoa, L. (2009). How do emotion and motivation direct executive control? *Trends in Cognitive Sciences*, *13*(4), 160–166. https://doi.org/10.1016/j.tics.2009.01.006

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

Rushworth, M. F. S., Walton, M. E., Kennerley, S. W., & Bannerman, D. M. (2004). Action sets and decisions in the medial frontal cortex. *Trends in Cognitive Sciences*, *8*(9), 410–417. https://doi.org/10.1016/j.tics.2004.07.009

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

Shashidhara, S., Spronkers, F. S., & Erez, Y. (2019). Localizing the “multiple-demand” frontoparietal network in individual subjects. *BioRxiv*. https://doi.org/10.1101/661934

Shenhav, A., Botvinick, M. M., & Cohen, J. D. (2013). The expected value of control: An integrative theory of anterior cingulate cortex function. *Neuron*, *79*(2), 217–240. https://doi.org/10.1016/j.neuron.2013.07.007

Simon, H. A. (1967). Motivational and emotional controls of cognition. *Psychological Review*, *74*(1),

29–39. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/5341441

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

Stokes, M. G., Kusunoki, M., Sigala, N., Nili, H., Gaffan, D., & Duncan, J. (2013). Dynamic coding for cognitive control in prefrontal cortex. *Neuron*, *78*(2), 364–375. https://doi.org/10.1016/j.neuron.2013.01.039

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

Taylor, S. F., Welsh, R. C., Wager, T. D., Luan Phan, K., Fitzgerald, K. D., & Gehring, W. J. (2004). A functional neuroimaging study of motivation and executive function. *NeuroImage*, *21*(3), 1045–1054. https://doi.org/10.1016/J.NEUROIMAGE.2003.10.032

Thurley, K., Senn, W., & Lüscher, H.-R. (2008). Dopamine Increases the Gain of the Input-Output Response of Rat Prefrontal Pyramidal Neurons. *Journal of Neurophysiology*, *99*(6), 2985–2997. https://doi.org/10.1152/jn.01098.2007

van der Kouwe, A. J. W., Benner, T., Salat, D. H., & Fischl, B. (2008). Brain morphometry with multiecho MPRAGE. *NeuroImage*, *40*(2), 559–569. https://doi.org/10.1016/j.neuroimage.2007.12.025

Vergauwe, E., & Cowan, N. (2015). Attending to items in working memory: evidence that refreshing and memory search are closely related. *Psychonomic Bulletin & Review*, *22*(4), 1001–1006. https://doi.org/10.3758/s13423-014-0755-6

Vijayraghavan, S., Wang, M., Birnbaum, S. G., Williams, G. V, & Arnsten, A. F. T. (2007). Inverted-U dopamine D1 receptor actions on prefrontal neurons engaged in working memory. *Nature Neuroscience*, *10*(3), 376–384. https://doi.org/10.1038/nn1846

Wallace, A. F. C. (1960). : Plans and the Structure of Behavior . George A. Miller, Eugene Galanter, Karl H. Pribram. *American Anthropologist*, *62*(6), 1065–1067. https://doi.org/10.1525/aa.1960.62.6.02a00190

Wallis, J. D., Anderson, K. C., & Miller, E. K. (2001). Single neurons in prefrontal cortex encode abstract rules. *Nature*, *411*(6840), 953–956. https://doi.org/10.1038/35082081

Watanabe, M. (1996). Reward expectancy in primate prefrental neurons. *Nature*, *382*(6592), 629–632. https://doi.org/10.1038/382629a0

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. https://doi.org/10.1016/J.NEUROIMAGE.2016.04.044

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. https://doi.org/10.1016/j.neuroimage.2014.04.059

Woolgar, A., Hampshire, A., Thompson, R., & Duncan, J. (2011). Adaptive Coding of Task-Relevant Information in Human Frontoparietal Cortex. *Journal of Neuroscience*, *31*(41), 14592–14599. https://doi.org/10.1523/JNEUROSCI.2616-11.2011

Woolgar, A., Thompson, R., Bor, D., & Duncan, J. (2011). Multi-voxel coding of stimuli, rules, and responses in human frontoparietal cortex. *NeuroImage*, *56*(2), 744–752. https://doi.org/10.1016/j.neuroimage.2010.04.035

Woolgar, A., Williams, M. A., & Rich, A. N. (2015). Attention enhances multi-voxel representation of novel objects in frontal, parietal and visual cortices. *NeuroImage*, *109*, 429–437. https://doi.org/10.1016/j.neuroimage.2014.12.083

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. This work was also supported by the Medical Research Council (UK) Intramural Program MC-A060-5PQ10. We thank John Duncan and Daniel Mitchell for fruitful discussions and advice throughout the study.

The authors declare no competing financial interests.