

# Adaptive Coding of Task-Relevant Information in Human Frontoparietal Cortex

Alexandra Woolgar, Adam Hampshire, Russell Thompson, and John Duncan

Medical Research Council Cognition and Brain Sciences Unit, Cambridge, CB2 7EF, United Kingdom

Frontoparietal cortex is thought to be essential for flexible behavior, but the mechanism for control remains elusive. Here, we demonstrate a potentially critical property of this cortex: its dynamic configuration for coding of task-critical information. Using multivoxel pattern analysis of human functional imaging data, we demonstrate an adaptive change in the patterns of activation coding task-relevant stimulus distinctions. When task demands made perceptual information more difficult to discriminate, frontoparietal regions showed increased coding of this information. Visual cortices showed the opposite result: a weaker representation of perceptual information in line with the physical change in the stimulus. On a longer timescale, a rebalancing of coding was also seen after practice, with a diminished representation of task rules as they became familiar. The results suggest a flexible neural system, exerting cognitive control in a wide range of tasks by adaptively representing the task features most challenging for successful goal-directed behavior.

## Introduction

Frontoparietal cortex is important in cognitive control, but the mechanism for control remains elusive. A critical component may be selective attention to task-relevant information. On this view, cells in many frontal and parietal regions show highly dynamic response properties, selectively coding the information required for current behavior (Duncan, 2001). This adaptive frontoparietal representation may serve as a source of bias to other brain systems, driving widespread focus on task-relevant processing (Desimone and Duncan, 1995; Dehaene et al., 1998; Miller and Cohen, 2001).

Support comes from single-unit data in the behaving monkey. Activity of frontal and parietal cells represents many different task features, including stimuli, responses, rules, and rewards (Sakagami and Niki, 1994; Asaad et al., 1998; White and Wise, 1999; Wallis et al., 2001; Stoet and Snyder, 2004). Changes in task relevance bring corresponding changes in cell activity (Freedman et al., 2001; Freedman and Assad, 2006).

In human functional imaging, selected regions of frontoparietal cortex show similar response to many different kinds of cognitive demand, including perceptual discrimination, response conflict, working memory, and more (Duncan and Owen, 2000; Nyberg et al., 2003; Dosenbach et al., 2006; Duncan, 2006). Included among these “multiple-demand” or MD regions (Dun-

can, 2006) are inferior frontal sulcus (IFS), anterior insula/frontal operculum (AI/FO), dorsal anterior cingulate/presupplementary motor area (ACC/pre-SMA), and intraparietal sulcus (IPS). Such regions are strong candidates for adaptive involvement in cognitive control (Miller and Cohen, 2001; Dosenbach et al., 2006). Recent work using multivoxel pattern analysis (MVPA) suggests that MD regions code many different task features. In MVPA, coding is revealed by regularities in fine-grained activity patterns evoked by different stimulus events (Haynes and Rees, 2006). The voxelwise pattern of activity in frontoparietal regions can discriminate task-relevant visual features (Li et al., 2007), task sets (Bode and Haynes, 2009) and rules (Haynes et al., 2007). Using a simple stimulus–response task, Woolgar et al. (2011) demonstrated MD coding of all task features necessary for behavior: stimulus position, stimulus–response mapping rule, and response.

The adaptive coding hypothesis predicts that frontoparietal representations will dynamically adjust to task demands. Much previous work shows increased MD activity with increasing demand (Duncan and Owen, 2000; Duncan 2006). Here we use MVPA to explore whether these regions also show improved discrimination of demanding task features. We predicted that, as the processing demand of some task feature increases, MD representations should adjust to give improved attention to, or coding of, that feature. To address this, we varied the perceptual demands of a stimulus–response task. Strikingly, we found improved MD discrimination of different stimulus positions when they were more similar, i.e., when behaviorally they were more difficult to distinguish. Second, we analyzed MD representations after participants became familiar with the task through practice. The result was a rebalancing of MD resources: when task rules were unfamiliar they were strongly coded in MD activity, but rule coding diminished with experience. Our results confirm an extensive pattern of dynamic representation in frontoparietal cortex, with selective focus on demanding aspects of current behavior.

Received May 24, 2011; revised July 28, 2011; accepted Aug. 16, 2011.

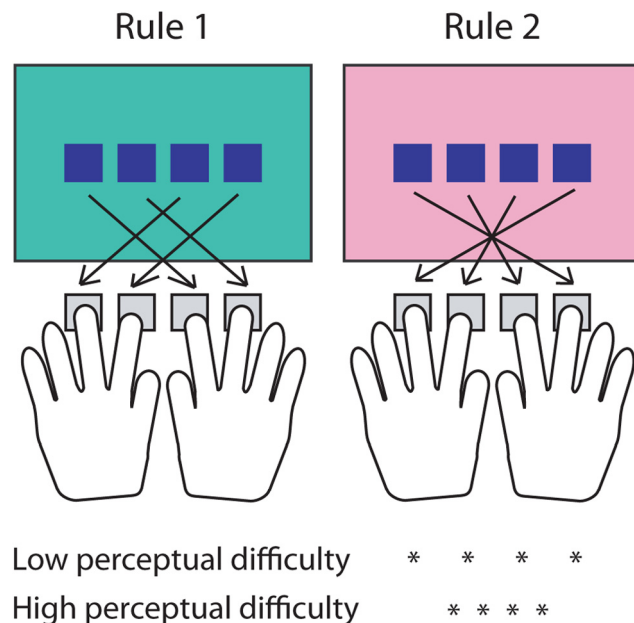
Author contributions: A.W., R.T., and J.D. designed research; A.W. and A.H. performed research; A.W. analyzed data; A.W. and J.D. wrote the paper.

This work was funded by the Medical Research Council (United Kingdom) intramural program (MC\_US\_A060\_0001). A.W. was supported by a Domestic Research Studentship/Millennium Scholarship funded by the University of Cambridge and the Newton Trust. Web-based participant training was supported by the Cambridge Brain Sciences website.

Correspondence should be addressed to Alexandra Woolgar at her present address: Macquarie Centre for Cognitive Science, Macquarie University, Sydney, New South Wales 2109, Australia. E-mail: alexandra.woolgar@mq.edu.au.

DOI:10.1523/JNEUROSCI.2616-11.2011

Copyright © 2011 the authors 0270-6474/11/3114592-08\$15.00/0



**Figure 1.** Stimulus–response task. There were two incompatible stimulus–response mappings between the four stimulus positions and the four response keys. The background color of the screen indicated which rule to use on the current trial: green indicated rule 1, and pink indicated rule 2. Participants responded with the index and middle finger of each hand. On low perceptual difficulty blocks, the four stimulus positions were separated by 3°; on high difficulty blocks, this was reduced to 1°.

## Materials and Methods

**Participants.** Eighteen participants (10 female; mean  $\pm$  SD age, 22.9  $\pm$  3.84 years) were recruited from the Medical Research Council Cognition and Brain Sciences Unit volunteer panel. Participants were right handed and had normal or corrected-to-normal vision. All participants gave written informed consent to take part and were reimbursed for their time. The study was approved by the Hertfordshire Local Research Ethics Committee.

**Task design.** Participants were scanned while performing a simple visual stimulus–response task that we used previously to separate coding of visual stimulus features, task rules, and button-press responses (Woolgar et al., 2011). On each trial, the stimulus was a blue square measuring  $\sim 2 \times 2^\circ$  presented on a projector and viewed through a head-coil-mounted mirror in the scanner. It could appear in one of four positions, which were indicated at the start of each block by four white squares with a black outline. The four positions were arranged in a horizontal row in the center of the screen. Participants responded by pressing one of four response keys using index and middle fingers from each hand. There were two incompatible stimulus–response mappings between the four stimulus positions and the four response keys (Fig. 1). The current rule to use was indicated by the background color of the screen: green indicated rule 1, and pink indicated rule 2.

To manipulate perceptual difficulty, we varied the distance between the four stimulus positions (Fig. 1). In blocks of low perceptual difficulty, adjacent stimulus positions were separated by 3° (center to center); in blocks of high perceptual difficulty, this was reduced to 1°.

Participants learned the rules outside the scanner and practiced the task for 20 min before each scanning session. Practice blocks alternated between high and low perceptual difficulty (five blocks of each), each lasting 2 min. Within each block, the eight stimuli (four positions  $\times$  two background colors) were presented in random order. Participants were instructed to respond as quickly as possible without making any mistakes and were shown feedback (number of trials completed and percentage correct) after each block of trials.

**Acquisition.** fMRI data were acquired using a Siemens 3 T TimTrio scanner with a 12-channel head coil. We used a sequential descending T2\*-weighted echo planar imaging (EPI) acquisition sequence with the

following parameters: acquisition time, 2000 ms; echo time, 30 ms; 32 oblique axial slices with a slice thickness of 3.0 mm and a 0.75 mm interslice gap; in-plane resolution,  $3.0 \times 3.0$  mm; matrix,  $64 \times 64$ ; field of view, 192 mm; flip angle, 78°. T1-weighted MPRAGE structural images were also acquired for all participants (slice thickness, 1.0 mm; resolution,  $1.0 \times 1.0 \times 1.5$  mm; field of view, 256 mm; 160 slices).

Participants performed alternating blocks of high and low perceptual difficulty; block order was counterbalanced across subjects. The block type (high or low difficulty) and the corresponding stimulus positions were cued at the start of each block. Within each block, the eight stimuli (four positions  $\times$  two background colors) were presented in random order. Stimuli remained visible until the participant responded. There was an interval of 1000 ms between response and display of the subsequent stimulus, during which time the screen was white. Participants performed four runs of 10 blocks over two scanning sessions. Block length was fixed at 2 min, in which time participants completed a varying number of trials (mean  $\pm$  SD number of trials per session, 975  $\pm$  166). There was a 20 s gap between blocks. The EPI time was 46 min 36 s per session.

The two scanning sessions were 1 week apart, and participants practiced the task for 20 min per day over the Internet for the 6 intervening days. Practice sessions consisted of 10 blocks of trials, identical to a single scanning run except that, during practice, auditory feedback (single high tone for correct, double low tone for incorrect) was given on each trial.

**Analysis.** A combination of univariate and multivariate analyses techniques were used to explore complementary aspects of the data. Conventional univariate analyses examined overall differences in BOLD response in high and low perceptual difficulty conditions and in the two scanning sessions. MVPA was used to discriminate fine-grained activation patterns pertaining to different task features. Three task features were investigated: stimulus position, rule, and response. Because position and response were partially confounded, we compared inner with outer positions (which have equal contributions from each of the four responses and each of the two rules) and inner with outer responses (which have equal contributions from each of the four stimulus positions, each of the two hands, and each of the two rules). Multivoxel coding of each task feature was compared between high and low perceptual difficulty conditions and between the two scanning sessions using ANOVA. Because the central aim of the study was to investigate the representational content of MD cortex, the main analyses focused on prefrontal and parietal regions of interest (see below). Whole-brain analyses were also performed using a searchlight method (Kriegeskorte et al., 2006) to identify any additional regions showing task-relevant feature coding.

**Preprocessing.** Image realignment, slice timing correction, and coregistration to structural images was performed using Automatic Analysis version 2.0 for SPM5 (<http://imaging.mrc-cbu.cam.ac.uk/imaging/AutomaticAnalysisIntroduction>). For univariate analyses, data were additionally normalized (simultaneous gray/white matter segment and normalize) and smoothed (10 mm FWHM Gaussian kernel) using the same software. In all cases, data were high-pass filtered (128 s).

**Regions of interest.** MD regions of interest (ROIs) were defined using data from a previous review of activity associated with a diverse set of cognitive demands (Duncan and Owen, 2000). We used the kernel method described by Cusack et al. (2010). To ensure symmetrical ROIs, all peaks from the original review were first projected onto a single hemisphere. A point was placed at the location of each peak, and the resulting image was smoothed (15 mm FWHM Gaussian kernel) and thresholded at 3.5 times the height of a single smoothed point. The resulting regions were then duplicated in the opposite hemisphere by reflection across the midline. A plane at the local minimum was used to divide lateral prefrontal regions into a more dorsal part, in and around the IFS, and a more ventral part, focused around the AI/FO. The two left and right medial ROIs abutting each other at the midline were unified into a single ACC/pre-SMA region. The procedure yielded a total of seven ROIs (see Fig. 3): left and right IFS (center of mass,  $\pm 38, 26, 24$ ; volume, 17,000 mm<sup>3</sup>); left and right AI/FO ( $\pm 35, 19, 3$ ; 3000 mm<sup>3</sup>); left and right IPS ( $\pm 35, -58, 41$ ; 7000 mm<sup>3</sup>), and ACC/pre-SMA (0, 23, 39; 21,000 mm<sup>3</sup>). In addition, left and right visual cortex ROIs were derived from the Brodmann tem-

plate provided with MRICro (Rorden and Brett, 2000): Brodmann area (BA) 17/18 (center of mass,  $-13, -81, 3$ ;  $16, -79, 3$ ; volume,  $54,000 \text{ mm}^3$ ). All coordinates are given in MNI152 space (McConnell Brain Imaging Centre, Montreal Neurological Institute).

**Univariate analyses.** Univariate analyses compared task-related activity in the two perceptual difficulty conditions and two sessions using a factorial ANOVA. The standard multiple regression approach of SPM5 (Wellcome Department of Imaging Neuroscience, London, UK; [www.fil.ion.ucl.ac.uk](http://www.fil.ion.ucl.ac.uk)) was used to estimate  $\beta$  values pertaining to the high and low perceptual difficulty conditions in each of the four runs separately. Trials were modeled as epochs lasting from stimulus onset until response. Movement parameters and run means were included as covariates of no interest. Whole-brain analyses compared voxelwise BOLD response in the two difficulty conditions and the two sessions using a two-way ANOVA with factors difficulty (high, low) and session (session 1, session 2). For ROI analyses,  $\beta$  estimates were averaged across each region. An additional factor, region (ACC/pre-SMA, IFS, AI/FO, and IPS; data collapsed across hemisphere when appropriate), was included in ROI-based ANOVAs. Additionally, to check for any univariate changes that might contribute to differences in multivoxel coding between perceptual difficulty conditions or between sessions, three four-way ANOVAs were also performed, one for each task feature. These had the following factors: task feature level (e.g., rule 1, rule 2), region (ACC/pre-SMA, IFS, AI/FO, and IPS), difficulty (high, low), and session (session 1, session 2). For this analysis,  $\beta$  estimates were derived as described below for multivariate analyses, using normalized and smoothed data.

**Multivoxel pattern analyses.** Multivoxel pattern analyses were performed using MultiVariate Pattern Analysis in Python (PyMVPA) software (Hanke et al., 2009), in which support vector machine classification is implemented by wrapping the LIBSVM library (Chang and Lin, 2011). We used a linear support vector machine, LinearCSVMC (<http://www.pympva.org/api/mvpa.cifs.svm.LinearCSVMC-class.html>; cost parameter  $C = 1$ ).  $\beta$  estimation and second-level random-effects analyses were performed using SPM5 (Wellcome Department of Imaging Neuroscience; [www.fil.ion.ucl.ac.uk](http://www.fil.ion.ucl.ac.uk)).

The standard multiple regression approach of SPM5 (Wellcome Department of Imaging Neuroscience; [www.fil.ion.ucl.ac.uk](http://www.fil.ion.ucl.ac.uk)) was used to estimate  $\beta$  values pertaining to inner and outer positions, inner and outer responses, rule 1 and rule 2, in each of the 40 blocks. Trials were again modeled as epochs lasting from stimulus onset until response, and each trial contributed to the estimation of three  $\beta$  values (inner or outer stimulus position, inner or outer response, and rule 1 or rule 2). Error trials were excluded from analyses.

ROI analyses proceeded as follows. For each participant, the nine ROIs were deformed by applying the inverse of the participant's normalization parameters. This allowed us to perform pattern classification analysis directly on the native space data for each participant. For each participant, classification of position was performed in each of the high and low perceptual difficulty conditions and each of the two sessions separately. For a given ROI, the pattern of  $\beta$  values across the relevant voxels was extracted from each of the 20 relevant  $\beta$  images (e.g., 10 blocks of low perceptual difficulty in session 1  $\times$  two positions), yielding 20 multivoxel vectors. One hundred percent of the voxels in each ROI contributed to each vector, without feature selection. The linear support vector machine was trained to discriminate between the vectors pertaining to inner positions and those pertaining to outer positions. We used a leave-one-out 10-fold splitter: the classifier was trained using the data from 9 of the 10 blocks and was subsequently tested on its accuracy at classifying the unseen data from the remaining block. This process was performed in 10 iterations, using all 10 possible combinations of train and test blocks. The classification accuracies from the 10 iterations were then averaged to give a mean accuracy score for that participant. This procedure was repeated for each feature (position, rule, response), for each level of difficulty (high, low), and each session (session 1, session 2).

For each task feature, classification accuracies from each participant were then entered into three-way ANOVAs with factors perceptual difficulty (high, low), session (session 1, session 2), and region (ACC/pre-SMA, IFS, AI/FO, and IPS; data collapsed across hemisphere as appropriate). When appropriate, the relevant ANOVA was also run in each region individually. To explore any hemisphere effects, we ran an

**Table 1. RT and percentage correct scores for low and high perceptual difficulty conditions in session 1 and session 2**

	Low, session 1		High, session 1		Low, session 2		High, session 2	
	RT (ms)	%	RT (ms)	%	RT (ms)	%	RT (ms)	%
Mean	1094	96.3	1564	88.0	798	96.4	1078	90.3
Rule 1	1206	95.1	1728	84.8	853	96.0	1169	89.1
Rule 2	982	97.5	1401	91.2	742	96.7	986	91.5
Position inner	1126	96.1	1553	91.1	808	96.9	1092	91.6
Position outer	1061	96.6	1575	85.0	787	95.8	1063	89.0
Response inner	1098	96.3	1565	88.0	804	96.3	1057	90.0
Response outer	1089	96.4	1563	88.1	791	96.4	1098	90.6

additional ANOVA with factors region (IFS, AI/FO, IPS), difficulty (high, low), session (session 1, session 2), and hemisphere (left, right). Finally, to compare coding of the different task features and whether this changed with perceptual difficulty or practice, we ran a single four-way ANOVA with factors perceptual difficulty (high, low), session (session 1, session 2), region (IFS, AI/FO, ACC/pre-SMA, IPS), and task feature (position, rule, response).

To identify any additional regions showing flexible coding of task-relevant information and to be sensitive to more restricted regions of information coding, pattern classification was also performed across the whole brain using a roaming spotlight (Kriegeskorte et al., 2006). For each participant, data were extracted from a spherical ROI (radius, 5 mm; volume, 19 voxels) centered in turn on each voxel in the brain. A linear support vector machine was trained and tested as before, using data from each sphere, and the classification accuracy value for that sphere was assigned to the central voxel. This yielded whole-brain classification accuracy maps for each individual for each task feature in each condition and session separately. To combine data across individuals, classification accuracy maps were normalized by applying the normalization parameters extracted at the preprocessing stage of the univariate analyses and were subsequently smoothed using a 10 mm FWHM Gaussian kernel. For each feature, these data were entered into a two-way ANOVA equivalent to that described for the ROI analyses. All whole-brain results were thresholded at  $p < 0.01$ , with false discovery rate correction, with an extent threshold of 100 voxels.

## Results

### Behavioral results

Behavioral data are shown in Table 1. As expected, reaction times (RTs) were substantially longer, and accuracy lower, in the high perceptual difficulty condition. RTs also decreased with practice. Rule 2 was appreciably easier than rule 1, whereas there were only minor differences between inner and outer stimulus positions or between inner and outer responses.

Data were analyzed using a series of three-way ANOVAs. In the first analyses, the factors were perceptual difficulty (low, high), session (session 1, session 2), and rule (rule 1, rule 2). Participants were significantly slower (main effect of difficulty,  $F_{(1,17)} = 84.3, p < 0.001$ ) and less accurate ( $F_{(1,17)} = 30.8, p < 0.001$ ) in the high perceptual difficulty condition. There was also a significant main effect of session on reaction time ( $F_{(1,17)} = 29.3, p < 0.001$ ), indicating that participants were significantly faster after practice. There was no main effect of session on percentage correct ( $F_{(1,17)} = 1.77, p = 0.20$ ). The difference in reaction time attributable to the perceptual difficulty manipulation was significantly reduced in the second session (session  $\times$  difficulty interaction,  $F_{(1,17)} = 27.5, p < 0.001$ ), although it was still highly significant (two-way ANOVA on RT data from second session, main effect of difficulty,  $F_{(1,17)} = 36.0, p < 0.001$ ). For percentage correct, the session  $\times$  difficulty interaction was marginally significant ( $F_{(1,17)} = 3.93, p = 0.06$ ), with the trend in the same direction. Finally, participants were faster and more accu-

rate in rule 2 compared with rule 1 (RT,  $F_{(1,17)} = 31.4$ ,  $p < 0.001$ ; accuracy,  $F_{(1,17)} = 21.9$ ,  $p < 0.001$ ).

A second set of analyses was identical but replacing the rule factor with stimulus position (inner vs outer). Results for difficulty and session factors were necessarily identical to those described above. Participants tended to be more accurate in responding to inner positions ( $F_{(1,17)} = 8.06$ ,  $p = 0.011$ ), although there was no difference in reaction times ( $F_{(1,17)} = 1.08$ ,  $p = 0.31$ ). In a final set of analyses, the third factor was response rather than stimulus position. There was no significant effect of this factor in either speed or accuracy (RT,  $F_{(1,17)} = 0.10$ ,  $p = 0.76$ ; accuracy,  $F_{(1,17)} = 0.13$ ,  $p = 0.73$ ).

### Univariate results

Univariate analyses compared MD BOLD responses in the high and low difficulty conditions and the two sessions (see Materials and Methods). Given our a priori hypothesis, analyses were performed first on an ROI basis. This was also supplemented by a more exploratory whole-brain analysis.

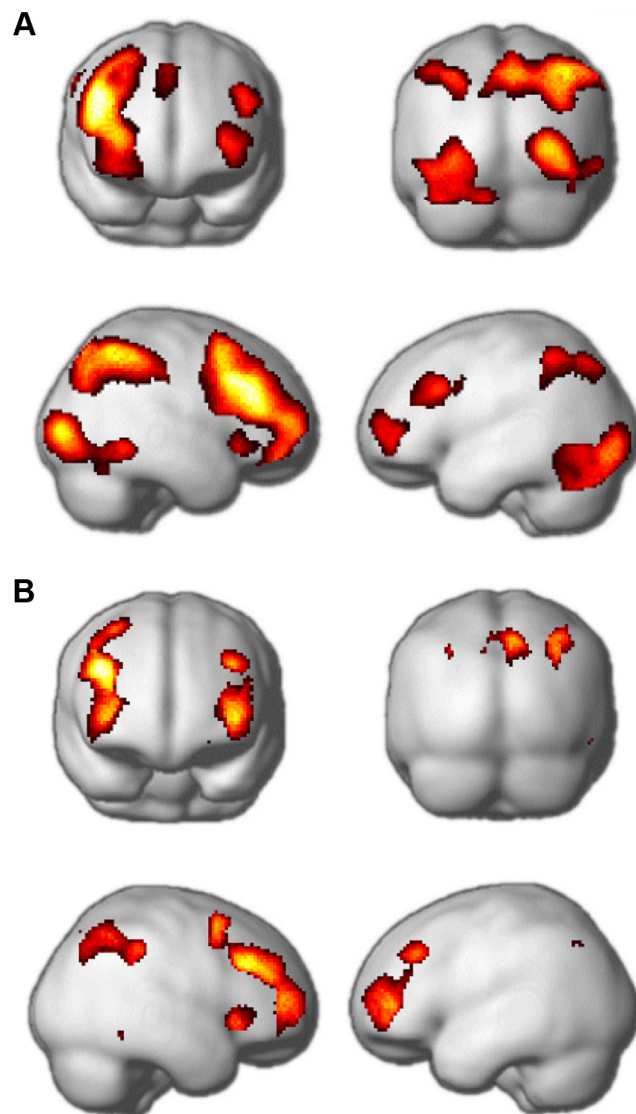
To compare MD activation in the high and low difficulty conditions, we performed an ANOVA with factors difficulty (high, low), session (session1, session 2), and region (IFS, AI/FO, ACC/pre-SMA, and IPS; averaged across hemisphere when appropriate). The ROI analysis revealed significantly greater MD activity overall in the high compared with low difficulty condition (main effect of difficulty,  $F_{(1,17)} = 14.0$ ,  $p = 0.002$ ). This difference was also significant in the IFS ( $F_{(1,17)} = 22.4$ ,  $p < 0.001$ ), AI/FO ( $F_{(1,17)} = 5.66$ ,  $p = 0.029$ ), and IPS ( $F_{(1,17)} = 29.3$ ,  $p < 0.001$ ) individually. The whole-brain analysis similarly showed regions of increased activation for the high perceptual difficulty condition in a large area of the left and right lateral frontal surfaces (peaks: 44, 30, 34, BA 45; 46, 20, 38, BA 44; –46, 28, 34, BA 45; –40, 6, 34, BA 44), the ACC/pre-SMA (peak: 6, 30, 44, BA 8), and left and right IPS (peaks: 40, –52, 46, BA 40; –30, –52, 42, BA 40), as well as left and right higher visual cortex (peaks: 30, –90, 2, BA 18; –32, –90, –6, BA 19) (Fig. 2A).

A significant main effect of session in the same ANOVA indicated that task-related MD activity was reduced overall in the second session ( $F_{(1,17)} = 6.31$ ,  $p = 0.022$ ), as expected. This difference was also significant in the IPS ROI individually ( $F_{(1,17)} = 14.8$ ,  $p = 0.001$ ) and approached significance in the IFS ( $F_{(1,17)} = 4.23$ ,  $p = 0.055$ ) and AI/FO ( $F_{(1,17)} = 3.82$ ,  $p = 0.067$ ). The whole-brain analyses mimicked these results, showing greater task-related BOLD signal in the first session in the left and right lateral frontal surface (peaks: 44, 32, 36, BA 45; 40, 42, 28, BA 46; –42, 54, –2, BA 46) and right IPS (peak: 12, –64, 44, BA 7) (Fig. 2B). There was no session  $\times$  difficulty interaction ( $F_{(1,17)} < 0.01$ ,  $p = 0.995$ ).

To check for any univariate activation that might contribute to differences in multivoxel coding between perceptual difficulty conditions or sessions, three additional ANOVAs were performed, one for each task feature [factors: difficulty (high, low), session (session 1, session 2), region (IFS, AI/FO, ACC/pre-SMA, IPS), and feature level (rule 1, rule 2); see Materials and Methods]. There were no significant interactions with difficulty or session for any task feature (position,  $p$  values  $> 0.74$ ; rule,  $p$  values  $> 0.29$ ; response,  $p$  values  $> 0.17$ ).

### Multivariate results

Of central interest was the flexibility of MD coding in response to changing task demands. MVPA was used to quantify the discriminability of multivoxel patterns pertaining to different task events



**Figure 2.** Whole-brain univariate analyses for high minus low perceptual difficulty (A) and session 1 minus session 2 (B). Data are thresholded at  $p < 0.01$ , with false discovery rate correction for multiple comparisons and an extent threshold of 100 voxels. Coordinates of peak activations are given in the Results (see Univariate results).

(e.g., stimulus positions), in the two perceptual difficulty conditions: classification accuracy indicated the relative strength of coding.

We predicted that, in the high perceptual difficulty condition, the MD system would show increased representation of stimulus position relative to the low perceptual difficulty condition. The results, shown in Figure 3, were in line with this hypothesis. In the MD system as a whole, there was significantly more coding of position information in the high relative to the low perceptual difficulty condition (mean classification accuracy for low difficulty, 49.9%; high, 58.3%;  $F_{(1,17)} = 11.6$ ,  $p = 0.003$ ). This trend was consistent across the MD ROIs (difficulty  $\times$  region interaction  $F_{(3,51)} = 0.20$ ,  $p = 0.90$ ). Moreover, the difference was significant in the IFS, IPS, and ACC/pre-SMA ROIs individually (main effect of difficulty for each region separately: IFS,  $F_{(1,17)} = 9.99$ ,  $p = 0.006$ ; IPS,  $F_{(1,17)} = 6.87$ ,  $p = 0.018$ ; ACC/pre-SMA,  $F_{(1,17)} = 5.93$ ,  $p = 0.026$ ) and approached significance in the AI/FO ( $F_{(1,17)} = 3.37$ ,  $p = 0.084$ ).

Greater coding of physically less discriminable stimuli is striking. To emphasize this, we examined position coding in the visual

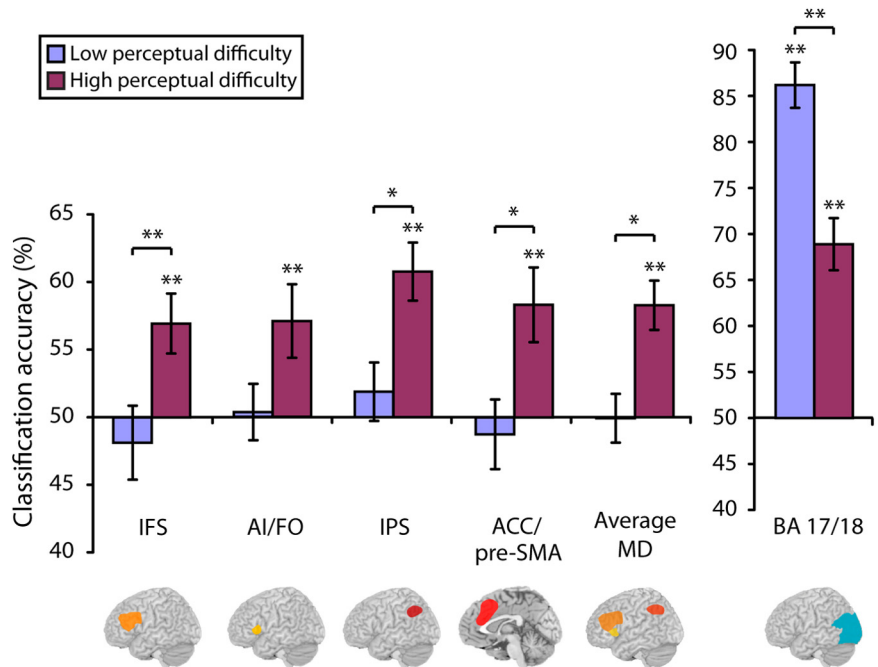
cortex using an anatomically defined ROI taken from the Brodmann template: areas 17 and 18. As expected, we saw good position coding overall in this ROI. In contrast to the MD result, in the visual ROI, there was significantly less coding of position in the high perceptual difficulty condition (low, 86.2%; high, 68.9%;  $F_{(1,17)} = 61.1$ ,  $p < 0.001$ ), in line with the change in physical discriminability of the stimulus.

Because we excluded error trials and because (depending on RT) a variable proportion of time in each block was devoted to task performance versus inter-trial interval, a potential concern was differential reliability of  $\beta$  estimates between conditions. In turn, differential reliability of  $\beta$  estimates could affect differences in classification accuracy in MVPA. To address this, we ran a second model in which we equated the total scanning time (summed RT) contributing to the estimation of task performance  $\beta$  values in the high and low perceptual difficulty conditions. To achieve this, for each subject and block, trials from the condition with greater summed RT were dropped until conditions were matched. This did not change the pattern of results (main effect of perceptual difficulty on coding of position in MD regions: low, 50.4%; high, 56.7%,  $F_{(1,17)} = 6.57$ ,  $p = 0.02$ ; difficulty  $\times$  MD region interaction,  $F_{(3,51)} = 0.29$ ,  $p = 0.83$ ; BA 17/18: low, 86.5%; high, 66.25%,  $F_{(1,17)} = 61.7$ ,  $p > 0.001$ ).

To check for hemispheric differences, we ran an additional ANOVA with factors difficulty (high, low), session (session 1, session 2), region (IFS, AI/FO, IPS), and hemisphere (left, right). There was a main effect of hemisphere ( $F_{(1,17)} = 10.7$ ,  $p = 0.004$ ), indicating more coding of position information overall in the right relative to left hemisphere. The hemisphere  $\times$  difficulty interaction was not significant ( $F_{(1,17)} = 0.11$ ,  $p = 0.74$ ), suggesting that there was no difference in the extent to which responses from each hemisphere adapted to the perceptual difficulty manipulation.

Our second question concerned whether the other task features, rule and response, continued to be represented in the high perceptual difficulty condition. The pattern of representation of rule and response information is shown in Figure 4. Because they were still relevant for behavior, we predicted that these task features would continue to be represented in the system. Accordingly, there was no significant effect of perceptual difficulty on coding of rule ( $F_{(1,17)} = 0.42$ ,  $p = 0.53$ ) or response ( $F_{(1,17)} = 0.001$ ,  $p = 0.98$ ; difficulty  $\times$  session  $\times$  region ANOVA for rule and response separately).

Finally, we turned to the effect of practice on multivoxel coding. For position, there was no difference (numerical increase) in position coding across the two session (52.5 to 55.7%,  $F_{(1,17)} = 1.36$ ,  $p = 0.26$ ). There was also no change in the coding of response (53.7 to 52.1%,  $F_{(1,17)} = 1.10$ ,  $p = 0.31$ ). However, there was a significant reduction in rule coding in the second session (65.2 to 58.0%, three-way ANOVA for rule, main effect of session:  $F_{(1,17)} = 5.35$ ,  $p = 0.033$ ). This trend was consistent across the MD

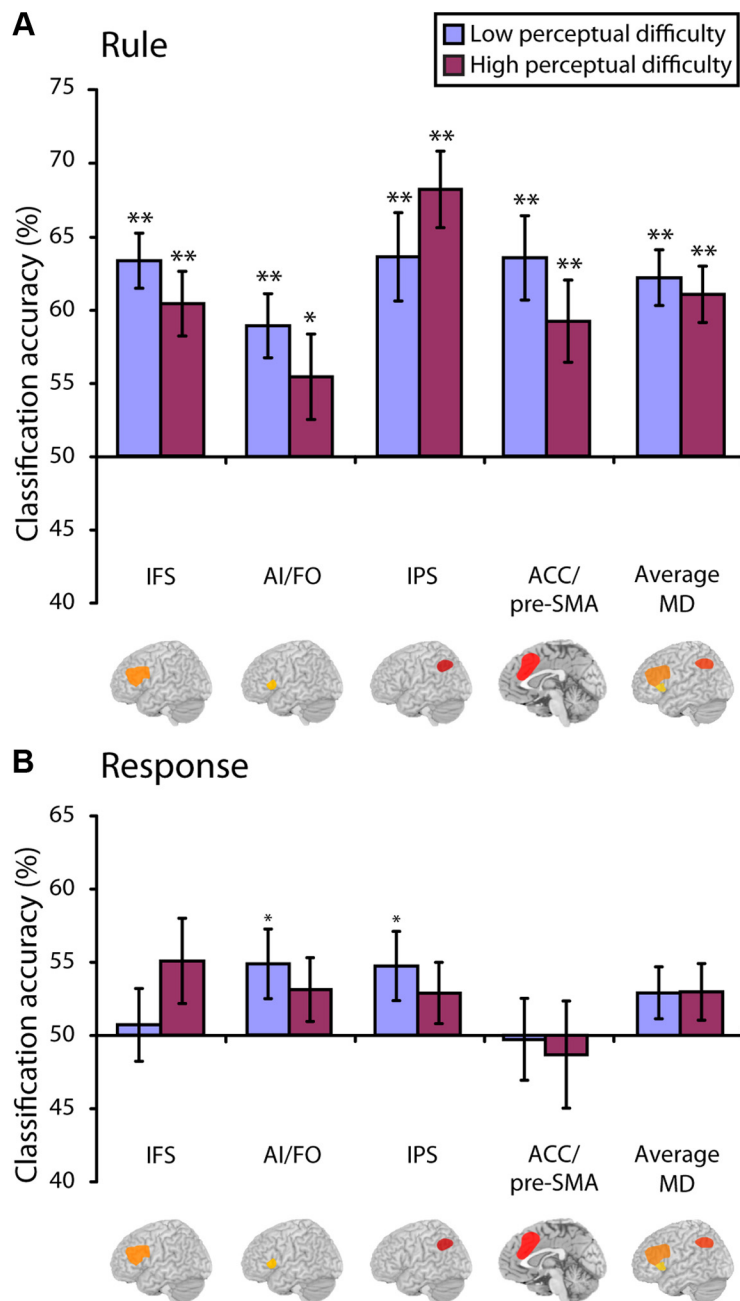


**Figure 3.** Position coding in the MD system, under conditions of high and low perceptual difficulty. Bars indicate classification accuracy for inner versus outer position in high and low perceptual difficulty conditions in each of the MD ROIs, collapsed across session and hemisphere when appropriate. Error bars indicate SE. Significance markings between bars indicate change in classification accuracy between high and low perceptual difficulty conditions, tested with ANOVA (factors: difficulty, session) in each region separately or ANOVA (factors: difficulty, region, session) for average MD. Significance markings for individual bars indicate where position coding was significantly greater than chance in that region and condition (one-sample  $t$  test against chance, 50%). \* $p < 0.05$ , \*\* $p < 0.01$ .

regions (Fig. 5) and significant in the IFS ( $F_{(1,17)} = 4.55$ ,  $p = 0.048$ ) and IPS ( $F_{(1,17)} = 10.1$ ,  $p = 0.006$ ) individually. The results indicate that, with practice, MD coding of task rules decreased, whereas coding of specific stimuli and responses was relatively unaffected.

In these ANOVAs, there were no session  $\times$  difficulty interactions (all  $p$  values  $> 0.17$ ), suggesting that the perceptual difficulty manipulation had a similar effect on coding in each session. A four-way ANOVA with factors difficulty (high, low), session (session 1, session 2), region (IFS, AI/FO, ACC/pre-SMA, IPS), and task feature (rule, position, response) confirmed that the interaction between session and task feature was significant ( $F_{(2,34)} = 3.61$ ,  $p < 0.038$ ), suggesting a rebalancing of MD resources after practice. There was no main effect of session ( $F_{(1,17)} = 2.87$ ,  $p = 0.11$ ) in this ANOVA; overall task-relevant information continued to be represented to a similar extent in the second session. The four-way ANOVA also revealed a highly significant effect of feature ( $F_{(2,32)} = 13.2$ ,  $p < 0.001$ ), which indicated that coding of rule was significantly greater than coding of position or response.

Whole-brain MVPA analyses, performed to check for additional regions behaving adaptively, did not reveal any additional areas of interest. The high minus low perceptual difficulty contrast revealed increased position coding in bilateral IPS (peaks: 52,  $-50$ , 34, BA 40;  $-50$ ,  $-48$ , 38, BA 40) and no differences in rule or response coding. For low minus high, there was increased position coding in the visual cortices (peak: 10,  $-82$ , 10, BA 17), as seen in the ROI analysis, and no differences in rule or response coding. For the effect of practice (session 2 minus session 1), no voxels survived correction for position, rule, or response. In the converse contrast (session 1 minus session 2), there was a small



**Figure 4.** Rule (**A**) and response (**B**) coding in the MD system, under conditions of high and low perceptual difficulty. Bars indicate classification accuracy for rule 1 versus rule 2 (**A**) or inner versus outer responses in high and low perceptual difficulty conditions (**B**) in each of the MD ROIs. Data are collapsed across session and hemisphere when appropriate. Error bars indicate SE. The significance markings for individual bars indicate whether coding of that task features was significantly greater than chance (one-sample *t* test against chance, 50%) in that region in that condition. There were no significant changes in classification accuracy between high and low perceptual difficulty conditions. \* $p < 0.05$ , \*\* $p < 0.01$ .

cluster of voxels showing increased position coding in first session in the right visual cortex (peak: 22, −78, −8, BA 18). As in the ROI analysis, there was increased rule coding in the first session compared with the second session in regions of the lateral frontal surface (peaks: −46, 14, 16, BA 44; 46, 20, 34, BA 44; −40, 50, 0, BA 46; 38, 04, 46, BA 47), ACC/pre-SMA (6, 8, 60, BA 6), and a large cluster of voxels around the temporo-parietal junction (−50, −64, 18, BA 39; 48, −66, 40, BA 39). No voxels survived correction for this contrast for response coding.

## Discussion

The adaptive coding hypothesis predicts that the coding of information in the MD system is sensitive to task demands (Duncan, 2001). In line with this hypothesis, the representation of stimulus position information in the MD system increased adaptively when the perceptual difficulty of the task was increased. In contrast, in the visual cortex, position coding significantly decreased when perceptual difficulty was increased, in line with the physical attributes of the stimuli. These changes occurred dynamically, between alternating blocks of high and low perceptual difficulty each lasting 2 min.

Many previous studies have shown selective coding of task-relevant information in single neurons of the monkey prefrontal cortex (Rao et al., 1997; Duncan, 2001; Freedman et al., 2001). In humans, MVPA of frontal activity recorded with fMRI has also shown that different types of task-relevant information can be represented (Haynes et al., 2007; Li et al., 2007; Bode and Haynes, 2009; Woolgar et al., 2011). Here, we show the effect of demand on these representations. When perceptual stimuli were more difficult to distinguish we saw a greater representation of perceptual information, despite weaker representation of this information in earlier processing areas. Moreover, we show that this effect is not restricted to lateral frontal brain regions but occurs across the MD network.

It is worth noting that the change in information coding was not a general increase, as might be expected in the case of a general increase in effort or attention to the task. Instead, the results suggest a highly specific adaptation to increased demand for stimulus identification, with stronger coding of stimulus position but unchanged coding of other task features. One possibility is that, when additional attention must be allocated specifically to stimulus position, the MD regions adjust to give a greater representation of this information. Additional work is needed to disentangle whether this representation itself reflects amplified sensory information (for example, compensating for the lack of perceptual information coded in the visual cortex) or some form of more considered perceptual decision regarding the stimulus position.

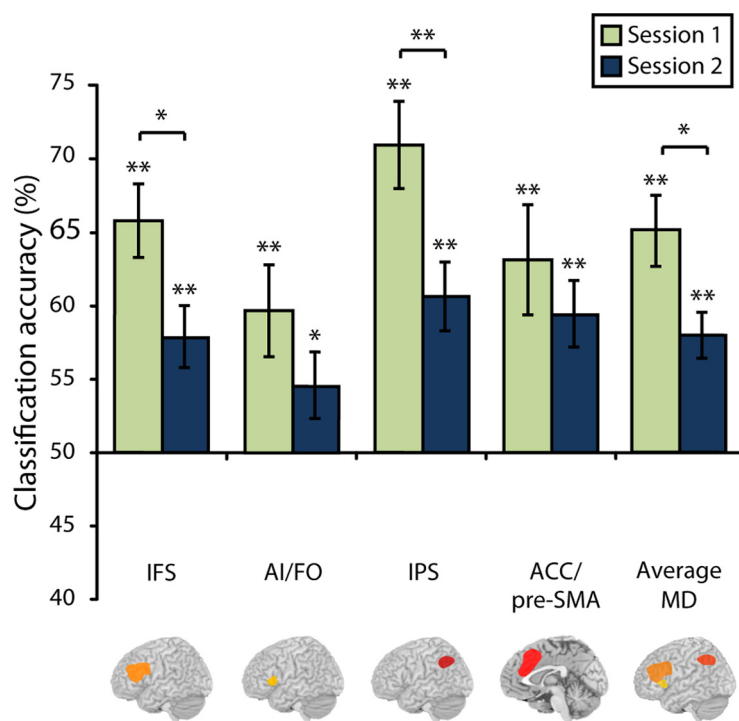
In traditional univariate fMRI studies, increased MD activity is associated with many kinds of task difficulty (Duncan and Owen, 2000). In the present data, the MD system indeed showed the expected increase in overall activity under conditions of increased task demand. The MVPA results provide a possible explanation of what this increased activity reflects, namely an

increased representation of the task feature to which additional processing capacity must be applied.

Previous investigation of adaptive coding has focused primarily on the properties of the non-human primate prefrontal cortex, leaving the flexibility of coding in the parietal lobe less thoroughly explored. Our data suggest that, in the human brain, the IPS adaptively increases its representation of task-relevant information in line with task demands. That the IPS region should respond much as the rest of the MD system does is in line with the common coactivation of IPS with IFS regions (Duncan, 2006), as well as demonstrations of similar patterns of responses in frontal and parietal cortex at the level of the single neuron (Quintana and Fuster, 1992; Chafee and Goldman-Rakic, 1998). Because the parietal lobe has been suggested to be somewhat specialized for spatial information (Mishkin et al., 1983; Milner and Goodale, 1995; Corbetta and Shulman, 2002; Rizzolatti and Matelli, 2003), it remains an open question as to whether this region would flexibly adapt to code other types of information as they became relevant for the task, or demand additional attention. Certainly, however, there is also considerable evidence for nonspatial parietal functions (Duncan, 2006; Nachev and Husain, 2006; Husain and Nachev, 2007).

The current study also casts light on adaptive MD coding occurring over increased practice. After 1 week, participants were substantially faster on the visual stimulus–response task. Concurrently, the MD system showed reduced univariate task-related activity, in line with previous literature. Meanwhile, the MVPA results suggest a rebalancing of MD resources. Although MD representation of stimuli and responses was relatively unaffected by practice, the MD system exhibited strong coding of rule information before practice when the task rules were unfamiliar, but, with experience, rule coding was much diminished. Familiarity with stimulus–response mapping rules is a strong determinant of performance. For unfamiliar mappings, reaction times are high and strongly influenced by the number of alternative responses but diminish and become independent of the number of alternatives when familiar (Mowbray, 1960; Brainard et al., 1962). Our task also required an unfamiliar choice between rules based on a novel cue (background color). Time to make such a choice also decreases rapidly with practice (Duncan, 1977). Our results suggest that, as mapping operations are speeded, MD coding of rules decreases.

Even within one task, our data show flexible coding of multiple task features across the MD system. It follows that general conclusions are unlikely to be drawn from specific consideration of how information is distributed across MD regions in any one task. However, it was striking that, in this study, as in our previous work (Woolgar et al., 2011), stimulus–response mapping rule was the most strongly represented task feature. Rule was significantly coded in all MD regions in both high and low perceptual difficulty conditions and, especially in the first session, was represented sig-



**Figure 5.** Effect of practice on rule coding in the MD system. Bars indicate classification accuracy for rule 1 versus rule 2 in the first and second scanning session. Data are collapsed across perceptual difficulty and hemisphere when appropriate. Error bars indicate SE. Significance markings between bars indicate change in classification accuracy between sessions, tested with ANOVA (factors: difficulty, session) in each region separately or ANOVA (factors: difficulty, region, session) for average MD. Significance markings for individual bars indicate rule coding significantly greater than chance (one-sample *t* test against chance, 50%). \**p* < 0.05, \*\**p* < 0.01.

nificantly more strongly than position or response across the MD system. In the current design, rule coding was confounded with background color, but our previous work suggests that color coding tends to be weak compared with rule coding and indeed that rule coding generalizes across different background colors (Woolgar et al., 2011). In the present experiment, the two rules were also of appreciably different difficulty, raising the possibility that a generalized processing increase (e.g., effort) in the harder rule could have contributed to the separation of multivoxel codes. However, the same result was seen in our previous work, in which the rules were more closely matched for difficulty (Woolgar et al., 2011), and, in the present case, the corresponding univariate analysis did not show significant differences that could account for the multivariate results. One possibility is that, despite adapting to represent different types of information as relevant for the current task context, the MD system may maintain a hierarchy of coding, with a stronger representation of task rules or general cognitive context and a weaker representation of particular stimulus–response instances (Miller and Cohen, 2001; Sigala et al., 2008). Another possibility—especially in the first session, before practice—is that rule choice and use may have been especially demanding in the current task.

The current data demonstrate a surprising effect of demand on MD representation of task-relevant information. In line with the adaptive coding hypothesis (Duncan, 2001), representation of stimulus position increased when stimulus position was more difficult to discern, despite decreased representation of this information in early visual cortex. This dynamic change occurred within a single task and was consistent across both frontal and parietal MD regions. After practice on the task, the result was a

rebalancing of MD resources, with a diminished representation of task rules. The results are consistent with the proposal that the MD regions constitute a flexible neural system, exerting cognitive control in a wide range of tasks by adaptively representing the task features relevant for successful goal-directed behavior.

## References

- Asaad WF, Rainer G, Miller EK (1998) Neural activity in the primate prefrontal cortex during associative learning. *Neuron* 21:1399–1407.
- Bode S, Haynes JD (2009) Decoding sequential stages of task preparation in the human brain. *Neuroimage* 45:606–613.
- Brainard RW, Irby TS, Fitts PM, Alluisi EA (1962) Some variables influencing the rate of gain of information. *J Exp Psychol* 63:105–110.
- Chafee MV, Goldman-Rakic PS (1998) Matching patterns of activity in primate prefrontal area 8a and parietal area 7ip neurons during a spatial working memory task. *J Neurophysiol* 79:2919–2940.
- Chang CC, Lin CJ (2011) LIBSVM: a library for support vector machines. *ACM Trans Intel Syst Technol* 2:27.
- Corbetta M, Shulman GL (2002) Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci* 3:201–215.
- Cusack R, Mitchell DJ, Duncan J (2010) Discrete object representation, attention switching, and task difficulty in the parietal lobe. *J Cogn Neurosci* 22:32–47.
- Dehaene S, Le Clec'H G, Cohen L, Poline JB, van de Moortele PF, Le Bihan D (1998) Inferring behavior from functional brain images. *Nat Neurosci* 1:549–550.
- Desimone R, Duncan J (1995) Neural mechanisms of selective visual attention. *Annu Rev Neurosci* 18:193–222.
- Dosenbach NU, Visscher KM, Palmer ED, Miezin FM, Wenger KK, Kang HC, Burgund ED, Grimes AL, Schlaggar BL, Petersen SE (2006) A core system for the implementation of task sets. *Neuron* 50:799–812.
- Duncan J (1977) Response selection rules in spatial choice reaction tasks. In: *Attention and performance VI* (Dornic S, ed), pp 49–61. Hillsdale, NJ: Erlbaum.
- Duncan J (2001) An adaptive coding model of neural function in prefrontal cortex. *Nat Rev Neurosci* 2:820–829.
- Duncan J (2006) EPS Mid-Career Award 2004: brain mechanisms of attention. *Q J Exp Psychol (Colchester)* 59:2–27.
- Duncan J, Owen AM (2000) Common regions of the human frontal lobe recruited by diverse cognitive demands. *Trends Neurosci* 23:475–483.
- Freedman DJ, Assad JA (2006) Experience-dependent representation of visual categories in parietal cortex. *Nature* 443:85–88.
- Freedman DJ, Riesenhuber M, Poggio T, Miller EK (2001) Categorical representation of visual stimuli in the primate prefrontal cortex. *Science* 291:312–316.
- Hanke M, Halchenko YO, Sederberg PB, Hanson SJ, Haxby JV, Pollmann S (2009) PyMVPA: a python toolbox for multivariate pattern analysis of fMRI data. *Neuroinformatics* 7:37–53.
- Haynes JD, Rees G (2006) Decoding mental states from brain activity in humans. *Nat Rev Neurosci* 7:523–534.
- Haynes JD, Sakai K, Rees G, Gilbert S, Frith C, Passingham RE (2007) Reading hidden intentions in the human brain. *Curr Biol* 17:323–328.
- Husain M, Nachev P (2007) Space and the parietal cortex. *Trends Cogn Sci* 11:30–36.
- Kriegeskorte N, Goebel R, Bandettini P (2006) Information-based functional brain mapping. *Proc Natl Acad Sci U S A* 103:3863–3868.
- Li S, Ostwald D, Giese M, Kourtzi Z (2007) Flexible coding for categorical decisions in the human brain. *J Neurosci* 27:12321–12330.
- Miller EK, Cohen JD (2001) An integrative theory of prefrontal cortex function. *Annu Rev Neurosci* 24:167–202.
- Milner AD, Goodale MA (1995) *The visual brain in action*. Oxford: Oxford UP.
- Mishkin M, Ungerleider LG, Macko KA (1983) Object vision and spatial vision—2 cortical pathways. *Trends Neurosci* 6:414–417.
- Mowbray GH (1960) Choice reaction times for skilled responses. *Q J Exp Psychol* 12:193–202.
- Nachev P, Husain M (2006) Disorders of visual attention and the posterior parietal cortex. *Cortex* 42:766–773.
- Nyberg L, Marklund P, Persson J, Cabeza R, Forkstam C, Petersson KM, Ingvar M (2003) Common prefrontal activations during working memory, episodic memory, and semantic memory. *Neuropsychologia* 41:371–377.
- Quintana J, Fuster JM (1992) Mnemonic and predictive functions of cortical-neurons in a memory task. *Neuroreport* 3:721–724.
- Rao SC, Rainer G, Miller EK (1997) Integration of what and where in the primate prefrontal cortex. *Science* 276:821–824.
- Rizzolatti G, Matelli M (2003) Two different streams form the dorsal visual system: anatomy and functions. *Exp Brain Res* 153:146–157.
- Rorden C, Brett M (2000) Stereotaxic display of brain lesions. *Behav Neurol* 12:191–200.
- Sakagami M, Niki H (1994) Encoding of behavioral significance of visual stimuli by primate prefrontal neurons: relation to relevant task conditions. *Exp Brain Res* 97:423–436.
- Sigala N, Kusunoki M, Nimmo-Smith I, Gaffan D, Duncan J (2008) Hierarchical coding for sequential task events in the monkey prefrontal cortex. *Proc Natl Acad Sci U S A* 105:11969–11974.
- Stoet G, Snyder LH (2004) Single neurons in posterior parietal cortex of monkeys encode cognitive set. *Neuron* 42:1003–1012.
- Wallis JD, Anderson KC, Miller EK (2001) Single neurons in prefrontal cortex encode abstract rules. *Nature* 411:953–956.
- White IM, Wise SP (1999) Rule-dependent neuronal activity in the prefrontal cortex. *Exp Brain Res* 126:315–335.
- Woolgar A, Thompson R, Bor D, Duncan J (2011) Multi-voxel coding of stimuli, rules, and responses in human frontoparietal cortex. *Neuroimage* 56:744–752.