

Feature-selective Attention in Frontoparietal Cortex: Multivoxel Codes Adjust to Prioritize Task-relevant Information

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Abstract

■ Human cognition is characterized by astounding flexibility, enabling us to select appropriate information according to the objectives of our current task. A circuit of frontal and parietal brain regions, often referred to as the frontoparietal attention network or multiple-demand (MD) regions, are believed to play a fundamental role in this flexibility. There is evidence that these regions dynamically adjust their responses to selectively process information that is currently relevant for behavior, as proposed by the “adaptive coding hypothesis” [Duncan, J. An adaptive coding model of neural function in prefrontal cortex. *Nature Reviews Neuroscience*, 2, 820–829, 2001]. Could this provide a neural mechanism for feature-selective attention, the process by which we preferentially process one feature of a stimulus over another? We used multivariate pattern analysis of fMRI data during a perceptually challenging categorization task to in-

vestigate whether the representation of visual object features in the MD regions flexibly adjusts according to task relevance. Participants were trained to categorize visually similar novel objects along two orthogonal stimulus dimensions (length/orientation) and performed short alternating blocks in which only one of these dimensions was relevant. We found that multivoxel patterns of activation in the MD regions encoded the task-relevant distinctions more strongly than the task-irrelevant distinctions: The MD regions discriminated between stimuli of different lengths when length was relevant and between the same objects according to orientation when orientation was relevant. The data suggest a flexible neural system that adjusts its representation of visual objects to preferentially encode stimulus features that are currently relevant for behavior, providing a neural mechanism for feature-selective attention. ■

INTRODUCTION

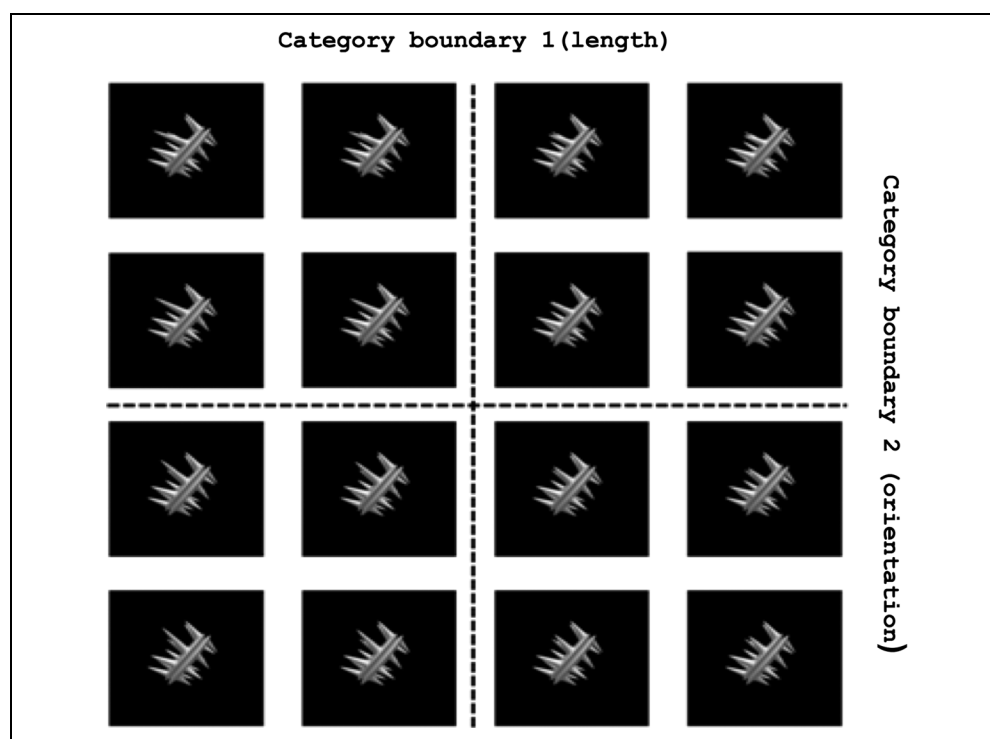
We live in a complex dynamic environment where the behavioral relevance of different sensory input changes rapidly. To function successfully, we need a cognitive system that can select what is currently relevant, ignore distraction, and update its responses in accordance with events in the world. The selection of relevant information can be specific to different features of visual objects depending on the current goal. For example, if I am looking for my blue cup among other cups, color is the relevant dimension. When I find my cup and reach to pick it up, other features of the cup are now relevant (e.g., orientation). Following Chen, Hoffmann, Albright, and Thiele (2012), we refer to the process of attending to and making a decision about one feature of an object, while ignoring other features of that object, as feature-selective attention. We use this nomenclature to differentiate it from feature-based attention, in which a relevant feature is used to select what object or location to attend to (e.g., attend to the red object). In feature-based attention, attention is directed toward objects and/or locations matching a cued value (e.g., red), while objects of a dif-

ferent color are ignored. In feature-selective attention, attention is instead directed toward a particular stimulus dimension (e.g., color), in preference to other dimensions (e.g., shape), to make a judgment about the relevant feature of a stimulus (Chen et al., 2012).

The adaptive coding hypothesis (Duncan, 2001) offers a possible neural mechanism for feature-selective attention. It holds that, within higher cortical regions, the response properties of single neurons are highly adaptable such that, in any particular task context, many cells become tuned to code information that is currently relevant. Evidence of such “adaptive coding” comes primarily from single-unit work with non-human primates in which neurons in higher cortical regions have been shown to alter coding as needed for behavior (Stokes et al., 2013; Cromer, Roy, & Miller, 2010; Roy, Riesenhuber, Poggio, & Miller, 2010; Freedman & Assad, 2006; Freedman, 2001; Sakagami & Niki, 1994). For example, in a go/no-go discrimination task where the relevant feature of a cue changed between three task contexts (Sakagami & Niki, 1994), 72% of PFC neurons showed different responses during the cue period for each task condition. In another example, Roy et al. (2010) demonstrated that 24% of PFC neurons had a distinct firing rate in response to one category of visual stimuli over another. These neurons responded to the relevant

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Figure 1. The stimulus set consisted of 16 spiky objects with eight objects on either side of two orthogonal category boundaries. Category boundaries were defined based on the length (horizontal axis) or orientation (vertical axis) of the third spike from the bottom on the left side of the object. Spike length and orientation were titrated on an individual-participant basis to equate the difficulty of categorization across the two dimensions.



Stimuli

Stimuli were abstract novel “spiky” objects created using custom MATLAB scripts (Op de Beeck, Baker, DiCarlo, & Kanwisher, 2006). The stimulus set consisted of 16 objects (Figure 1) in which one spike varied along two dimensions (its length and orientation). Participants learnt to discriminate between the 16 objects across two orthogonal decision boundaries (task contexts) based on the length and orientation dimensions. The relevant visual feature of the stimuli therefore varied depending on the current decision boundary. The stimuli were aligned so that the main stem of the objects appeared at an angle of $+37^\circ$ from vertical. During both the training and scanning sessions, the visual angle (VA) of the spiky object’s length along its main axis was 8.07° . Stimulus presentation was controlled by a PC running the Psychophysics Toolbox 3 package (Brainard, 1997) in MATLAB (The MathWorks, Inc, Natick, MA). Stimuli were presented at central fixation on a screen and viewed through a mirror mounted on the head coil in the scanner.

Titration Task Difficulty

Less than 1 week (1–7 days) before scanning, participants completed a behavioral testing session in which we titrated the discriminability of the stimuli to ensure that the length and orientation tasks were of comparable difficulty on an individual participant level. We started with a difference of 1.26° VA between the shortest and longest lengths of the spike and a maximum difference of 27.02° in the angle of orientation. After 192 trials, the range of

lengths or orientations in the stimulus set was adjusted if there was a significant difference in the participant’s RTs between the two tasks ($p < .05$). For this, we increased the difficulty of the task that had the lower average RT. This procedure was repeated until there was no difference in RT between the two task contexts, as assessed with Bayes factor (BF) analysis (Love et al., 2015) in each participant separately (BF < 1 taken as evidence for no difference between conditions; Dienes 2011). The difficulty of the orientation context was increased for 11 participants (the maximum angle decreased to 21.92° for six participants and 13.86° for five participants), and the difficulty of the length context was increased for five participants (the maximum difference in VA was decreased to 1.06° for two participants and 0.95° for three participants).

Procedure

Before titrating the stimuli, participants completed six blocks of practice trials to learn the task. Stimuli were initially presented for 400 msec until participants achieved $>80\%$ correct, after which objects were presented for 216 msec. Feedback (correct/incorrect) was presented after each response until participants achieved $>80\%$ performance, after which feedback (percent correct) was only given at the end of each block. Once participants reached a high performance level ($>80\%$ correct) in both task contexts, we then titrated the stimuli to ensure equal performance in RTs (as described above). During titration, participants only received feedback at the end of each block. Immediately before entering the scanner, participants

interval, a blank black screen was shown for the remainder of the trial time. Feedback (accuracy score) was presented at the end of each block for 6000 msec, after which there was a delay of 4000 msec before the start of the next block. At the end of each run, a blank black screen was shown for 4000 msec.

After completion of the main task during the scanning session, we ran a localizer task to functionally identify the LOC as an a priori ROI. Participants viewed central intact and scrambled versions of black and white common objects in 16.8-sec blocks of 16 trials (1100 msec/trial), while fixating on a central cross. Participants had to indicate via a button response when the fixation cross changed color to remind them to fixate centrally. There were 21 blocks consisting of alternating blocks of whole objects, scrambled objects, and rest blocks (counterbalanced across participants). The EPI (acquisition time) for the localizer task was 6.25 min.

Data Acquisition

The data were collected using a 3-T Verio Siemens (Erlangen, Germany) MRI scanner at Macquarie Medical Imaging, Macquarie University Hospital, Sydney, Australia. We used a sequential descending T2*-weighted EPI acquisition sequence with the following parameters: acquisition time = 2000 msec, echo time = 30 msec, 34 oblique axial slices with a slice thickness of 3.0 mm and a 0.70-mm interslice gap, in-plane resolution = 3.0×3.0 mm, matrix = 64×64 , field of view = 210 mm, and flip angle = 78° . T1-weighted magnetization prepared rapid gradient echo structural images were also acquired for all participants (slice thickness = 1.0 mm, resolution = 1.0×1.0 mm).

Preprocessing

MRI data were preprocessed using SPM 5 (Wellcome Department of Imaging Neuroscience, London, UK; www.fil.ion.ucl.ac.uk/spm) in MATLAB 2011b. Functional MRI data were converted from DICOM to NIFTII format, spatially realigned to the first functional scan and slice timing corrected, and structural images were co-registered to the mean EPI. EPIs from the main experiment were smoothed slightly (4-mm FWHM Gaussian kernel) to improve signal-to-noise ratio. LOC localizer EPIs were also smoothed (8-mm FWHM Gaussian kernel), and, in all cases, the data were high-pass filtered (128 sec). Structural scans were additionally normalized, using the segment and normalize routine of SPM5, to derive the individual participant normalization parameters needed for ROI definition (below).

ROIs

MD ROIs were defined using coordinates from a previous review of activity associated with a diverse set of cognitive demands (Duncan & Owen, 2000) using the kernel

method described in Cusack, Mitchell, and Duncan (2010), as in our previous work (Woolgar, Williams, et al., 2015; Woolgar, Hampshire, et al., 2011; Woolgar, Thompson, et al., 2011). The procedure yielded seven ROIs: left and right IFS (center of mass = $\pm 38, 26, 24$; volume = 17 cm^3), left and right AI/FO ($\pm 35, 19, 3$; 3 cm^3), left and right IPS ($\pm 35, -58, 41$; 7 cm^3), and ACC/pre-SMA ($0, 23, 39$; 21 cm^3).

Left and right visual cortex ROIs were derived from the Brodmann's template provided with MRICro (Rorden & Brett, 2000; Brodmann's area [BA] 17; center of mass = $-13, -81, 3/16, -79, 3$; volume = 54 cm^3). All coordinates are given in MNI152 space (McConnell Brain Imaging Centre, Montreal Neurological Institute). MD and BA 17 ROIs were deformed for each participant by applying the inverse of the participant's normalization parameters. This allowed analyses to be carried out using native space (i.e., nonnormalized) EPI data.

Using the functional localizer scan data, we defined LOC for each participant as the brain area that responded more strongly to whole objects than to scrambled versions of the same objects. We used the standard multiple regression approach of SPM5 (Wellcome Department of Imaging Neuroscience, London, UK; www.fil.ion.ucl.ac.uk) to estimate values pertaining to the whole and scrambled object conditions (block design). Blocks were modeled using a box car function lasting 16 sec convolved with the hemodynamic response of SPM5. The run mean was included in the model as a covariate of no interest. Whole-brain analyses (paired *t* tests) compared voxelwise BOLD response in the two conditions (whole objects minus scrambled objects). The resulting map was thresholded such that there was at least one cluster with a minimum size of 20 voxels. These clusters were then imported into MarsBaR (Brett, Anton, Valabregue, & Poline, 2002), and those active voxel clusters close to anatomical LOC coordinates from previous studies (Grill-Spector, Kushnir, Hendler, & Malach, 2000; Grill-Spector et al., 1999) were selected to form the ROI.

First-level Model

To obtain estimated activation patterns for multivariate analysis, a general linear model was estimated for each participant using the realigned, slice-time-corrected, and smoothed native space EPIs using SPM5 (Wellcome Department of Imaging Neuroscience, London, UK; www.fil.ion.ucl.ac.uk). We classified each stimulus as either "short" or "long" on the length dimension and "rotated clockwise" or "rotated anticlockwise" relative to the category boundary on the orientation dimension. Trials were modeled as events of zero duration convolved with the hemodynamic response of SPM5. Each trial contributed to the estimation of two beta values, the relevant feature (short or long for length context blocks and clockwise or anticlockwise for orientation context blocks) and the irrelevant feature (short or long for orientation context blocks and clockwise

region. Furthermore, BA 17 did not show categorical discrimination of these visually similar objects according to either the task-relevant (relative to chance; mean classification accuracy = 52.91%, $t(25) = 1.62$, $p = .14$) or task-irrelevant (relative to chance; mean classification accuracy = 52.31%, $t(25) = 1.17$, $p = .25$) stimulus features. The two-step permutation tests similarly showed no evidence that BA 17 coded the task-relevant over the task-irrelevant features ($p = .41$). In addition, coding of relevant ($p = .08$) and irrelevant ($p = .12$) features did not reach significance. As the stimuli were identical in the different task contexts, it is not at all surprising to find that the early visual cortex information does not distinguish between these stimuli, although, as with all null effects, we must be cautious about interpretation.

Coding of Category Placement

On each trial, participants had to categorize the object according to the relevant feature dimension (e.g., short/long on length blocks), associate that decision with the number representing the chosen category (1 or 2, e.g., short = 1 in half of the participants), and then use the response mapping screen to transform their choice into the appropriate button press response (left or right, 1 = left in half of the trials). Therefore, it is possible that, as well as the categorization decision at the level of the stimulus, participants also held a category number in mind on each trial. To test for representation at this higher level of abstraction, we ran an additional analysis where we trained the classifier on the data representing the category number decisions in one task context and tested this on the category number decisions participants made in the other task context. We were not able to decode the category number placement of the objects in the MD system (mean classification accuracy = 50.54%, $t(25) = 1.31$, $p = .21$). To interpret this null effect, we calculated the BF. Coding of category number placement revealed a BF_{10} of 0.44. As this is less than 1 (Dienes, 2011) and approaches the level of 0.33 suggested by Jeffreys (1998) to represent significant evidence for the null hypothesis, we interpret this as evidence that, although the MD regions encode task-relevant stimulus distinctions, the representation is not abstracted to the level of categorical number placement.

DISCUSSION

The adaptive coding hypothesis (Duncan, 2001) proposes that neural populations dynamically adjust their responses to selectively code information that is currently relevant for our behavior. This provides a possible mechanism for feature-selective attention, which allows information about task-relevant stimulus features to be processed in preference to irrelevant attributes. We examined the responses of the MD regions in a difficult visual object

categorization task in which the relevant stimulus dimension varied on physically identical stimuli. The MD system adjusted its representation of these novel objects to preferentially encode feature distinctions that were relevant for the task. When the task required participants to categorize the objects based on length, the MD regions coded length information more strongly than orientation information, but when the task was to categorize based on orientation, orientation was encoded in preference to length. Thus, the MD system adjusted its representation of the features of an object to encode the discrimination necessary for the current task. Consistent with the proposal that the cognitive flexibility of these regions underlies their involvement in a wide range of tasks (e.g., Duncan, 2010; Cole & Schneider, 2007; Duncan & Owen, 2000), our data suggest that the coding of this adaptive system adjusts to hold the currently relevant features of a stimulus as needed for behavior.

Electrophysiology studies in nonhuman primates have previously shown that neurons in higher cortical regions adapt their tuning profiles to respond most strongly to the information that is currently relevant (Stokes et al., 2013; Cromer et al., 2010; Roy et al., 2010; Freedman & Assad, 2006; Freedman, 2001; Sakagami & Niki, 1994). The implementation of MVPA for fMRI has shown similar results in humans: Patterns of activation in the MD regions code a range of different types of task-related information (e.g., Woolgar, Williams, et al., 2015; Nee & Brown, 2012; Reverberi et al., 2011; Woolgar, Hampshire, et al., 2011; Woolgar, Thompson, et al., 2011; Bode & Haynes, 2009; Haynes et al., 2007; Li et al., 2007) and adjust their responses when task demands vary (Woolgar, Afshar, et al., 2015; Woolgar, Williams, et al., 2015; Woolgar, Hampshire, et al., 2011; Li et al., 2007). The MD regions also encode attended objects in preference to unattended objects (Woolgar, Williams, et al., 2015), and a previous adaptation study demonstrated that these regions show greater responses to changes in attended stimulus features (color/shape) than to changes in unattended stimulus features (Thompson & Duncan, 2009). Here, we find that these regions can also flexibly adapt their representations of single objects to emphasize task-relevant stimulus distinctions, resulting in preferential coding of attended stimulus features.

Our data align with a recent study in which objects were strongly represented in LPFC in individual task contexts, but the representation did not generalize between task contexts (Harel et al., 2014). Those data suggested that the same set of objects may be represented differently as task contexts change. Here, we tested this possibility directly by specifying the specific stimulus distinctions that an adaptive system should make in each task context. We found that the MD system adjusted its representation of the set of novel objects to make the specific distinctions needed for the task. In a related study (Peelen & Caramazza, 2012), participants responded to one of two semantic dimensions of an object (how the object is used or where the object is found) in a 1-back task. Results from a

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