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Attention enhances multi-voxel representation of novel objects in frontal, parietal and visual cortices

Alexandra Woolgar *, Mark A. Williams, Anina N. Rich

Perception in Action Research Centre & Department of Cognitive Science, Faculty of Human Sciences, Macquarie University, Sydney, NSW 2109, Australia
ARC Centre of Excellence in Cognition and Its Disorders, Macquarie University, Sydney, NSW 2109, Australia

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ABSTRACT

Selective attention is fundamental for human activity, but the details of its neural implementation remain elusive. One influential theory, the adaptive coding hypothesis (Duncan, 2001, An adaptive coding model of neural function in prefrontal cortex, Nature Reviews Neuroscience 2:820–829), proposes that single neurons in certain frontal and parietal regions dynamically adjust their responses to selectively encode relevant information. This selective representation may in turn support selective processing in more specialized brain regions such as the visual cortices. Here, we use multi-voxel decoding of functional magnetic resonance images to demonstrate selective representation of attended – and not distractor – objects in frontal, parietal, and visual cortices. In addition, we highlight a critical role for task demands in determining which brain regions exhibit selective coding. Strikingly, representation of attended objects in frontoparietal cortex was highest under conditions of high perceptual demand, when stimuli were hard to perceive and coding in early visual cortex was weak. Coding in early visual cortex varied as a function of attention and perceptual demand, while coding in higher visual areas was sensitive to the allocation of attention but robust to changes in perceptual difficulty. Consistent with high-profile reports, peripherally presented objects could also be decoded from activity at the occipital pole, a region which corresponds to the fovea. Our results emphasize the flexibility of frontoparietal and visual systems. They support the hypothesis that attention enhances the multi-voxel representation of information in the brain, and suggest that the engagement of this attentional mechanism depends critically on current task demands.

Introduction

Our ability to selectively attend to relevant information is fundamental to perceiving and interacting with the world, but we do not fully understand how it is implemented in the brain. Several theories implicate frontoparietal cortex as a source of top-down attention (e.g. Kastner and Ungerleider, 2000; Corbetta and Shulman, 2002). For example, frontoparietal cortex is activated by tasks requiring endogenously directed attention (Pessoa et al., 2003), even before stimuli are presented (Kastner et al., 1999; Hopfinger et al., 2000). One influential proposal is that frontoparietal neurons adjust their responses to favor information that is currently relevant for behavior (Duncan, 2001, 2010, 2013). This selective representation may serve as a source of bias, prioritizing processing of task-relevant information across the brain (Desimone and Duncan, 1995; Dehaene et al., 1998; Miller and Cohen, 2001).

Support for an adaptive view of frontoparietal function comes from single unit data. In non-human primates, frontal and parietal neurons discriminate a wide range of task features (Duncan, 2001; Rigotti et al., 2013). Moreover, coding adjusts to make different task-relevant distinctions during single trials as attentional focus is established (Kadohisa et al., 2013), as dictated by the current phase of the task (Rao et al., 1997; Sigala et al., 2008; Stokes et al., 2013), and after animals are retrained to make different stimulus distinctions (Freedman et al., 2001; Freedman and Assad, 2006).

In humans, candidate regions for adaptive coding are restricted regions of frontoparietal cortex in the inferior frontal sulcus (IFS), anterior insular/frontal operculum (AI/FO), anterior cingulate cortex/pre-supplementary motor area (ACC/pre-SMA), and the intraparietal sulcus (IPS). These 'multiple-demand' or MD (Duncan, 2010) regions are active during a wide range of cognitive tasks including perceptual discrimination, response conflict, working memory, episodic memory, and semantic memory (Duncan and Owen, 2000; Nyberg et al., 2003; Dosenbach et al., 2006; Duncan, 2006; Stiers et al., 2010; Niendam et al., 2012; Yeo et al., 2014). The generality of this response holds across tasks for single voxels in single subjects (Fedorenko et al., 2013). These regions are widely implicated in neural models of executive function and cognitive control (e.g. Dehaene and Naccache, 2001; Miller and Cohen, 2001;

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* Corresponding author at: Perception in Action Research Centre & Department of Cognitive Science, Faculty of Human Sciences, Macquarie University, Sydney, NSW 2109, Australia.
E-mail address: Alexandra.woolgar@mq.edu.au (A. Woolgar).

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Corbetta and Shulman, 2002; Cole and Schneider, 2007) and have been referred to variously as the “cognitive control network” (Cole and Schneider, 2007), “task positive network” (Fox et al., 2005), “task activation ensemble” (Seeley et al., 2007), or “frontoparietal control system” (Vincent et al., 2008). A recent study suggested that these frontoparietal regions comprise “flexible hubs” that adjust their pattern of functional connectivity according to task demands (Cole et al., 2013). In line with an adaptive view of MD function, work using multi-voxel pattern analysis (MVPA) of fMRI data has demonstrated MD discrimination of a range of task elements including stimuli, rules, and responses (Haynes et al., 2007; Li et al., 2007; Bode and Haynes, 2009; Woolgar et al., 2011b), and dynamic adjustment of coding when task demands are manipulated (Woolgar et al., 2011a).

Adaptive coding in MD cortex may provide a mechanism for selective attention (Duncan, 2001). For example, selective MD discrimination of information may support task-relevant decision making processes necessary for solving the task at hand. Additionally, selective MD representation may support selective processing in more specialized cortices such as the visual cortex (e.g. Desimone and Duncan, 1995; Dehaene et al., 1998; Miller and Cohen, 2001). Traditionally, top-down feedback of this sort has been difficult to examine using fMRI but the recent discovery that the foveal region of visual cortex is critical for discrimination of objects presented in the periphery (Williams et al., 2008; Chambers et al., 2013) provides an opportunity. In foveal cortex, the retinotopic mapping of visual input can be separated from the feedback representation.

Here, we test three elements of this account of selective attention. First, we predicted that if MD cortex is involved in selecting between simultaneously available information, it would show preferential coding of attended over distractor stimuli. Thus, the same object should be better discriminated by frontoparietal regions when it is attended compared to when it is ignored. Second, we reasoned that an adaptive MD response should be augmented when perceptual demand is high and top-down attention is more necessary. Third, we examined whether feedback played a role in determining the patterns of response of the visual cortex. We reasoned that preferential coding of attended information in visual cortex or any representation of peripherally represented objects in foveal cortex must be due to feedback.

Participants attended to one of two simultaneously presented objects under conditions of low or high perceptual difficulty. MD cortex indeed showed selective focus on attended stimuli, but only when perceptual demand was high and coding in early visual cortex was weak. We also saw selective coding for attended objects in early visual cortex, but, in contrast to MD cortex, object coding here was diminished when perceptual difficulty was increased. Feedback to the fovea was similarly only present for low perceptual difficulty, and only reached significance for attended objects, whereas object-selective higher visual cortex showed selective representation of attended information across perceptual difficulty conditions. Our results suggest a flexible distribution of information across MD and visual cortex that varies with attention and perceptual demand.

Materials and methods

Participants

38 healthy participants (13 male, 25 female; mean age 23.7, SD 4.41 years) took part in this experiment. Participants were right handed and had normal or corrected to normal vision. They gave written informed consent and were reimbursed for their time. The study was approved by the Macquarie University Ethics Review Committee.

Task design

The task was to identify one of two simultaneously presented novel objects. We manipulated two factors: (1) which object was the target (attended) and (2) the perceptual quality of the stimuli (manipulated between subjects).

There were three possible objects (a 'cubie', a ‘spikie’ and a ‘smoothie’; mean width: 4 degrees of visual angle; Fig. 1A) selected from the novel object set of Op de Beeck et al. (2006). On each trial two objects were presented, one on each side of a white central fixation cross (6 degrees eccentricity). One object was colored blue and the other green. In separate blocks, participants were cued to attend to either the blue or the green object. On each trial, participants identified the relevant object by pressing one of three response keys operated with the index, middle, and ring fingers of the right hand. Thus on each trial, the object in the relevant color was the target (‘attended object’) and the object in the other color was to be ignored (‘distractor’).

To allow separate estimation of the BOLD response to the three objects from that of the three button presses, object-button associations were counterbalanced within participants across scanning runs. Each participant learnt 3 different stimulus–response mappings (mapping 1: ‘button 1 for spikie, button 2 for cubie and button 3 for smoothie’; mapping 2: ‘button 1 for cubie, button 2 for smoothie and button 3 for spikie’; mapping 3: ‘button 1 for smoothie, button 2 for spikie and button 3 for cubie’). Across stimulus–response mappings, each object was equally associated with each of the three button press responses. A different mapping was used for each of 3 scanning runs carried out in a single session. Each run consisted of 4 blocks of trials. Blocks began with a 4 s cue, ‘Attend BLUE’ or ‘Attend GREEN’, which indicated the color of the target for the entire block (Fig. 1B). There were 72 trials in each block. On each trial, a white central fixation cross was presented for a variable delay of 1–3 s, after which it changed to either green or blue (in attend green and attend blue blocks respectively) for 500 ms before the pair of objects appeared. The object display was visible for 100 ms. Note that the change in fixation cross color cued the participants as to *when* the target would appear, and served to remind them of the color they should attend to, but did not inform them *where* the target item would appear as the configuration of green and blue objects varied randomly from trial to trial.

We manipulated the perceptual demand of the task by superimposing Gaussian noise in front of the stimuli (Fig. 1A). To maximize the amount of data available for the multi-voxel classification of object, which is carried out on individual subject data in each condition separately (see below), perceptual difficulty was manipulated as between-subject factor. Participants were randomly assigned to one of two experimental groups: 19 participants saw the stimuli with noise (high perceptual demand condition); the other 19 participants saw the stimuli without noise (low perceptual demand condition).

Participants learnt the 3 stimulus–response mappings before scanning and practiced the task for approximately 20 min. The order in which rules were learnt and used was counterbalanced between participants. Objects were not explicitly named at any point. Participants were instructed to respond as quickly as possible without making any mistakes and were told not to move their eyes. Stimuli were briefly presented (100 ms) and the target could be left or right of fixation with equal probability, making eye movements counterproductive.

Acquisition

FMRI scans were acquired using a Siemens 3 T Verio scanner with 32-channel head coil, at the Macquarie Medical Imaging center in Macquarie University Hospital. We used a high resolution interleaved ascending T2*-weighted echo planar imaging (EPI) acquisition sequence with the following parameters: repetition time (TR), 3000 ms; echo time (TE), 36 ms; 36 slices of 2.0 mm slice thickness with a 0.4 mm interslice gap; in-plane resolution, 1.77 × 1.77 mm; field of view, 191 mm. We also acquired T1-weighted MPRAGE structural images for all participants (non-selective inversion recovery, resolution 0.94 × 0.94 × 0.9 mm).