



Attentional modulation of background connectivity between ventral visual cortex and the medial temporal lobe



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ARTICLE INFO

Article history:

Received 18 September 2015

Revised 3 June 2016

Accepted 13 June 2016

Available online 15 June 2016

Keywords:

Top-down attention

fMRI

Functional connectivity

Hippocampus

Faces

Scenes

ABSTRACT

Attention prioritizes information that is most relevant to current behavioral goals. This prioritization can be accomplished by amplifying neural responses to goal-relevant information and by strengthening coupling between regions involved in processing this information. Such modulation occurs within and between areas of visual cortex, and relates to behavioral effects of attention on perception. However, attention also has powerful effects on learning and memory behavior, suggesting that similar modulation may occur for memory systems. We used fMRI to investigate this possibility, examining how visual information is prioritized for processing in the medial temporal lobe (MTL). We hypothesized that the way in which ventral visual cortex couples with MTL input structures will depend on the kind of information being attended. Indeed, visual cortex was more coupled with parahippocampal cortex when scenes were attended and more coupled with perirhinal cortex when faces were attended. This switching of MTL connectivity was more pronounced for visual voxels with weak selectivity, suggesting that connectivity might help disambiguate sensory signals. These findings provide an initial window into an attentional mechanism that could have consequences for learning and memory.

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1. Introduction

Attention during encoding enhances subsequent recognition memory and can modulate activity in regions of the medial temporal lobe (MTL) that support such memory (Carr, Engel, & Knowlton, 2013; Dudukovic, Preston, Archie, Glover, & Wagner, 2011; Uncapher & Rugg, 2009; Yi & Chun, 2005). The purpose of the current study was to investigate a particular way in which attention might enhance MTL processing, inspired by studies about how attention modulates the visual system. Specifically, top-down attention has been shown to modulate the coupling between visual areas, strengthening functional connectivity between areas that code for attended information (Al-Aidroos, Said, & Turk-Browne, 2012; Bosman et al., 2012). By establishing such functional pathways, attention may improve the transmission of task-relevant information (Fries, 2005).

If attention modulates coupling at the highest levels of the visual hierarchy, this mechanism could also prioritize which information is transmitted to the MTL and ultimately the hippocampus. Parahippocampal cortex (PHC) and perirhinal cortex (PRC) provide

an interface between the visual system and the hippocampus and thus are good targets for evaluating attentional modulation of functional connectivity. PHC and PRC have different functional characteristics (Eichenbaum, Yonelinas, & Ranganath, 2007; Ranganath & Ritchey, 2012): for example, PHC processes spatial and contextual information such as scenes, whereas PRC processes items, such as objects and faces (Davachi, 2006; Lee, Yeung, & Barense, 2012).

We thus manipulated selective attention to scenes and faces in composite images (Al-Aidroos et al., 2012; O'Craven et al., 1999; Yi & Chun, 2005), predicting that this would influence functional connectivity with PHC and PRC. Much of ventral visual cortex processes low- and mid-level features that are common to both scenes and faces (e.g., contours, colors, textures) and these areas might couple with distinct MTL regions depending on attention. In particular, we hypothesized that ventral visual cortex would show stronger functional connectivity with PHC during scene attention and with PRC during face attention.

To measure functional connectivity, we examined the correlation of BOLD activity over time between regions or voxels. This approach has long been used to uncover the coupling between brain regions during rest (Fox & Raichle, 2007). However, such measures can be confounded during tasks because regions that

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respond synchronously to stimuli will be spuriously correlated over time even in the absence of any interaction. There are several approaches for dealing with this issue (Friston et al., 1997; Rissman, Gazzaley, & D'Esposito, 2004). Here we adopt a “background connectivity” approach in which stimulus-evoked responses and noise sources are projected out of the data and correlations are calculated in the residuals during different experimental conditions (Al-Aidroos et al., 2012; Duncan, Tompary, & Davachi, 2014; Griffis, Elkhetafi, Burge, Chen, & Visscher, 2015; Norman-Haignere, McCarthy, Chun, & Turk-Browne, 2012; Tompary, Duncan, & Davachi, 2015). The resulting connectivity reflects spontaneous, intrinsic interactions within the functional networks engaged by each condition.

By comparing background connectivity across epochs in which attention was oriented to scenes vs. faces, we identified patterns of PHC and PRC connectivity selective to each attentional state. We predicted that areas of ventral visual cortex would show higher background connectivity both with PHC during scene attention and with PRC during face attention. Moreover, we predicted that such switching would be most pronounced for voxels in ventral visual cortex that responded robustly to both scenes and faces, as connectivity is needed in such cases to determine how the information conveyed by this activity will be processed (Fries, 2005). That is, the influence of voxels with unselective evoked activity in broader networks might arise from selective functional connectivity.

2. Materials and methods

2.1. Participants

Twelve participants (7 females, ages 18–26), with normal or corrected-to-normal vision, participated for monetary compensation. The study was approved by the Princeton University Institutional Review Board and all participants provided informed consent.

2.2. Attention runs

Functional runs followed an on-off block design with 18 s of stimulation interleaved with 18 s of fixation. Stimulation blocks contained 12 face/scene composite stimuli selected pseudorandomly, presented sequentially for 1 s each separated by a 500-ms interstimulus interval (Fig. 1). Each run contained 12 blocks and lasted 7.2 min.

To create the composite stimuli, we drew from a set of 24 house photographs (from image searches on the Internet) and 24 face photographs (neutral expression, equal number of males and females, from www.macbrain.org/resources.htm). All photographs were equated in terms of mean luminance. For each run, 16 of the houses and 16 of the faces were selected randomly. Four of the photographs from each category were presented in a given block (three times each). The sequence of 12 photographs was determined separately for each category and included adjacent repetitions for the attention task (described below). The two streams were then combined by averaging the pair of house and face photographs at each serial position. This averaging involved simply taking the mean of the intensity values at each pixel. Because the two photographs had the same mean luminance, they made approximately equal contributions to the composite image. The photographs differed in other ways of course, which were preserved in the composite image, including: spatial frequency, central vs. peripheral information, number of objects, etc. Such differences were unavoidable to some extent, as they were what made the photographs depictions of houses and faces. Stimuli were

presented on a projection screen at the back of the scanner bore ($6 \times 6^\circ$), viewed through a mirror attached to the head coil.

To manipulate attention, participants performed a one-back task on the photographs from one category for an entire run, while ignoring the photographs from the other category. During face-attention runs, for example, participants pressed a button with their right index finger when the face component of two successive composite images matched, irrespective of whether the house changed. Participants had 1 s to respond. One-back targets occurred once or twice per block (with equal probability) in both of the categories. During fixation periods, the only stimulus was a central fixation point.

There are two noteworthy properties of this task: First, bottom-up stimulation was identical across attentional states, allowing neural differences to be interpreted as reflective of top-down attention. Second, by holding attention on one category throughout each run, we encouraged participants to adopt strong attentional states that could modulate connectivity in a persisting manner. Although similar in design to one of our previous studies about retinotopic visual cortex (Al-Aidroos et al., 2012), a new dataset was collected for this study with high-resolution coverage of the MTL.

2.3. Rest runs

Additional rest runs of the same length as the attention runs were collected as a connectivity baseline, containing only the fixation point. Participants completed two rest runs first, followed by alternating face-attention and scene-attention runs (two each, order counterbalanced).

2.4. Localizer run

The localizer used the same stimuli, design, and task as the attention runs, but with house and face photographs presented individually in separate, alternating blocks (starting block counterbalanced).

2.5. Data acquisition

Data were acquired with a 3T Siemens Skyra scanner. Functional images were collected with a gradient-echo EPI sequence (TE = 28 ms; TR = 2000 ms; FA = 71° ; matrix = 96×96). Each of 221 volumes contained 32 slices (2×2 mm in-plane, 3 mm thickness) perpendicular to the long axis of the hippocampus. A high-resolution 3D T1-weighted MPRAGE scan was collected for registration. A high-resolution T2-weighted TSE scan (32 slices; 0.4×0.4 mm in-plane; 3 mm thickness) was collected for manual MTL segmentation.

2.6. Preprocessing

Data were analyzed with FSL and MATLAB. The first 5 volumes of each run were discarded. All images were skull-stripped to improve registration. The images were preprocessed with motion correction (MCFLIRT), slice timing correction, spatial smoothing (4-mm FWHM), high-pass filtering (144-s cutoff), and FILM prewhitening. Functional images were registered to the MPRAGE and then the Montreal Neurological Institute (MNI) standard brain.

2.7. MTL segmentation

We manually segmented PRC and PHC on the TSE scan of each participant using published criteria (Insausti et al., 1998; Pruessner et al., 2002; see also Aly & Turk-Browne, 2016a). The anterior border of PRC was defined as the slice with the anterior-most tip of the

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