

Spatial encoding and underlying circuitry in scene-selective cortex



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ABSTRACT

Three cortical areas (Retro-Splenial Cortex (RSC), Transverse Occipital Sulcus (TOS) and Parahippocampal Place Area (PPA)) respond selectively to scenes. However, their wider role in spatial encoding and their functional connectivity remain unclear. Using fMRI, first we tested the responses of these areas during spatial comparison tasks using dot targets on white noise. Activity increased during task performance in both RSC and TOS, but not in PPA. However, the amplitude of task-driven activity and behavioral measures of task demand were correlated only in RSC. A control experiment showed that none of these areas were activated during a comparable shape comparison task.

Secondly, we analyzed functional connectivity of these areas during the resting state. Results revealed a significant connection between RSC and frontal association areas (known to be involved in perceptual decision-making). In contrast, TOS showed functional connections dorsally with the Inferior Parietal Sulcus, and ventrally with the Lateral Occipital Complex – but not with RSC and/or frontal association areas. Moreover, RSC and TOS showed differentiable functional connections with the anterior-medial and posterior-lateral parts of PPA, respectively. These results suggest two parallel pathways for spatial encoding, including RSC and TOS respectively. Only the RSC network was involved in active spatial comparisons.

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Introduction

Neuroimaging evidence suggests that at least three visual cortical areas respond selectively to ‘scenes’, compared to images from other semantic categories. These areas are typically termed the Parahippocampal Place Area (PPA), Retrosplenial Cortex (RSC) and the Transverse Occipital Sulcus (TOS), respectively located in ventral, medial and dorsal regions of the visual cortex (Aguirre et al., 1998; Epstein and Kanwisher, 1998; Epstein et al., 2007; Grill-Spector, 2003; Maguire et al., 1998; Nasr et al., 2011; Park and Chun, 2009). Neuroimaging and neuropsychological studies have concluded that PPA is selectively involved in scene perception, whereas RSC contributes more during scene navigation (Epstein, 2008; Epstein et al., 1999, 2007; Kravitz et al., 2011; Maguire, 2001; Park and Chun, 2009; Spiers and Maguire, 2006; Takahashi et al., 1997; Vann et al., 2009). For instance, RSC responds more strongly to familiar scenes rather than to unfamiliar ones, whereas PPA activity does not vary with scene familiarity (Epstein et al., 2007). Furthermore, RSC shows more viewpoint invariance, compared to PPA (Epstein et al., 2003, 2007; Park and Chun, 2009).

In addition to the above evidence for a role of RSC in scene-based navigation, some evidence suggests that RSC may be activated across a wide range of non-scene-specific spatial encoding tasks. For instance, it has been reported that isolated visual objects can activate RSC (and PPA) when they are associated with spatial context (Aminoff et al.,

2007; Bar and Aminoff, 2003). Another study reported that RSC (but not PPA) is activated by haptic input when blind humans try to discriminate spatial layouts (Wolbers et al., 2011). A recent study by Harel et al. (2013) reported that RSC activity contained information about spatial layout but no information about the objects within the presented scene. Additionally, lesions including RSC affect non-navigational tasks, impairing the integration of spatial information with egocentric heading/position (Hashimoto et al., 2010 but see Ino et al., 2007).

In contrast to RSC and PPA, the dorsal scene-selective area (TOS) is explicitly retinotopic (Grill-Spector, 2003; Levy et al., 2004; Nasr et al., 2011). Partly for this reason, TOS has been regarded as ‘transitional’ between lower (i.e. retinotopic) and higher (e.g. scene-selective) cortical levels (Hasson et al., 2003). However, recent TMS studies suggested a causal link between TOS activity and scene perception in human subjects (Dilks et al., 2013). Other studies have also shown that, to the extent that TOS does respond to higher-order variables, those TOS responses are usually similar to responses in PPA rather than RSC (Epstein et al., 2007; Park and Chun, 2009).

In the first part of this study, we tested whether spatial comparison tasks activated scene-selective areas (RSC, TOS and PPA) in the absence of scenes. If so, does the amplitude of this task-driven activity vary with the level of spatial encoding demand? Secondly, if information encoded in RSC (and/or other areas that show task-driven responses) is used for decision-making, then one might expect to see functional connections between these sensory- and task-driven areas, relative to higher-level association areas responsible for decision-making (Badre

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and D'Esposito, 2009; Heekeren et al., 2008; Kayser et al., 2010). To test this, we analyzed resting state functional connections by independently seeding RSC, PPA and TOS.

Methods

Participants

In different experiments, participants were selected from a total pool of 17 subjects (ages 22 to 36). Among these subjects, 14 subjects participated in experiment 1, and 11 subjects participated in experiment 2 (8 subjects in common with experiment 1). All subjects had normal or corrected-to-normal visual acuity and radiologically normal brains, without history of neuropsychological disorders. All experimental procedures conformed to NIH guidelines and were approved by Massachusetts General Hospital protocols. Informed written consent was obtained from all subjects.

Stimuli and procedure

In spatial comparison tasks, stimuli were two colored semi-transparent square dots (one red, and the other blue) that were presented simultaneously in randomized locations within each image ($20 \times 20^\circ$ of visual angle) during central fixation (Fig. 1A). In the control shape comparison tasks, stimuli were two colored semi-transparent objects (one red, and the other blue) and their shape (square or triangle) varied randomly from trial to trial (Fig. S1).

In each trial, dot size was scaled with eccentricity (range = $0.33\text{--}0.57^\circ$ of visual angle). Dots were presented simultaneously for 100 ms at the beginning of each trial (Fig. 1A) while the white noise background remained constant throughout the 1000 ms trial interval. This short dot presentation discouraged saccades toward the target dots. A white noise background was generated independently for each trial. Stimuli were presented via LCD projector (Sharp XG-P25, 1024×768 pixel resolution, 60 Hz refresh rate) onto a rear-projection screen. Matlab 7.8 (MathWorks, US) and Psychophysics Toolbox were used to control stimulus presentation.

Trials were blocked according to the task. Each block consisted of 15 s of fixation on a uniform gray screen ('fixation only'), followed by 30 stimulus presentation trials at 1 s each. The fixation point was white during the fixation-only period, and green during the stimulus presentation trials. Each run consisted of 5 blocks, and the subjects' task did not change within a run.

Tasks

During the spatial comparison sessions, subjects were cued at the beginning of each run to make either (1) a spatial comparison *within images*, (2) a spatial comparison *between images* (1-back task), or (3) a simple target detection. During the *within image* comparison, subjects were required to report if the two simultaneously presented dots in each trial were located on the same side of the fixation point (i.e., both on the left or both on the right), or on different sides. During the *between image* comparison task, subjects compared the location of the target dot (blue dot for half of the subjects and red dot for the rest) between each two consecutive trials (1-back) and reported if they were presented on the same side of the fixation point or not. During target detection trials, they reported if they could see the target dot or not. These target detection trials were used as the baseline to reduce (if not eliminate) the impact of the sensory-related activity relative to activity evoked during 'within' and 'between' image comparison tasks. Importantly, the visual stimuli were identical across all three tasks, except for the very small ($0.33\text{--}0.57^\circ$) target dots, whose average contrast varied between tasks (Results).

During the shape comparison sessions, subjects were cued to make (1) a shape comparison between images (1-back), or (2) a simple target

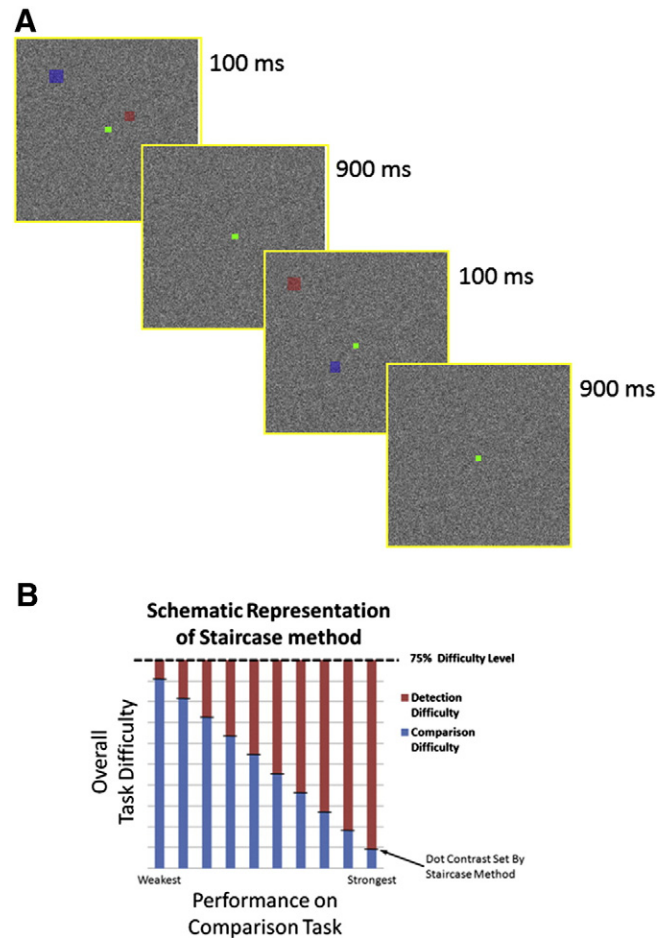


Fig. 1. Panel A shows a schematic representation of experimental trials. In different blocks, subjects compared the locations of dot targets either 1) within or 2) between images, when presented against a white noise background, in the absence of any scene. In each trial, dots were presented simultaneously during the first 100 ms, and the background remained otherwise constant throughout the trial (i.e. 1 s). In separate blocks, subjects performed a simple dot detection control task. For each subject, the response accuracy converged towards 75%. Panel B shows a schematic representation of staircase method used to control subjects response accuracy. Since performance on the spatial comparison task varied between subjects, we adjusted the "overall load" by varying the target dot contrast. Thus, for those subjects that had more difficulty in the spatial comparison (i.e. higher spatial comparison demand), dot contrast was increased to ease dot detection. Conversely, for those subjects performed the spatial comparison task more easily (i.e. lower spatial comparison demand), we reduced the dot contrast to make dot detection harder. According to this paradigm, dot contrast varied positively correlated to spatial comparison demand.

detection. During the comparison between images, subjects were required to report if each two consecutively presented target objects had the same shape (i.e. if they were both squares or triangles) or not. During target-detection trials, subjects reported if they could see the target object or not. Again, the visual stimuli were identical (again excepting the *small* areas subtended by target objects) across both these tasks. The target detection trials were used as the baseline condition for analysis, to reduce/eliminate the impact of the sensory-related activity from the shape comparison trials.

For all tasks, subjects were instructed to maintain their gaze at the central fixation point and to report their answers by pressing one of the two keys on a key pad (two-alternative forced choice). Accuracy was stressed more than speed. Subjects' performance during the scans converged towards 75% by manipulating the contrast between the dots and background using a staircase design. The task sequence was selected pseudo-randomly, without immediate repeats. Subjects practiced with the stimuli and tasks for 20–30 min prior to scanning.

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