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Occipital place area represents the local elements of scenes

By

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Abstract

The occipital place area represents the local elements of scenes

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Frederik S. Kamps

Neuroimaging studies have identified three scene-selective regions in human cortex: parahippocampal place area (PPA), retrosplenial complex (RSC), and occipital place area (OPA). However, the particular scene information represented in each region is unknown, especially for the least-studied OPA. Here we investigate how OPA represents two critical sources of scene information: i) spatial boundary (e.g., the external shape of the space) and ii) content (i.e., the internal elements such as furniture). To test spatial boundary representation, we examined responses in OPA to images of intact rooms and these same rooms in which the walls, floors, and ceilings were fractured and rearranged, disrupting spatial boundary. OPA responded similarly to intact and fractured rooms, suggesting OPA does not represent spatial boundary per se, but rather the local elements that compose the space themselves, independent of their spatial arrangement. By contrast, PPA and RSC were sensitive to spatial boundary, responding more to intact than fractured rooms. Next, to test scene content representation, we examined responses in OPA to images of furniture and non-furniture objects. We found OPA (and PPA) responded selectively to furniture. However, while both OPA and PPA represent scene content, they do so differently; in another test, only OPA was sensitive to the number of pieces of furniture, suggesting OPA represents the local elements of scene content, responding more when more such elements were presented. Taken together, these findings reveal that OPA analyzes local scene elements – both in spatial boundary and scene content representation – while PPA and RSC represent global scene properties.

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Introduction

Behavioral and computational research has proposed that a scene (e.g., a kitchen) can be represented by two independent, yet complementary descriptors: i) its *spatial boundary* (i.e., the external shape, size, and scope of the space) and ii) its *content* (i.e., the internal elements encompassing objects, textures, colors, and materials) (Oliva and Torralba, 2001, 2002). But how does the brain represent these descriptors? A central hypothesis is that one scene-selective region – the parahippocampal place area (PPA) – represents spatial boundary information. Supporting this hypothesis, Epstein and Kanwisher (1998) found that PPA responds significantly more to images of intact, empty apartment rooms than to these same rooms in which the walls, floors, and ceilings were fractured and rearranged, such that they no longer defined a coherent space. Two other studies using multivoxel pattern analysis (MVPA) found distinct patterns of activity in PPA related to closed (e.g., a cave) versus open (e.g., a hilly landscape) scenes (Kravitz et al., 2011; Park et al., 2011), further supporting the idea that PPA is sensitive to spatial boundary information in scenes. However, spatial boundary representation in PPA may not be the whole story; mounting evidence suggests that PPA also represents scene content information. For example, PPA is sensitive to single pieces of furniture (Harel et al., 2012; Bettencourt and Xu, 2013), objects strongly associated with particular scenes (e.g., a stove) (Bar and Aminoff, 2003), objects that are large and not portable (e.g., a sofa) (Mullally and Maguire, 2011; Konkle and Oliva, 2012), and objects relevant for navigation (Janzen and van Turennout, 2004). By contrast, retrosplenial complex (RSC) represents spatial boundary, but not content (Harel et al., 2012). Finally, spatial boundary and content representation in occipital place area (OPA), formerly referred to as transverse occipital sulcus (Grill-Spector, 2003), have never been explored.

Here we investigate how OPA (as well as PPA and RSC) represents both spatial boundary and scene content information. To test spatial boundary representation in OPA, we examined responses to images of ‘intact’, empty rooms and these same rooms ‘fractured’ and rearranged. We hypothesized that if a region is sensitive to spatial boundary, then it will respond more to intact rooms than fractured rooms. To test scene content representation in OPA, we compared responses to images of single, nonfurniture objects (e.g., a hammer) and single pieces of furniture (e.g., a sofa). We hypothesized that if a region is sensitive to scene content, it should respond more to furniture than non-furniture objects. Finally, as an additional test of scene content representation, we explored whether the three scene-selective regions were sensitive to the amount of content information in a scene by examining the responses in OPA, PPA, and RSC to images of single pieces of furniture and multiple pieces of furniture, a question which to our knowledge has never been addressed (Figure 2).

Methods

Participants. Twenty-five participants (Age: 18-25; 12 from Emory, 13 from MIT; 13 females, 12 males) were recruited for this experiment. Two participants were excluded from further analyses because of nonsignificant localizer results, and one for excessive motion during scanning, yielding a total of 22 participants reported here. All participants gave informed consent and had normal or corrected-to-normal vision.

Design. We used a region of interest (ROI) approach in which we localized category-selective regions (Localizer runs) and then used an independent set of runs to investigate their responses to a variety of stimulus categories (Experimental runs). For both Localizer and Experimental runs, participants performed a one-back task, responding every time the same image was presented twice in a row.

For the localizer scans, ROIs were identified using a standard method described previously (Epstein & Kanwisher, 1998). Specifically, a blocked design was used in which participants viewed images of faces, objects, scenes, and scrambled objects. Each participant completed either 2 (Emory) or 3 (MIT) runs. Each run was 336 s long and consisted of 4 blocks per stimulus category. The order of blocks in each run was palindromic (e.g., faces, objects, scenes, scrambled objects, scrambled objects, scenes, objects, faces) and randomized across runs. Each block contained 20 images from the same category for a total of 16 s blocks. Each image was presented for 300 ms, followed by a 500 ms interstimulus interval. We also included five 16 s fixation blocks: one at the beginning, three in the middle interleaved between each palindrome, and one at the end of each run.

For the Experimental scans, participants viewed runs during which 16 s blocks (20 stimuli per block) of either 8 (at Emory) or 12 (at MIT) categories of images were presented. Five of the categories were common between Emory and MIT, and tested the central hypotheses described here; the additional categories tested unrelated hypotheses. Each image was on for 300 ms followed by a 500 ms inter-stimulus interval. At Emory, participants viewed 8 runs, and each run contained 21 blocks (2 blocks of each condition, plus 5 blocks of fixation), totaling 344 s. At MIT, participants viewed 12 runs, and each run contained 16 blocks (one block of each of the 12 different stimulus categories, and 4 blocks of fixation), totaling 256 s.

For the five categories of interest, we used the same stimuli presented in Epstein and Kanwisher (1998; indicated with an asterisk), as well as one other category (Figure 2): (1*) photographs of apartment rooms with all furniture and objects removed (intact rooms); (2*) the same rooms but fractured into their component surfaces and rearranged such that they no longer defined a coherent space (fractured rooms); (3*) single non-furniture objects (single objects); (4) single items of furniture (single furniture); and (5*) arrays of all of the objects from one of the furnished rooms cut out from the original background and rearranged in a random configuration (multiple furniture).

fMRI scanning. All scanning was performed on a 3T Siemens Trio scanner. At Emory, scans were conducted in the Facility for Education and Research in Neuroscience. Functional images were acquired using a 32-channel head matrix coil and a gradient-echo single-shot echoplanar imaging sequence (28 slices, TR = 2 s, TE = 30 ms, voxel size = 1.5 x 1.5 x 2.5 mm, and a 0.25 interslice gap). At MIT, scans were conducted at the Athinoula A. Martinos Imaging Center at the McGovern Institute for Brain Research. Functional images were acquired using a 32-channel head matrix coil and a gradient-echo single-shot echoplanar imaging sequence (28 slices, TR = 2 s, TE = 30 ms, voxel size = 1.4 x 1.4 x 2.0 mm, and a 0.2 interslice gap). For all scans, slices were oriented approximately between perpendicular and parallel to the calcarine sulcus, covering the occipital and temporal lobes. Whole-brain, high-resolution anatomical images were also acquired for each participant for purposes of registration and anatomical localization (see Data analysis).

Data analysis. fMRI data analysis was conducted using the FSL software (FMRIB's Software Library; www.fmrib.ox.ac.uk/fsl) (Smith et al., 2004) and the

FreeSurfer Functional Analysis Stream (FS-FAST; http://surfer.nmr.mgh.harvard.edu/). ROI analysis was conducted using the FS-FAST ROI toolbox. Before statistical analysis, images were motion corrected (Cox and Jesmanowicz, 1999). Data were then detrended and fit using a double gamma function. Localizer data, but not experimental data, were spatially smoothed (5-mm kernel). After preprocessing, scene-selective regions OPA, PPA, and RSC were bilaterally defined in each participant (using data from the independent localizer scans) as those regions that responded more strongly to scenes than objects ($p < 10^{-4}$, uncorrected), as described previously (Epstein and Kanwisher, 1998). OPA, PPA, and RSC were identified in at least one hemisphere in all participants. Within each ROI, we then calculated the magnitude of response (percent signal change, or PSC) to the five categories of interest, using the data from the experimental runs. A 2 (hemisphere: Left, Right) x 5 (condition: intact rooms, fractured rooms, single objects, single furniture, multiple furniture) repeated-measures ANOVA for each scene ROI was conducted. We found no significant hemisphere x condition interaction in OPA (p = .615), PPA (p = .083), or RSC (p = .427). Thus, both hemispheres were collapsed for further analyses. As a control region, we anatomically defined bilateral early visual cortex (EVC). Specifically, a spherical ROI (6 mm radius, 941 voxels) was drawn in each subject in each hemisphere along the calcarine sulcus just anterior to the occipital pole, and then collapsed across hemisphere for further analysis.

Results

Spatial boundary representation

To test spatial boundary representation in OPA (as well as PPA and RSC), we compared responses in each scene-selective ROI to images of intact, empty rooms (intact rooms) with responses to images of fractured and rearranged rooms in which spatial boundary information was disrupted (fractured rooms) (Figure 2). Interestingly, for OPA, a paired t-test revealed no significant difference between responses to intact and fractured rooms ($t_{(21)} = 0.89$, $p = 0.39$). This finding suggests OPA is not sensitive to the coherent spatial arrangement of walls, floors, and ceilings, but rather represents these local scene elements independent of their spatial arrangement relative to one another. By contrast, PPA responded significantly more to intact rooms than fractured rooms ($t_{(21)} = 5.68$, $p < 0.001$), replicating previous findings (Epstein & Kanwisher, 1998). Likewise, RSC responded significantly more to intact rooms than fractured rooms ($t_{(21)} = 8.81$, $p < 0.001$), consistent with previous reports (Harel et al., 2012).

The analyses above suggest that the three scene-selective regions represent spatial boundary information differently, so next we directly compared their response profiles. A 3 (ROI: OPA, PPA, RSC) x 2 (room type: intact, fractured) repeated measures ANOVA revealed a significant interaction ($F_{(2, 42)} = 33.66$, $p < 0.001$), with OPA responding significantly more than both PPA and RSC to fractured rooms relative to intact rooms (main effect contrasts, both p values < 0.001). This result suggests that the scene-selective regions represent spatial boundary differently, with OPA representing the local elements (e.g., walls, floors, ceilings) that compose the spatial boundary, and PPA and RSC representing the coherent spatial arrangement of these elements relative to one another.

Scene content representation

To test scene content representation in the three scene-selective regions, we compared responses in each of these regions to images of single, non-furniture objects (single objects) with responses to images of single pieces of furniture (single furniture) (Figure 2). For OPA, a paired t-test revealed a significantly greater response to single furniture than to single objects ($t_{(21)} = 8.18, p < 0.001$), indicating that OPA selectively represents scene content. Similarly, for PPA, we found a significantly greater response to single furniture than to single objects ($t_{(21)} = 10.26, p < 0.001$), consistent with previous reports of scene content representation in PPA (Bar and Aminoff, 2003; Mullally and Maguire, 2011; Harel et al., 2012; Konkle and Oliva, 2012; Bettencourt and Xu, 2013). Finally, RSC did not respond above baseline to either single furniture or single objects, consistent with previous findings that RSC is not sensitive to scene content (Harel et al., 2012).

The above analyses suggest that the three scene-selective regions encode scene content differently, so next we directly tested this suggestion. A 3 (ROI: OPA, PPA, RSC) x 2 (condition: single objects; single furniture) repeated measures ANOVA revealed a significant interaction of ROI and condition ($F_{(2, 42)} = 17.65, p < 0.001$), with both OPA and PPA responding significantly more than RSC to single furniture relative to single objects (main effect contrasts, both p values < 0.001). OPA and PPA responded similarly to single furniture relative to single objects ($p = 0.31$). These findings indicate that OPA and PPA are more sensitive to scene content than RSC.

As an additional exploratory test of content representation in scene processing, we asked whether any scene-selective region might further be sensitive to the amount of scene content. To test sensitivity to amount of scene content, we compared responses in each region to images of single pieces of furniture (single furniture) and multiple pieces of furniture (multiple furniture). For OPA, a paired t-test revealed a significantly greater response to multiple furniture than single furniture ($t_{(21)} = 5.95, p < 0.001$), indicating that

OPA is sensitive to the amount of scene content information presented. But might OPA be sensitive to the amount of any object information more generally, and not the amount of scene content information in particular? To address this question, in ten of our participants, we included an additional condition – images of multiple non-furniture objects (multiple objects). Importantly, the number and position of objects in the multiple object images was matched with the number and position of pieces of furniture in the multiple furniture images. In OPA, a paired t-test revealed a significantly greater response to multiple furniture than multiple objects ($t_{(9)} = 4.342, p = 0.002$), suggesting that OPA does not simply represent the number of any sort of objects, but rather scene-related objects in particular. This finding dovetails with a recent study that also found a significantly greater response to images of multiple furniture than multiple objects in OPA (referred to as 'TOS') (Bettencourt and Xu, 2013). For PPA, we found a marginal difference in responses to single furniture and multiple furniture ($t_{(21)} = 1.96, p = 0.06$), suggesting that representation of scene content in PPA may be independent of the amount of content presented. Finally, RSC did not respond above baseline to either single furniture or multiple furniture, again consistent with previous findings that RSC does not represent scene content (Harel et al., 2012).

The findings above suggest that OPA, PPA, and RSC are differentially sensitive to the amount of content information presented, so next we directly tested this suggestion. A 3 (ROI: OPA, PPA, RSC) x 2 (condition: single furniture, multiple furniture) repeated-measures ANOVA revealed a significant interaction of ROI and condition ($F_{(2, 42)} = 9.527$, $p < 0.001$), with OPA responding significantly more than both PPA and RSC to multiple furniture versus single furniture (main effect contrasts, both p values < 0.01). PPA and

RSC responded similarly to multiple and single furniture ($p = 0.46$). This finding presents evidence of differential scene content representation across scene-selective cortex, with OPA more sensitive than both PPA and RSC to the amount of scene content information.

Finally, might the findings in OPA be explained by retinotopic information simply inherited from early visual cortex? To address this concern, we compared responses in OPA with those in EVC to all five conditions (Figure 4). A 2 (ROI: OPA, EVC) x 5 (condition: intact rooms, fractured rooms, single objects, single furniture, multiple furniture) repeated measures ANOVA revealed a significant interaction of ROI and condition ($F_{(4,84)} = 75.73$, $p < 0.001$), indicating that the pattern of responses in OPA was not as expected for a retinotopic region.

Discussion

The present study explored how two crucial sources of scene information, spatial boundary and scene content, are represented in OPA (as well as PPA and RSC). The results indicate differential representation of spatial boundary and scene content across scene-selective cortex. Specifically, we found sensitivity to spatial boundary in PPA and RSC, but no such sensitivity in OPA. Rather, OPA may represent scenes at the level of local elements (e.g., walls, floors, ceilings), independent of the coherent spatial arrangement of these elements. Next, we found sensitivity to scene content (i.e., furniture) in both OPA and PPA, but not in RSC. Importantly, however, while both OPA and PPA respond selectively to scene content, they represent such information differently: OPA was additionally sensitive to the amount of content information in a scene, while PPA was not. This finding suggests that OPA represents scene content (e.g., furniture) at the level of local elements, insofar as a region sensitive to local elements of content should respond more when more such elements are present. By contrast, PPA encodes global representations of content that are independent of the number of elements making them up. RSC did not respond above baseline to any of the 'object' conditions, indicating that RSC is not sensitive to scene content information.

Together, these findings suggest a novel division of labor in the human scene processing system, with OPA representing the local elements of scenes, and PPA and RSC representing global scene properties. This hypothesis not only enriches our understanding of the functional organization of the scene-processing system in particular, but may also inform our knowledge of the functional organization of high-level visual processing in human cortex more generally. Specifically, across the face and body systems, more posterior cortical regions (i.e., the occipital face area, OFA, and the extrastriate body area, EBA) are sensitive to local elements, while the more anterior cortical regions (the fusiform face area, FFA, and the fusiform body area, FBA) represent the global configuration of local elements (Yovel and Kanwisher, 2004; Pitcher et al., 2007; Taylor et al., 2007; Liu et al., 2009). While this posterior to anterior organizational scheme is well established in low- and mid-level vision, particularly on the basis of anatomical criteria such as receptive field properties and connectivity (Hubel and Wiesel, 1962, 1965; Felleman and Van Essen, 1991), the present data provide an important and previously missing piece of functional evidence to suggest this principle can be extended to high-level visual systems as well.

Our findings showing that PPA represents both spatial boundary and scene content are consistent with many other studies (Epstein and Kanwisher, 1998; Janzen and van Turennout, 2004; Kravitz et al., 2011; MacEvoy and Epstein, 2011; Mullally and

Maguire, 2011; Park et al., 2011; Harel et al., 2012; Bettencourt and Xu, 2013). Further, our finding that RSC selectively responded to intact over fractured rooms, and not at all to scene content, is consistent with previous reports of spatial boundary sensitivity, but not scene content sensitivity, in RSC (Maguire, 2001; Ino et al., 2002; Epstein et al., 2007; Park and Chun, 2009; Harel et al., 2012). While little is known about information processing in OPA, two recent studies have reported that OPA encodes 'sense' (left/right) (Dilks et al., 2011) and egocentric distance information (Persichetti and Dilks, submitted), suggesting a role for OPA in navigation. At first glance, our finding that OPA is relatively insensitive to spatial boundary appears inconsistent with the role of OPA in navigation, since fractured rooms do not imply a navigable space. However, we propose that while OPA may not represent allocentric spatial relationships between local components of scenes, such as how floors are arranged relative to walls, it may nevertheless represent egocentric spatial information about local scene elements, such as the distance and direction of boundaries (e.g., walls) and obstacles (e.g., furniture) relative to the viewer. Thus, our hypothesis that OPA represents the local elements of scenes is compatible with the proposed role of OPA in navigation, and may point to a role for OPA in locally guided navigation and obstacle avoidance.

In conclusion, we found differential sensitivity to spatial boundary and scene content information across scene-selective cortex. Unlike PPA and RSC, OPA does not represent spatial boundary information, but rather may represent the local elements that compose the spatial boundary (e.g., walls, floors, ceilings), independent of their coherent spatial arrangement. Further, unlike PPA and RSC, OPA not only represents scene content, but also is sensitive to the amount of content information in a scene, suggesting that OPA represents scene content information at the level of local elements, responding more when such elements are present. Based on these findings, we propose a novel division of labor in the scene processing system, with OPA representing the local elements of scenes, and PPA and RSC representing global scene properties.

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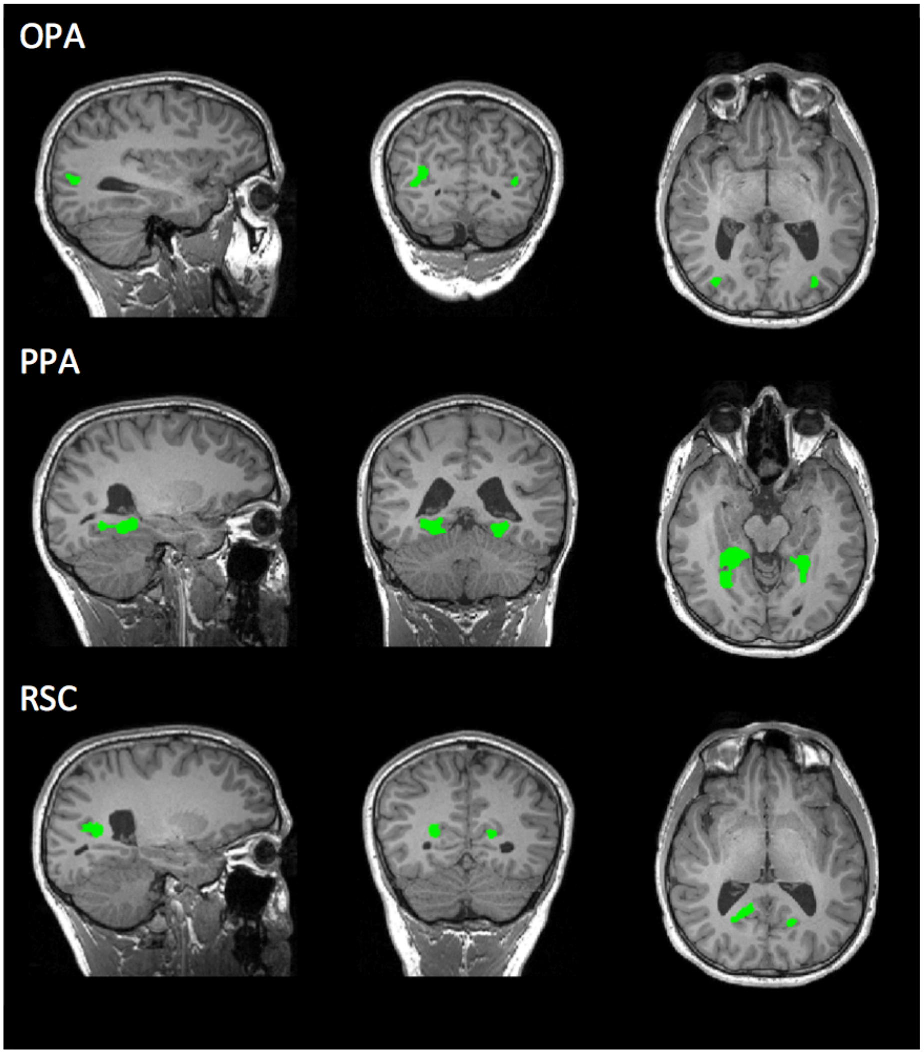

Figure 1.
Scene-selective regions of interest in a sample participant. Occipital Place Area (OPA), Parahippocampal Place Area (PPA), and Retrosplenial Complex (RSC), labeled accordingly. Regions of interest were selected as those regions responding significantly more to scenes then objects ($p < .0001$). Responses of each region to the experimental conditions were then tested in an independent set of data.

Figure 2.
Example stimuli used in the study. From top row to bottom row: 1) intact, empty apartment rooms (intact rooms); 2) indoor rooms whose walls, floors, and ceilings were fractured and rearranged such that they no longer defined a coherent space (fractured rooms); 3) single, non-furniture objects (single objects); 4) single pieces of furniture (single furniture); and 5) multiple pieces of furniture (multiple furniture).

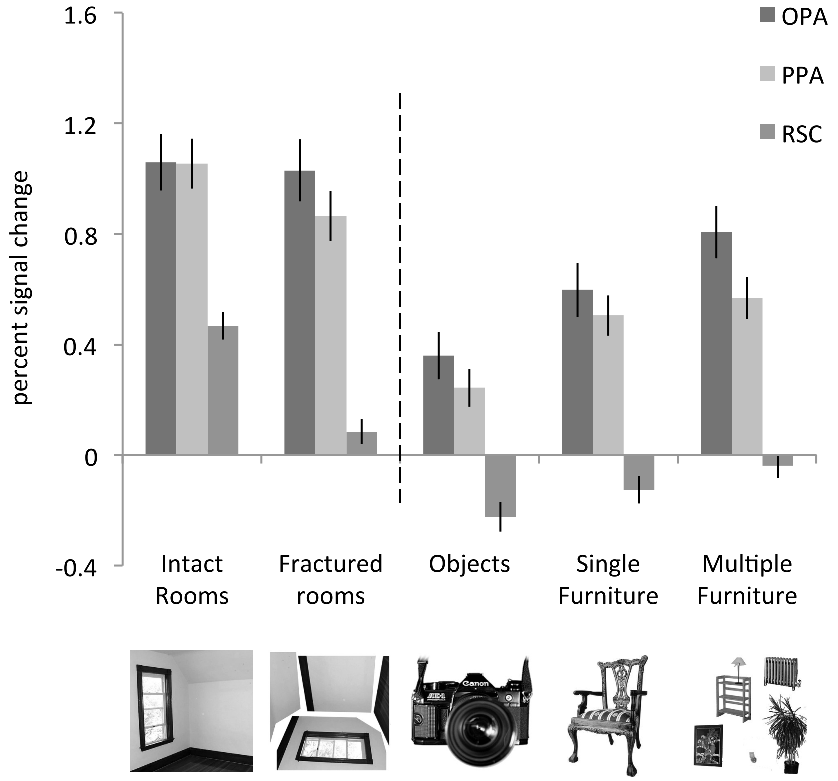

Figure 3.
Average percent signal change in OPA, PPA, and RSC to the five conditions. Error bars indicate the standard error of the mean. First, a 3 (ROI: OPA, PPA, RSC) x 2 (room type: intact, fractured) repeated measures ANOVA revealed a significant interaction ($F_{(2, 42)} = 33.66$, $p < 0.001$), with OPA responding significantly more than both PPA and RSC to fractured rooms relative to intact rooms (main effect contrasts, both p values < 0.001). Second, a 3 (ROI: OPA, PPA, RSC) x 2 (condition: single furniture, multiple furniture) repeated-measures ANOVA revealed a significant interaction of ROI and condition ($F_{(2, 42)} = 9.527$, $p < 0.001$), with OPA responding significantly more than both PPA and RSC to multiple furniture versus single furniture (main effect contrasts, both p values < 0.01). PPA and RSC responded similarly to multiple and single furniture (p = 0.46). Taken together, these results suggest that OPA represents the local elements of both spatial boundary (i.e., walls, floors, ceilings) and scene content (i.e., furniture), while PPA and RSC encode global representations of the scene.

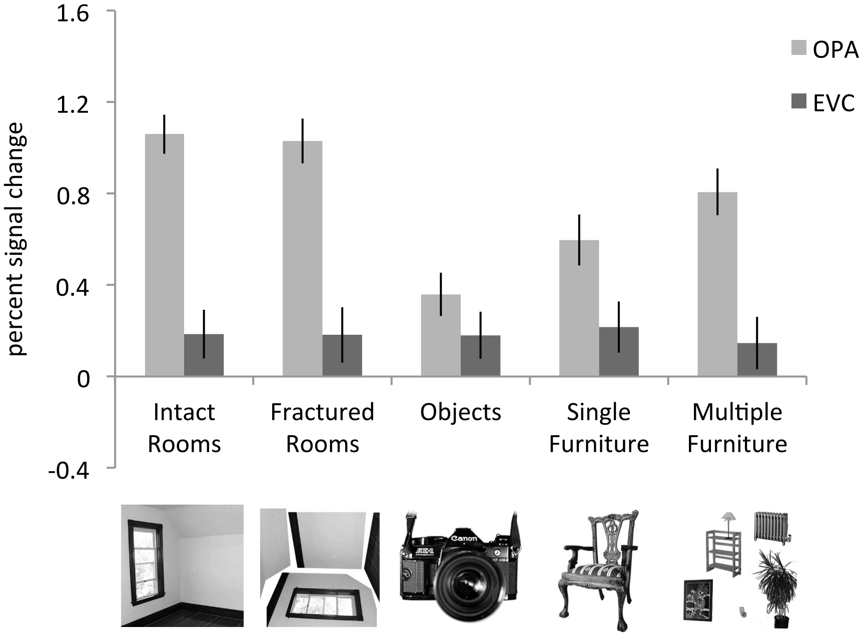

Figure 4.
Average percent signal change in OPA and EVC to the five conditions. Error bars indicate the standard error of the mean. A 2 (ROI: OPA, EVC) x 5 (condition: intact rooms, fractured rooms, single objects, single furniture, multiple furniture) repeated measures ANOVA revealed a significant interaction of ROI and condition ($F_{(4,84)} = -75.73$, $p < 0.001$), indicating that the pattern of responses in OPA was not as expected for a retinotopic region.