Disentangling scene content from its spatial boundary: Complementary roles for the PPA and LOC in representing real-world scenes

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Detailed Terms
Behavioral and computational studies suggest that visual scene analysis rapidly produces a rich description of both the objects and the spatial layout of surfaces in a scene. However, there is still a large gap in our understanding of how the human brain accomplishes these diverse functions of scene understanding. Here we probe the nature of real-world scene representations using multivoxel functional magnetic resonance imaging pattern analysis. We show that natural scenes are analyzed in a distributed and complementary manner by the parahippocampal place area (PPA) and the lateral occipital complex (LOC) in particular, as well as other regions in the ventral stream.

Specifically, we study the classification performance of different scene-selective regions using images that vary in spatial boundary and naturalness content. We discover that, whereas both the PPA and LOC can accurately classify scenes, they make different errors: the PPA more often confuses scenes that have the same spatial boundaries, whereas the LOC more often confuses scenes that have the same content. By demonstrating that visual scene analysis recruits distinct and complementary high-level representations, our results testify to distinct neural pathways for representing the spatial boundaries and content of a visual scene.

Introduction

Behavioral studies have shown that, in a brief glance at a scene, a rich representation is built comprising spatial layout, the degree of human manufacture, and a few prominent objects (Oliva and Torralba, 2001; Renninger and Malik, 2004; Fei-Fei et al., 2007; Greene and Oliva, 2009a,b). In parallel, neuroimaging investigations have identified specific brain regions involved in scene perception. Among these regions is the parahippocampal place area (PPA), which responds preferentially to pictures of scenes and landmarks and shows selectivity to the geometric layout of the scene but not the quantity of objects (Aguirre et al., 1998; Epstein and Kanwisher, 1998; Epstein et al., 1999; Janzen and van Turennout, 2004) and the retrosplenial complex (RSC), which also responds to scenes and navigationally relevant tasks (Epstein, 2008; Park and Chun, 2009) in addition to processing context (Bar and Aminoff, 2003). In contrast, the lateral occipital complex (LOC) has been found to represent object shapes and categories (Malach et al., 1995; Grill-Spector et al., 1998; Kourtzi and Kanwisher, 2000; Eger et al., 2008; Vinberg and Grill-Spector, 2008). Recent studies have found that activity in early visual areas PPA and LOC is discriminative enough to allow scene classification into a handful of semantic categories (Naselaris et al., 2009; Walther et al., 2009). However, we do not yet know how the brain accomplishes the diverse functions involved in scene understanding.

Here, we examined scene representation using functional magnetic resonance imaging (fMRI) pattern analysis, demonstrating the existence of high-level neural representations of visual environments that uncouple processing of the spatial boundaries of a scene from its content. Just as external shape and internal features are separable dimensions of face encoding, an environmental space can be represented by two separable and complementary descriptors (Oliva and Torralba, 2001): its spatial boundary (i.e., the shape and size of the scene’s space) and its content (textures, surfaces, materials and objects). As illustrated in Figure 1, the shape of a scene may be expansive and open to the horizon, as in a field or highway, or closed and bounded by frontal and lateral surfaces, as in forests or streets. For a given spatial boundary, a scene may comprise natural or urban (manufactured) objects. Analyzing the types of errors produced by the PPA and LOC in this two-dimensional space allows us distinguish whether the PPA and LOC represent a scene in an overlapping manner (e.g., both produce similar errors when classifying scenes) or in a complementary manner (e.g., specialization in representing boundaries and content).

We show that, although both the PPA and the LOC classify scenes with the same level of accuracy, these regions show opposite patterns of classification errors. Therefore, our work provides
Fourier space and then rescaled so the luminance of each pixel ranged a random phase. Finally, the image was reconstructed from this modified spectrum and phase. Next, the phase at each frequency was replaced with high-level scene information. The grayscale images from experiment 1 phase scrambled, so as to keep second-order image statistics but remove luminance scale. In the first control experiment, the same images were presented in grayscale with a mean luminance averaging 127 (on a 0 – 255 scale). There were 140 test images, “open urban” images, and “closed urban” images (Oliva and Torralba, 2001; Greene and Oliva, 2009a) and visual search (Torralba, 2003; Torralba et al., 2006).

Materials and Methods

Subjects. Eight participants (two females; one left-handed; ages, 19–28 years) for the main experiment, six participants (three females; ages, 18–29 years) for the first control experiment (using phase-scrambled images), and seven participants (three females; ages, 20–35 years) for the second control experiment (using added vertical and horizontal bars) were recruited from the Massachusetts Institute of Technology community for financial compensation. All had normal or corrected-to-normal vision. Informed consent was obtained, and the study protocol was approved by the Institutional Review Board of the Massachusetts Institute of Technology. One participant for the main experiment was excluded from the analyses because of excessive head movement (over 8 mm across runs).

Visual stimuli. Scenes were carefully chosen to represent each of the following four scene groups: “open natural” images, “closed natural” images, “open urban” images, and “closed urban” images (Oliva and Torralba, 2001; Greene and Oliva, 2009a). Images were visually matched for spatial boundary and content across these groups (see examples in Figs. 1, 3a). Importantly, each scene group included multiple basic-level scene categories. For example, open and closed natural images included different views of fields, oceans, forests, creeks, mountains, and deserts, whereas open and closed urban images included views of highways, parking lots, streets, city canals, buildings, and airports. There were 140 test images per scene group. In the main experiment, photographs were 256 × 256 pixels resolution (4.5° × 4.5° of visual angle) and were presented in grayscale with a mean luminance averaging 127 (on a 0 – 255 luminance scale). In the first control experiment, the same images were phase scrambled, so as to keep second-order image statistics but remove high-level scene information. The grayscale images from experiment 1 were first Fourier transformed to decompose them into their amplitude spectrum and phase. Next, the phase at each frequency was replaced with a random phase. Finally, the image was reconstructed from this modified Fourier space and then rescaled so the luminance of each pixel ranged from 0 to 255, and the overall image had mean luminance of 127. In the second control experiment, horizontal or vertical lines were superposed on top of the images and were presented 300 × 300 pixels resolution to maximize the visibility of lines (for control experiment stimuli, see Fig. 6). The same orientation lines were added on top of either all of the natural scenes or all of the urban scenes to increase the within-content low-level image similarity across these two sets of conditions. Images were presented in the scanner using a Hitachi (CP-X1200 series) rear-projection screen.

Experimental design. Twenty images from an image group were presented in blocks of 20 s each. The order of block conditions was randomized within each run. Each block was followed by a 10 s fixation period. Within a block, each scene was displayed for 800 ms, followed by 200 ms blank. The entire image set (560 images) was presented across two runs with a break between: the first run was composed of 16 blocks with four blocks per condition, acquiring 245 image volumes; the second run was composed of 12 blocks with three blocks per condition, acquiring 185 image volumes. This set of two runs was repeated four times within a session, totaling eight runs, to increase the number of samples and power. Accordingly, participants saw the same image four times across runs at different time points for each run. Twenty-eight blocks per each condition were acquired and used as training samples throughout the experiment. Participants performed a one-back repetition detection task to maintain attention.

The experimental design for the first and second control experiments were identical to the main experiment except that participants in the first control experiment performed a red-frame detection task rather than a one-back repetition task to maintain attention on the phase scrambled images. MRI acquisition and preprocessing. Imaging data were acquired with a 3 T Siemens fMRI scanner with 32-channel phased-array head coil (Siemens) at the Martinos Center at the McGovern Institute for Brain Research at Massachusetts Institute of Technology. Anatomical images were acquired using a high-resolution (1 × 1 × 1 mm voxel) magnetization-prepared rapid-acquisition gradient echo structural scan. Functional images were acquired with a gradient echo-planar T2* sequence [repetition time (TR), 2 s; echo time, 30 ms; field of view, 200 mm; 64 × 64 matrix; flip angle, 90°; in-plane resolution, 3.1 × 3.1 × 3.1 mm; 33 axial 3.1 mm slices with no gap; acquired parallel to the anterior commissure–posterior commissure line].
Functional data were preprocessed using Brain Voyager QX software (Brain Innovation). Preprocessing included slice scan-time correction, linear trend removal, and three-dimensional motion correction. No additional spatial or temporal smoothing was performed. For retinotopic analysis, we mapped data from a functional retinotopic localizer (see below) onto a surface-rendered brain of each individual.

Pattern analysis. For multivariate pattern analysis, we extracted MRI signal intensity from each voxel within the region of interest (ROI) across all time points and transformed the MRI signal intensity within each voxel into z-scores so that the mean activity is set to 0 and the SD is set to 1. This helps mitigate overall differences in fMRI signal across different regions of interests and across runs and sessions (Kamitani and Tong, 2005). Activity level for each block of each individual voxel was labeled with condition, which spanned 20 s (10 TR) in all experiments. In labeling the condition, we added 4 s (2 TR) to each time points, to account for the hemodynamic delay of the blood oxygenation level-dependent (BOLD) response (4–6 s) so that we are targeting the correct period corresponding to each block of samples. We did not do a voxel selection, and the entire cluster that passed the threshold of an ROI localizer was used. This eliminates problems with “double-dipping” as a result of non-independence in feature selection (Kriegeskorte et al., 2009; Vul et al., 2009).

The average number of voxels for each of the ROIs in the main experiment were as follows (after mapping into the structural 1 × 1 × 1 voxel space; for voxel counts in the original functional space, divide by 2009). The average number of voxels for each of the ROIs in the main experiment was calculated for each region but is organized in a distributed manner across multiple visual areas.

Patterns of interest. For each participant, we used a separate linear SVM classifier based on LIBSVM (http://sourceforge.net/projects/svm/). For each block, we computed the average pattern activity across the voxels. An SVM classifier was trained to classify the four conditions using all time points and transformed the MRI signal intensity within each voxel into z-scores so that the mean activity is set to 0 and the SD is set to 1. This helps mitigate overall differences in fMRI signal across different regions of interests and across runs and sessions (Kamitani and Tong, 2005). Activity level for each block of each individual voxel was labeled with condition, which spanned 20 s (10 TR) in all experiments. In labeling the condition, we added 4 s (2 TR) to each time points, to account for the hemodynamic delay of the blood oxygenation level-dependent (BOLD) response (4–6 s) so that we are targeting the correct period corresponding to each block of samples. We did not do a voxel selection, and the entire cluster that passed the threshold of an ROI localizer was used. This eliminates problems with “double-dipping” as a result of non-independence in feature selection (Kriegeskorte et al., 2009; Vul et al., 2009).

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Results. We extracted multivoxel fMRI activity from our ROIs (PPA, LOC, V1, RSC, and FFA). For each region in each participant, we used a separate linear SVM to classify each block of scenes as closed natural images, closed urban images, open natural images, or open urban images (Fig. 3a). As shown in Figure 3b, classification accuracy in all of the ROIs was significantly above chance (25%): PPA, LOC, V1, RSC, and FFA had respective classification accuracies of 51% (t(6) = 7.1, p < 0.001), 45% (t(6) = 4.0, p < 0.01), 50% (t(6) = 6.1, p < 0.001), 37% (t(4) = 4.4, p < 0.05), and 43% (t(6) = 4.1, p < 0.01). These results show that these regions can distinguish between scenes varying in spatial and content properties. Furthermore, these results suggest that the analysis of scene information is not processed by a single scene-specific region but is organized in a distributed manner across multiple visual areas.
Classification errors

Classification accuracy does not inform about the nature of the scene representation in each region. For example, the spatial boundary (open or closed) and the content (natural or urban) may have contributed equally to the classification performance across different regions. Conversely, the spatial boundary and the content may have contributed differently to the classification performance across different areas. We examined this contribution by studying the types of errors made by the classifier. If the classifier shows systematic confusions between two conditions in a particular brain region, this suggests that the region has similar representations of the scenes from these two conditions.

Figure 4a illustrates two possible orthogonal patterns of errors. First, if a particular brain region is sensitive to the spatial boundaries of a scene, it should confuse images with the same global structure, regardless of the content or objects in the scene. For instance, scenes representing closed urban environments (e.g., street, buildings, or city canal) might be confused with closed natural scenes that have similar spatial boundaries (e.g., forest, mountain, or canyon) but not with open urban scenes that have similar content (e.g., highways, parking lot, or airport). In Figure 4a, we refer to these errors as confusions within the same spatial boundary. Conversely, if a given brain region is more sensitive to the content of a scene than its structure, it should confuse images with the same content, regardless of their spatial boundaries (e.g., fields, deserts, or ocean would be confused with forest, mountain, or canyons but not with highways, parking lots, or airports that have urban contents). We refer to these errors as confusion within the same content.

Figure 4b shows the types of errors made by different regions of interest. First, as we hypothesized, we observed a striking dissociation between the main regions under investigation, the PPA and the LOC: whereas the PPA made the most errors between scenes that shared the same spatial boundaries, regardless of content (e.g., confusing open natural and open urban scenes), the LOC made the most errors between scenes that shared the same content, regardless of the spatial boundary (e.g., confusing open natural and closed natural scenes). Most importantly, there was a significant interaction across area (PPA or LOC) and types of errors (confusion within the same boundary vs confusion within the same content), \( t(6) = 4.6, p < 0.005 \) and in the opposite direction in the LOC (\( t(6) = -6.6, p < 0.001 \)). Additionally, other regions of interest also show a specific pattern of errors: the FFA made more confusion errors within the same scene content, similar to the LOC (\( t(6) = -3.3, p < 0.05 \)). RSC showed a numerical pattern of greater confusion within the same spatial layout, like the PPA pattern, but not as dominant as found in the PPA, and this pattern was not significant (\( t(6) = 1.2, p > 0.2 \)). On average, more than 72% of errors were confusions within the same spatial boundary or within the same content. Double errors, in which both content and layout were incorrect, were the least frequent (21, 27, 16, 25, and 23% in the PPA, LOC, V1, RSC, and FFA, respectively) and did not show any interaction across areas.

The overall performance was the same when we have normalized the number of voxels across the different regions of interest (Fig. 5). We randomly sampled different numbers of voxels (from 10 to 1000) from each ROI, and this process was repeated 200 times for each number of voxels within each ROI in each observer. The classification accuracy plateaued at 500 voxels and was equal to the classification performance when all the voxels
a Hypothetical Patterns of Errors

**Confusion within the same Spatial Boundary**

<table>
<thead>
<tr>
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<th>Closed</th>
<th>Natural</th>
<th>Urban</th>
<th>Open</th>
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<td>Confusion</td>
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**Confusion within the same Content**

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<th>Closed</th>
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<td>Confusion</td>
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Figure 4.  

b Results

**Main ROIs**

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<tr>
<th></th>
<th>PPA</th>
<th>LOC</th>
<th>V1</th>
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<tr>
<td>% of Confusion Errors</td>
<td>40%</td>
<td>50%</td>
<td>60%</td>
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**Additional Areas**

<table>
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<th>RSC</th>
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<tr>
<td>% of Confusion Errors</td>
<td>30%</td>
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Correlation analysis

In addition to looking at the confusions made by a classifier, we can also examine the similarity in the patterns across voxels in the different conditions using a correlation-based analysis (Haxby et al., 2001). When we conducted the split-half correlation analysis, results showed similar conclusions to the classifier-based analysis. Within-condition correlation for the PPA, RSC, LOC, FFA, and V1, respectively, were 0.74, 0.64, 0.64, 0.44, and 0.83. Most importantly, the across-condition correlation patterns showed the same pattern as in the SVM confusion error analysis. There was a significant crossover interaction between the PPA and LOC, such that the correlation of images that shared the spatial boundary is higher in PPA and the correlation of images with shared content is higher in LOC ($F_{(1,6)} = 12.8, p < 0.05$). Thus, the two results provide similar conclusions. They differ in that the classifier confusions weigh informative voxels only, do not discard differences between the mean activity level of the two conditions, and, in addition, provide interpretable effect sizes (in terms of percentage correct) rather than differences in correlation $r$ values (which do not indicate how separable the sets actually are).

Contribution of low-level visual properties

As shown in Figures 3b and 4b, V1 had the same overall pattern of classification and confusion errors as the PPA, confusing scenes with similar boundaries more often than scenes with similar content. The high level of accuracy of V1 is not surprising given that previous studies observed high classification for natural images using patterns of activity of retinotopic areas (Kay et al., 2008; Naselaris et al., 2009) and the fact that the poles of the two spatial boundary properties contain distinctive and diagnostic low-level features (Oliva and Torralba, 2001; Torralba and Oliva, 2003). Given the dissociation in the types of confusion between the PPA and LOC (and other ROIs), it is unlikely that the patterns of activity of PPA result only from the PPA mirroring a straightforward influence of V1. Previous studies have demonstrated the high-level nature of the responses of PPA, including its sensitivity to spatial layout (Epstein, 2005) and its responses during binocular rivalry of scenes and faces, which reflects the perceived representation rather than direct physical input (Tong et al., 1998). Nevertheless, to empirically address the possibility that the greater confusion of PPA within spatial layout was a byproduct of the low-level properties of the stimuli, we conducted two control experiments. These experiments manipulated the low-level properties of the images to decipher the nature of the representations in the PPA and V1. Specifically, in the first control experiment, we expect the removal of high-level im-

within ROIs were accounted (PPA, LOC, V1, RSC, and FFA classification accuracies were, respectively, 50.4, 45, 49, 37, and 42%).

Moreover, we observed significantly higher classification accuracy for a combined region of interest merging PPA and LOC voxels (an average of 56%, after randomly sampling 500 voxels from the combined ROI and repeating this process 200 times) compared with when only 500 PPA voxels were included in the original analysis ($50.4\%, t_{(5)} = 2.5, p = 0.05$) or when only 500 LOC voxels were included ($45\%, t_{(5)} = 3.4, p < 0.05$). The fact that the addition of LOC voxels to PPA voxels increases classification accuracy suggests that the neural representation of scenes within these regions is complementary. Altogether, the results provide the first evidence that the PPA and LOC represent complementary properties of real-world scenes, with PPA holding a representation of spatial boundaries and LOC simultaneously holding a representation of scene content.
low-level visual differences across conditions, then we would expect the classification performance in both areas to significantly improve compared with the original images that had less visual difference for the four conditions overall. Contrary to this prediction, we observed a significant boost of performance in V1 compared with the original experiment (64 vs 50% in the main experiment) but not in the PPA (54 vs 51% in the main experiment; interaction of the PPA and V1 across experiments was significant, $F_{(1,12)} = 5.6, p < 0.05$). V1 accuracy was also significantly higher than the PPA in control experiment 2 ($t_{(6)} = 2.7, p < 0.05$). Thus, the fact that adding low-level image features, such as oriented bars, improved V1 but not PPA performance strengthens the conclusion that the PPA is sensitive to higher-level scene information, not simply the low-level statistics of the images (Epstein, 2005). Moreover, the confusion errors for the PPA and LOC completely replicated the main experiment, because these areas are essentially invariant to the addition of the lines. There was a significant interaction across area (PPA or LOC) and types of errors (confusion within the same boundary vs confusion within the same content, $F_{(1,6)} = 24.7, p < 0.005$). The $t$ tests between the two types of errors (confusion within the same boundary vs confusion within the same content) within each ROI was also significant in the PPA (48% confusion within the same boundary vs 32% confusion within the same content; $t_{(6)} = 3.2, p < 0.05$) and in the opposite direction in the LOC (30% confusion within the same boundary vs 49% confusion within the same content; $t_{(6)} = -2.6, p < 0.05$).

Together, these additional experiments show that, although V1 classification primarily relies on low-level image statistics independent of the scene spatial layout or content, the PPA is sensitive to the removal of higher-order information (control experiment 1) but not the addition of low-level features (control experiment 2). Therefore, the results support our hypothesis that the PPA represents higher-level scene information, such as the spatial boundaries, and does not merely reflect V1 representations.

Discussion
Using multivoxel pattern analysis to examine the neural basis of natural scene representation, we found a differential coding of scene features throughout the ventral visual cortex, including V1, PPA, LOC, RSC, and FFA. Interestingly, all these regions accurately classified the spatial boundary and content of a scene, across different semantic categories, suggesting that these brain regions are sensitive to both of these high-level scene properties. Importantly, the degree to which a specific property was used to classify scenes was different across the regions of interest. We found that spatial boundary information was primarily represented in the PPA and RSC and scene content primarily represented in the LOC and FFA. This suggests a complementary role for scene-selective areas and object-related areas in scene representation.

The possibility of a complementary scene representation with objects and scene content processed in a separate pathway from the spatial boundary is similar to that proposed by recent models of scene recognition and visual search (Torralba, 2003; Torralba et al., 2006; Vogel and Schiele, 2007; Greene and Oliva, 2009a). In such models, both spatial boundary and object information is extracted from a scene, often in parallel, and then integrated to arrive at a decision about the identity of the scene or where to search for a particular object. This convergence between fMRI data and scene recognition models suggests a possible computa-
tional role for the separate representations observed in many studies of the LOC and PPA.

Multivoxel pattern analysis and confusion errors
Previous studies using multivoxel pattern classification found that activity patterns in fMRI data can accurately classify between oriented lines (Kamitani and Tong, 2005; Kamitani and Tong, 2006), object categories (Haxby et al., 2001), and even object exemplars within a category (Eger et al., 2008). Recent fMRI studies with natural images have shown that high-level scene processing areas can classify across basic-level scene categories, such as mountains, beaches, or buildings (Walther et al., 2009). In addition, using generative models of the fMRI response in early visual cortex has allowed the prediction of a viewed image from brain data (Kay et al., 2008) and even some reconstruction of images from these data (Naselaris et al., 2009).

In the present study, rather than attempt to classify images into semantic categories or to recognize their identity exactly, we focus on global properties of scenes (Oliva and Torralba, 2001; Greene and Oliva 2009a). We thus provide the first neural evidence of a coding scheme of visual scenes based on structural and content properties. In other words, we show that scene and object areas in the brain not only represent the semantic category of a scene (forest, mountain) but also its spatial boundaries (open, closed) and degree of naturalness (urban, natural).

Analyzing the errors made by a classifier demonstrates that it is possible to probe the nature of neural representations in various ventral visual areas beyond the level of classification accuracy. By examining the different pattern of errors for our conditions, we can dissociate multiple levels of image representation coexisting within a single image and test the extent to which a specific property is coded in the brain. Reliable patterns of errors between scenes with a shared visual property (such as similar boundaries or content) provide evidence for that property being coded.

Naturalness and the role of objects
Throughout the paper, we have focused on naturalness as expressing the content of the scene: tree, bush, rock, grass, etc., make the scene content natural, whereas manufactured surfaces and man-made objects create urban content. However, we are not suggesting that the naturalness dimension reflects solely object processing. Naturalness is correlated with visual features at all levels of processing, from different distributions of orientations (Torralba and Oliva, 2003; Kaping et al., 2007) to different textural and surface components (Torralba and Oliva, 2002) in addition to different objects.

Recent behavioral work suggests a prominent role for global properties in the rapid analysis of visual scenes (Renninger and Malik, 2004; Greene and Oliva, 2009a,b). Indeed, global properties of scene shape boundary, such as openness, perspective, or mean depth, and global properties of scene content, such as the naturalness of an environment can influence rapid basic-level scene categorization. Human observers are more likely to confuse scenes that share a similar global scene property (e.g., a field and a coast are both open environments) than scenes that share same regions (e.g., trees can be shared by field and forest). In addition, human observers can classify the naturalness of a scene after a briefer exposure than is required for individual objects to be recognized (Joubr et al., 2007; Greene and Oliva, 2009b), and the naturalness of a scene is a property that is selectively adaptable (Greene and Oliva, 2010), suggesting that, at a high level of visual processing, naturalness is a unified construct.

The fact that LOC is both responsive to scenes and can accurately classify scene categories based on either content or spatial boundary provides some suggestive evidence that this region might play a more integrative role in scene understanding than simply representing object form information.

The role of other regions
It is interesting to note that all the visual regions we examined, including those that were not part of our original hypothesis, showed above-chance classification for scene properties. Of particular interest is the RSC, which has been found to be involved in processing navigationally relevant properties of scenes (Epstein, 2008; Park and Chun, 2009; Vann et al., 2009) and context (Bar and Aminoff, 2003). Indeed, the patterns of confusion errors in RSC were similar to the pattern observed in the PPA. However, the overall classification performance of RSC was significantly lower than the PPA ($t(4) = 6, p < 0.01$), and the difference in confusion errors between spatial boundary confusions and content confusions were not significant. This suggests that, although the RSC may be involved in representing spatial boundary or correlated dimensions, it is less consistent across observers than the PPA.

The FFA also performed above-chance level for scene classification, with more confusion errors among scene content. This fits with similar results finding above-chance classification performance for object categories in FFA that have been reported by...
Haxby et al. (2001) and Reddy and Kanwisher (2007). However, we should remain cautious about potential involvement of the FFA in scene processing. For example, the current result could potentially be triggered by the presence of pedestrians in urban scenes (indeed, people are a consistent object for outdoor urban environments). In addition, there is strong evidence in the literature for the face selectivity of the FFA (for review, Kanwisher, 2010), and it is important to note that the overall BOLD response in FFA for scenes is well below that for faces (in both our own data and that of many previous studies, including Kanwisher et al., 1997). In contrast, regions such as LOC respond nearly as strongly to scenes as to objects, even in data specifically selected to show a large response to objects (data from localizer vs main experiment).

Conclusion
In summary, the current study demonstrates a distributed and complementary neural coding of scene information, mediated via global properties of spatial boundary and content. By studying the patterns of errors made by a classifier, we conclude that the spatial boundary information was primarily used in the PPA for scene classification, whereas the content was primarily used in the LOC. Such complementary functions of these regions support the idea that observers concurrently process the global spatial boundary of a scene, which is important for navigation, as well as the content properties of a scene, which may be important for object identification and directed action.

References