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Beyond the Edges of a View: Boundary Extension in Human Scene-Selective Visual Cortex

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SUMMARY

To allow perception of a continuous world, cortical mechanisms extrapolate missing information with highly constrained predictions about the environment just beyond the edges of a view. Here, we report functional magnetic resonance imaging evidence for extrapolation of scene layout information beyond what was physically presented, an illusion known as boundary extension. Consistent with behavioral reports, we observed boundary extension for scene-selective attenuation in the parahippocampal place area (PPA) and retrosplenial cortex (RSC), but no such extrapolation of object representations in the lateral occipital complex (LOC). These results demonstrate that scene layout representations are extrapolated beyond the confines of the perceptual input. Such extrapolation may facilitate perception of a continuous world from discontinuous views.

INTRODUCTION

A central question in human visual cognition is how we perceive a coherent, continuous world despite multiple physiological constraints on vision. The visual field itself is spatially limited, with the best acuity restricted to the small foveal region, thus causing the viewer to sample the world through movements of the head and eyes. Furthermore, vision is suppressed during the 30–50 ms that the eyes are in motion—shifting fixation from one location to another. Yet, in spite of this succession of discrete sensory inputs, interrupted by eye movements, we perceive a continuous perceptual representation of our surroundings. How is the brain capable of creating a rich and continuous visual experience with limited input?

The powerful way that the brain overcomes many types of physical limitation (including occlusion) is by making predictions about the visual world beyond the sensory input. The visual system constantly extrapolates beyond the constraints of an aperture-like visual input, making associations with visual or semantic context (Palmer, 1975;

Chun, 2000; Bar, 2004), recent experience (Miller and Gazzaniga, 1998), or expectations about the broader visual world. Most times, these expectations help the visual system to overcome the ambiguity of perception (Hochberg, 1978, 1986; Kanizsa and Gerbino, 1982), but oftentimes, these expectations beyond the input distort perception (Simons and Levin, 1997; Miller and Gazzaniga, 1998) and, as we will describe, *memory*. Here, we investigate how the brain represents scene information that is extrapolated beyond what is physically present so that moments after viewing, the observer remembers seeing more of the scene than was present in the physical input, an illusion known as boundary extension (Intraub and Richardson, 1989; Intraub, 1997).

When asked to remember a photograph of a scene, people remember a more expansive view than was shown in the original photograph. The representation extends beyond the picture's boundaries—particularly when the view is a close-up (Figure 1). For example, if the background is homogeneous, viewers remember seeing more space beyond the edges of the view. If the background includes more complex information, such as a fence and trees, viewers remember seeing a greater expanse of the fence and more trees (Intraub and Richardson, 1989). When asked to recreate it in reconstruction tasks, viewers will draw the additional information (Intraub, 2002), and when given the opportunity to adjust the location of borders on a computer display, they will show more of the scene than had been visible, moments after offset of the view (Intraub et al., 2006). This occurs for pictures presented for as little as 250 ms (an eye fixation's worth of viewing), just 42 ms following offset (C.A. Dickinson et al., 2006, Vision Sciences Society, abstract).

In fact, if shown a close-up followed by a slightly more wide-angle view of the same scene, people often will not notice a difference. In contrast, if the wider view is presented first, the difference is readily noted. This asymmetry occurs because people falsely remember the first view as having shown more of the scene that it actually had. This *boundary-extension effect* suggests that scene representation is not limited to the physical input but instead projects outward to integrate the sampled view into a broader real-world environment (Intraub, 1997). This interpretation is bolstered by the generality of the phenomena
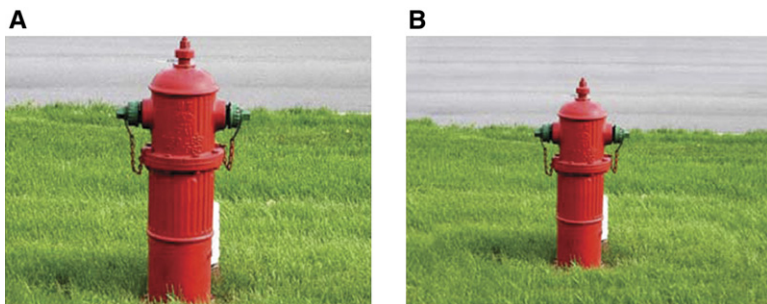
Figure 1. Example of Boundary Extension

After viewing a close-up view of a scene (A), observers tend to report an extended representation (B). For example, when participants were later shown the physically identical scene (A), they rated it as looking more close-up. An extended view of the original scene (B) was perceived as identical to the original (A).

(occurring both in the case of 2D images and real 3D spaces viewed through a window [Intraub, 2004]), and the fact that it does not occur if the same-sized objects are presented on a blank background with no scene context (Gottesman and Intraub, 2002). In other words, viewers don't remember objects as being smaller; they remember having seen more of the surrounding background layout.

Boundary extension is a powerful tool with which to investigate scene representation in the brain because it allows us to contrast neural responses to scene pairs that are physically the same but elicit different patterns of spatial extrapolation in the mind. Are there neural processes that signal the spatial extrapolation of physically absent but mentally represented regions of a scene's layout in the viewer's memory?

We used event-related functional magnetic resonance imaging (fMRI) to probe the precise nature of scene representation in a cortical region that is selectively active in scene perception and memory. A region of the medial temporal lobe—the parahippocampal place area (PPA)—selectively responds when viewing scenes such as landscapes, rooms, or buildings (Epstein and Kanwisher, 1998). The retrosplenial cortex (RSC) is another region of interest (ROI) that is responsive to scene layout and important for navigation (Epstein et al., 2005; Maguire, 2001).

fMRI can reveal the properties of scene-specific representations, as activity is lower for repeated items compared to novel items (Wiggs and Martin, 1998; Schacter and Buckner, 1998). For example, the fMRI response in the PPA shows less activity for repeated scenes than for novel scenes (Epstein et al., 2003; Yi et al., 2004; Yi and Chun, 2005). This repetition attenuation can be used to infer whether a particular neuronal population treats two stimuli as the same or different from each other (Grill-Spector and Malach, 2001). In other words, we can use fMRI attenuation to estimate what information is included in the representation and what information is not (Kourtzi and Kanwisher, 2001; Grill-Spector et al., 1999). We exploited this attenuation to determine if the scene-selective ROIs respond to the physical view or to the boundary-extended view that includes information beyond the physical input.

Eighteen participants viewed series of scene photographs with a main object situated in a natural background (Figure 1). Each scene was repeated once within a scan run across trials, and the brain activity was measured for every scene presentation. We tested four conditions of scene repetition across trials. In the two critical conditions a close-up and a wider-angle view of the same scene were presented in one of two different orders: (1) close-up then wide-angle or (2) wide-angle then close-up. In two control conditions (1) the same close-up or (2) the same wide-angle view was presented twice.

If the PPA and RSC respond to the physical expanse encompassed by the view, we should observe little attenuation for close-wide and for wide-close views, and the degree of any attenuation observed for these views should be equivalent. However, if the PPA and RSC respond to the filled-out layout in the representation (i.e., boundary extension), then we should observe attenuation in the close-wide condition but not in the wide-close condition. This is because in the close-wide condition, boundary extension of the initial close-up image would cause it to match the perceived view presented in the wide angle image, whereas in the wide-close condition, any boundary extension would tend to increase the perceived disparity between the two.

Functional differences between the PPA and RSC are under investigation, but current evidence suggests that RSC integrates a local scene into a broader, abstract representation of spatial layout, while the PPA is more involved in the perceptual processing of the local scene (Bar and Aminoff, 2003; Epstein and Higgins, 2006). If so, the PPA may be more sensitive to physical repetition than RSC is, revealing attenuation in close-close and wide-wide conditions as well.

In addition to the PPA and RSC, we investigated responses in the lateral occipital complex (LOC), a region known to specifically respond to objects (Malach et al., 1995; Grill-Spector et al., 1999). As mentioned earlier, previous behavioral results showed that boundary extension was elicited when objects were embedded in a scene context, but not when the same objects were perceived to appear in isolation on a blank background (Gottesman and Intraub, 2002). This leads to the prediction that boundary-extension effects should be restricted to the PPA or RSC that process scene layout and should not generalize to other visual processing areas that only process objects and surfaces, such as the LOC (Intraub, 2002). In other

words, the LOC should reveal attenuation in all four conditions because the main objects in the scenes are always repeated.

RESULTS

fMRI Measurements of Boundary Extension

A repeated-measures ANOVA and paired t tests between conditions were performed on the average of the peak amplitude responses in all three ROIs. There was no main effect of hemisphere in any of the ROIs, and hemisphere did not interact with any combination of the other factors (F's < 2.6, p's > 0.1). Thus, both hemispheres were collapsed for analysis.

PPA activations revealed a marginally significant main effect of viewing condition (close-wide, wide-close, close-close, wide-wide; $F_{3,51} = 2.87$, $p = 0.07$) and a significant main effect of scene repetition (first appearance versus second appearance; $F_{1,17} = 25.8$, $p < 0.01$), the latter providing evidence for neural attenuation. No differences in activation were found between novel close-up scenes and novel wide-view scenes ($F_{1,17} < 0.1$, $p > 0.9$). Most importantly, there was a significant interaction between the viewing condition and scene repetition factors ($F_{3,51} = 4.2$, $p < 0.01$). Figure 2A shows that the BOLD signal in the PPA in the critical experimental conditions mirrored the response asymmetry observed in behavioral studies. Paired comparisons showed that attenuation occurred in the close-wide condition ($t_{17} = 6.7$, $p < 0.001$), but not in the wide-close condition ($t_{17} < 1$, $p = 0.85$), even though the stimuli were identical and only their order of presentation was switched. Attenuation occurred in both control conditions: close-close ($t_{17} = 2.2$, $p < 0.05$) and wide-wide ($t_{17} = 2.6$, $p < 0.02$) conditions. Significant attenuation in the close-wide condition indicates that the PPA treated the wide scene as identical to the close view seen before. On the other hand, the wide-close condition did not show any attenuation. To specifically test the different patterns of attenuation across conditions of viewpoint change, we conducted an ANOVA (condition × repetition) for only close-wide and wide-close conditions. The interaction was significant ($F_{1,17} = 18$, $p < 0.01$), that is, there was attenuation in the close-wide, but not the wide-close condition. Thus, the release of adaptation in the wide-close condition cannot be due to a change in viewpoint per se. Rather, the asymmetry demonstrates boundary extension in the PPA. This interpretation was supported by greater attenuation in the close-wide condition than in the close-close condition (condition × repetition interaction, $F_{1,17} = 6.5$, $p < 0.05$). Thus, close-wide image pairs were treated as more similar than physically identical close-close pairs. In addition, significant condition × repetition interactions revealed that the wide-wide condition showed greater attenuation than the wide-close condition ($F_{1,17} = 7$, $p < 0.05$) and marginally bigger attenuation than the close-close condition ($F_{1,17} = 4$, $p = 0.07$). Accordingly, the behavioral boundary extension test, which we will report in more detail later, showed margin-

ally greater boundary extension in the close-close condition than in the wide-wide condition ($t_{23} = 1.8$, $p = 0.06$). This is consistent with previous behavioral findings that the boundary extension is more prominent with close-up images than wide-view images (Gottesman and Intraub, 2002; Intraub, 2002; Intraub et al., 1992).

The RSC ROI also showed the largest attenuation in the close-wide condition (Figure 2B). There were no significant main effects of viewing condition ($F_{3,48} = 0.7$, $p = 0.59$) or scene repetition ($F_{1,16} = 1.5$, $p = 0.23$), but there was a marginally significant interaction between these factors ($F_{3,48} = 3.4$, $p = 0.07$). As in the PPA, the RSC ROI revealed a significant difference between the amount of attenuation for close-wide condition and the amount of attenuation for wide-close condition (condition × repetition interaction, $F_{1,16} = 4.4$, $p < 0.01$) and between the close-wide condition and the close-close condition ($F_{1,16} = 6.63$, $p < 0.05$). However, an interesting difference between the PPA and RSC suggested that RSC is more specifically involved in the extrapolation of a scene to a broader layout. RSC showed robust attenuation in the close-wide condition ($t_{16} = 3.2$, $p < 0.01$), but not in any of the three other conditions ($t_{16} < 1.6$, $p > 0.1$). This contrasts with the significant attenuation for close-close and wide-wide conditions in the PPA, reflecting the PPA's sensitivity to perceptual repetition as well as boundary extension. The three-way interaction between the two scene-specific areas (PPA and RSC), viewing condition, and repetition was significant ($F_{3,48} = 3.4$, $p < 0.05$), indicating that the PPA was sensitive to physical repetition while RSC was not in this experiment.

Critically, as predicted, boundary extension was not observed in the LOC (Figure 2C). The LOC ROI showed no main effect of viewing condition ($F_{3,51} < 1$, $p = 0.8$) and a significant main effect of scene repetition ($F_{1,17} = 24$, $p < 0.01$). There was no interaction between these factors ($F_{3,51} < 1$, $p = 0.8$). In contrast to the PPA and the RSC, all four viewing conditions including the wide-close condition showed a significant attenuation in the LOC (all t's > 2.1, p's < 0.05). These results are consistent with previous findings that the fMRI response in the LOC is invariant to object size changes (Grill-Spector et al., 1999). The specificity of boundary extension for scene layout processing in the brain is in line with a previous behavioral study showing that boundary extension only occurs for pictures of scenes (i.e., views sampled from a broader layout); there was no boundary extension for pictures of objects presented in isolation (Gottesman and Intraub, 2002). There was a significant three-way interaction between ROI (PPA, RSC, and LOC), viewing condition, and repetition ($F_{6,96} = 3.1$, $p < 0.01$). Furthermore, the three-way interaction between ROI, viewing condition, and repetition was significant both for the PPA and the LOC ($F_{3,48} = 4.8$, $p < 0.01$) and for RSC and the LOC ($F_{3,48} = 2.8$, $p < 0.05$).

Random-effects analyses revealed significant attenuation effects for close-wide repetition in our primary regions of interests: left and right PPA, left and right retrosplenial
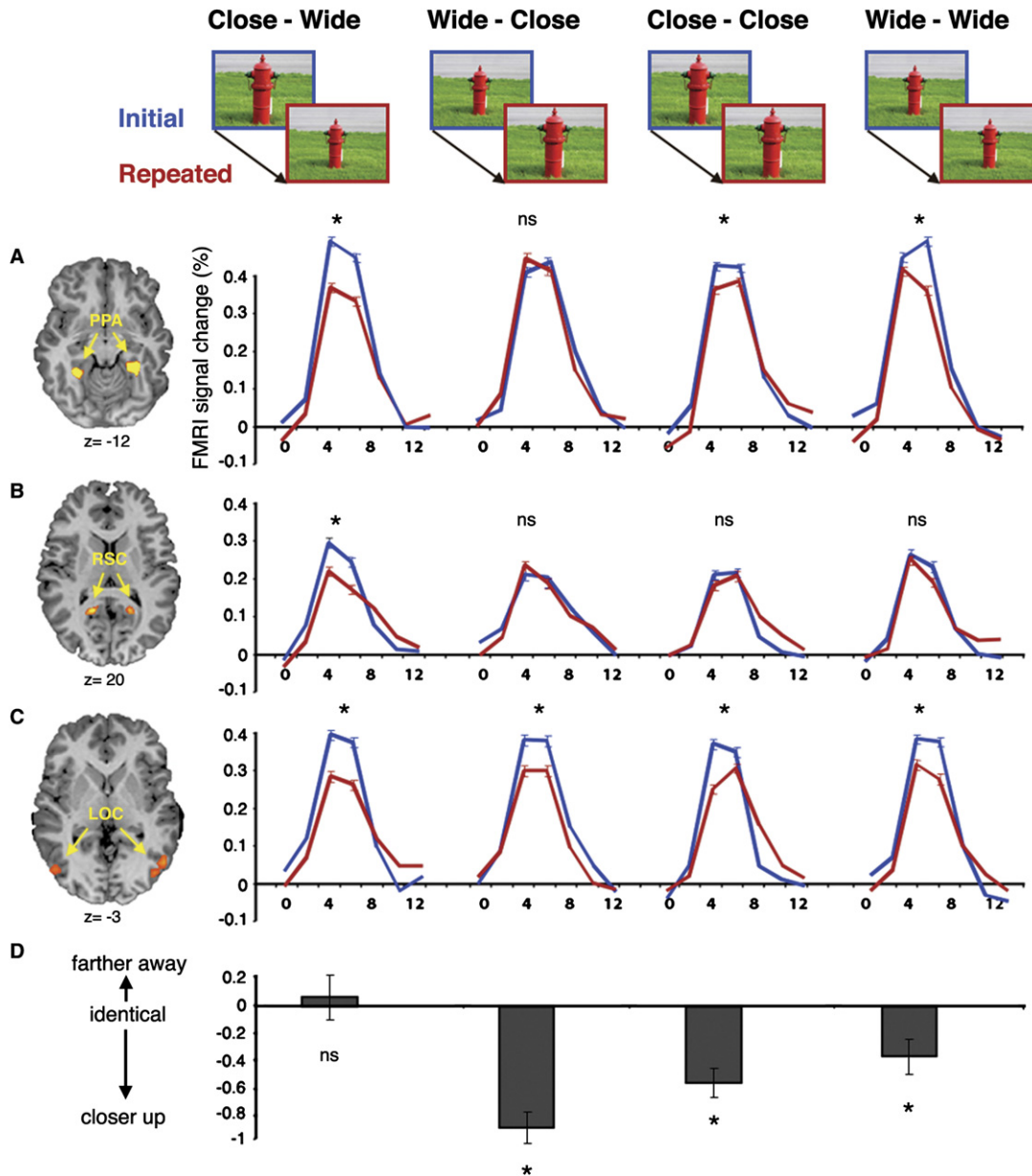
Figure 2. Boundary Extension in the PPA and RSC but Not in the LOC

A representative participant's PPA, RSC, and LOC ROIs are shown on a Talairach-transformed brain. Examples of each viewing condition are presented in the top row. Hemodynamic responses for close-wide, wide-close, close-close, and wide-wide conditions are shown for each ROI. Error bars indicate standard error (±SEM).

(A) Parahippocampal place area (PPA). Paired comparisons between initial and repeated scenes show significant neural attenuation in the close-wide, close-close, and wide-wide conditions. There was no attenuation in the wide-close condition. The attenuation in the close-wide condition was significantly larger than the wide-close condition and the close-close condition.

(B) Retrosplenial cortex (RSC). Paired comparisons between initial and repeated scenes show significant neural attenuation only in the close-wide condition, but not in the three other conditions.

(C) Lateral occipital complex (LOC). Paired comparisons between initial and repeated scenes show significant or marginally significant neural attenuation in all four conditions. There was no interaction between conditions.

(D) Behavioral boundary-extension scores for each condition. The participants answered with five-scale ratings if a test picture was much too close (−2), slightly closer (−1), the same (0), slightly farther away (+1), or much too far (+2) than the original picture. The boundary score for close-wide condition was not significantly different from 0, indicating that the participants rated the repeated wide image as identical to the original close image. In addition, there was a significant boundary-extension effect both in close-close and wide-wide conditions; the significantly negative scores indicate that the repetitions appeared closer than the initial view.

cortex, and left and right LOC (p < 0.001, uncorrected, cluster threshold k = 5 voxels). In addition to these regions of interest, significant neural attenuation was found in left and right superior frontal cortex (−14, 47, 35; 14, 43, 37; Talairach and Tournoux, 1988) and right inferior parietal cortex (44, −35, 50). All of these areas also appeared with the overall novel-repeated attenuation contrast, suggesting that these areas are involved in explicit or implicit recognition of the repeated stimuli. This replicates previous findings with attenuated activity for repeated items in inferior parietal cortex in association with implicit memory, and the attenuated activity in frontal cortex in association with explicit memory (Turk-Browne et al., 2006; Wagner et al., 2000). Brain regions that revealed a significant interaction between repetition and close-wide and wide-close conditions (the critical boundary-extension effect) include left and right PPA, left and right retrosplenial cortex, and cingulate and anterior cingulate gyri (−4, 18, 31; −10, 33, 23). Cingulate and anterior cingulate gyri activity were attenuated for close-wide repetition but were increased for wide-close repetition, causing the interaction. It is possible that the discrepancy across wide-close images activated the cingulate gyrus, which is known to be activated in the presence of conflicting input. No interaction was found in the LOC.

Finally, a retinotopic analysis was conducted to explore boundary-extension effects in early visual areas. Even with a highly liberal threshold (p < 0.05, uncorrected, cluster threshold k = 5 voxels), no interactions for close-wide and wide-close conditions with repetition were found in any of the retinotopic areas that were localized using a separate retinotopic localizer (see Supplemental Data available with this article online). These early visual area results, taken with our LOC patterns of activation, indicate that the boundary-extension effects are mainly restricted to scene selective cortical areas such as the PPA and retrosplenial cortex.

Behavioral Measurements of Boundary Extension

We additionally confirmed reliable boundary extension using the same recognition memory procedure as in prior behavioral research. After the fMRI scan, 36 new scenes were presented without repetition, and observers were instructed to remember the objects, background, and layout of each scene image (see Experimental Procedures for more detail). At test, either the opposite view was presented (e.g., close-wide condition, close-up during viewing but wide-angle view during the rating test), or the same view was repeated (e.g., close-close condition, close-up during viewing and then repeated as a close-up during the rating test). Participants rated each test picture as being the same view as before or as revealing a closer or wider expanse of the scene on a five-point scale. Specifically, they were asked if in comparison to its placement in the original view, the camera was *much too close* (−2), *slightly closer* (−1), *the same* (0), *slightly farther away* (+1), or *much too far* (+2). To increase the statistical power of the behavioral recognition test, in addition to

the 18 fMRI participants reported above, six additional participants were tested only in the behavioral session. Figure 2D illustrates boundary-extension scores for each viewing condition; zero indicates that participants recognized the second picture as identical to the original picture, while negative scores indicate that participants recognized the repeated picture as looking closer up than the original picture. We found a significant asymmetry in ratings between the close-wide and wide-close conditions consistent with prior behavioral research (Gottesman and Intraub, 2002; Intraub, 2002; Intraub et al., 1992). When the closer view was presented first, people were unable to distinguish a difference between the wide-angle and close-up views (t_{23} = 0.44, p = 0.6), whereas when the wide-angle was presented first, they readily noticed that the second view was closer (t_{23} = 3.6, p < 0.001). The mean ratings were strikingly different (t_{23} = 6.7, p < .001; see bar graphs in Figure 2). In addition, we found significant boundary extension in both the close-close and wide-wide conditions (t_{23} > 3, p < 0.01). Boundary extension in the close-close condition was marginally greater than the boundary extension in wide-wide condition (t_{23} = 1.8, p = 0.06). Thus, the scene boundary is extrapolated for both close-view and wide-view images, but it is stronger for close-view images that are more constrained in view.

DISCUSSION

The present results provide novel evidence that high-level visual mechanisms extrapolate spatial layout beyond the confines of a given view. The enhanced representation impacts neural responses in the PPA and RSC selectively seconds later, exerting no influence whatsoever on object-specific activity in the LOC or early visual areas.

The absence of boundary-extension effects in early visual areas rules out the possibility that the boundary-extension effects in the PPA and RSC simply reflect attenuation to object size changes or center-peripheral changes over the repetition sequence. This is consistent with behavioral research, showing that boundary extension does not reflect changes in object size but extension of layout at the edges of the view (Gottesman and Intraub, 2002). Most importantly, the boundary error was unidirectional, only showing an extension effect from close to wide images and never a restriction effect from wide to close, even though only the latter case preserved all the features present in the initial presentation. If the boundary-extension effects here simply reflected attenuation to repeated features, then equal degrees of attenuation should have been observed for the wide-close repetitions. Furthermore, the absence of attenuation or behavioral boundary restriction for wide-close repetitions rules out the alternative possibility that the participants were simply representing prototypic distance of a scene, a hypothesis that has been tested and rejected in prior behavioral work (Intraub et al., 1992; Intraub and Berkowits, 1996).

Although our retinotopic mapping analyses did not reveal boundary-extension effects in early visual areas, this issue deserves further research. There is growing evidence that activity in primary visual cortex (V1) reflects what people consciously perceive, rather than simply registering physical retinal input. Murray and colleagues (2006) showed that V1 activity was closely linked to perceived angular size rather than the physical angular size of an object when a size illusion was induced. This shows that activity in early visual areas such as V1 does not just simply reflect feed-forward signals, but also feedback influence from higher areas (Tong, 2003; Hupé et al., 1998). In fact, many studies have demonstrated neural completion processes for early visual features such as illusory color, brightness, or contours (Mendola et al., 1999; Perna et al., 2005; Sasaki and Watanabe, 2004, Meng et al., 2005).

Thus, the lack of scene extrapolation effects in early visual areas may reflect key differences between boundary extension and perceptual filling-in, such as neon color effects of filling-in of the blindspot. Such perceptual effects occur on-line while the stimulus is still present. In contrast, boundary extension does not occur while sensory information is present, but rather involves distortion of the scene representation over time in perceptual memory. Consistent with these differences, the boundary-extension effects were restricted to higher-level scene-processing areas. We did not find boundary-extension effect in early visual areas, which reveal illusory effects for other types of on-line filling-in experiments (Mendola et al., 1999; Ramachandran, 1992; Sasaki and Watanabe, 2004, Meng et al., 2005). Yet despite these differences, there are also interesting functional commonalities between boundary extension and perceptual filling-in. Both phenomena involve neural representation of physically absent but perceived or remembered information. Also, this flexible nature of neural processing reflects the brain's effort to overcome physical constraints of our visual system to represent a continuous and complete visual world. Our study provides novel evidence that higher visual processing systems, such as the PPA and RSC, can also respond to physically absent information beyond a view.

Viewed as a distortion of perceptual memory, these results provide an interesting new window on neural representation of false memories in general. For example, there is evidence that responses in different regions of the medial temporal lobe (MTL) can distinguish between correct recognition and false recognition of words (Cabeza et al., 2001). In the case of boundary extension, however, the PPA and RSC treat a picture that reflects false memory for unseen layout (i.e., a wider view), as more similar to the original view than a physically identical picture: greater attenuation occurred in the close-wide conditions than the close-close conditions. Note that, although boundary extension is a type of false memory (Intraub et al., 1996; Roediger, 1996), it has adaptive value, providing anticipatory representation of upcoming layout that may be fundamental to the integration of successive views.

The responses in the PPA and RSC deserve careful comparison. Both regions showed significant attenuation to close-wide pairs, indicating that these regions are responding to an extended representation of the initial view. Neither region showed attenuated responses to the opposite ordering: wide-close pairs. However, the two regions showed differential sensitivity to perceptual repetition. The PPA showed attenuation to close-close and wide-wide pairs, while RSC did not, presumably because the repetition of the same view did not match the extrapolated scene representation in RSC. This suggests that RSC is more sensitive to boundary extension than the PPA, although we do not claim that RSC will never show attenuation to repeated scene images. However, the results do suggest that the PPA is relatively more strongly tuned to perceptual features in a scene's spatial layout (Bar, 2004; Epstein and Higgins, 2006), making it more responsive to physical repetition.

Future research should further clarify how the PPA and RSC interact in scene perception. One hypothesis is that the PPA responds to local layout information, while RSC, which plays a role in general navigation (Maguire, 2001), may further integrate local scene information into a global environmental representation (Epstein and Higgins, 2006). Another line of research has shown that the parahippocampal cortex and the retrosplenial cortex are highly involved in analyzing long-term associations or contextual associations between object representations (Bar and Aminoff, 2003; Bar, 2004). These previous studies are consistent with our finding of stronger sensitivity to boundary-extended images than to identically repeated images in RSC.

In terms of scene representation, these results converge with behavioral studies suggesting that the representation of a view combines sensory input with highly constrained predictions about the environment just beyond the edges of a view. Extrapolation of layout may thus provide a means by which the visual system can integrate discrete samples of surrounding space that are drawn from successive movements of the eyes and head, enabling perception of a richly detailed and continuous world.

EXPERIMENTAL PROCEDURES

Experimental Design and Procedure

Nineteen participants (11 females, 21–29 years old) from the Yale University community participated for financial compensation. All had normal or corrected-to-normal vision. Informed consent was obtained, and the study protocol was approved by the Yale University Human Investigation Committee at the School of Medicine.

Participants completed three runs of scene viewing in the scanner with 54 trials per run. Each event-related trial began with a green fixation point for 1 s, followed by a 500 ms blank interval. A scene (24° × 18°) was then presented for 500 ms. Participants were instructed to memorize the overall layout and details of the scene. Participants did not make any responses during the main experiment, and their memory for the scenes was not behaviorally tested at any point during the main experiment. The scene was followed by a white fixation dot that remained for 2, 4, or 6 s. Scenes were repeated once within a run at an

average lag of 32 s in one of the four following viewing-angle conditions: close-wide (close-up the first time and wide view of the same scene the second time), wide-close, close-close, or wide-wide (Intraub et al., 1992). The average lag was not different across conditions both in time and in the number of intervening trials (t's < 1.4, p's > 0.2). Scenes were counterbalanced so that each scene appeared equally in each condition across six participants.

When participants came out of the scanner, they participated in an additional test that was designed to measure behavioral reports of boundary extension. Participants first viewed 36 new scenes, each for 500 ms, and then performed 36 trials of a view-angle rating (boundary-extension) task, which tested four conditions: (1) close-wide (close-up angle during viewing and then repeated as a wide view during the rating test); (2) wide-close; (3) close-close; (4) wide-wide. The participants answered with five-scale ratings if the camera that took the picture was much closer than before, slightly closer, the same, slightly farther away, or much too far than the original picture. Participants gave confidence ratings for each recognition judgment as "sure," "pretty sure," "not sure," or "don't remember at all." Confidence ratings indicated that participants were sure or pretty sure of their memory for scenes 84% of the time. To increase the power of behavioral effect, we also tested six more behavioral participants with the same design and stimuli. Data from these participants were added to the behavioral data collected outside the scanner from the brain-imaging participants, resulting in a total number of 24 participants for behavioral analysis. Scenes were counterbalanced so that each scene appeared equally often during initial presentation in the behavioral test.

fMRI Data Acquisition
Participants were scanned in a Siemens Trio 3T scanner with a standard birdcage head coil. Stimuli were presented through an LCD projector on a rear-projection screen. Data from one participant were excluded from the analyses because no time-locked hemodynamic responses were found even when averaged across all the conditions. A high-resolution T1-weighted anatomical image was collected with a 3D MPRAGE protocol ($256 \times 256 \times 256$, 1 mm^3 isometric voxel size). Then, 19 axial slices were defined (7 mm thickness, no gap), parallel to the anterior commissure-posterior commissure line with a T1-FLASH sequence. The main experiment was conducted in the first three functional scan runs, each acquiring 159 image volumes. Subsequent two scans were for the PPA, RSC, and LOC localizers, each acquiring 255 image volumes. In these localizer runs, participants performed repetition detection of faces and scenes or objects and scrambled objects (Kourtzi and Kanwisher, 2001; Yi and Chun, 2005). Each functional volume comprised 19 axial slices (2 s repetition time; 25 ms echo time; 80° flip angle; 7 mm thickness with no gap) acquired parallel to the anterior commissure-posterior commissure line. The first five image volumes of each functional scan were discarded to allow for T1 equilibration effects. After the object localizer run, a new anatomical scan defined new sets of 34 slices perpendicular to the calcarine sulcus, using a T1-FLASH sequence. This was followed by two functional retinotopic mapping runs (see Supplemental Data).

fMRI Data Analysis
Image preprocessing and statistical analyses were conducted using BrainVoyager QX 1.3 (www.brainvoyager.com). Data preprocessing included 3D motion correction, slice acquisition time correction, linear trend removal, and Talairach space transformation. The PPA, RSC, and the LOC ROIs were functionally localized for individual participants based on the independent localizer scan. Linear contrasts (p < 0.0001, uncorrected, cluster threshold k = 5) were used to identify clusters of contiguous voxels in bilateral occipital temporal regions that responded significantly more to (1) scenes compared to faces (PPA, −26, −42, −12; 26, −42, −11 and RSC, −16, −55, 20; 15, −51, 22) and (2) objects compared to scrambled objects (−46, −66, −3; 47, −64, −1), showing regions consistent with prior studies (Grill-

Spector et al., 1999; Maguire, 2001; Yi et al., 2004; Xu and Chun, 2006). Bilateral PPA and LOC were found in all 18 participants examined; however, bilateral RSC was found in 17 out of 18 participants, consistent with previous reports (Epstein et al., 2005). All eight conditions were modeled using 13 finite impulse response (FIR) functions with six motion parameters as covariates of no interest. For each ROI of each participant, the mean time courses for the eight main events were extracted across voxels. To determine the time point to include in ANOVA, the time courses were averaged across conditions and hemispheres, and the numerical peak was compared to each of the other time points. After the comparison of time points, the peak of the PPA, RSC, and the LOC response included the time points 4 and 6, which were significantly different from the others (t test, p < 0.05, one-tailed) (Epstein et al., 2003; Marois et al., 2004).

Random-effects analyses were conducted to study the boundary-extension effects outside of our ROIs (p < 0.001, uncorrected, cluster threshold k = 5). The fMRI data were modeled with an HRF including time derivatives and used as regressors in a multiple regression analysis, along with six movement parameter regressors.

Supplemental Data
The Supplemental Data for this article can be found online at http://www.neuron.org/cgi/content/full/54/2/335/DC1/.

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