Report

Current Biology

Neural Representations Integrate the Current Field of View with the Remembered 360° Panorama in Scene-Selective Cortex

Highlights

- Visual experience of a 360° panorama forges memory associations between scene views
- Representations of discrete views of a 360° environment overlap in RSC and OPA
- The scene currently in view primes associated views of the 360° environment

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In Brief

How is panoramic visual memory formed in the brain? Robertson et al. report that specific regions of the brain—the RSC and OPA—integrate discrete views of a 360° environment. Subsequently, the scene in the current field of view implicitly triggers associated views of the panoramic environment, facilitating ongoing perception.

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Neural Representations Integrate the Current Field of View with the Remembered 360° Panorama in Scene-Selective Cortex

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SUMMARY

We experience our visual environment as a seamless, immersive panorama. Yet, each view is discrete and fleeting, separated by expansive eye movements and discontinuous views of our spatial surroundings. How are discrete views of a panoramic environment knit together into a broad, unified memory representation? Regions of the brain's "scene network" are well poised to integrate retinal input and memory [1]: they are visually driven [2, 3] but also densely interconnected with memory structures in the medial temporal lobe [4]. Further, these regions harbor memory signals relevant for navigation [5–8] and adapt across overlapping shifts in scene viewpoint [9, 10]. However, it is unknown whether regions of the scene network support visual memory for the panoramic environment outside of the current field of view and, further, how memory for the surrounding environment influences ongoing perception. Here, we demonstrate that specific regions of the scene network—the retrosplenial complex (RSC) and occipital place area (OPA)—unite discrete views of a 360° panoramic environment, both current and out of sight, in a common representational space. Further, individual scene views prime associated representations of the panoramic environment in behavior, facilitating subsequent perceptual judgments. We propose that this dynamic interplay between memory and perception plays an important role in weaving the fabric of continuous visual experience.

RESULTS AND DISCUSSION

How is memory of our broad panoramic environment built from discrete and fleeting views of our spatial surroundings? Here, we sought to understand the psychological and neural mechanisms by which different views of a 360° panoramic environment are linked in memory. We further asked whether memory for the surrounding environment plays an important functional role in naturalistic scene perception, enabling the scene within the current field of view to prime views of the environment that are currently out of sight.

Participants studied novel 360° panoramic environments: photospheres of real-world locations, which were either dynamically revealed across a panoramic display (experiments 1 and 3) or actively explored using a virtual reality (VR) headset (experiments 2 and 4). These naturalistic, egocentric viewing experiences enabled participants to experience a seamless transition between the poles of each immersive panoramic scene (Figure 1; Movies S1 and S2). Written consent was obtained from all participants in accordance with a protocol approved by the Massachusetts Institute of Technology Institutional Review Board.

Controlled manipulation of these panoramic environments allowed us to ask three questions. First, how do discrete views of a panoramic environment become linked in memory? Second, once memory for a broad panoramic environment is formed, which regions of the brain represent the association between different views from within that environment? Finally, how is memory for the panoramic environment brought to bear on the scene within the current field of view during perception?

To address these questions, we first aimed to determine whether visual experience of a panoramic environment could link discrete views from within that environment in memory ($n = 21$, experiment 1). On each trial of the study phase, participants viewed two movie segments on a panoramic display (Figure 1A). These segments depicted two overlapping or non-overlapping quarters of a broad panoramic environment, dynamically revealed through a restricted sliding window on a computer screen (Figures 1B and 1C; Movie S1). We later tested whether scene views from opposite poles of this environment, 180° degrees apart, became associated in memory as a function of direct visual experience of their mutual panoramic context (overlap condition versus no-overlap condition; Figure 1C). Note that the studied panoramic environments were visually similar to each other (all came from a homogeneous urban neighborhood; Figure S1). Therefore, associations between test image pairs in this stimulus set could only be inferred from their remembered shared panoramic context (overlap versus no-overlap condition; Figure 1C).

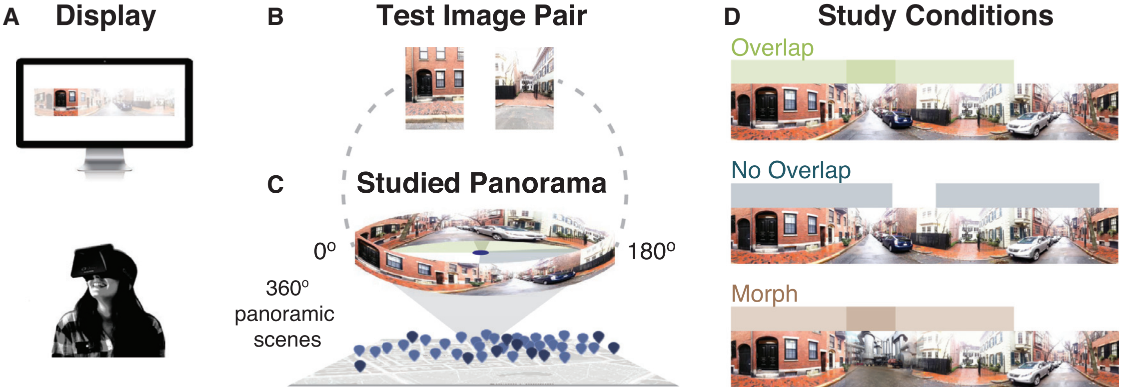

Figure 1. Experimental Paradigm and Stimuli

(A) Participants studied novel, 360° panoramic scenes, either dynamically revealed through a restricted, sliding window on a panoramic display (experiments 1 and 3, top) or actively explored using a virtual reality headset (experiments 2 and 4, bottom).

(B and C) During the memory tests, we presented 20 pairs of images, drawn from opposite poles of 360° panoramic scenes.

(D) For half of these pairs, the panoramic visual information linking them was known because participants had extensively studied overlapping quarters of the scene, for example, the 0–100° and 80°–180° quadrants of the 360° panorama (Overlap study condition, top panel, green). For the other half, the panoramic visual information linking them was unknown, either because participants had studied two non-overlapping quarters of the scene, for example, the 0–100° and 170°–270° quadrants of the 360° panorama (No-Overlap study condition, experiments 1 and 3, middle panel, blue), or because participants had studied spliced panoramas that smoothly morphed between two panoramic scenes (Morph study condition, experiment 2, bottom panel, brown).

See Movies S1 and S2 for screen videos of study trials, Figure S1 for examples of all test images, and Supplemental Experimental Procedures for further experimental details.

On each trial of a subsequent memory test, participants were shown two images, drawn from opposite poles of the studied panoramas (Figure 2A), and asked to report whether the two images came from the same panoramic scene. Participants successfully formed memory associations between two images from the same scene as a function of panoramic visual experience: explicit memory (d′) for the association between two images was significant for both the overlap and no-overlap conditions (overlap: t(18) = 4.19, Cohen's d = 0.96, p = 0.001; no-overlap: t(18) = 2.43, Cohen's d = 0.56, p = 0.026; Figure 2B). Importantly, though, memory performance was significantly stronger for the overlap compared with the no-overlap condition (overlap mean and SEM: 0.63 ± 0.13, no-overlap: 0.25 ± 0.08; repeated-measures ANOVA F(1,18) = 4.09, η_p^2 = 0.30, p = 0.001; Figure 2A). These results indicate that direct visual experience of a broad panoramic environment serves to associate discrete views from within that environment in memory.

But which components of panoramic visual experience drive associative learning in natural scene perception? Thus far, our results argue that continuous visual experience through common visual content causes a stronger association between scene views than mere temporal co-occurrence on study trials, which was equivalent in the overlap and no-overlap conditions. This finding distinguishes panoramic visual learning from demonstrations of paired associative learning based on temporal co-occurrence, for example, between views of objects or faces [11] and their concomitant cortical changes [12, 13]. Next, we asked whether opposite poles of a panoramic expanse could be associated with each other via mutual association with common, but not panoramically consistent, visual content (i.e., via transitive learning). We also tested whether our finding from experiment 1—that continuous visual experience links scene views in memory—would extend to fully egocentric, active viewing conditions using a VR headset.

To test these hypotheses, we ran a control experiment (n = 18, experiment 2; Supplemental Experimental Procedures) in which participants actively explored novel panoramic environments using a VR headset (Figure 1A). In this experiment, half of the panoramas were continuously experienced as in experiment 1 (overlap condition; Figure 1D; Movie S2), and half were spliced in the middle with foreign panoramas (morph condition; Figure 1D; Movie S2). In theory, the two images on opposite poles of these panoramas could be associated via their mutual association with a common middle image, although this spliced image was from an obviously different place (e.g., a plaza or a factory setting) (Figure 1C; Movie S2).

However, continuous panoramic experience (overlap condition) led to significantly stronger associations between scene views than transitive experience (morph condition). Participants' sensitivity (d′) to detect that two images came from the same panoramic environment was significant for both the overlap and morph conditions (overlap: t(19) = 3.27, Cohen's d = 0.73, p = 0.004; no-overlap: t(19) = 3.74, Cohen's d = 0.84, p = 0.001; Figure 2B). Critically, associative memory was significantly higher for the overlap compared with the morph condition (overlap mean d′ and SEM: 1.61 ± 0.50, morph: 0.63 ± 0.17, repeated-measures ANOVA F(1,19) = 2.218, η_p^2 = 0.21, p = 0.01; Figure 2B). All in all, these results demonstrate that continuous, panoramic visual experience links individual scene views from within that panorama in memory under both passive (experiment 1) and active (experiment 2) viewing conditions, going beyond either associative or transitive learning. These findings lend support to models of memory integration that posit that graded exposure to continuous, morphed intermediate states between two distinct stimuli supports the merging of these representations in memory [14–16]. Future work should explore the benefits of active over passive viewing conditions on scene memory formation.

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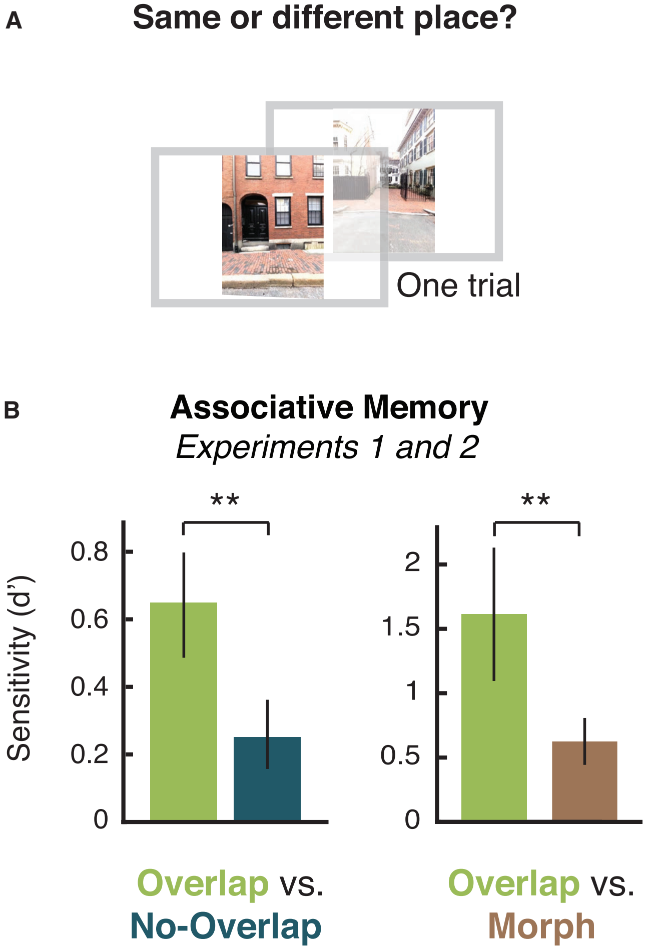

Figure 2. Panoramic Visual Experience Forges Associations between Scene Views in Behavior

(A) In the memory tests of both experiments 1 and 2, participants were asked whether two scene views, drawn from opposite poles of a 360° panoramic environment, depicted the same place or two different places.

(B) In both experiments, sensitivity (d′) to detect that two images came from the same panoramic environment was higher for the Overlap condition (light green) compared with control conditions (Overlap vs. No-Overlap: $F(1,18) = 4.09$, $\eta_p^2 = 0.30$, $p = 0.001$; Overlap vs. Morph: $F(1,19) = 2.218$, $\eta_p^2 = 0.21$, $p = 0.01$). These results demonstrate that discrete views of a panoramic environment become associated in memory as a result of direct visual experience of the panoramic content that unites them (Overlap condition). Further, these effects go beyond simple temporal co-occurrence between scene views on study trials (No-Overlap condition) or transitive learning between views with intermediate visual content (Morph condition).

In all plots, error bars represent 1 SEM. $^{**}p \leq 0.01$, $^{***}p \leq 0.001$ difference between the two conditions. See also Movies S1 and S2 for screen videos of study trials and Figure S2 for replication of experiment 1.

Having demonstrated the conditions under which two discrete views from opposite poles of a 360° panoramic environment are integrated into a broad structural representation of a scene in memory, distinct from either associative or transitive representations, we aimed to determine the neural substrate of this visual memory for views of a panoramic environment. We specifically predicted that this effect would manifest in certain regions of the scene network of the brain—the parahippocampal place area (PPA), the retrosplenial complex (RSC), and the occipital place area (OPA)—which are visually selective for scenes [2, 3] but also sensitive to memory for navigationally relevant information, such as landmark familiarity (PPA) [5, 6] and known position on an allocentric map (RSC) [7, 8] and hence serve as candidate loci for integrated representations between retinal input and memory.

After studying the panoramas, participants were scanned in an event-related fMRI paradigm (n = 12, experiment 3; Supplemental Experimental Procedures; see also Figure S2 for behavioral replication of experiment 1). On each trial, participants viewed a discrete scene view from the studied panoramas and indicated whether it had appeared on the left or the right side of the studied panorama. Crucially, this question did not require explicit recall of the associated scene view (the other pole of the 360° panoramic environment).

Using multivariate pattern analysis, we tested whether representational similarity was stronger for pairs of scene views whose shared panoramic context was known (overlap condition) compared to unknown (no-overlap condition), demonstrating representational overlap between discrete scene views that were associated in memory (Supplemental Experimental Procedures). We first computed panorama decoding indices for each region of interest (ROI): the average correlation in the pattern of fMRI response between two different views from the same panorama minus the correlation between two views from different panoramas. Panorama decoding indices significantly greater than zero indicate greater similarity between the response patterns evoked by two scene views that shared panoramic context than two scenes that did not.

A two-way ANOVA on these panorama decoding indices, with ROI (PPA, RSC, and OPA) and memory condition (overlap versus no-overlap) as repeated-measures factors, revealed a significant main effect of overlap versus no-overlap ($F(1,11) = 6.8687$, $\eta_p^2 = 0.38$, $p = 0.026$), which was qualified by an interaction with ROI ($F(2,22) = 3.66$, $\eta_p^2 = 0.41$, $p = 0.038$). We therefore investigated each region of the scene-responsive network separately in a series of post hoc comparisons.

Our results demonstrate a robust effect of memory for the panoramic environment on the visual responses of two regions of the scene network: RSC and OPA (Figure 3). Specifically, these regions demonstrated a stronger similarity for pairs of images from the overlap compared with the no-overlap condition: OPA ($F(1,11) = 2.07$, $\eta_p^2 = 0.28$, $p = 0.003$) and RSC ($F(1,11) = 2.65$, $\eta_p^2 = 0.39$ $p = 0.001$). These results indicate that the RSC and OPA represent scene views in the context of visual memory for the broader panoramic environment outside of the current field of view.

These effects were specific to RSC and OPA: responses in PPA were not modulated by memory for the broader panoramic scene (Figure 3). In PPA, responses between pairs of scene views were equally similar for pairs whose panoramic context was known (overlap condition) as opposed to unknown (no-overlap condition) ($F(1,11) = 0.048$, $\eta_p^2 = 0.0$, $p = 0.928$). The absence of these effects in PPA is consistent with previous literature: the PPA is particularly implicated in visual recognition of landmarks [5, 17]—objects or buildings of navigational relevance that typically appear in the distance and rarely span multiple fields of view [1]. Further, control analyses revealed that face-selective

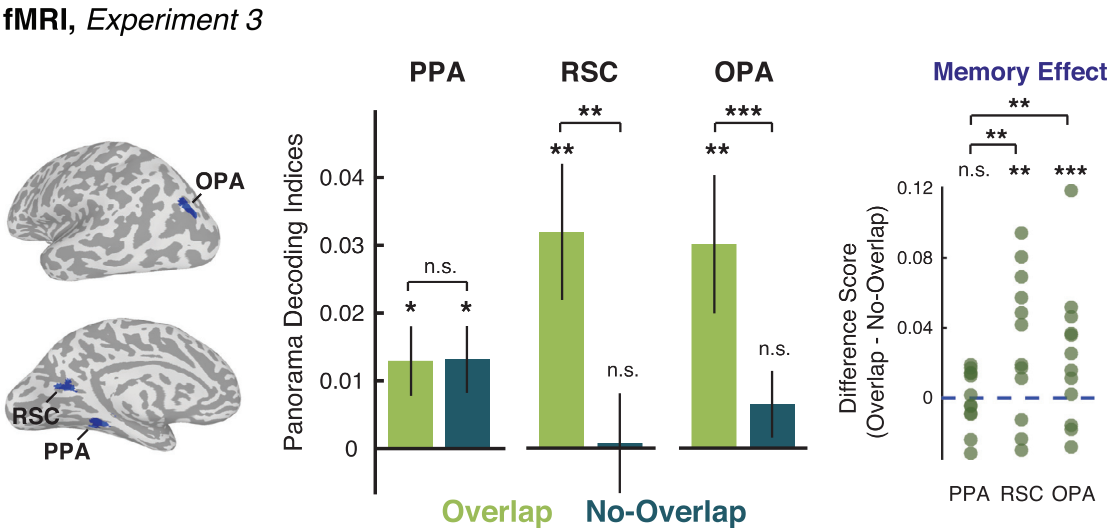

Figure 3. Memory for the Panoramic Environment Forges Representational Similarity between Scene Views in RSC and OPA

Two specific regions of the scene network evidenced stronger similarity for pairs of images from the Overlap as compared with the No-Overlap condition: RSC (F(1,11) = 2.65, $\eta_p^2 = 0.39$ p = 0.001) and OPA (F(1,11) = 2.07, $\eta_p^2 = 0.28$, p = 0.003). Conversely, responses in PPA were not modulated by memory for the broader panoramic scene (F(1,11) = −0.048, p = 0.928). Individual difference scores for each individual subject are plotted in the far right panel. These results demonstrate that discrete views of a panoramic environment increase in representational similarity in two specific regions of the scene network, the RSC and OPA, as a function of visual memory for the spatial information that unites them. In all plots, error bars represent 1 SEM. $^{**}p \leq 0.01$, $^{***}p \leq 0.001$ difference between the two conditions. See also Movie S1 for screen videos of study trials and Figure S2 for behavioral data.

(FFA) and early visual (V1) regions of the brain were not modulated by memory condition (FFA: F(1,11) = 0.067, $\eta_p^2 = 0$, p = 0.899; V1: F(1,11) = −1.085, $\eta_p^2 = 0.06$, p = 0.20).

Finally, it should be noted that all scene ROIs displayed stereotypical signatures of scene-selective visual regions [18–20]: sensitivity to the identity of each scene view across repetitions (all t > 3.80; p = 0.001) as well as the spatial layout within each scene view (open versus closed, PPA: t = 2.20, p = 0.049; OPA: t = 5.22, p = 0.007; RSC: t = 3.49, p = 0.023). Importantly, neither of these signatures (image discrimination or spatial layout discrimination) interacted with our main condition of interest, memory condition (both p > 0.340).

These results demonstrate neural representations of the scene within the current field of view are imbued with our memory for the broader panoramic environment. We hypothesized that this association might serve an important functional role in scene perception, causing non-overlapping views of a learned panoramic environment to automatically prime each other in perception. We tested this hypothesis in a final behavioral experiment (n = 20, experiment 4; Supplemental Experimental Procedures). On each trial of experiment 4, participants were shown an image from one of the studied panoramas and asked to remember the position of the image (whether it had been shown on the left or right side of the panoramic scene at study). Critically, the image was briefly primed (300 ms) by a task-irrelevant stimulus: either another image from the same panorama (valid prime) or a black square (neutral prime) (Figures 4A and 4B).

Overall, memory accuracy for where a scene view had appeared in the broader panorama (left or right side) was high for both the panoramic and morph conditions (overlap mean and SEM: 0.81 ± 0.03, morph: 0.81 ± 0.02, F(1,18) = 0.03, $\eta_p^2 = 0.0$, p = 0.9), indicating that location memory for discrete scene views was similar between the conditions. Critically, however, the perceptual priming effect (efficiency valid prime – efficiency neutral prime) was significantly stronger in the overlap condition compared to the morph condition (mean and SEM, overlap: 0.046 ± 0.016; morph: −0.003 ± 0.02; F(1,18) = 1.43, $\eta_p^2 = 0.27$, p = 0.02; Figure 4C). Post hoc comparisons revealed a significant effect of perceptual priming in the overlap condition (F(1,18) = 2.15, $\eta_p^2 = 0.33$, p = 0.008), but not in the morph condition (F(1,18) = 0.14, $\eta_p^2 = 0.0$, p = 0.82). An additional control study demonstrated that the perceptual priming we observed in the overlap condition was specific to primes that share panoramic context with the target, as compared with invalid primes from another panorama (see Supplemental Information). These results demonstrate that memory for a broad, panoramic environment causes discrete views from within this environment to prime each other in subsequent perception, facilitating perceptual judgments.

Our findings dovetail with predictions from integrative encoding models of memory, which posit that memory representations of prior related events are reactivated during encoding of novel events, contextualizing ongoing experience [21–23]. Neural support for such models derives from associative inference paradigms, where discrete stimuli (e.g., a baseball and a hat) are paired via mutual association with a third stimulus (e.g., a car) [24, 25]. Here, we present a concrete example of integrative memory encoding in naturalistic visual experience: the scene within the current field of view triggers memory of the broader panoramic environment, priming perception of associated views.

Much of the content of a visual percept is based on inference and memory that goes far beyond the information available from retinal input [26]. Here, we demonstrate that the percept of the current field of view is imbued with memory of the broader

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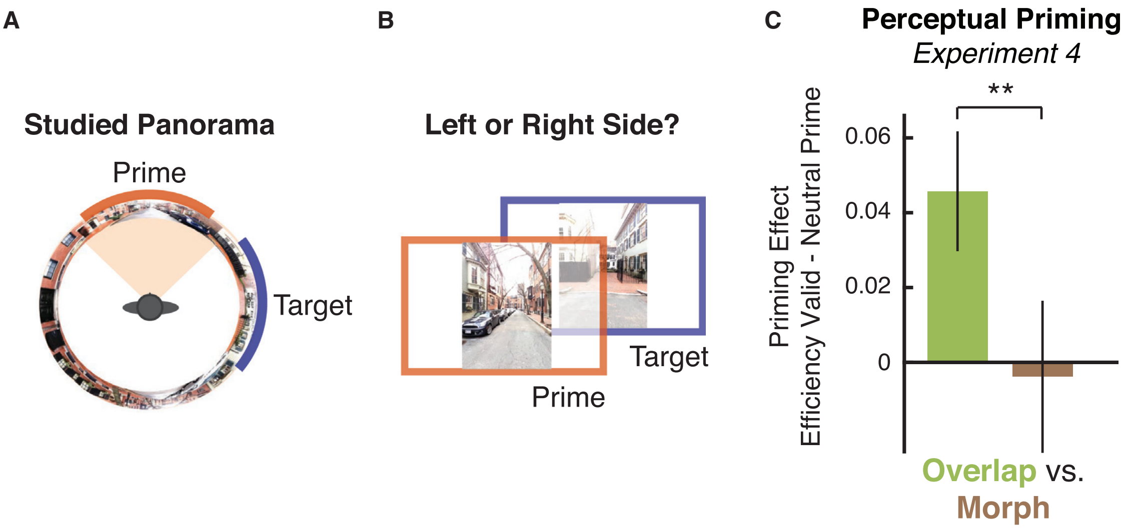

Figure 4. Associated Scene Views Prime Each Other in Perception

(A–C) Participants were faster and more accurate to remember the spatiotopic location of a scene view (Target, A) if it was briefly primed by another view from the broader panoramic environment (Prime, B). Performance was measured as efficiency scores (accuracy / reaction time). The perceptual priming effect (efficiency valid prime – efficiency neutral prime) was significantly stronger in the Overlap condition compared with the no-Overlap condition ($F(1,18) = 1.43$, $\eta_p^2 = 0.27$, $p = 0.02$). These results demonstrate that the scene within the current field of view implicitly triggers memory for associated views of the panoramic environment. In all plots, error bars represent 1 SEM. $^{**}p \leq 0.01$, $^{***}p \leq 0.001$ difference between the two conditions. See also Movie S2 for screen videos of study trials.

panoramic environment. In this way, ongoing scene representations are affixed to a broader representation of the surrounding environment, which may help to support our sense of a seamless panoramic visual expanse.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, two figures, one table, and two movies and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.07.002.

AUTHOR CONTRIBUTIONS

Conceptualization, C.E.R., N.K., and D.J.K.; Methodology, C.E.R., K.L.H., N.K., and D.J.K.; Investigation, C.E.R., A.M., and K.L.H.; Formal Analysis, C.E.R. and D.J.K.; Visualization, C.E.R. and A.M.; Writing – Original Draft, C.E.R.; Writing – Review & Editing, C.E.R., N.K., D.J.K., K.L.H., and A.M.

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