Journal Club

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Memory Retrieval of Visuospatial Context is Supported by the Anterior Portions of High-Level Visual Cortex

Sabina Srokova
Psychology Department, University of Arizona, Tucson 85721, Arizona
Review of Steel et al.

Memory retrieval is believed to be accompanied by a reactivation (reinstatement) of the neuronal populations that were active when the event was initially experienced (for review, see Rugg et al., 2015). The notion of retrieval-related neural reinstatement has been well supported by neuroimaging research over the last two decades. Recent findings, however, point to systematic differences in the localization of content-selective cortical activity evoked during initial perception and memory retrieval. Specifically, it has been shown that neural activity associated with the retrieval and mental imagery of visuospatial information is present in cortical regions that sit immediately anterior to those areas that are typically recruited during visual perception. This phenomenon has been termed retrieval-related "anterior shift" (Bainbridge et al., 2021; Steel et al., 2021).

The idea that visual perception and mental imagery are supported by dissociable neural mechanisms initially emerged from single-case neuropsychological investigations. The case of patient C.K., described by Behrmann et al. (1992), is a notable example. Following a traumatic head injury that resulted in bilateral occipital cortex atrophy, patient C.K. exhibited profound deficits in his ability to recognize objects from vision (visual object agnosia). Remarkably, his ability to retrieve details of the visual properties of objects, when assessed across a variety of mental imagery tasks, remained largely intact. Evidence for the reverse pattern has been documented in several other studies, which reported cases of impaired mental imagery but intact visual object recognition (Farah, 1988). Thus, these results provide support for a double dissociation between perception and imagery.

The natural separation of the visual system into perception and imagery networks was later corroborated by resting state connectivity analyses reported by Baldassano et al. (2016). The proposed framework subdivided the scene-selective parahippocampal place area (PPA) into the posterior PPA, a retinotopically organized cortex that is functionally interconnected with the early visual areas, and the anterior PPA, which exhibits strong coupling with the hippocampus and retrosplenial complex. Based on this functional organization, it was proposed that the neural populations of the posterior scene-selective network process *perceptual* information within the immediate visual field, whereas the anterior regions form a *mnemonic* network that supports neural computations pertinent to the environment beyond the observer's view. This notion was strengthened by recent task-related fMRI studies demonstrating that scene-sensitive neural activity elicited during recall of natural scenes occurs immediately anterior and adjacent to the classical scene-perception areas within the visual cortex. The anterior shift has been proposed to reflect a systematic spatial transformation of the experienced event, such that the contents of the retrieved representation weigh conceptual and semantic information more heavily relative to perceptual detail (Favila et al., 2020). However, prior research has not definitively established whether the neural patterns arising from the anterior portions of the visual cortex contain visuospatial information specific to the retrieved scene, and as such the evidence for the representational transformation account has remained limited.

To address this shortfall, Steel et al. (2023) recently used fMRI and immersive virtual reality to test the hypothesis that the regions anterior and immediately adjacent to canonical scene-perception areas represent the broader visuospatial context of retrieved scenes. Seventeen healthy young participants studied real-world scenes using head-mounted immersive virtual reality. The stimuli comprised 20 panoramic "photospheres" categorized into three visuospatial context conditions. The "image" condition provided the least contextual information, as only a 45° portion of the photosphere was visible to the participant. The "panorama" condition provided a scene view of 270°, and the "street" condition comprised three contiguous 360° photospheres placed along a single street. Participants underwent fMRI as they completed two memory tasks. During the memory recall task, participants recalled scenes associated with verbal cues presented on the screen.

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Correspondence should be addressed to Sabina Srokova at sabinasrokova@arizona.edu.
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During the recognition task, participants viewed scene images (45°) and made old/new judgements. Additionally, participants completed a scene-perception localizer task that involved passively viewing images of scenes, faces, and objects, as well as a place memory localizer task, during which participants recalled familiar places and people. The scene-perception localizer was used to define three posterior "scene-perception" regions-of-interest (ROIs): PPA, occipital place area (OPA), and the medial place area (MPA). The place memory localizer was used to identify the ventral, lateral, and medial "place memory areas", each localized at the anterior edge of the PPA, OPA, and MPA, respectively.

Motivated by previous work demonstrating that neural activity within scene-selective cortical regions is modulated by the amount of associated visuospatial context (Bar and Aminoff, 2003), the authors used univariate analyses to examine whether the amplitude of fMRI BOLD within the place memory areas differed according to the three spatial context conditions. The univariate analyses were motivated by the prediction that, if the anterior "place memory areas" represent the content of a retrieved scene, then the activity within these regions should increase when participants retrieve scenes associated with greater visuospatial context. Indeed, during scene recall, whole-brain, and ROI univariate analyses indicated that the activity in all anterior "place memory areas" increased with visuospatial context. In contrast, activity in the posterior scene-perception areas did not differ according to context, and in fact, these regions were not significantly activated above baseline (except for the MPA). Similar results arose during scene recognition: activity within the place memory areas was modulated by visuospatial context to a greater extent than in the scene-perception areas. This outcome signifies that the broader visuospatial information outside of the visible field of view (a 45° image) is implicitly reactivated in the anterior place memory areas. Finally, the authors applied multivoxel correlation analyses to the memory recall data to determine whether the anterior edge of the visual cortex represents visuospatial information specific to the retrieved environment. In keeping with their predictions, the identity discrimination index (computed as the similarity in neural patterns elicited across retrieval trials of the same scene minus the similarity with other scenes belonging to the same context condition) revealed that the identity of a given environment could be reliably decoded from all perception and memory areas.

Taken together, the univariate and multivariate results provide converging evidence that the anterior edge of the visual cortex represents visuospatial information specific to the retrieved environment. Firstly, these results point to a neural mechanism through which the brain may resolve interference from competing perception and memory signals. Next, while the posterior "scene-perception areas" showed robust scene-selectivity as participants perceived images of scenes (during the perceptual localizer task), these same regions were not significantly activated above baseline during memory recall. This finding, along with the robust context effects in the anterior place memory areas, is consistent with the hypothesis that perception and retrieval of visuospatial information occur in dissociable cortical regions. Therefore, this study joins the recent literature on anterior shift by potentially challenging the neural reinstatement hypothesis and its primary assumption that the neuronal populations that are active during encoding are also reactivated during retrieval. The phenomenon of anterior shift potentially calls into question the wealth of empirical work that examined retrieval-related reinstatement only in those regions which were most active when visual information was initially perceived and encoded. Such studies are likely to be confounded by differences in the localization of retrieval-related neural activity, especially in cases where anterior shift could be exaggerated (e.g., in older age, Srokova et al., 2022).

For the reasons outlined above, future research examining the neural correlates of memory retrieval might benefit from defining functional ROIs using data obtained from "memory localizers" (akin to the place memory localizer used in Steel et al., 2021, 2023). This approach may be helpful in identifying the areas that are most responsive to retrieval-related signals. However, it remains unclear whether a dichotomy between perception and memory networks accurately depicts the functional organization of the visual system. Do the anterior and posterior regions reflect a cytoarchitectonically meaningful separation between two functionally dissociable networks? Or is the visual cortex better thought of as exhibiting a posterior-to-anterior functional gradient? A dichotomy may be valid in the case of the anterior neighbor of the OPA, the lateral place memory area, as this area possibly corresponds with the caudal inferior parietal lobule, a separate region previously implicated in the recall of familiar places (for discussion, see Baldassano et al., 2016). On the other hand, if the neural organizations of the PPA (or the MPA) reflects a gradient of increasing abstraction towards more semantic and language-based information (Favila et al., 2020), treating the posterior and anterior PPA as two functionally distinct regions could obscure important information pertaining to how representational content transforms as neural activity gradually shifts from the posterior to anterior cortex.

Although Steel et al. (2023) make an important step towards unraveling the content of neural patterns arising from the anterior edge of high-level visual cortex, the nature of these representations remains unknown. Do the neuronal populations of the anterior cortex support relatively high-level language-based information at the expense of low-level perceptual detail? Under this assumption, the univariate and multivariate results described above may reflect stimulus-unique semantic content which increases in quantity as the field of view broadens. Although disentangling the roles of semantic and visual information in modulating activity in visually responsive cortex may prove to be challenging, this hypothesis may be a promising focus for future research. An additional prospective avenue pertains to the possibility that the magnitude of the anterior shift differs as a function of the retrieval task. For example, it would be of interest to determine whether incentivizing participants to retrieve high-fi delity perceptual detail of a studied scene results in the recruitment of relatively more posterior cortical regions. While many intriguing questions remain, the article by Steel et al. (2023) serves as a crucial foundation for potential future work that may be aimed at broadening our understanding of the neural mechanisms underlying the anterior shift.

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