Relating scene memory and perception activity to functional properties, networks, and landmarks of posterior cerebral cortex - a probabilistic atlas

Adam Steel[1,2,*], Deepa Prasad[3], Brenda D. Garcia[4], Caroline E. Robertson[3]

[1]Department of Psychology, University of Illinois

[2]Beckman Institute for Advanced Science and Technology, University of Illinois

[3]Department of Psychology, Dartmouth College

[4]University of California San Diego Medical School, University of California San Diego

*Corresponding author: adamdanielsteel@gmail.com

Competing interests: The authors declare no competing interests.

Data availability: Probabilistic parcels and fMRI localizer tasks are available from https://osf.io/xmhn7/. Other supporting data will be made available upon publication.

Code availability: This data does not use any original code. Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

Acknowledgements: This work was supported by an award from the National Institutes of Mental Health (R01MH130529) to CER. AS was supported by the Neukom Institute for Computational Sciences.

Number of Figures: 12

Number of Tables: 2

Abstract word count: 285

Introduction/Discussion text word count: 883/2398

Author contributions: AS and CER designed the research. AS, DP, BDG collected and processed the data. AS analyzed the data. AS and CER wrote the manuscript. All authors reviewed and edited the manuscript.

During the preparation of this work, the author(s) used Claude (Anthropic) to assist in revising the manuscript. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

Abstract

Adaptive behavior in complex environments requires integrating visual perception with memory of our spatial environment. Recent work has implicated three brain areas in posterior cerebral cortex — the place memory areas (PMAs) that are anterior to the three visual scene perception areas (SPAs) – in this function. However, PMAs' relationship to the broader cortical hierarchy remains unclear due to limited group-level characterization. Here, we examined the PMA and SPA locations across three fMRI datasets (44 participants, 29 female). SPAs were identified using a standard visual localizer where participants viewed scenes versus faces. PMAs were identified by contrasting activity when participants recalled personally familiar places versus familiar faces (Datasets 1-2) or places versus multiple categories (familiar faces, bodies, and objects, and famous faces; Dataset 3). Across datasets, the PMAs were located anterior to the SPAs on the ventral and lateral cortical surfaces. The anterior displacement between PMAs and SPAs was highly reproducible. Compared to public atlases, the PMAs fell at the boundary between externally-oriented networks (dorsal attention) and internally-oriented networks (default mode). Additionally, while SPAs overlapped with retinotopic maps, the PMAs were consistently located anterior to mapped visual cortex. These results establish the anatomical position of the PMAs at inflection points along the cortical hierarchy between unimodal sensory and transmodal, apical regions, which informs broader theories of how the brain integrates perception and memory for scenes. We have released probabilistic parcels of these regions to facilitate future research into their roles in spatial cognition.

Significance statement

Complex behavior requires the dynamic interplay between mnemonic and perceptual information. For example, navigation requires representation of the current visual scene and its relationship to the surrounding visuospatial context. We have suggested that the place memory areas, three brain areas located anterior to the scene perception areas in visual cortex, are well-positioned to serve this role. Here, in a large group of participants, we show that the place memory areas are robustly localizable, and that their position at the interface of multiple distributed brain networks is uniquely suited to mnemonic-perceptual integration. We have released probabilistic regions-of-interest and localization procedure so that others can identify these areas in their own participants.

61 Introduction

The integration of perception and memory is a fundamental challenge for the brain, requiring
neural systems to simultaneously maintain current sensory input while accessing relevant
stored information(Rust and Palmer, 2021). This integration is particularly evident during
spatial navigation, where we dynamically exchange information between the immediate
visual scene and memory of the broader environment to interpret visible features, predict
unseen elements, and guide attentional and motor decisions(Robertson et al., 2016; Brunec
et al., 2018; Haskins et al., 2020; Berens et al., 2021; Draschkow et al., 2022). Understanding
how the brain's functional architecture enables perceptual and mnemonic representations
to effectively interface, while also avoiding interference, is therefore a central question in
cognitive neuroscience(Summerfield and De Lange, 2014; Kiyonaga et al., 2017; Favila et al.,
2020; Libby and Buschman, 2021).

Recent work has identified a network of three brain areas in posterior cerebral cortex that
may play a crucial role in bridging perception and memory in the domain of scenes(Steel et
al., 2021, 2023, 2024b). These "place memory areas", on the lateral, ventral, and medial
surfaces (LPMA, VPMA, MPMA, respectively), selectively activate when individuals recall
familiar places (e.g., their house) compared to other memorable stimuli like familiar people
(e.g., their mother) (Steel et al., 2021). Critically, each place memory area is located
immediately anterior and adjacent to one of the three functionally-defined "scene
perception areas" in high-level visual cortex - the occipital place area (OPA),
parahippocampal place area (PPA), and medial place area (MPA, also known as retrosplenial
complex), on the brain's lateral, ventral, and medial surfaces, respectively (Epstein and
Kanwisher, 1998; Hasson et al., 2003; Epstein et al., 2007; Dilks et al., 2013; Silson et al.,
2016). This systematic topographical relationship suggests the place memory areas are
anatomically positioned to directly access perceptual representations of scenes(Steel et al.,
2023), which may change with age (Srokova et al., 2022).

Functionally, the place memory areas exhibit several key properties that highlight their role
in bridging perception and memory. The PMAs areas contain multivariate representations of
specific remembered scene views(Bainbridge et al., 2020; Steel et al., 2023), and activation
in these areas scales with the amount of remembered visuospatial context associated with
a viewed scene (Steel et al., 2023). Connectivity analyses show that the PMAs constitute a
distinct functional network from the SPAs, which is more strongly connected with spatial
memory structures like the hippocampus compared to early visual cortex (Baldassano et al.,
2016; Silson et al., 2016, 2019; Steel et al., 2021). Additionally, PMAs are dynamically
connected to SPAs through voxel-wise retinotopically opponent patterns during tasks
requiring perceptual-mnemonic interaction, such as recognizing familiar scenes (Steel et

al., 2024b, 2024a). Finally, the anterior shift of memory compared with perception may be
specific to scene stimuli as compared with faces (Steel et al., 2021; Chen et al., 2024). Taken
together, this organization aligns with a specialized role in processing out-of-view spatial
information during navigation (Steel et al., 2023).

While these properties make the place memory areas compelling candidates for integrating
perceptual and mnemonic representations of scenes, their broader relationship to large-
scale cortical topography remains unclear. This gap stems partly from methodological
choices in prior research. Given the individualized functional location of category-selective
areas in high-level visual cortex (Kanwisher et al., 1997; Epstein and Kanwisher, 1998; Grill-
Spector and Weiner, 2014; Kanwisher, 2017), most investigations have employed subject-
specific localization approaches to define these areas (Steel et al., 2021, 2023, 2024b;
Srokova et al., 2022), leaving open questions about whether the PMAs represent a
fundamental feature of human cortical organization or whether their location varies
substantially across individuals and methodological approaches. Additionally, because
group-level analyses have been limited, the place memory areas' relationships with other
known anatomical and functional landmarks (e.g., retinotopic maps(Wandell et al., 2007;
Wang et al., 2015) or large-scale cortical networks (Raichle et al., 2001; Fox et al., 2005;
Thomas Yeo et al., 2011; Yeo et al., 2015; Braga and Buckner, 2017; DiNicola et al., 2020; Du
et al., 2024) and functional gradients(Margulies et al., 2016; Huntenburg et al., 2018; Reznik
et al., 2024)) remain poorly characterized. Understanding these relationships can provide
important insight into the role of these memory areas in the brain outside of the visual
system and shed light on the relationship between spatial memory processes and broader
large-scale organizing principles of the human brain.

Here we address these open questions by characterizing the topography of place memory
areas across three independent datasets that vary in their fMRI acquisition parameters,
preprocessing approaches, and experimental designs. This approach allows us to establish
the consistency of these areas' locations relative to scene perception areas and other
cortical landmarks, while controlling for methodology-specific effects. Our results suggest
the place memory areas – each located immediately anterior to a classic scene perception
area on the ventral and dorsal surface of the human brain – represent a robust and consistent
feature of human functional cortical organization. Further, we establish their anatomical
position at inflection points along the cortical hierarchy between unimodal sensory and
transmodal, apical regions, which informs broader theories of how the brain integrates
perception and memory. Finally, we have made probabilistic parcels defining their locations
freely available to the research community to facilitate future research on these areas, and
to better understand their probabilistic relationship with reference to other probabilistic

atlases of functional areas in the human visual system (Julian et al., 2012; Wang et al., 2015;
Rosenke et al., 2021).

Methods

Procedure

The data for this study comprised functional localizers from three independent datasets.
Dataset 1 and Dataset 3 shared 3 participants, otherwise, all participants were non-
overlapping. Dataset 1 (Steel et al., 2021)and Dataset 2 (Steel et al., 2022, 2023, 2024b)were
analyzed for different studies that have been previously published. Dataset 3 was collected
for a separate study that has not been published.

The datasets in this study differed on their imaging parameters and task paradigms, which
enabled us to test the impact of these factors on the robustness of the place memory and
scene perception area location. Datasets 1 and 2 had different imaging parameters but
identical task paradigms. Datasets 2 and 3 had identical imaging parameters but different
task paradigms. Datasets 1 and 3 had different imaging parameters and task paradigms. A
general description of the relationships between these datasets is detailed in Table 1, and a
detailed description of all relevant details are reported below.

Table 1. Relationship between Datasets 1-3.

Dataset	Number of participants	MRI acquisition / processing	Task conditions (imagery)	Total data acquired (Perception task)	Total data acquired (Memory task)	Publications
Dataset 1	14	Single echo Standard	Familiar places Familiar faces	2 runs, 226 TRs (run duration 552 s)	4 runs, 155 TRs (run duration 310 s)	Steel et al., 2021
Dataset 2	23	Multi-echo ME-ICA	Familiar places Familiar faces	2 runs, 226 TRs (run duration 552 s)	4 runs, 155 TRs (run duration 310 s)	Steel et al., 2022; Steel et al., 2023; Steel*, Silson*, et al., 2024
Dataset 3	10 (3 shared with Dataset 1)	Multi-echo ME-ICA	Familiar places Familiar faces Familiar bodies Familiar objects Famous faces	-	6 runs, 234 TRs (run duration 768 s)	Unpublished

Participants

Data from 44 unique participants (Age: 24.9±6.1 s.d., 15 male) comprise this study and are
distributed across three different datasets (Dataset 1: N = 14, Age: 25.6±4.1 s.d., 5 male;
Dataset 2: N = 23, Age: 24.6±7.7 s.d., 8 male; Dataset 3: N =10, Age: 25.8±3.3 s.d., 4 male).

Three participants were present in both Dataset 1 and Dataset 3. All subjects had normal or
correct to normal vision, were not colorblind, and were free from neurological or psychiatric
conditions. Written consent was obtained from all participants in accordance with the
Declaration of Helsinki and with a protocol and consent form approved by the Dartmouth
College Institutional Review Board (Protocol #31288). Participants were compensated for
their time at a rate of $20/hr. No statistical methods were used to pre-determine sample
sizes.

162 Visual Stimuli and Tasks

163 Perception and memory tasks - Datasets 1 and 2

Static scene perception area localizer

The scene perception areas (SPAs, i.e. occipital place area, OPA; parahippocampal place
area, PPA; medial place area, MPA) are regions that selectively activate when an individual
perceives places (i.e., a kitchen) compared with other categories of visual stimuli (i.e., faces,
objects, bodies) (Epstein and Kanwisher, 1998; Silson et al., 2016; Weiner et al., 2018; Steel
et al., 2021). To identify these areas in each person, participants performed an independent
functional localizer scan. On each run of the localizer (2 runs), participants passively viewed
blocks of scene, face, and object images presented in rapid succession (500 ms stimulus,
500 ms ISI). Blocks were 24 s long, and each run comprised 12 blocks (4 blocks/condition).
There was no interval between blocks.

Place memory area localizer

The place memory areas (PMAs) are defined as regions that selectively activate when a
person recalls personally familiar places (i.e., their kitchen) compared with personally
familiar people (i.e., their mother)(Steel et al., 2021). To identify these areas in each person,
participants performed an independent functional localizer scan. Prior to fMRI scanning,
participants generated a list of 36 personally familiar people and places to establish
individualized stimuli (72 stimuli total). These stimuli were generated based on the following
instructions.

"For your scan, you will be asked to visualize people and places that are personally
familiar to you. So, we need you to provide these lists for us. For personally familiar
people, please choose people that you know in real life (no celebrities) that you can
visualize in great detail. You do not need to be contact with these people now, as
long as you knew them personally and remember what they look like. So, you could
choose a childhood friend even if you are no longer in touch with this person.
Likewise, for personally familiar places, please list places that you have been to and
can richly visualize. You should choose places that are personally relevant to you,

so you should avoid choosing places that you have only been to one time. You
should not choose famous places where you have never been. You can choose
places that span your whole life, so you could do your current kitchen, as well as
the kitchen from your childhood home."

During fMRI scanning, participants recalled these people and places. On each trial,
participants saw the name of a person or place and recalled them in as much detail as
possible for the duration that the name appeared on the screen (10 s). Trials were separated
by a variable ISI (4-8 s). Place memory areas were localized by contrasting activity when
participants recalled personally familiar places compared with people (see ROI definitions
section). All trials were unique stimuli, and conditions (i.e., people or place stimuli) were
pseudo-randomly intermixed so that no more than two repeats per condition occurred in a
row.

Memory task - Dataset 3

203   Dataset 3 comprised two tasks, a multi-category dynamic perception task and a multi-
204   category dynamic memory task. The data from the multi-category perception task is being
205   reported in a separate publication and will not be discussed here.

Multi-category place memory localizer

Prior to fMRI scanning, participants generated a list of 5 examples from 5 categories:
personally familiar people's faces (e.g., wife's face, sister's face), familiar people's body
parts (e.g., mother's hands, father's feet), familiar places (e.g., my kitchen, college library),
familiar objects roughly the size of a person's face (e.g., laptop, rugby ball), and famous
people's faces (Beyonce's face, Obama's face) to establish individualized stimuli (72 stimuli
total). These stimuli were generated based on the following instructions.

"For your scan, you will be asked to visualize people's faces and bodies, places, and
objects that are familiar to you. So, we need you to provide these lists for us. For
personally familiar people's faces, please choose people that you know in real life
(no celebrities) that you can visualize in great detail. You do not need to be contact
with these people now, as long as you knew them personally and remember what
they look like. So, you could choose a childhood friend even if you are no longer in
touch with this person.

For bodies, you will choose 5 familiar parts of bodies that are specific to someone
you know (e.g., the hands or feet of your parents). The parts of the body you choose
do not have to belong to the personally familiar people you chose. Please do not
include explicit body parts. Some examples of body parts specific to a person could
be hands, feet, legs, arms, whole bodies etc., but not faces.

For familiar objects, or objects, choose 5 personally familiar objects that are about
the size of a toaster (e.g., your favorite mug, a coffee maker). These objects should be
personal items that you know very well and interact with fairly regularly (e.g., your
personal hairbrush or your soccer ball). You should also be familiar with from multiple
visual angles or viewpoints.

For personally familiar places, please list places that you have been to and can
richly visualize. You should choose places that are personally relevant to you, so
you should avoid choosing places that you have only been to one time. You should
not choose famous places where you have never been. You can choose places that
span your whole life, so you could do your current kitchen, as well as the kitchen
from your childhood home.

For famous people, list some celebrities that you do not know personally whose
faces you can visualize richly. You should be able to imagine their faces and bodies
moving. For example, if you can imagine Beyonce's face, then she would be a good
choice. However, if you could only imagine Beyonce's body while she is dancing,
then you should pick a different celebrity."

During fMRI scanning, participants performed 6 runs of the imagery task. During each run,
participants recalled these people, body parts, objects, and places. All stimuli were
presented in each run, and trials were pseudo-randomized so that no category could appear
on more than 2 consecutive trials.

The trial sequence was modelled off our prior work (Steel et al., 2023). On each trial,
participants saw the name of a person or place and recalled them in as much detail as
possible. The name of the stimulus was displayed for 1 second, followed by a 1 second
dynamic mask (mix of ascii characters approximately the same length as the stimulus cue),
followed by four circles ('oooo'). Participants were instructed to maintain imagery for as long
as the circles remained on the screen (10 s). Trials were separated by a variable ISI (4-8 s).

MRI acquisition

T1-weighted anatomical scan

For registration purposes, a high-resolution T1-weighted magnetization-prepared rapid
acquisition gradient echo (MPRAGE) imaging sequence was acquired (TR = 2300 ms,
TE = 2.32 ms, inversion time = 933 ms, Flip angle = 8°, FOV = 256 × 256 mm, slices = 255,
voxel size = 1 ×1 × 1 mm). T1 images were segmented and surfaces were generated using
Freesurfer (Dale et al., 1999; Fischl et al., 2002; Fischl, 2012) (version 6.0) and aligned to the

fMRI   data   using   AFNI   programs   (Cox,   1996)   align_epi_anat.py   and

@SUMA_AlignToExperiment(Saad and Reynolds, 2012).

260   Dataset 1 – Single Echo EPI

Single-echo T2*-weighted echo-planar images covering the temporal, parietal, and frontal

cortices were acquired using the following parameters: TR=2000 ms, TE=32 ms, GRAPPA=2,

Flip angle=75°, FOV=240 x 240 mm, Matrix size=80 x 80, slices=34, voxel size=3 x 3 x 3 mm.

To minimize dropout caused by the ear canals, slices were oriented parallel to temporal

lobe(Weiskopf et al., 2006). The initial two frames were discarded by the scanner to achieve

steady state.

268   Dataset 2 & 3 – Multi Echo EPI

269   Multi-echo T2*-weighted sequence. The sequence parameters were: TR=2000 ms,

270   TEs=[14.6, 32.84, 51.08], GRAPPA factor=2, Flip angle=70°, FOV=240 x 192 mm, Matrix

271   size=90 x 72, slices=52, Multi-band factor=2, voxel size=2.7 mm isotropic. The initial two

272   frames of data acquisition were discarded by the scanner to allow the signal to reach steady

273   state.

274   MRI Preprocessing

275   Dataset 1 – Single Echo EPI

Data was preprocessed using AFNI (version 20.3.02 'Vespasian')(Cox, 1996). In addition to

the frames discarded by the fMRI scanner during acquisition, the initial two frames were

discarded to allow T1 signal to achieve steady state. Signal outliers were attenuated

(3dDespike). Motion correction was applied, and parameters were stored for use as

nuisance regressors (3dVolreg). Data were then iteratively smoothed to achieve a uniform

smoothness of 5mm FWHM (3dBlurToFWHM).

282   Dataset 2 & 3 – Multi Echo EPI

Multi-echo data processing was implemented based on the multi-echo preprocessing

pipeline from afni_proc.py in AFNI (version 21.3.10 'Trajan')(Cox, 1996). Signal outliers in the

data were attenuated (3dDespike(Jo et al., 2013)). Motion correction was calculated based

on the second echo, and these alignment parameters were applied to all runs. The optimal

combination of the three echoes was calculated, and the echoes were combined to form a

single, optimally weighted time series (T2smap.py). Multi-echo ICA denoising(Kundu et al.,

2012; Evans et al., 2015; DuPre et al., 2019, 2021) was then performed (see *Multi-echo ICA*,

below). Following denoising, signals were normalized to percent signal change, and data
were smoothed with a 3mm Gaussian kernel (3dBlurInMask).

Multi-echo ICA

The data were denoised using multi-echo ICA denoising (tedana.py(Kundu et al., 2012;
Evans et al., 2015; DuPre et al., 2019; Steel et al., 2022), version 0.0.12). In brief, PCA was
applied, and thermal noise was removed using the Kundu decision tree method.
Subsequently, data were decomposed using ICA, and the resulting components were
classified as signal and noise based on the known properties of the T2* signal decay of the
BOLD signal versus noise. Components classified as noise were discarded, and the
remaining components were recombined to construct the optimally combined, denoised
timeseries.

MRI analysis

Dataset 1 & 2 GLM and ROI definition

Scene perception area localizer

To define scene perceptual areas, the scene perception localizer was modeled by fitting
gamma function of the block duration with a square wave for each condition (Scenes, Faces,
and Objects) using 3dDeconvolve. Estimated motion parameters were included as
additional regressors of no-interest along with 4th order polynomials. Scene areas were
drawn based on a general linear test comparing the coefficients of the GLM during scene
versus face blocks. These contrast maps were then transferred to the SUMA standard mesh
(std.141) using @SUMA_Make_Spec_FS and @Suma_AlignToExperiment.

Initial ROIs were hand drawn using a vertex-wise significance of p<0.001 (t-statistic > 3.3)
along with expected anatomical locations (e.g., PPA was not permitted to extend posteriorly
beyond the edge of the collateral sulcus, was used to define the pre-constrained regions of
interest (Weiner et al., 2018; Steel et al., 2021).

Place memory area localizer

To define place memory areas, the familiar people/places memory data was modeled by
fitting a gamma function of the trial duration for trials of each condition (people and places)
using 3dDeconvolve. Estimated motion parameters were included as additional regressors
of no-interest along with 4th order polynomials. Activation maps were then transferred to the
suma standard mesh (std.141) using @SUMA_Make_Spec_FS and
@Suma_AlignToExperiment.

People and place memory areas were drawn based on a general linear test comparing
coefficients of the GLM for people and place memory. Initial ROIs were hand drawn using a
vertex-wise significance threshold of p<0.001 (t-statistic > 3.3). These ROIs were
subsequently constrained to the top 800 most selective vertices before aggregating at the
group level (see below)

328   Dataset 3 GLM and ROI definition

Dynamic place memory area localizer

To define place memory areas, the familiar people/places memory data was modeled by
fitting a gamma function of the trial duration for trials of each condition (famous faces,
familiar faces, familiar bodies, familiar objects, familiar places) using 3dDeconvolve (10 s).
We included a single regressor to model the cue onset and stimulus mask for all trials (2 s).
Estimated motion parameters were included as additional regressors of no-interest along
with 4th order polynomials. Activation maps were then transferred to the suma standard
mesh (std.141) using @SUMA_Make_Spec_FS and @Suma_AlignToExperiment.

People and place memory areas were drawn based on a general linear test comparing
coefficients of the GLM for place memory versus all other categories (personally familiar
faces, body parts, objects, and famous faces). A vertex-wise significance threshold of
p<0.001 was used to draw the pre-constrained ROIs.

341   ROI aggregation across participants

Below we detail the procedure for establishing the probabilistic group definition for all
regions of interest (scene perception areas: OPA, PPA, MPA; place memory areas: LPMA,
VPMA, MPMA).

Individual participants exhibit a wide spectrum of activation extent and magnitude during
the localizer tasks. To ensure that that these differences did not skew our results and that all
individuals contributed equally to the probabilistic parcellation, we constrained the large
ROIs drawn from the GLM to the subset of the top 800 most selective surface vertices in each
region in their respective task. These vertices had the maximum difference between the
category of interest compared to other categories in the task of interest (e.g., in perception,
the vertices with the largest difference between scene perception vs face images in Datasets
1&2). If the region of interest had fewer than 800 vertices, all vertices were taken.

We chose a fixed number of vertices for all participants and regions to ensure that no
participant biases the overall spatial extent of the final parcels. Since all participants
contribute the same number of vertices, the parcel extent and peak of overlap reflect the
pattern across the whole group. Using a percentage of vertices causes spatial extent of the

parcel to overrepresent participants who have larger ROIs. Because the goal of generating
the parcels was to provide a representative spatial location to help guide ROI drawing, we
considered it essential that the parcels reflect the overall pattern of the constituent
participant's regions' spatial extent in this unbiased way. Across subjects included in the
parcels, the mean ROI size was greater than 1000 vertices (mean±std ROI size – MPA:
1135±891, PPA: 2597±880, OPA: 2181±1161, MPMA: 3444±1.304, VPMA: 2147±624; LPMA
3039±1053), and most regions had greater than 800 vertices for most participants (Figure 1).

Figure 1. In most cases, participants had greater than 800 vertices in the hand drawn ROI prior to constraining. Histograms
show the size of the hand drawn region for all participants included in the final parcellation (N=37). Red dotted line marks
800 vertices. The mean number of vertices for all regions was greater than 800, and only MPA had a significant proportion
of participants with fewer than 800 vertices (median =746 vertices).

The size of the constrained region (800 vertices) was chosen to balance the size of the
regions across subjects, the desire to have the most selective vertices represented, and the
desire for contiguity across the vertices. Our prior publications have considered the top 300
most selective vertices (Steel et al., 2021, 2023), but this constraint has generally resulted in
incontiguous sets of vertices. This led to the adoption of the new, larger set of vertices for
parcel definition.

We refer to the top 800 most selective vertices as the individualized regions of interest. We
aggregated these individualized regions of interest within Datasets 1, 2, and 3 for
comparison. We also aggregated across all datasets to form the final probabilistic group
parcel definition. We refer to these final probabilistic overlap maps of the individualized
regions of interest as "parcels".

Comparison across parcels across datasets

We evaluated the success of our parcel definitions for the scene perception and place
memory areas by comparing the location of the parcels across Datasets 1-3. For these
analyses, we focused on Dataset 1 as the basis for comparison for two reasons. First,
Dataset 1 was originally used to establish the place memory areas, and we wanted to
confirm that this original definition was consistent. Second, Datasets 2 had the largest

number of participants to serve as test cases for the generalization of the established
parcels.

We performed three different quantifications: 1) overlap between group-level probabilistic
maps across datasets, 2) proportion of individual constrained ROIs captured by the group
parcel across tasks (i.e., how much did individual participants' constrained ROIs from
Dataset 2 & 3 overlap with the group parcel from Dataset 1), and 3) whether the individual
participants' peak of selectivity was captured by the group parcel across tasks (i.e., did the
individual participants' peak of selectivity from Dataset 2 & 3 fall within the group parcel from
Dataset 1). These metrics provide a comprehensive view of the generalization of the parcels
in independent data.

Shift between scene perception and place memory selectivity

In addition to comparing the parcels across datasets, we also compared the spatial
dissociation between the scene perception and place memory areas in all participants. We
compared the weighted center-of-mass of the scene perception and place memory areas
using the individualized regions of interest from Datasets 1 & 2 (using the methods described
in (Steel et al., 2021)). Specifically, we calculated the center of mass of the individualized
scene perception and place memory parcels, with the spatial position of each vertex
weighted by its selectivity magnitude (i.e., activation for scene versus face perception or
place versus face memory).

Comparison with other scene perception area parcellations

Several groups have published publicly available parcels of the probabilistic locations of PPA
and OPA, defined by contrasting activation during place images compared to other
categories using different localizer stimuli and scan parameters (Julian et al., 2012; Weiner
et al., 2018; Rosenke et al., 2021). To determine how our parcels compare with existing
parcels, we systematically compared the location or our probabilistic parcels with the
location of these previously established parcels. Below we briefly describe the data yielding
the parcels in the previous studies (paraphrased from their methods sections) for
convenience of the readers.

Probabilistic PPA (Weiner et al., 2018)

12 participants underwent two runs of a functional localizer task from (Stigliani et al., 2015),
in which they viewed gray-scale natural images of faces (adult and child faces), scenes
(corridors and houses), bodies (limbs and headless bodies), characters (numbers and
pseudowords), and objects (cars and guitars). Stimuli were shown in 16 second blocks, and
images from each category were on the screen for 1 second (1Hz presentation rate).

Participants were instructed to fixate on a red dot during the task while performing an oddball
task in which they pressed a button whenever they detected phase scrambled images, which
occurred 0-2 times per block. The total scan duration was not given in this study.

PPA was defined in each participant based on the contrast of scenes > faces, objects,
places, bodies, and characters with a voxel-wise threshold of t > 3. The full extent of each
participant's ROI was used to generate the overlap map.

VisF atlas (Rosenke et al., 2021)

19 participants underwent three runs of a multicategory localizer to define visual areas in
lateral and ventral occipitotemporal cortex. This study used the same localizer task and
stimuli used to define the probabilistic PPA by Weiner and colleagues, but with a different
timing (Stigliani et al., 2015). Eight stimuli of one of the five categories (characters
(pseudowords and numbers), bodies (whole bodies and limbs), scenes (houses and
corridors), faces (child and adult), and objects (cars and instruments)) were presented in
each miniblock design, each mini-block holding a duration of 4 s. Participants performed an
oddball task while fixating, where they indicated the presence of a phase scrambled image
using a button press. Each run consisted of 150 MRI volumes (total duration 300s).

OPA and PPA were defined by contrasting activity during scene blocks compared with all
others (t > 3). The full extent of each participant's ROI was used to generate the overlap map.

Julien parcels (Julian et al., 2012)

35 participants underwent four runs of fMRI scanning on a dynamic multicategory localizer
task. Stimuli were three second movie clips of children's faces, children's bodies, objects
(children's toys), scrambled objects, and pastoral scenes used in previous studies (Pitcher
et al., 2011). Within each imaging run, participants saw two blocks of each category, where
six videos clips were shown (block duration = 18s). Three 18 second rest blocks were
included at the beginning, middle, and end of the run, where the screen alternated between
different full-screen colors once every three seconds. Each run consisted of 117 volumes
(total duration 234 seconds). No task details (e.g., 1-back or oddball) were detailed in the
methods section.

Statistical analysis

Statistics were calculated using MATLAB code (Version 2022a, MathWorks). Data
distributions were assumed to be normal, but this was not statistically tested. Individual
data points are shown. Raleigh's tests were used to assess the consistency of the direction
of the shift from perception to memory. Otherwise, paired t-tests were used where indicated.

Alpha level of p < 0.05 was used to assess significance, and Bonferroni correction was
applied where appropriate.

Results

The current study had four aims. First, we wanted to establish the localization of the place
memory areas across multiple datasets with different data acquisition parameters and
experimental design considerations. Second, we wanted to show the consistent
topographic extent and location of the place memory areas with respect to their relationship
with the scene perception areas at an individual subject level. Third, we wanted to compare
the location of the place memory and scene perception areas to other established parcels
involved in scene perception at a group level (Julian et al., 2012; Weiner et al., 2018; Rosenke
et al., 2021). Finally, we wanted to contextualize the place memory and scene perception
areas' locations within the cortical organization more generally, including their anatomical
locations, and their location compared to large scale cortical networks and gradients. In
addition, we have released a publicly available parcel for the scene perception and place
memory areas for general use that can be downloaded from https://osf.io/xmhn7/.

We defined the place memory areas in individual participants by comparing fMRI activity
when participants recalled personally familiar places compared with other categories. In
Dataset 1 & 2, we contrasted activation when participants recalled places compared with
familiar people's faces. In Dataset 3, we compared activity when participants recalled
places versus multiple other categories (places versus faces, objects, bodies, and famous
faces).

In all Datasets, we defined an initial region of interest for each participant on their lateral,
ventral and medial surfaces, which was hand drawn based on a contrast of t > 3.3 (p = 0.001,
uncorrected) for people versus place memory (place memory localizer) or viewing scene
versus face images/videos (scene perception localizer). This hand drawn region of interest
was further constrained to the top 800 most selective surface vertices as each participant's
"individualized region of interest". These individualized regions of interest served as the
basis for comparing across datasets.

The place memory areas' location is consistent across datasets

We began by comparing the location of the most probable location of the place memory
areas across our datasets. Within each dataset (datasets 1-3), we aggregated all
participants' individualized regions of interest to derive a probabilistic surface map. In this
map, vertices were assigned the probability that they were located within the place memory
areas across all individuals in the dataset. We refer to these probabilistic areas as

parcels(Rosenke et al., 2021). The probabilistic maps for each parcel and their overlap are
shown in Figure 2.

We observed a high degree of overlap in place memory parcel's location across the datasets,
despite that the datasets considered different data acquisition, processing methods, and
task conditions. Qualitatively, the spatial location of the parcels was highly similar, as was
the general shape of the cluster. This confirms that the place memory area activation is
highly reproducible, which suggests that these regions are a general feature of cortex and do
not depend on specific design or acquisition/processing methods. We explore the location
of the place memory parcels in greater detail below.

Figure 2. The most probable location of the place memory selective activity is consistent across datasets. The most
probable location of the lateral, ventral, and medial place memory areas (LPMA, VPMA, MPMA) was based on the
intersection of the top 800 most selective surface vertices for each participant. Probabilistic maps show vertices where
greater than 15% of participants were represented. The extent of these regions for all datasets are outlined in the upper right
panel (Dataset 1: Yellow, Dataset 2: Red, Dataset 3, Blue). The boxed portion of the image is enlarged in the insets (right).

Place memory area parcels capture individualized ROIs across datasets

Having confirmed that we could reproduce the most probable location of the place memory
areas across datasets, we next quantified how well the probabilistic parcels captured the
variability of the place memory region of interests' locations in independent participants. We
asked two questions: 1) would the probabilistic parcels capture the location of the most-
selective vertices from individual-participants from a separate dataset, and 2) how well do
the parcels capture the spatial extent of the individualized regions of interest from an

independent dataset? Answering these questions will establish whether the most probable
location of the parcels is an adequate description of the topography of these functionally
defined areas.

For these analyses we used Dataset 1 as the basis for comparison, and we restricted the
probabilistic parcels from Dataset 1 with greater than 15% of participants. We used Dataset
1 as the basis for comparison for two reasons. First, we used Dataset 1 to establish the
location of the place memory areas in our original study (Steel et al., 2021), so this analysis
would confirm that our original definition would generalize to new data. Second, Datasets 2
and 3 were more appropriate test datasets. Because Dataset 2 had the most participants, it
provided the most opportunities to test the generalization of the parcel to new individuals.
In addition, because Dataset 3 used a different experimental design, it provided an
opportunity to test whether the location of the individualized regions of interest depended
on the conditions used to localize these areas. Importantly, three subjects from Dataset 1
were also included in Dataset 3; however, because Datasets 1 and 3 used different
conditions and came from separate testing sessions, they are still independent. Results
were comparable when these participants were removed from the analysis of Dataset 3.

Overall, the place memory parcels derived from Dataset 1 generalized to individual
participants from Datasets 2 and 3. Across all of the memory areas, the parcels from Dataset
1 captured the surface vertex with the greatest selectivity to place memory in the majority of
participants in Dataset 2 (Left hemisphere – MPMA: 78%, VPMA: 87%, LPMA: 87%; Right
hemisphere – MPMA: 78%, VPMA: 91%; LPMA: 100%) and Dataset 3 (Left hemisphere –
MPMA: 80%, VPMA: 100%, LPMA: 60%; Right hemisphere – MPMA: 80%, VPMA: 100%; LPMA:
80%) (Figure 3A-B). Qualitatively, most maxima that fell outside of the parcel were very close
to parcels' edges (Figure 3A). So, it is possible that these peaks could be captured by the
parcel if a more liberal threshold were used.

Likewise, the participants' individualized regions of interest from Dataset 2 and 3 (top 800
most selective vertices) overlapped substantially with the parcel from Dataset 1 (Figure 3B).
We observed significant overlap (> 50%) between individual participants from Dataset 2 and
parcel from Dataset 1 in all regions and all hemispheres (Dataset 2: ts(23) > 3.54, ps <
0.0018). For Dataset 3, we observed significant overlap (> 50%) between individual
participants in all regions in the right hemisphere (ts(9) > 3.88, ps < 0.004), and in the place
memory parcel on the medial and ventral surfaces in the left hemisphere (ts(9) > 8, ps <
0.001); however, the place memory parcel on the lateral surface did not significantly capture
greater than 50% of the individualized parcels across participants in Dataset 3 (t(9) = 1.62, p
= 0.141). The results for Dataset 3 were similar when overlapping participants were excluded
(Left hemisphere – MPMA: t(7) = 4.99, p = 0.003; VPMA: t(7) = 22.90, p < 0.001; LPMA: t(7) =

1.33, p = 0.23; Right hemisphere – MPMA: t(7) = 6.30, p < 0.001; VPMA: t(7) = 31.84, p < 0.001;
LPMA: t(7) = 3.44, p = 0.014). Across both datasets, only one participant (Dataset 2) had zero
vertices of their ROI confined to the LPMA parcel in the left hemisphere, which was due to
the atypically anterior location of their LPMA ROI compared to other participants.

Collectively, these results show that the original place memory parcels established in the
subjects from Steel et al., 2021 generalize to new datasets with different data acquisition,
processing, and experimental design choices. This suggests that the place memory parcels
from one dataset are adequate descriptors of these areas in new datasets, opening the
possibility of algorithmic region of interest definition based on these established parcels.

Figure 3. Location of place memory areas is consistent across datasets. A. Location of the peaks in place memory area
parcels (red outline) compared with the individual participant peaks in place memory selective activity from an independent
set of participants using different fMRI processing and analysis methods (Dataset 2, red) and experimental design (Dataset
3, blue). Participants with peaks within the parcel are shown in red/blue, peaks outside the parcel are shown in yellow/cyan
for Datasets 2 and 3, respectively. Only the left hemisphere is shown. These data are summarized as pie charts for both
hemispheres in panel B and C. B and C. Overlap between the place memory area parcels with individual participant defined
place memory area ROIs (top 800 memory selective surface vertices) from Dataset 2 (B) and Dataset 3 (C). Pie charts show
the percentage of participants with peak selectivity contained within the group parcel. Dotted line indicates 50% overlap
(400 vertices).

Anterior shift for place memory vs. scene perception is reproducible

The place memory areas are thought to support mnemonic processes relevant to visual
scene analysis, and one key piece of supporting evidence is their proximity to the scene
perception areas(Steel et al., 2021). In individual studies, the place memory areas are
reported to lie consistently anterior and adjacent to the scene perception areas on their
respective cortical surfaces (Steel et al., 2021; Srokova et al., 2022). Next, we tested whether
the anterior topographic shift for PMAs relative to SPAs is reproducible across participants
in our three datasets. For these analyses, we considered Datasets 1 and 2, which used the
same experimental design. The results from Dataset 3 will be reported separately in a future
publication.

We addressed the relative location of the place memory and scene perception areas in two
ways. First, in Datasets 1 and 2, we considered the most probable location of the place
memory areas compared to the most probable location of their functionally paired scene

perception areas in the same group of participants. Given the similarity of the place memory
areas' locations in Datasets 1 and 2 described above, we combined the individualized
regions of interest from both Datasets. We then compared topography of the scene
perception and place memory area parcels constructed from these combined datasets,
including the location of the maximum probability. To evaluate overlap, we thresholded the
probabilistic place memory and scene perception parcels to represent at least 33% of
participants, a threshold that is consistent with prior publications (Julian et al., 2012; Weiner
et al., 2018; Rosenke et al., 2021). The peak probability for the place memory and scene
perception parcels are shown in Table 2).

Table 2. Peak probability for perception and memory parcels across cortical surfaces. Coordinates are in MNI space
referenced to the MNI-N27 atlas.

Surface	REGION	LH			RH		
		X	Y	Z	X	Y	Z
Medial	Medial place area	-14	-60	12	14	-59	14
	Medial place memory area	-9	-59	12	14	-51	17
Ventral	Parahippocampal place area	-26	-43	-9	29	-41	-10
	Ventral place memory area	-23	-40	-11	21	-34	-18
Lateral	Occipital place area	-30	-91	21	29	-86	19
	Lateral place memory area	-33	-81	35	37	-79	31

We found that the place memory parcel was located anterior to the scene perception area
parcel on all cortical surfaces (Figure 4). On the lateral surface, we observed an anterior and
dorsal shift of the place memory parcel compared with scene perception, and we saw a
relatively small amount of overlap between the memory and perception parcels (Percent of
LPMA shared – Left hemisphere = 4.4%; Right hemisphere shared = 8.4%). On the ventral
surface, we observed a nearly veridical anterior shift of place memory compared with scene
perception and approximately half of the memory parcel was shared with the perception
area parcel (Percent of VPMA shared – Left hemisphere = 41.3%; Right hemisphere = 42.9%).
On the medial surface, we observed an anterior and dorsal shift in the peak probability
between the parcel perception and memory parcels, but these parcels had a high degree of
overlap (Percent of MPMA shared – Left hemisphere = 35.6%; Right hemisphere = 61.6%;
note that the small amount of LPMA shared is due to the relatively small size of left MPA at
an overlap of 33%). These results confirm the spatial dissociation between the place
memory and scene perception areas on the lateral surface but suggest a less strong
distinction between the memory and perception responses on the medial surface.

The prior analysis shows an anterior shift of scene perception and place memory activity at
the group level, but it does not capture the consistency of the shift at the individual

participant level. We tested the consistency of this shift in a second analysis by comparing
the location of the weighted center of mass of each participant's individualized perception
and place memory area regions of interests for each cortical surface (Steel et al., 2021). This
analysis considers the degree of selectivity for the category of places/scenes versus
people/faces during memory and perception, and therefore provides a sensitive measure of
activation shifts between conditions in regions with a high degree of intersubject variability.
Note that this analysis has been previously published using Dataset 1 with a different ROI
definition method (Steel et al., 2021). Here, we replicate that analysis using a new ROI
definition (top 800 most selective scene perception and place memory area vertices), and
we extend that analysis by considering a new set of participants from Dataset 2. A
comparison between scene perception and place memory area activity in Dataset 3 will be
presented elsewhere. The results were consistent across hemispheres, so we report the
average results across hemispheres.

With this approach, we observed a systematic shift of place memory compared with scene
perception activation on the lateral and ventral surfaces of the brain (Figure 4). In Datasets 1
and 2, on both lateral and ventral surfaces, the individualized weighted center of mass was
significantly anterior to the scene perception area (Dataset 1 – Lateral: t(13) = 10.22, p <
0.001; Ventral: t(13) = 10.11, p < 0.001; Dataset 2 – Lateral: t(22) = 15.94, p < 0.001; Ventral:
t(22) = 12.17, p < 0.001). On the lateral surface, the angle of this shift was anterior and dorsal,
and it highly consistent across individuals (Dataset 1 – mean±s.d. shift distance = 20.6 ±8.4
mm., Raleigh's test: z = 13.05, p < 0.001; Dataset 2 – mean±s.d. shift distance = 21.4±9.6
mm, Raleigh's test: z = 22.24, p < 0.001). On the ventral surface, the shift was largely anterior,
with little medial-lateral variation (Dataset 1 – mean±s.d. shift distance = 17.5±7.5 mm,
Raleigh's test: z = 13.86, p < 0.001; Dataset 2 – mean±s.d. shift distance = 16.9±7.8 mm,
Raleigh's test: z = 22.71, p < 0.001). This replicates the anterior shift previously reported
(Steel et al., 2021) using this new individualized ROI definition. Further, this shows that the
magnitude of the shift replicates to a larger sample of participants collected using different
fMRI acquisition and processing methods.

On the medial surface, the displacement of the place memory compared with scene
perception activity was less pronounced. We found a significant anterior shift of the place
memory compared with scene perception activation on the medial surface in Dataset 1
(t(13) = 2.47, p =0.03) along a consistent anterior and ventral angle (Mean±s.d. shift distance
= 6.22±3.0 mm; Raleigh's test: z = 8.74, p < 0.001), which replicated our prior result with the
new individualized region of interest definition (Steel et al., 2021). However, we did not
observe an anterior shift on the medial surface in Dataset 2. While the activity was shifted
(Mean shift distance = 7.8±6.2 mm; Raleigh's test: z = 7.76, p < 0.001), the shift of memory
compared to perception was more ventral (t(22) = 5.90, p < 0.001) rather than anterior (t(22)

= 0.79, p = 0.43). Note that the ventral shift of place memory compared with scene
perception activity is not consistent with the most probable location of the cluster reported
above, where the most probable location of the scene perception area was ventral and
posterior to the most probable location of the place memory area. It is likely that the
additional information provided by using magnitude of selectivity to weight the center of
mass for this analysis led to this discrepancy.

Taken together, these results replicate prior work investigating the difference in topography
between scene perception and place memory activation in posterior cerebral cortex(Steel
et al., 2021). Specifically, the anterior shift for place memory vs. scene perception is most
prominent on the lateral surface and ventral surfaces, as compared with the medial surface.
This difference between cortical surfaces could belie a difference in the functional
distinction between the perception and memory areas across the cortical surfaces (see
Discussion).

Figure 4. Place memory areas are consistently anterior to scene perception areas. Brain images depict the most probable
location of the place memory (yellow) and scene perception (purple) areas on the brain's lateral, medial, and ventral
surfaces based on the overlap of the top 800 most selective vertices for each task across all participants. Rose plots depict
the shift in the weighted center of mass oof place memory compared to scene perception activation in individual
participants, split between Datasets 1 and 2 (yellow and red, respectively). This individualized analysis revealed a
consistent shift of place memory compared to scene perception activity on all surfaces (Raleigh's tests: zs > 7.6, ps < 0.001).
This shift was anterior and dorsal for the lateral surface, anterior on the ventral surface, and ventral on the medial surface.
Note that rose plots orientation is aligned to the respective brain surface plot. Probability maps for parcels are thresholded
at 0.33 overlap across participants, consistent with prior work establishing probabilistic locations of functional areas in
occipito-temporal cortex(Julian et al., 2012; Wang et al., 2015; Weiner et al., 2018; Rosenke et al., 2021).

Location of the place memory areas compared to established scene
perception area definitions

The parahippocampal place area (PPA) and occipital place areas (OPA) are critical parts of
the scene perception system. These regions can be reliably localized by contrasting brain
activity to images of scenes compared to images of other categories like faces, bodies, or

objects; however, the precise contrast used varies between research groups. In an effort to
standardize the definition of these areas, several groups have published publicly available
parcels of the probabilistic locations of PPA and OPA, defined by contrasting activation
during place images compared to other categories using different localizer stimuli and scan
parameters (Julian et al., 2012; Weiner et al., 2018; Rosenke et al., 2021). How do the place
memory and scene perception parcels defined in this study compare with the probabilistic
locations of parahippocampal place area and occipital place areas from these independent
functional parcels? Specifically, do the place memory areas fall anterior to the probabilistic
location of PPA and OPA as defined by these independent datasets? For these analyses, we
thresholded our probabilistic parcels to at 33% overlap across participants, consistent with
prior work establishing probabilistic locations of functional areas in occipito-temporal
cortex(Julian et al., 2012; Wang et al., 2015; Weiner et al., 2018; Rosenke et al., 2021).

We compared the location of the place memory and scene perception area parcels to three
different publicly available group-defined parahippocampal place areas and two different
occipital place areas. First, for parahippocampal place area, we considered a probabilistic
definition of this region from Weiner and colleagues (henceforth wPPA) (Weiner et al., 2018).
Second, for both parahippocampal place area and occipital place area, we considered an
atlas of functionally-defined category selective areas, known as the visf atlas (Rosenke et
al., 2021), that includes a scene selective area on the ventral and lateral surfaces (COS-
places and TOS-places, respectively). Third, we considered the parahippocampal place area
and occipital place area from Julian and colleagues (Julian et al., 2012).

In sum, we found that the peak of both our ventral and lateral place memory parcels fell
anterior to the peak of every other previously published PPA and OPA/TOS parcel,
respectively (Figures 5-7). With reference to the wPPA parcel from Weiner and colleagues
(Weiner et al., 2018), we found that the peak of our ventral scene perception parcel
corresponded closely to the peak location of the wPPA (Figure 5) (Weiner et al., 2018). While
our scene perception parcel extended posteriorly beyond the wPPA, the maximum
probability was well aligned between these areas. Importantly, the place memory parcel
extended anteriorly beyond the wPPA, and the peak in probability of the place memory
parcel was anterior to peak in probability from the wPPA. This suggests that the scene
perception parcels we defined are well aligned with this definition of the parahippocampal
place area (as previously shown) (Steel et al., 2021).

Figure 5. Location of most probable location of the place memory and scene perception parcels compared
parahippocampal place area defined by Weiner and colleagues (red outline) (Weiner et al., 2018). Place memory area
parcels combine the most probable locations of participants in Datasets 1 and 2 (33% of participants). Probable location
data is reproduced from Figure 4.

Second, we considered the visf atlas (Rosenke et al., 2021), which contained a ventral and

lateral scene selective area analogous to the parahippocampal place area and occipital

place area (referred to as COS-places and TOS-places); notably COS-places from has a

significantly greater anterior extent compared to the wPPA (Rosenke et al., 2021). We found

that COS-places extended anteriorly beyond our ventral scene perception area parcel

(Figure 6). Consequently, we observed more overlap between the place memory area parcel

with COS-places. TOS-places also had a greater anterior extent than the lateral scene

perception area parcel, and therefore also overlapped more with the place memory parcel.

We found that the TOS-places region of interest overlapped with the peak of probability of

both the scene perception and place memory parcels on the lateral surface. Importantly, the

place memory parcels were still anteriorly shifted compared to COS-places and TOS-

places, which supports our conclusion that the place memory parcels are distinct from

functionally localized visual areas.

Figure 6. Location of most probable location of the place memory and scene perception parcels compared to COS-places and TOS-places defined in the visf atlas (red outline) (Rosenke et al., 2021). Place memory area parcels combine the most probable locations of participants in Datasets 1 and 2 (33% of participants). Probable location data is reproduced from Figure 4.

Third, we considered the parcels from Julian and colleagues (Julian et al., 2012), which contained parahippocampal place area and occipital place area atlas regions of interest (henceforth jPPA and jOPA, respectively). Interestingly, we found mixed topographic relationship between our scene perception and place memory area parcels and the Julian regions of interest (Figure 7). Although we found that the jPPA captured the maximum probability of our ventral scene perception parcel, our parcel had a larger anterior and posterior extent, and we observed relatively little overlap between the jPPA and our place memory parcel. On the lateral surface, the jOPA was shifted anteriorly compared to our lateral scene perception parcel. Like TOS-places from the visf atlas, the jOPA overlapped with the maximum probability of both our scene perception and place memory parcel. However, the lateral place memory parcel was distinct from the jOPA: the lateral place memory parcel had a greater dorsal-ventral extent compared to the jOPA, and the lateral place memory parcel was shifted anteriorly compared with the jOPA. Thus, the Julian scene perception area regions of interest were qualitatively different in their topographic extent from the parcels defined from our data.

Place memory areas are at an inflection point between unimodal and transmodal cortex

The previous results demonstrated the robust localization of place memory selective areas showed the consistent topographic distinction (anterior shift) between the place memory activity compared with scene perception activity. Next, we investigated the location of the place memory and scene perception parcels compared with other proposed anatomical and functional landmarks of cerebral cortex. Comparing the locations to established landmarks will provide a more comprehensive understanding the place memory area's position cortex more generally.

Glasser atlas

First, to better understand the place memory and scene perception location relative to known anatomical landmarks, we compared these parcels to the multimodal atlas from Glasser and colleagues (Glasser et al., 2016). We used the probability maps for the place memory and scene perception areas combined from Datasets 1 and 2 thresholded to consider only vertices with greater than 33% of participants represented.

The place memory and scene perception areas were largely centered on different known anatomical landmarks from the Glasser parcellation (Figure 8). On the lateral surface, the place memory parcel was situated over PGp and only minimally overlapped with other areas posterior to PGp. The place memory parcel did extend anteriorly and dorsally into PGs and intraparietal area 0 and 1. Overall the place memory parcel location may be qualitatively similar location to the tertiary sulcus slocs-v, based on visual comparison with published maps (Willbrand et al., 2024). On the other hand, the lateral scene perception parcel was situated more posteriorly, falling largely within area V3CD and posteriorly into the fourth

visual area. The portion of the scene perception parcel shared with the place memory parcel
did extend anteriorly into PGp and interparietal area 0, ventrally into LO1, dorsally into V3B.

On the ventral surface, the place memory parcel began at the anterior portion of the
ventromedial visual areas 1-3 and covered the full extent of parahippocampal areas 1-3. The
medial portion of the place memory parcel crossed minimally into presubiculum. The
anterior portion did not overlap with entorhinal or perirhinal cortex, and the posterior extent
of the place memory parcel only minimally overlapped with the ventromedial visual areas 1-
3. In contrast, the ventral scene perception parcel was situated within the ventromedial
visual areas 1-3, and centered on ventromedial visual area 2. The scene perception parcel
did extend anteriorly into the middle of parahippocampal areas 1-3.

On the medial surface, both the medial place memory and scene perception parcels
covered the full extent of parieto-occipital area sulcus area 1 and terminated prior to
retrosplenal complex. Both parcels overlapped with the transitional visual area and parieto-
occipital sulcus area 2. Neither the place memory or scene perception parcel extended
anterior-dorsally into area 23 A/B or area 7M.

Figure 8. Location of most probable location of the place memory and scene perception parcels compared to the
anatomical regions from the Glasser MPM atlas (Glasser et al., 2016) (Glasser 2016). A. Probabilistic parcels for perception
and memory areas with Glasser atlas regions outlined. B. Pie charts showing distribution of vertices within the Glasser atlas
regions. On the lateral and ventral surfaces, the peak probability of the place memory area was centered in a region anterior
to the scene perception area. On the lateral surface, the maximal probability was at the boundary between PGp and PGs,
while the scene perception area peak was in V3CD. On the ventral surface, the place memory area parcel was centered on
PHC1-3, while the scene perception area was located primarily within the VMVA1-3. On the medial surface, both the scene
perception and place memory area were largely confined within POS1. Place memory area parcels combine the most
probable locations of participants in Datasets 1 and 2 (33% of participants). Probable location data is reproduced from
Figure 4. Pie charts contain data from left and right hemispheres.

Retinotopic maps (Wang atlas)

Retinotopic maps, topographic recapitulations of the retina based on voxels' preferential
responses to stimulation of portions of the visual field, are a hallmark of visual cortical
organization. Although the visual field preferences are shared between retinotopic maps,
many of the retinotopic maps have dissociable roles in visual processing (e.g., the
independent processing of orientation and shape in LO1 versus LO2 (Silson et al., 2013)).
Understanding the location of the scene perception and place memory parcels relative to
these retinotopic maps will help understand these areas' locations compared to these well-
characterized sub-regions of classically visually responsive cortex. To this end, we
compared the most probable location of these parcels with the most probable location of
the retinotopic maps using the atlas from (Wang et al., 2015).

We found that the scene perception parcel largely fell within the retinotopic maps, while the
place memory parcel was generally anterior to these maps, consistent with their respective
roles in perception and memory (Figure 9). On the ventral surface, the peak of scene
perception area probability fell within map PHC2, and the parcel extended posteriorly as far
as map VO1. In contrast, the peak probability of the ventral place memory area parcel was
anterior to map PHC2. The place memory area parcel did extend posteriorly into the PHC2
parcel, but much of the parcel was anterior to the map.

On the lateral surface, the location of the perception and memory parcels followed a similar
pattern to the ventral surface. Most of the scene perception parcel fell within the retinotopic
maps LO1, V3A, and V3B, and the peak of scene perception parcel probability fell within V3A.
On the other hand, the place memory parcel was anterior to these maps, nestled within the
space not considered classically visually responsive between maps LO2, LO1, V3A, V3B,
IPS0, and IPS1.

Taken together, these results show that the place memory parcels are largely anterior to
classic retinotopic maps. This is generally consistent with the assumed dissociation with
their functional roles. Notably, recent work has shown that the place memory areas have
nontraditional visual responses, including systematic negative BOLD responses to
stimulation of positions on the retina (negative retinotopic coding) (Angeli et al., 2024; Steel
et al., 2024b, 2024a), consistent with much of the default mode network of the brain (Szinte
and Knapen, 2020; Christiaan Klink et al., 2021). The difference in visual coding between the
scene perception and place memory areas adds to the evidence for their distinct roles in
cognition.

Figure 9. The place memory areas fall outside of the retinotopic maps, while the scene perception areas fall largely within
these maps. A. Probabilistic parcels for lateral and ventral scene perception and place memory areas with retinotopic maps
overlaid. Retinotopic maps were defined using a maximum probability projection from a standard atlas (Wang et al., 2015).
B. Distribution of vertices within each retinotopic map combined across hemispheres. Place memory area parcels combine
the most probable locations of participants in Datasets 1 and 2 (33% of participants). Probable location data is reproduced
from Figure 4.

Large-scale cortical networks (Yeo HCP 15)

Within human cognitive neuroscience, there is a growing consensus that the coordinated activity across large-scale distributed networks of brain areas underpins cognitive processes like external attention, episodic projection, social processing, and language comprehension and production (Fox et al., 2005; Buckner et al., 2011; Power et al., 2011; Braga and Buckner, 2017; DiNicola et al., 2020; DiNicola and Buckner, 2021; Du et al., 2024; Steel et al., 2024a). Establishing where the place memory and scene perception parcels are located compared to these distributed networks will help contextualize how these regions contribute to the brain's large-scale activity. Importantly, these distributed cortical networks can be defined within individual participants with sufficient resting-state fMRI data(Laumann et al., 2015; Braga and Buckner, 2017; Gordon et al., 2017; Gratton et al., 2018; DiNicola and Buckner, 2021; Du et al., 2024). However, it is also common to use established templates of these networks for group analysis (Buckner et al., 2011) or as priors for individualized network definition (Kong et al., 2021; Du et al., 2024). So, here we compared the most probable location of the place memory and scene perception parcels to a commonly used template from Yeo and colleagues (Buckner et al., 2011).

Overall, the scene perception and place memory parcels were associated with networks involved in external and internally oriented attention, respectively (Raichle et al., 2001; Fox et al., 2005, 2006; Steel et al., 2024a) (Figure 10). Specifically, the peak probability of the scene perception area parcels on the lateral and ventral surfaces fell within the dorsal

attention network A, a network typically associated with externally oriented attention due to
its activation during attentionally-demanding visual tasks (e.g., visual search) (Fox et al.,
2005, 2006). On the other hand, the place memory parcels tended to fall at the boundary
between the dorsal attention network B and the default network A, generally associated with
high-level visual processing and episodic projection and scene construction tasks,
respectively (Braga and Buckner, 2017; Dixon et al., 2017; DiNicola et al., 2020). On the
medial surface, both place memory and scene perception parcels were at the posterior-
ventral edge of the large default network A cluster in posterior parietal cortex.

These data are consistent with the role of the scene perception area in high-level visual
analysis. Moreover, they suggest that the place memory parcels may be a transitional zone
between external and internally oriented neural systems that are not well captured by the
canonical networks. However, this should be interpreted with caution, as the topography of
these networks is more accurate when defined in individual participants (Gordon et al.,
2017).

Figure 10. Location of most probable location of the place memory and scene perception parcels compared to the large-
scale distributed cortical networks defined by Yeo and colleagues (colored outlines) (Thomas Yeo et al., 2011). A.
Probabilistic parcels of the scene perception and place memory areas with the resting-state networks from Yeo and
colleagues overlaid. B. Pie charts showing the distribution of vertices from each parcel within the Yeo networks. On the
lateral and ventral surfaces, the scene perception areas fell largely within sensory grounded cortical networks, specifically
dATN-B. On the other hand, the place memory area parcels fell within networks associated with more abstract, mnemonic
processing, including the DN-A and dATN-A. On the medial surface, both the scene perception and place memory area
parcels fell within DN-A. Place memory area parcels combine the most probable locations of participants in Datasets 1 and
2 (33% of participants). Probable location data is reproduced from Figure 4.

Principal gradient (Margulies et al., 2016)

Beyond discrete networks, cortical organization can be characterized by continuous gradients that transition from unimodal sensory/motor areas to transmodal association areas. These gradients are thought to reflect increasingly abstract and integrated information processing (Margulies et al., 2016; Huntenburg et al., 2018; Murphy et al., 2018, 2019). Given that place memory areas appear to bridge perceptual and mnemonic processes, understanding their position along this gradient could provide insight into their functional role. Using the principal gradient framework established by Margulies et al., we examined where scene perception and place memory areas fall along this unimodal-to-transmodal axis (Margulies et al., 2016). We hypothesized that scene perception areas, which process immediate visual input, would occupy a relatively unimodal position. In contrast, we predicted place memory areas would fall further along the gradient toward transmodal cortex, reflecting their role in integrating visual and mnemonic information.

For this analysis, we compared the location of the place memory and scene perception parcels with the first principal gradient published by Margulies and colleagues (Margulies et al., 2016). We restricted these parcels to surface vertices with greater than 33% of participants.

We found that the place memory and scene perception parcels were in distinct portions of the unimodal-to-transmodal axis (Figure 11), which we quantified by comparing the distributions of vertex-wise gradient score for between the perception and memory areas on each surface using two-sample Kolmogorov-Smirnov tests (lateral surface: $D(3130)=0.90$, $p<0.001$; ventral: $D(3777)=0.53$, $p<0.001$; medial: $D(2819)=0.31$), $p<0.001$. Consistent with our hypothesis, the scene perception parcels on the lateral and ventral surfaces fell largely within unimodal cortex, while the MPA parcel tended to have an elevated position on the principal gradient compared with the other scene perception areas. Intriguingly, all place memory parcels and the MPA parcel fell at the inflection point between unimodal and transmodal cortex, and the parcels spanned the dominantly unimodal to more dominantly transmodal cortical territory (Figure 11B-D). This is further support for the distinct roles of the lateral and ventral scene perception compared with MPA and the place memory areas, and specifically that MPA and the place memory areas may constitute a unique transition zone between sensory and abstract representations.

Figure 11. The scene perception and place memory areas are located at different points along the unimodal-to-transmodal principal gradient. A. Distribution of the principal gradient on the cortical surface with scene perception and place memory area parcels overlaid. B-C. Histograms depicting the relative frequency of vertex-wise principal gradient scores for scene perception (grey) and place memory area parcels (black, colored fill). On the lateral and ventral surfaces, the scene perception parcels are largely confined to unimodal cortical territory. In contrast, the place memory parcels and the MPA parcel fall at the inflection point between unimodal and transmodal cortical territory. Principal gradient data are taken from Margulies et al., 2016(Margulies et al., 2016). Place memory and scene perception parcels were binarized probability maps containing at least 33% of participant's individualized perception or memory area regions of interest. Histograms show data from both hemispheres.

Place memory and scene perception parcel availability and access

Taken together, these data support the distinction between scene perception and place memory related activity on the lateral and ventral surfaces. Figure 12 shows a binarized mask of the probabilistic definition of the scene perception and place memory parcels for both hemispheres reported here (thresholded at 15% participants), which are available for download here: https://osf.io/xmhn7/. The 15% threshold was chosen because of the relative success in capturing the individual local maxima across independent datasets (Figure 3, above). Parcels are available as volume (nifti) and surface files (SUMA's NIML standard mesh 141 density (Argall et al., 2006; Saad and Reynolds, 2012) and Gifti formatted for the fsaverage template (Fischl, 2012)). We have released a probabilistic definition of these parcels for users who wish to set their own parcel probability criteria. Finally, we have released stimulus presentation code and instructions to run the place memory localizer used in this study.

938   Discussion

Here, we characterized the anatomical locations of the place memory areas, a set of brain
areas that respond more when participants recall personally familiar places compared with
other types of stimuli (Steel et al., 2021), across a relatively large group of participants
spanning three different studies. We made three central observations. First, the place
memory areas' locations are consistent across participants and different fMRI acquisition
parameters, localizer tasks, and statistical contrasts. Second, within a participant, the place
memory areas lie systematically anterior to the scene perception areas on the lateral and
ventral surfaces. Third, at the group-level, compared with the scene perception areas, the
place memory areas are in regions associated with memory processes. Specifically, the
place memory areas are immediately anterior to the retinotopic maps and previous
published definitions of the scene perception areas(Julian et al., 2012; Wang et al., 2015;
Weiner et al., 2018; Rosenke et al., 2021), at the boundary between Dorsal Attention Network
B and the Default Network A (Buckner et al., 2011), and span the transition between
unimodal and transmodal cortex(Margulies et al., 2016). These group analyses support the
hypothesis that the place memory areas serve as a bridge between perceptual and
mnemonic processes in cortex(Steel et al., 2021, 2023, 2024b, 2024a; Angeli et al., 2024).

955   Place memory areas are consistently anterior to scene perception areas
956   on the lateral and ventral surfaces

A striking feature of the place memory and scene perception areas is their topographic
arrangement in cortex. Our initial description revealed that the place memory areas were
located immediately anterior and adjacent to the scene perception areas within individual
subjects (Steel et al., 2021), which was subsequently replicated by our group and others

(Srokova et al., 2022; Steel et al., 2023, 2024b). The precise arrangement between
perception and mnemonic areas varies by cortical surface: the trajectory between from
scene perception to place memory area is dorsal and anterior on the lateral surface, anterior
and ventral on the medial surface, and anterior on the ventral surface. In addition, earlier
studies found a larger anterior shift for the lateral and ventral place memory areas vs. their
corresponding scene perception areas, as compared with the medial areas (Steel et al.,
2021; Srokova et al., 2022). Our findings here replicate these prior findings, with remarkable
consistency between the Datasets. The reproducibility of this shift across participants and
paradigms suggests that a neuroanatomical linking mechanism (e.g., structural
connectivity) may underpin their co-localization.

Unlike the lateral and ventral surfaces, the medial place memory and scene perception
areas were highly overlapping, and the shift of memory versus perception was smaller and
less consistent. The findings from Dataset 1 replicate the original observation of an anterior
(and ventral) shift for the center of mass of memory compared with perception on the medial
surface (Steel et al., 2021). However, we found no anterior shift in Dataset 2. Instead, we
observed a ventral shift of memory compared with perception in Dataset 2, but this shift was
small compared with the shift on the other cortical surfaces (approximately 7mm shift on
the medial versus 18 or 21 mm shift on the ventral and lateral surfaces). In both Datasets,
we observed a considerably more overlap between the perception and memory areas on the
medial surface compared with the lateral and ventral surfaces. As noted in the initial studies
of these areas, these differences suggest that the relationship between memory and
perception on the medial surface may be categorically different than the lateral and ventral
surfaces(Steel et al., 2021, 2023).

What does the co-localization memory and perceptual activity for scenes on the medial
surface imply about the medial scene regions' functions? The retrosplenial cortex (RSC), an
anatomical region in the posterior medial parietal cortex near the parietooccipital sulcus
near MPA, receives input from, among other areas, parahippocampal cortex, suggesting that
this area may be higher in the visual hierarchy compared to this area (Kobayashi and Amaral,
2003; Alexander et al., 2023). Indeed, prior work suggests that the medial scene perception
area may not be involved in visual analysis, per se, like image processing related to structure
identification (i.e., "this is a tower") or path detection, associated with the ventral and lateral
surfaces, respectively (Marchette et al., 2015; Julian et al., 2016; Kamps et al., 2016;
Persichetti and Dilks, 2016, 2019; Bonner and Epstein, 2017; Epstein and Baker, 2019;
Henriksson et al., 2019; Lescroart and Gallant, 2019; Dilks et al., 2022). Instead, the medial
scene perception area may be involved with more abstract processes related to joint visuo-
mnemonic representation(Epstein et al., 2007; Park et al., 2007; Baumann and Mattingley,
2010; Vass and Epstein, 2013; Marchette et al., 2014; Robertson et al., 2016; Silson et al.,

2018; Berens et al., 2021). Likewise, RSC/MPA has been implicated in scene memory and
navigation (Maguire et al., 1998; Epstein et al., 2007; Auger et al., 2015; Chrastil et al., 2018;
Steel et al., 2019, 2021; Foster et al., 2023). RSC/MPA is more active when viewing images of
familiar scenes compared with unknown scenes(Epstein et al., 2007; Steel et al., 2021), and
when viewing familiar scenes the posterior medial parietal cortex represents allocentric
position of that scene in the environment (Baumann and Mattingley, 2010; Vass and Epstein,
2013; Marchette et al., 2014; Nau et al., 2020). In addition, if the spatial relationship between
scenes is known (e.g., they appear on opposite sides of a street), the MPA represents the
spatial relationship between these viewpoints within a larger panoramic environment
(Robertson et al., 2016; Berens et al., 2021). This portion of cortex also activates during
mental imagery of scenes, when recalling past events, and imagining future events (Gilmore
et al., 2015, 2016; Vass and Epstein, 2017; Silson et al., 2018, 2019; Barry et al., 2019;
DiNicola et al., 2020). Collectively, these functions rely on mnemonic information
associated with familiarity.

Taken together, these results show a qualitative distinction between the importance of
memory in MPA, and they suggest that MPA could be viewed as a region further down the
visual hierarchy and not a core sensory region. Consistent with this view, in our data, we
observe little distinction between perceptual and mnemonic activity on the medial surface,
with visual scene perception tasks activating just a small portion of this larger, memory
responsive region. Therefore, we suggest that future work distinguishing between mnemonic
and perceptual processing in scenes might jointly consider this scene perception area
(MPA/RSC) and its mnemonic counterpart MPMA as single memory area, akin to LPMA and
VPMA, and separate from scene perception areas on the ventral and lateral surface (PPA and
OPA). Notably, at a finer scale, the anterior and posterior banks of the parietooccipital sulcus
may be differentially involved in memory and perception (Silson et al., 2016, 2018), and it is
possible that these fine-grained distinctions have been blurred at 3T resolution used in this
study. Future work using high- or layer- resolution fMRI may more clearly characterize the
visual selectivity and processes in the medial scene perception and place memory areas.

Place memory areas span the transition from unimodal to transmodal cortex

Our analyses revealed the place memory areas' intriguing position at the intersection of
perceptual and mnemonic cortical systems. Rather than simply activating either sensory
regions or memory-related networks like the default network(DiNicola et al., 2020; Du et al.,
2024), these areas emerge at their intersection, suggesting they may serve as a functional
bridge between these systems. This pattern was particularly clear in our large-scale network
analyses, where both VPMA and LPMA peaked at the boundary between the dorsal attention

network B and the default network A, which are associated with external and internally
oriented attention respectively(Fox et al., 2005; Dixon et al., 2017; Murphy et al., 2018, 2019).
Likewise, the place memory areas fell at the inflection point between unimodal and
transmodal cortical territory (Margulies et al., 2016). This position allows these areas serve
as a topographic link between perceptual and mnemonic systems to facilitate their
interaction during complex behaviors like navigation that require continuous interplay
between perception and memory.

The transitional nature of the place memory areas was further supported by their
relationship to know retinotopic maps (Wandell et al., 2007; Wang et al., 2015). Our group
analysis underscored that the memory areas fell at the anterior edge of the known
retinotopic maps, implying that they are interfacing with retinotopic information. However,
these areas may not have a map-like topographic layout typically associated with visually
responsive areas. Instead, our previous work has shown that these regions have a significant
proportion of negative retinotopic voxels (Steel et al., 2024b). Recent work has shown that
this bivalent (negative vs. positive) retinotopic code underpins voxel-scale interactions
across place memory and scene perception areas (Steel et al., 2024b), and broader
perceptual-mnemonic interactions in the brain, including interactions between the default
network and dorsal attention network (Steel et al., 2024a) and between the hippocampus
and cortex (Angeli et al., 2024). The place memory areas' position at the edge retinotopic
cortex and their mixed response properties suggests that they may organize the retinotopic
information transfer across cortical systems. However, because these results consider
group-aligned data, future work with high-resolution fMRI with dense sampling individual
participants will be critical to investigate these areas' possible role in bridging perceptual
and mnemonic representation and whether these transitional areas are a general motif of
cortical organization.

An important contribution of this work is characterizing place memory areas within
previously established anatomical atlases and functional frameworks. For example, one
prominent framework of perceptual-mnemonic systems, the PMAT framework (Ranganath
and Ritchey, 2012; Ritchey et al., 2015; Reagh and Ranganath, 2018, 2023; Barnett et al.,
2021), posits a "medial temporal network" (MTN), a set of brain areas including the
parahippocampal cortex and precuneus, bridges visual areas to the DMN and the
hippocampus ((Barnett et al., 2021), see also (Andrews-Hanna et al., 2014; Gilmore et al.,
2016)). Additionally, within the DMN, two subsystems – the posterior medial networks (PMN)
and the anterior temporal network (ANT) – are thought to represent place (i.e., location,
situation) and item information (i.e., objects and people), respectively (Ranganath and
Ritchey, 2012; Ritchey et al., 2015; Reagh and Ranganath, 2018; Cooper and Ritchey, 2019;
Ritchey and Cooper, 2020). Consistent with the PMAT framework, our group analysis shows

that the place memory areas overlap with the MTN described by Barnett and colleagues
based on their associated Glasser parcels (Glasser et al., 2016). Specifically, both the place
memory areas and the MTN are associated with the parahippocampal areas 1-3 and the PGp
on the ventral and lateral surface, respectively. Showing this correspondence deepens our
understanding of the place memory areas broader functional profile, implicating them more
directly in autobiographical memory, scene construction, and navigation (Ranganath and
Ritchey, 2012; Cooper and Ritchey, 2019; Ritchey and Cooper, 2020; Barnett et al., 2021). It
also suggests that the place memory areas' visual properties and functions during memory-
guided visual tasks, including their retinotopic coding (Steel et al., 2024b) their role in
representing visuospatial context (Steel et al., 2023), could be integrated within the PMAT
framework. More broadly, this approach of situating brain areas within multiple reference
frameworks helps synthesize findings across different theoretical perspectives and
methodological approaches.

Place memory areas can be localized across different datasets and protocols

Our results show that the place memory areas are localizable in a larger group of
participants and when considering a broader set of categories in memory (as is common in
studies of perception, e.g., (Stigliani et al., 2015; Weiner et al., 2018; Gomez et al., 2019;
Allen et al., 2021; Rosenke et al., 2021)). Importantly, we found these areas in all 44
participants we scanned, and the location of the place memory areas was consistent
between groups using simple two-category contrast (familiar places versus familiar faces
memory recall) or multiple categories (familiar places versus familiar faces, objects, bodies,
famous faces). Taken together, these results show that the place memory areas a robust
feature of human functional brain organization.

Interestingly, although the place memory parcels were significantly more anterior than all
previous scene perception area parcels, including the wPPA (Weiner et al., 2018), CoS-
places and TOS-places region (visf atlas)(Rosenke et al., 2021), and jPPA and jOPA (Julian
parcels) (Julian et al., 2012), our lateral scene perception parcel was generally more
posterior than previous scene perception parcels (TOS-places and jOPA). Several
methodological differences may explain this partial discrepancy. First, these prior parcels
were defined by contrasting activation when participants viewed scenes versus multiple
other visual categories, while we used a more targeted scenes versus faces contrast to
match our place memory localizer (places versus people recall). Second, task demands
differed across studies - we used passive viewing whereas the data used to define the visf
atlas employed an oddball task (Rosenke et al., 2021); Julian et al. did not report task
details(Julian et al., 2012). These differences in stimuli and attention demands could

contribute to the observed variability in parcel location. Taken together, our results reinforce
the distinction between scene perception and place memory areas on both lateral and
ventral surfaces, and our publicly available probabilistic parcels complement existing
resources by providing bilateral, probabilistic ROIs that capture this distinction.

1111 Conclusion

To summarize, understanding the neural systems that subserve perceptual-mnemonic
interactions is a critical question for neuroscience. Here, we describe the anatomical
location of the place memory areas (PMAs) on the brain's lateral, ventral and medial surface,
which are well poised to facilitate perceptual-mnemonic interactions for scenes. Further
study of these brain areas could yield critical insights into neural processes underpinning
spatial cognition and other functions that require the dynamic interplay between perception
and memory. To support this, we have released the probabilistic maps and parcels defined
in the large group of participants for public use (https://osf.io/xmhn7/).

1120

1121 References

Alexander AS, Place R, Starrett MJ, Chrastil ER, Nitz DA (2023) Rethinking retrosplenial
cortex: Perspectives and predictions. Neuron 111:150–175.

Allen EJ, St-Yves G, Wu Y, Breedlove JL, Prince JS, Dowdle LT, Nau M, Caron B, Pestilli F,
Charest I, Hutchinson JB, Naselaris T, Kay K (2021) A massive 7T fMRI dataset to bridge
cognitive neuroscience and artificial intelligence. Nature Neuroscience 2021 25:1
25:116–126 Available at: https://www.nature.com/articles/s41593-021-00962-x
[Accessed April 16, 2024].

Andrews-Hanna JR, Smallwood J, Spreng RN (2014) The default network and self-generated
thought: Component processes, dynamic control, and clinical relevance. Ann N Y Acad
Sci 1316:29–52.

Angeli PA, Steel A, Silson EH, Robertson CE (2024) Positive and Negative Retinotopic Codes
in the Human Hippocampus. bioRxiv:2024.09.27.615397 Available at:
http://biorxiv.org/content/early/2024/10/05/2024.09.27.615397.abstract.

Argall BD, Saad ZS, Beauchamp MS (2006) Simplified intersubject averaging on the cortical
surface using SUMA. Hum Brain Mapp 27:14–27 Available at:
https://pubmed.ncbi.nlm.nih.gov/16035046/ [Accessed June 28, 2022].

Auger SD, Zeidman P, Maguire EA (2015) A central role for the retrosplenial cortex in de novo
environmental learning. Elife 4.

Bainbridge WA, Hall EH, Baker CI (2020) Distinct Representational Structure and
Localization for Visual Encoding and Recall during Visual Imagery. Cerebral Cortex
00:1–16 Available at:
http://fdslive.oup.com/www.oup.com/pdf/production_in_progress.pdf [Accessed
December 7, 2020].

Baldassano C, Esteva A, Fei-Fei L, Beck DM (2016) Two Distinct Scene-Processing Networks
Connecting Vision and Memory. eNeuro 3 Available at:
http://www.ncbi.nlm.nih.gov/pubmed/27822493 [Accessed August 18, 2019].

Barnett AJ, Reilly W, Dimsdale-Zucker HR, Mizrak E, Reagh Z, Ranganath C (2021) Intrinsic
connectivity reveals functionally distinct cortico-hippocampal networks in the human
brain. PLoS Biol 19:e3001275 Available at:
https://journals.plos.org/plosbiology/article?id=10.1371/journal.pbio.3001275
[Accessed April 17, 2024].

Barry DN, Barnes GR, Clark IA, Maguire EA (2019) The Neural Dynamics of Novel Scene
Imagery.   J   Neurosci   39:4375–4386   Available   at:
http://www.ncbi.nlm.nih.gov/pubmed/30902867 [Accessed August 18, 2019].

Baumann O, Mattingley JB (2010) Medial parietal cortex encodes perceived heading
direction in humans. Journal of Neuroscience 30:12897–12901.

Berens SC, Joensen BH, Horner AJ (2021) Tracking the Emergence of Location-based Spatial
Representations in Human Scene-Selective Cortex. J Cogn Neurosci 33:445–462
Available   at: https://direct.mit.edu/jocn/article/33/3/445/95543/Tracking-the-
Emergence-of-Location-based-Spatial [Accessed August 4, 2022].

Bonner MF, Epstein RA (2017) Coding of navigational affordances in the human visual
system.   Proc   Natl   Acad   Sci   U   S   A   114:4793–4798   Available   at:
www.pnas.org/cgi/doi/10.1073/pnas.1618228114 [Accessed December 9, 2020].

Braga RM, Buckner RL (2017) Parallel Interdigitated Distributed Networks within the
Individual Estimated by Intrinsic Functional Connectivity. Neuron 95:457-471.e5.

Brunec IK, Bellana B, Ozubko JD, Man V, Robin J, Liu ZX, Grady C, Rosenbaum RS, Winocur
G, Barense MD, Moscovitch M (2018) Multiple Scales of Representation along the
Hippocampal Anteroposterior Axis in Humans. Current Biology 28:2129-2135.e6.

Buckner RL, Krienen FM, Castellanos A, Diaz JC, Thomas Yeo BT (2011) The organization of
the human cerebellum estimated by intrinsic functional connectivity. J Neurophysiol
106:2322–2345.

Chen YY, Areti A, Yoshor D, Foster BL (2024) Perception and Memory Reinstatement Engage
Overlapping Face-Selective Regions within Human Ventral Temporal Cortex. The
Journal   of   Neuroscience   44:e2180232024   Available   at:
http://www.jneurosci.org/content/44/22/e2180232024.abstract.

Chrastil ER, Tobyne SM, Nauer RK, Chang AE, Stern CE (2018) Converging meta-analytic and
connectomic evidence for functional subregions within the human retrosplenial region.
Behavioral   Neuroscience   132:339–355   Available   at: /record/2018-51215-002
[Accessed November 4, 2020].

Christiaan Klink P, Chen X, Vanduffel W, Roelfsema PR (2021) Population receptive fields in
non-human primates from whole-brain fmri and large-scale neurophysiology in visual
cortex. Elife 10.

Cooper RA, Ritchey M (2019) Cortico-hippocampal network connections support the
multidimensional quality of episodic memory. Elife 8.

Cox RW (1996) AFNI: Software for analysis and visualization of functional magnetic
resonance neuroimages. Computers and Biomedical Research 29:162–173.

Dale AM, Fischl B, Sereno MI (1999) Cortical surface-based analysis: I. Segmentation and
surface reconstruction. Neuroimage 9:179–194.

Dilks DD, Julian JB, Paunov AM, Kanwisher N (2013) The occipital place area is causally and
selectively involved in scene perception. Journal of Neuroscience 33:1331–1336.

Dilks DD, Kamps FS, Persichetti AS (2022) Three cortical scene systems and their
development.   Trends   Cogn   Sci   26:117–127   Available   at:
http://www.cell.com/article/S1364661321002874/fulltext [Accessed January 17,
2022].

DiNicola LM, Braga RM, Buckner RL (2020) Parallel distributed networks dissociate episodic
and social functions within the individual. J Neurophysiol 123:1144–1179 Available at:
https://journals.physiology.org/doi/10.1152/jn.00529.2019 [Accessed March 19, 2020].

DiNicola LM, Buckner RL (2021) Precision estimates of parallel distributed association
networks: evidence for domain specialization and implications for evolution and
development.   Curr   Opin   Behav   Sci   40:120–129   Available   at:
https://linkinghub.elsevier.com/retrieve/pii/S2352154621000772 [Accessed May 18,
2021].

Dixon ML, Andrews-Hanna JR, Spreng RN, Irving ZC, Mills C, Girn M, Christoff K (2017)
Interactions between the default network and dorsal attention network vary across
default subsystems, time, and cognitive states. Neuroimage 147:632–649 Available at:
https://www.sciencedirect.com/science/article/pii/S1053811916307996.

Draschkow D, Nobre AC, van Ede F (2022) Multiple spatial frames for immersive working
memory.   Nature   Human   Behaviour   2022   6:4   6:536–544   Available   at:
https://www.nature.com/articles/s41562-021-01245-y [Accessed June 6, 2022].

Du J, DiNicola LM, Angeli PA, Saadon-Grosman N, Sun W, Kaiser S, Ladopoulou J, Xue A, Yeo
BTT, Eldaief MC, Buckner RL (2024) Organization of the human cerebral cortex
estimated within individuals: networks, global topography, and function. J Neurophysiol
131:1014–1082 Available at: https://doi.org/10.1152/jn.00308.2023.

DuPre E et al. (2021) TE-dependent analysis of multi-echo fMRI with *tedana*. J Open Source
Softw   6:3669   Available   at: https://joss.theoj.org/papers/10.21105/joss.03669
[Accessed June 26, 2022].

DuPre E, Salo T, Markello R, Kundu P, Whitaker K, Handwerker D (2019) ME-ICA/tedana: 0.0.6.
Available at: https://zenodo.org/record/2558498 [Accessed February 7, 2020].

Epstein R, Kanwisher N (1998) A cortical representation the local visual environment. Nature
392:598–601.

Epstein RA, Baker CI (2019) Scene Perception in the Human Brain. Annu Rev Vis Sci
5:annurev-vision-091718-014809   Available   at:
https://www.annualreviews.org/doi/10.1146/annurev-vision-091718-014809
[Accessed July 28, 2019].

Epstein RA, Higgins JS, Jablonski K, Feiler AM (2007) Visual Scene Processing in Familiar and
Unfamiliar   Environments.   J   Neurophysiol   97:3670–3683   Available   at:
https://www.physiology.org/doi/10.1152/jn.00003.2007 [Accessed April 22, 2020].

Evans JW, Kundu P, Horovitz SG, Bandettini PA (2015) Separating slow BOLD from non-BOLD
baseline drifts using multi-echo fMRI. Neuroimage 105:189–197.

Favila SE, Lee H, Kuhl BA (2020) Transforming the Concept of Memory Reactivation. Trends
Neurosci 43:939–950.

Fischl B (2012) FreeSurfer. Neuroimage 62:774–781.

Fischl B, Salat DH, Busa E, Albert M, Dieterich M, Haselgrove C, Van Der Kouwe A, Killiany R,
Kennedy D, Klaveness S, Montillo A, Makris N, Rosen B, Dale AM (2002) Whole brain
segmentation: Automated labeling of neuroanatomical structures in the human brain.
Neuron 33:341–355.

Foster BL, Koslov SR, Aponik-Gremillion L, Monko ME, Hayden BY, Heilbronner SR (2023) A
tripartite view of the posterior cingulate cortex. Nat Rev Neurosci 24:173–189 Available
at: https://doi.org/10.1038/s41583-022-00661-x.

Fox MD, Corbetta M, Snyder AZ, Vincent JL, Raichle ME (2006) Spontaneous neuronal activity
distinguishes human dorsal and ventral attention systems. Proceedings of the National
Academy   of   Sciences   103:10046–10051   Available   at:
https://doi.org/10.1073/pnas.0604187103.

Fox MD, Snyder AZ, Vincent JL, Corbetta M, Van Essen DC, Raichle ME (2005) The human
brain is intrinsically organized into dynamic, anticorrelated functional networks. Proc
Natl   Acad   Sci   U   S   A   102:9673–9678   Available   at:
https://pubmed.ncbi.nlm.nih.gov/15976020/ [Accessed July 13, 2022].

Gilmore AW, Nelson SM, McDermott KB (2015) A parietal memory network revealed by
multiple   MRI   methods.   Trends   Cogn   Sci   19:534–543   Available   at:

https://www.sciencedirect.com/science/article/pii/S1364661315001552   [Accessed
June 18, 2019].

Gilmore AW, Nelson SM, McDermott KB (2016) The Contextual Association Network
Activates More for Remembered than for Imagined Events. Cerebral Cortex 26:611–617
Available at: http://www.nil.wustl.edu/ [Accessed November 4, 2020].

Glasser MF, Coalson TS, Robinson EC, Hacker CD, Harwell J, Yacoub E, Ugurbil K, Andersson
J, Beckmann CF, Jenkinson M, Smith SM, Van Essen DC (2016) A multi-modal
parcellation of human cerebral cortex. Nature 536:171–178 Available at:
http://balsa.wustl.edu/WN56. [Accessed November 5, 2020].

Gomez J, Barnett M, Grill-Spector K (2019) Extensive childhood experience with Pokémon
suggests eccentricity drives organization of visual cortex. Nature Human Behaviour
2019:1 Available at: https://www.nature.com/articles/s41562-019-0592-8 [Accessed
May 5, 2019].

Gordon EM et al. (2017) Precision Functional Mapping of Individual Human Brains. Neuron
95:791-807.e7.

Gratton C, Laumann TO, Nielsen AN, Greene DJ, Gordon EM, Gilmore AW, Nelson SM,
Coalson RS, Snyder AZ, Schlaggar BL, Dosenbach NUF, Petersen SE (2018) Functional
Brain Networks Are Dominated by Stable Group and Individual Factors, Not Cognitive or
Daily Variation. Neuron 98:439-452.e5.

Grill-Spector K, Weiner KS (2014) The functional architecture of the ventral temporal cortex
and its role in categorization. Nat Rev Neurosci 15:536–548 Available at:
/pmc/articles/PMC4143420/?report=abstract [Accessed July 1, 2020].

Haskins AJ, Mentch J, Botch TL, Robertson CE (2020) Active vision in immersive, 360° real-
world environments. Scientific Reports 2020 10:1 10:1–11 Available at:
https://www.nature.com/articles/s41598-020-71125-4 [Accessed January 19, 2022].

Hasson U, Harel M, Levy I, Malach R (2003) Large-scale mirror-symmetry organization of
human occipito-temporal object areas. Neuron 37:1027–1041 Available at:
https://pubmed.ncbi.nlm.nih.gov/12670430/ [Accessed November 4, 2020].

Henriksson L, Mur M, Kriegeskorte N (2019) Rapid Invariant Encoding of Scene Layout in
Human OPA. Neuron Available at:
https://www.sciencedirect.com/science/article/pii/S0896627319303496   [Accessed
May 14, 2019].

Huntenburg JM, Bazin PL, Margulies DS (2018) Large-Scale Gradients in Human Cortical
Organization.   Trends   Cogn   Sci   22:21–31   Available   at:
http://www.cell.com/article/S1364661317302401/fulltext [Accessed June 21, 2022].

Jo HJ, Gotts SJ, Reynolds RC, Bandettini PA, Martin A, Cox RW, Saad ZS (2013) Effective
Preprocessing Procedures Virtually Eliminate Distance-Dependent Motion Artifacts in
Resting State FMRI. J Appl Math 2013 Available at: /pmc/articles/PMC3886863/
[Accessed June 21, 2022].

Julian JB, Fedorenko E, Webster J, Kanwisher N (2012) An algorithmic method for functionally
defining regions of interest in the ventral visual pathway. Available at:
http://web.mit.edu/bcs/nklab/GSS.shtml [Accessed January 20, 2022].

Julian JB, Ryan J, Hamilton RH, Epstein RA (2016) The Occipital Place Area Is Causally
Involved in Representing Environmental Boundaries during Navigation. Current Biology
26:1104–1109   Available   at: https://www.cell.com/current-biology/fulltext/S0960-
9822(16)30177-4 [Accessed May 15, 2019].

Kamps FS, Julian JB, Kubilius J, Kanwisher N, Dilks DD (2016) The occipital place area
represents the local elements of scenes. Neuroimage 132:417–424.

Kanwisher N (2017) The Quest for the FFA and Where It Led. The Journal of Neuroscience
37:1056 Available at: http://www.jneurosci.org/content/37/5/1056.abstract.

Kanwisher N, McDermott J, Chun MM (1997) The fusiform face area: A module in human
extrastriate cortex specialized for face perception. Journal of Neuroscience 17:4302–
4311 Available at: https://www.jneurosci.org/content/17/11/4302 [Accessed May 18,
2021].

Kiyonaga A, Scimeca JM, Bliss DP, Whitney D (2017) Serial dependence across perception,
attention,   and   memory.   Trends   Cogn   Sci   21:493   Available   at:
/pmc/articles/PMC5516910/ [Accessed July 17, 2022].

Kobayashi Y, Amaral DG (2003) Macaque monkey retrosplenial cortex: II. Cortical afferents.
Journal of Comparative Neurology 466:48–79.

Kong R, Yang Q, Gordon E, Xue A, Yan X, Orban C, Zuo X-N, Spreng N, Ge T, Holmes A, Eickhoff
S, Yeo BTT (2021) Individual-Specific Areal-Level Parcellations Improve Functional
Connectivity Prediction of Behavior. Cerebral Cortex 31:4477–4500 Available at:
https://doi.org/10.1093/cercor/bhab101.

Kundu P, Inati SJ, Evans JW, Luh WM, Bandettini PA (2012) Differentiating BOLD and non-
BOLD signals in fMRI time series using multi-echo EPI. Neuroimage 60:1759–1770.

Laumann TO, Gordon EM, Adeyemo B, Snyder AZ, Joo SJ, Chen MY, Gilmore AW, McDermott
KB, Nelson SM, Dosenbach NUF, Schlaggar BL, Mumford JA, Poldrack RA, Petersen SE
(2015) Functional System and Areal Organization of a Highly Sampled Individual Human
Brain. Neuron 87:657–670.

Lescroart MD, Gallant JL (2019) Human Scene-Selective Areas Represent 3D Configurations
of Surfaces. Neuron 101:178-192.e7.

Libby A, Buschman TJ (2021) Rotational dynamics reduce interference between sensory and
memory representations. Nature Neuroscience 2021 24:5 24:715–726 Available at:
https://www.nature.com/articles/s41593-021-00821-9 [Accessed April 16, 2024].

Maguire EA, Burgess N, Donnett JG, Frackowiak RSJ, Frith CD, O'Keefe J (1998) Knowing
where and getting there: A human navigation network. Science (1979) 280:921–924
Available at: https://pubmed.ncbi.nlm.nih.gov/9572740/ [Accessed November 4,
2020].

Marchette SA, Vass LK, Ryan J, Epstein RA (2014) Anchoring the neural compass: Coding of
local spatial reference frames in human medial parietal lobe. Nat Neurosci 17:1598–
1606   Available   at:
https://static1.squarespace.com/static/55aaa148e4b0ba360335ef21/t/55b07091e4b
0dd22812a8c37/1437626513802/Marchette-2014-Nature-Neuro.pdf [Accessed May
13, 2019].

Marchette SA, Vass LK, Ryan J, Epstein RA (2015) Outside looking in: Landmark
generalization in the human navigational system. Journal of Neuroscience 35:14896–
14908.

Margulies DS, Ghosh SS, Goulas A, Falkiewicz M, Huntenburg JM, Langs G, Bezgin G, Eickhoff
SB, Castellanos FX, Petrides M, Jefferies E, Smallwood J (2016) Situating the default-
mode network along a principal gradient of macroscale cortical organization. Proc Natl
Acad Sci U S A 113:12574–12579.

Murphy C, Jefferies E, Rueschemeyer SA, Sormaz M, Wang H ting, Margulies DS, Smallwood
J (2018) Distant from input: Evidence of regions within the default mode network
supporting perceptually-decoupled and conceptually-guided cognition. Neuroimage
171:393–401.

Murphy C, Wang H-T, Konu D, Lowndes R, Margulies DS, Jefferies E, Smallwood J (2019)
Modes of operation: A topographic neural gradient supporting stimulus dependent and
independent   cognition.   Neuroimage   186:487–496   Available   at:
https://doi.org/10.1016/j.neuroimage.2018.11.009 [Accessed June 17, 2019].

Nau M, Navarro Schröder T, Frey M, Doeller CF (2020) Behavior-dependent directional tuning
in the human visual-navigation network. Nat Commun 11:3247 Available at:
http://www.nature.com/articles/s41467-020-17000-2 [Accessed December 6, 2020].

Park S, Intraub H, Yi D-J, Widders D, Chun MM (2007) Beyond the Edges of a View: Boundary
Extension in Human Scene-Selective Visual Cortex. Neuron 54:335–342 Available at:
https://www.sciencedirect.com/science/article/pii/S0896627307002565   [Accessed
April 28, 2019].

Persichetti AS, Dilks DD (2016) Perceived egocentric distance sensitivity and invariance
across scene-selective cortex. Cortex 77:155–163.

Persichetti AS, Dilks DD (2019) Distinct representations of spatial and categorical
relationships across human scene-selective cortex. Proceedings of the National
Academy   of   Sciences:201903057   Available   at:
http://www.pnas.org/lookup/doi/10.1073/pnas.1903057116 [Accessed October 1,
2019].

Pitcher D, Dilks DD, Saxe RR, Triantafyllou C, Kanwisher N (2011) Differential selectivity for
dynamic versus static information in face-selective cortical regions. Neuroimage
56:2356–2363.

Power JD, Cohen AL, Nelson SM, Wig GS, Barnes KA, Church JA, Vogel AC, Laumann TO,
Miezin FM, Schlaggar BL, Petersen SE (2011) Functional Network Organization of the
Human Brain. Neuron 72:665–678.

Raichle ME, MacLeod AM, Snyder AZ, Powers WJ, Gusnard DA, Shulman GL (2001) A default
mode of brain function. Proceedings of the National Academy of Sciences 98:676–682
Available at: https://doi.org/10.1073/pnas.98.2.676.

Ranganath C, Ritchey M (2012) Two cortical systems for memory-guided behaviour. Nat Rev
Neurosci 13:713–726.

Reagh ZM, Ranganath C (2018) What does the functional organization of cortico-
hippocampal networks tell us about the functional organization of memory? Neurosci
Lett   680:69–76   Available   at:
https://www.sciencedirect.com/science/article/pii/S0304394018303136.

Reagh ZM, Ranganath C (2023) Flexible reuse of cortico-hippocampal representations
during encoding and recall of naturalistic events. Nature Communications 2023 14:1
14:1–15 Available at: https://www.nature.com/articles/s41467-023-36805-5 [Accessed
April 17, 2024].

Reznik D, Margulies DS, Witter MP, Doeller CF (2024) Evidence for convergence of distributed
cortical processing in band-like functional zones in human entorhinal cortex. Current
Biology 34:5457-5469.e2 Available at: https://doi.org/10.1016/j.cub.2024.10.020.

Ritchey M, Cooper RA (2020) Deconstructing the Posterior Medial Episodic Network. Trends
Cogn Sci xx Available at: https://doi.org/10.1016/j.tics.2020.03.006 [Accessed April 25,
2020].

Ritchey M, Libby LA, Ranganath C (2015) Cortico-hippocampal systems involved in memory
and   cognition: the   PMAT   framework   3.   Available   at:
http://dx.doi.org/10.1016/bs.pbr.2015.04.001 [Accessed September 2, 2019].

Robertson CE, Hermann KL, Mynick A, Kravitz DJ, Kanwisher N (2016) Neural
Representations Integrate the Current Field of View with the Remembered 360°
Panorama in Scene-Selective Cortex. Current Biology 26:2463–2468 Available at:
https://www.sciencedirect.com/science/article/pii/S0960982216307539   [Accessed
April 8, 2019].

Rosenke M, van Hoof R, van den Hurk J, Grill-Spector K, Goebel R (2021) A Probabilistic
Functional Atlas of Human Occipito-Temporal Visual Cortex. Cerebral Cortex 31:603–
619 Available at: https://doi.org/10.1093/cercor/bhaa246.

Rust   NC,   Palmer   SE   (2021)   Remembering   the   Past   to   See   the   Future.
https://doi.org/101146/annurev-vision-093019-112249   7   Available   at:
https://www.annualreviews.org/doi/abs/10.1146/annurev-vision-093019-112249
[Accessed September 7, 2021].

Saad ZS, Reynolds RC (2012) SUMA. Neuroimage 62:768–773.

Silson EH, Gilmore AW, Kalinowski SE, Steel A, Kidder A, Martin A, Baker CI (2018) A
posterior-anterior distinction between scene perception and scene construction in
human medial parietal cortex. Journal of Neuroscience 39:705–717 Available at:
https://www.jneurosci.org/content/early/2018/11/30/JNEUROSCI.1219-18.2018
[Accessed September 21, 2021].

Silson EH, McKeefry DJ, Rodgers J, Gouws AD, Hymers M, Morland AB (2013) Specialized and
independent processing of orientation and shape in visual field maps LO1 and LO2. Nat
Neurosci 16:267–269 Available at: https://doi.org/10.1038/nn.3327.

Silson EH, Steel A, Kidder A, Gilmore AW, Baker CI (2019) Distinct subdivisions of human
medial parietal cortex support recollection of people and places. Elife 8.

Silson EH, Steel AD, Baker CI (2016) Scene-Selectivity and Retinotopy in Medial Parietal
Cortex.   Front   Hum   Neurosci   10:412   Available   at:
http://journal.frontiersin.org/Article/10.3389/fnhum.2016.00412/abstract   [Accessed
April 8, 2019].

Srokova S, Hill PF, Rugg MD (2022) The Retrieval-related Anterior shift is Moderated by Age
and Correlates with Memory Performance. Journal of Neuroscience:JN-RM-1763-21
Available at: https://www.jneurosci.org/content/early/2022/01/06/JNEUROSCI.1763-
21.2021 [Accessed January 17, 2022].

Steel A, Angeli PA, Silson EH, Robertson CE (2024a) Retinotopic coding organizes the
interaction   between   internally   and   externally   oriented   brain   networks.
bioRxiv:2024.09.25.615084   Available   at:
http://biorxiv.org/content/early/2024/11/04/2024.09.25.615084.abstract.

Steel A, Billings MM, Silson EH, Robertson CE (2021) A network linking scene perception and
spatial memory systems in posterior cerebral cortex. Nature Communications 2021
12:1 12:1–13 Available at: https://doi.org/10.1038/s41467-021-22848-z [Accessed May
18, 2021].

Steel A, Garcia BD, Goyal K, Mynick A, Robertson CE (2023) Scene Perception and
Visuospatial Memory Converge at the Anterior Edge of Visually Responsive Cortex. The
Journal   of   Neuroscience   43:5723   Available   at:
http://www.jneurosci.org/content/43/31/5723.abstract.

Steel A, Garcia BD, Silson EH, Robertson CE (2022) Evaluating the efficacy of multi-echo ICA
denoising on model-based fMRI. Neuroimage 264:119723.

Steel A, Silson EH, Garcia BD, Robertson CE (2024b) A retinotopic code structures the
interaction   between   perception   and   memory   systems.   Nat   Neurosci   27:339–347
Available at: https://doi.org/10.1038/s41593-023-01512-3.

Steel A, Thomas C, Trefler A, Chen G, Baker CI (2019) Finding the baby in the bath water –
evidence for task-specific changes in resting state functional connectivity evoked by
training. Neuroimage 188:524–538.

Stigliani A, Weiner KS, Grill-Spector K (2015) Temporal Processing Capacity in High-Level
Visual Cortex Is Domain Specific. The Journal of Neuroscience 35:12412 Available at:
http://www.jneurosci.org/content/35/36/12412.abstract.

Summerfield C, De Lange FP (2014) Expectation in perceptual decision making: neural and
computational   mechanisms.   Nat   Rev   Neurosci   15:745–756   Available   at:
https://pubmed.ncbi.nlm.nih.gov/25315388/ [Accessed July 17, 2022].

Szinte M, Knapen T (2020) Visual Organization of the Default Network. Cerebral Cortex
30:3518–3527   Available   at:
https://academic.oup.com/cercor/article/30/6/3518/5685762 [Accessed July 13,
2022].

Thomas Yeo BT, Krienen FM, Sepulcre J, Sabuncu MR, Lashkari D, Hollinshead M, Roffman
JL, Smoller JW, Zöllei L, Polimeni JR, Fisch B, Liu H, Buckner RL (2011) The organization
of the human cerebral cortex estimated by intrinsic functional connectivity. J
Neurophysiol 106:1125–1165.

Vass LK, Epstein RA (2013) Abstract Representations of Location and Facing Direction in the
Human   Brain.   Journal   of   Neuroscience   33:6133–6142   Available   at:
https://www.jneurosci.org/content/33/14/6133 [Accessed April 13, 2022].

Vass LK, Epstein RA (2017) Common Neural Representations for Visually Guided
Reorientation and Spatial Imagery. Cerebral Cortex 27:1457–1471 Available at:
https://dx.doi.org/10.1093/cercor/bhv343 [Accessed April 17, 2024].

Wandell BA, Dumoulin SO, Brewer AA (2007) Visual field maps in human cortex. Neuron
56:366–383 Available at: https://pubmed.ncbi.nlm.nih.gov/17964252/ [Accessed July
13, 2022].

Wang L, Mruczek REB, Arcaro MJ, Kastner S (2015) Probabilistic maps of visual topography
in   human   cortex.   Cerebral   Cortex   25:3911–3931   Available   at:
/pmc/articles/PMC4585523/?report=abstract [Accessed November 4, 2020].

Weiner KS, Barnett MA, Witthoft N, Golarai G, Stigliani A, Kay KN, Gomez J, Natu VS, Amunts
K, Zilles K, Grill-Spector K (2018) Defining the most probable location of the
parahippocampal place area using cortex-based alignment and cross-validation.
Neuroimage 170:373–384 Available at: https://pubmed.ncbi.nlm.nih.gov/28435097/
[Accessed November 4, 2020].

Weiskopf N, Hutton C, Josephs O, Deichmann R (2006) Optimal EPI parameters for reduction
of susceptibility-induced BOLD sensitivity losses: A whole-brain analysis at 3 T and 1.5
T.

Willbrand EH, Tsai Y-H, Gagnant T, Weiner KS (2024) Updating the sulcal landscape of the
human lateral parieto-occipital junction provides anatomical, functional, and cognitive
insights. Available at: http://dx.doi.org/10.7554/eLife.90451.2.

Yeo BTT, Krienen FM, Eickhoff SB, Yaakub SN, Fox PT, Buckner RL, Asplund CL, Chee MWL
(2015) Functional Specialization and Flexibility in Human Association Cortex. Cerebral
Cortex 25:3654–3672 Available at: https://doi.org/10.1093/cercor/bhu217.

1483

1484