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Research Report

Sustained neural representations of personally familiar people and places during cued recall

Anna Corriveau [a,b,**,1], *Alexis Kidder* [a,c,*,1], *Lina Teichmann* [a],
Susan G. Wardle [a] *and Chris I. Baker* [a]

[a] *Laboratory of Brain and Cognition, National Institute of Mental Health, National Institutes of Health, Bethesda, MD, 20814, USA*
[b] *Department of Psychology, The University of Chicago, Chicago, IL 60637, USA*
[c] *Department of Psychological and Brain Sciences, Dartmouth College, Hanover, NH 03755, USA*

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ABSTRACT

The recall and visualization of people and places from memory is an everyday occurrence, yet the neural mechanisms underpinning this phenomenon are not well understood. In particular, the temporal characteristics of the internal representations generated by active recall are unclear. Here, we used magnetoencephalography (MEG) and multivariate pattern analysis to measure the evolving neural representation of familiar places and people across the whole brain when human participants engage in active recall. To isolate self-generated imagined representations, we used a retro-cue paradigm in which participants were first presented with two possible labels before being cued to recall either the first or second item. We collected personalized labels for specific locations and people familiar to each participant. Importantly, no visual stimuli were presented during the recall period, and the retro-cue paradigm allowed the dissociation of responses associated with the labels from those corresponding to the self-generated representations. First, we found that following the retro-cue it took on average ~1000 ms for distinct neural representations of freely recalled people or places to develop. Second, we found distinct representations of personally familiar concepts throughout the 4 s recall period. Finally, we found that these representations were highly stable and generalizable across time. These results suggest that self-generated visualizations and recall of familiar places and people are subserved by a stable neural mechanism that operates relatively slowly when under conscious control.

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[*] *Corresponding author*. Laboratory of Brain and Cognition, National Institute of Mental Health, National Institutes of Health, Bethesda, MD, 20814, USA

[**] *Corresponding author*. Laboratory of Brain and Cognition, National Institute of Mental Health, National Institutes of Health, Bethesda, MD, 20814, USA.

E-mail addresses: corriveaual@uchicago.edu (A. Corriveau), alexis.kidder.gr@dartmouth.edu (A. Kidder).

[1] AC and AK contributed equally to the study with shared first authorship.

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1. Introduction

The ability to recall and generate sustained representations from memory facilitates many everyday tasks, such as trying to locate a familiar person in a crowd or a specific house while driving. These internally generated representations also underlie our capacity to remember individual people and places that have personal significance. Regions within the medial temporal lobe, particularly the hippocampus, play an integral role in these memory processes and are fundamental to successful recollection of events, people and places (Diana et al., 2007; Liang & Preston, 2017; Ranganath & Ritchey, 2012; Yonelinas et al., 2019). In addition to the memory system within the medial temporal lobe, areas in lateral parietal cortex, medial parietal cortex and ventral temporal cortex also appear to support memory recall (Gilmore et al., 2015; Kim, 2013; Rugg & King, 2018; Silson et al., 2019; Vilberg & Rugg, 2008; Wagner et al., 2005). In particular, in medial parietal cortex the recall and mental visualization of people and places engages distinct anatomical regions (Peer et al., 2015; Silson et al., 2019; Woolnough et al., 2020).

While previous fMRI work has revealed a cortical locus for the recall of familiar people and places (Silson et al., 2019), the temporal dynamics of such recall remain unclear. Studies of event-related potentials have revealed that differences in slow wave amplitude and topography are present during recall of learned face stimuli and associated position from long-term memory (Khader et al., 2005), suggesting categorical differences may be present at a fine temporal scale. Characterization of the temporal properties of recalled representations is necessary to understand the complex neural mechanisms underlying this ability. For example, is there a sudden or gradual onset of information when we imagine locations or people that are familiar to us? Is the representation of recalled information brief and quickly evolving or does the recalled representation remain stable over time? These questions cannot be answered with the slow temporal resolution of fMRI. We address this gap through the use of whole-brain magnetoencephalography (MEG) to reveal the temporal evolution of self-generated imagined representations of personally familiar people and places.

A related but distinct area of research explores the neural mechanisms underlying visual mental imagery. Recent studies investigating the temporal dynamics of recall have primarily examined mental imagery for images presented during the experiment, with a focus on characterizing the similarity of mechanisms engaged in visual perception and visual imagery (Dijkstra et al., 2018, 2019, 2020; Shatek et al., 2019; Xie et al., 2020). For example, category membership (face vs house) can be decoded from whole-brain MEG when participants view face or house images, and when they subsequently imagine the same images (Dijkstra et al., 2018). Similarly, EEG recordings suggest shared mechanisms between imagery and perception in alpha oscillations (Xie et al., 2020). It is likely, however, that visual imagery of novel images learned during an experimental context primarily reflects the engagement of visual regions in ventral temporal cortex and not the extended network of regions implicated in memory recall (Kosslyn, 2005; O'Craven & Kanwisher, 2000). In contrast, we instead focus on revealing the temporal evolution of self-generated representations of people and places that are personally relevant, which are likely to engage rich and highly detailed memory representations. This is supported by the greater response previously observed in medial parietal and medial frontal cortex with fMRI during the recall of people and places that were personally familiar compared to those that were famous (Silson et al., 2019).

We used MEG and multivariate pattern analysis to measure dynamic neural activation patterns as participants recalled personally familiar people (e.g., parent, co-worker) and personally familiar places (e.g., bedroom, office) inside the scanner in a retro-cue paradigm. In sum, we find that distinct representations of familiar people and places take around 1 sec to develop and remain highly stable over time. These results suggest that the neural mechanisms supporting self-generated visualization and recall of familiar places and people operate relatively slowly when under conscious control. However, a potential benefit of this sluggishness is that the developed representations are highly consistent over time, as evident by the high temporal generalizability of the brain activation patterns over the duration of the recall period.

2. Materials and methods

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

2.1. *Participants*

Thirty-five healthy volunteers with normal or corrected-to-normal vision took part in this study. Five participants were excluded due to technical difficulties, MEG scanner malfunction, or incomplete recordings. Data from the remaining 30 participants (21 female, mean age 25.07, SD = 3.50) were included in all analyses throughout the study. Criteria for participant inclusion were determined prior to data collection according to the study population guidelines approved by the NIH Institutional Review Board as a part of the study protocol (93-M-0170, NCT00001360). All participants gave written informed consent prior to participation in the study, and were compensated monetarily for their time.

2.2. *Stimuli*

Cue stimuli consisted of the written names of 6 personally familiar people (2 family members, 2 friends, 2 coworkers) and 6 personally familiar places (2 home, 2 public, 2 work). The specific people and places included were provided by each participant through completion of a survey prior to the start of the MEG scan. Additionally, participants provided the length of time she/he had known the provided people and places. Participants were instructed to provide only people and places that were highly familiar. For privacy concerns, we do not include a full list of stimuli used. However, this list often included first names and titles such as “mom” and business names frequented by the participant.

2.3. VVIQ

Before the scan, participants completed the Vividness of Visual Imagery Questionnaire (VVIQ) (Marks, 1973). Legal copyright restrictions prevent public archiving of the VVIQ which can be obtained from the copyright holders in the cited references (Marks, 1973). The VVIQ is a 16-item questionnaire in which participants rate how vividly they are able to visualize specified prompts on a 5-point Likert scale (1 = 'No image at all'; 5 = 'Perfectly clear and as vivid as normal vision'), completed once with eyes open and once with eyes closed. Scores were calculated by averaging the sum of eyes-open and eyes-closed ratings.

2.4. Eye tracking

Eye position information was collected using the EyeLink 1000 Plus eye tracking system. Analyses were performed using two channels of the CTF 275 system, which correspond to *x* and *y*-positions of the pupil. Eye tracking control analyses are described in Supplementary Materials A.

2.5. Memory recall task

During the memory recall task, each participant saw two cues taken from the list of people and places they provided, separated by a fixation cross (Fig. 1a). If the first cue was the name of a person, the second cue was the name of a place, and vice versa. All stimuli were presented in the center of the screen in white Arial type against a dark grey background, using PsychoPy software (Peirce, 2007). Each of the cues was presented on the screen for 800 msec, separated by a fixation cross presented for 200 msec. Following the presentation of both cues and a second fixation cross presented for 400 msec, participants were presented with the number 1 or 2, which we refer to throughout the rest of the article as the "retro-cue" (Fig. 1a). The retro-cue was presented for 500 msec and was used to indicate which stimulus should be recalled and visualized following the offset of the retro-cue. The number "1" indicated that the participant should recall and visualize the item corresponding to the first cue presented in that trial, and a "2" indicated that the participant should recall and visualize the item corresponding to the second cue presented. The recall period was the 4000 msec following the offset of the retro-cue, during which a fixation cross was displayed on the screen. Participants were instructed to visualize the specific person or place cued as vividly as possible for 4000 msec, until the words "Get Ready" were presented on the screen, which indicated that the next trial was about to begin. This retro-cue paradigm was used to dissociate responses associated with the perception of the word cues from the representation of the person or place stimulus during the recall period. In order to

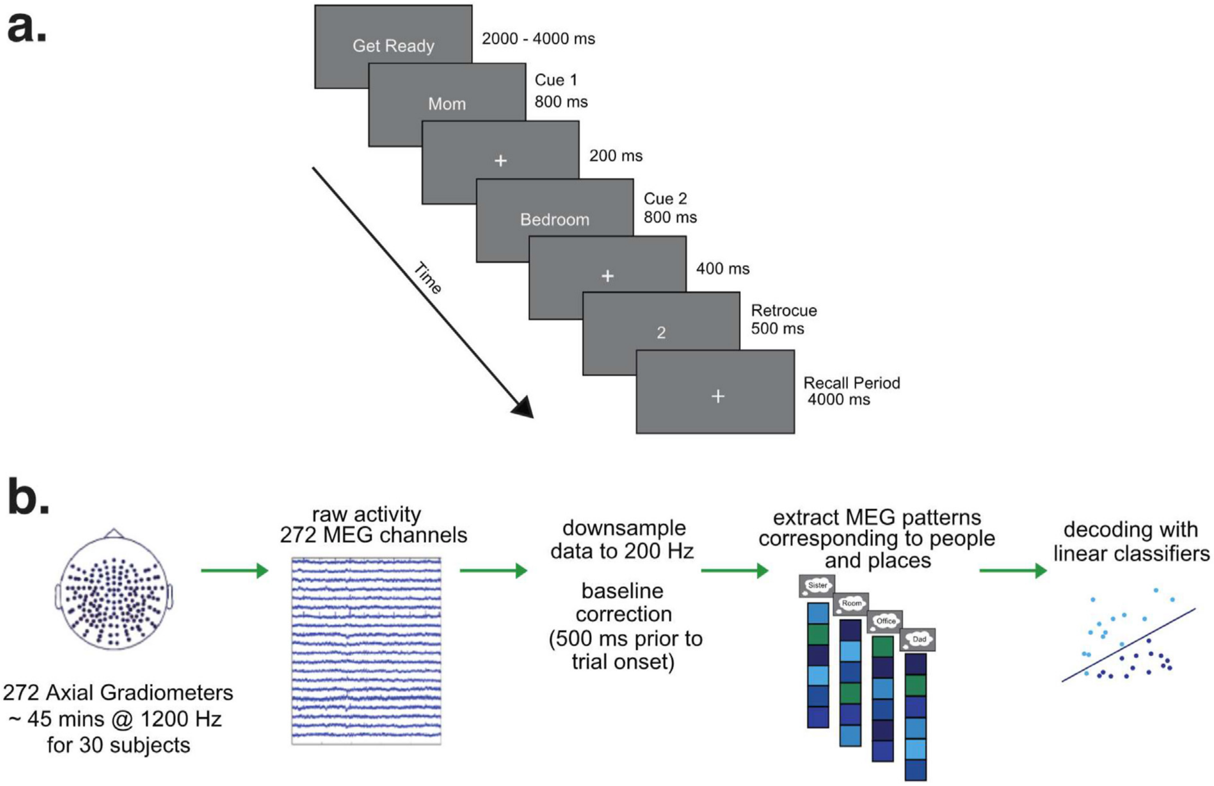


Fig. 1 – MEG cued recall experimental design and analysis pipeline. (a) Trial sequence for one example trial in the cued recall task. The cued stimuli for recall were people and places personally known to each participant. On each trial, the retro-cue "1" or "2" indicated whether the participant should recall and visualize the first or second cue during the subsequent recall period. (b) Schematic of the steps in the multivariate of MEG analysis pipeline used to extract the brain activation patterns across all sensors for every recalled person and place for each participant.

reduce anticipation effects, the "Get Ready" screen was presented for a variable time period, for either 2000, 3000 or 4000 msec, all of which were equally likely. Participants completed 24 of these trials in each run, resulting in runs that were just under 4 min long (232.8 sec). During each run, each cue was presented four times (twice in the first cue period, and twice in the second cue period), and recalled/visualized two times (once when presented in the first cue period and once when presented in the second cue period). There were 8 runs (192 trials) total, and each cue stimulus was seen a total of 32 times and recalled/visualized a total of 16 times. Including set up, scan sessions lasted approximately 40 min.

2.6. *Post-scan questionnaire*

Immediately following the scan, participants completed a questionnaire in which they rated how vividly they were able to visualize each cued item from memory during the MEG scan. The cues were listed in a randomized order and were rated on a 4-point Likert type scale (1 = not vivid at all; 4 = extremely vivid). If the participant could not visualize that stimulus during the scan they were instructed to check a box on the questionnaire. However, all participants rated the vividness of each cued stimulus between 1 and 4, and no one chose to check the optional box.

2.7. *MEG acquisition and preprocessing*

During MEG recordings, participants were seated in an upright position in an electromagnetically shielded MEG chamber. Stimuli were presented using a Panasonic DLP projector (model no. PT-D3500U, Panasonic) located outside of the chamber, which projected stimuli through a series of mirrors onto a back-projection screen in front of the participant. MEG data were continuously recorded at a sampling rate of 1200 Hz with a 275-channel CTF whole-head MEG system (MEG International Services, Ltd., Coquitlam, BC, Canada) with synthetic 3rd gradient filtering automatically applied online during acquisition. No other online filtering was applied. Recordings were available from 272 channels (dead channels: MLF25, MRF43, and MRO13).

We performed minimal preprocessing to keep MEG data in its rawest form (Grootswagers et al., 2017). Data were preprocessed using the FieldTrip (version 2, Oostenveld et al., 2011) toolbox in MATLAB (version 2018b, The Mathworks, Natick, MA). MEG triggers were temporally aligned to the onset of the first cue in each trial presented on the screen using an optical sensor attached to the projection mirror, except in the case of one participant for whom the optical sensor did not record. For this participant, trials were epoched based on a trigger sent by the code at the onset of each stimulus, with an additional lag of 50 samples (41.6 msec). This lag time was determined by taking the average delay of all other participants' recorded data between the trigger sent by the code and the presentation of the stimulus on the screen, as recorded by the optical sensor. To bring all sensor measurements on to the same scale, data were baseline corrected by subtracting the mean activity in each channel from the 500 msec prior to the onset of each trial (Hebart et al., 2018), when no category information was available to participants. Finally, in order to reduce computational load, data were downsampled to 200 Hz. We did not perform any other preprocessing steps or noise rejection in line with current studies using minimal preprocessing for the multivariate analysis of M/EEG data (e.g., Teichmann et al., 2021). The BIDS-formatted raw and preprocessed data (Appelhoff et al., 2019; Niso et al., 2018), and analyses code are available at the following URL: https://osf.io/4wupe/.

2.8. *Multivariate MEG decoding*

All analyses were performed using functions from the CoSMoMVPA toolbox (Oosterhof et al., 2016) with additional custom code written in MATLAB (The Mathworks, Natick, MA). To determine if representations of people and places from memory were distinct from each other, we first conducted a classification analysis. Next, to see if it was possible to differentiate individual stimuli within the people and place categories, we performed a classification analysis on all possible pairs of stimuli. Lastly, to understand how the neural information changed over time, we ran a temporal generalization analysis.

2.8.1. *Classification analysis*

A regularized linear discriminant analysis (LDA) classifier was trained to decode between whole-brain patterns of MEG signal across the 272 sensors at each time point of the trial individually (Fig. 1b). Using a leave-one-run-out cross-validation approach, a classifier was trained to discriminate between separate conditions at different time periods in the trial. Specifically, we used the conditions at three time periods to train the classifiers – the category of cue stimulus presented as the first cue (either "person" or "place"), the number presented in the retro-cue time period (either "1" or "2"), or the category of stimulus recalled and visualized in the recall period (either "person" or "place"). To keep training and testing data independent, all classifiers were trained on single trials in 7 of the 8 runs and tested on the left-out run, resulting in the accuracy at each time point (chance-level 50%). This process was repeated until each of the 8 runs served as the left-out run. The classifier accuracy for all 8 iterations was then averaged to obtain the mean classification accuracy at each time point across the trial. This time-resolved classification was performed for each participant separately and then averaged to find the mean classification accuracy across all participants. To ensure that classification was not influenced by training and testing on the same stimuli, we also performed a 6-fold cross-validation classification scheme, in which we trained on 5 of the 6 possible identities for both people and places and tested on the left-out identity. There was no noticeable difference between cross-validation schemes, and therefore we only show the results of the leave-one-run-out cross-validation approach.

2.9. *Sensor searchlight analysis*

In addition to the multivariate analysis across all sensors, we also ran a sensor-searchlight analysis (Carlson et al., 2019; Collins et al., 2018; Kaiser et al., 2016) to test whether observed effects are primarily driven by specific sensor clusters. We ran the same three analyses as outlined above, testing for information about the cue, retrocue, and the recall category in the signal. This time we used small clusters of nine MEG sensors and projected the effects back onto topographical plots. This analysis allows us to examine whether our effects can be related to distinct spatial distributions of the effect.

2.10. *Pairwise classification*

A classifier was then trained to decode between all pairs of stimuli (chance level 50%). We used a leave-one-run-out approach, performed the classification analysis for each participant separately, and then averaged to find the mean classification accuracy across all participants at every time point.

2.11. *Temporal generalization analysis*

To determine if the representations remained stable across the trial period or if they changed, we performed a temporal generalization analysis (Carlson et al., 2011; King & Dehaene, 2014). Testing whether the representational structure is consistent across the trial allows us to observe if the distinction between people and places transitions as recall occurs, or if the ability to distinguish people from places is stable across the entirety of recall. Regularized LDA classifiers were trained to discriminate between conditions at each individual time point and tested on all other time points across the trial. First, we used this approach to determine whether the representations elicited during the retro-cue period (1 or 2) generalized to other time points in the trial. We then tested the generalization of "person" or "place" recall and visualization information to other time points in the recall period.

2.12. *Statistical analysis*

To assess whether classification accuracy is above chance (alternative hypothesis) or at chance (null hypothesis), we calculated Bayes Factors (Jeffreys, 1935, 1939) at each timepoint. Bayes Factors allow us to directly compare two hypotheses and represent a measure that indicates how plausible each hypothesis is given the data (e.g., Ly et al., 2016; Dienes, 2011, 2014, 2016; Keysers et al., 2020; Morey et al., 2016; Wagenmakers et al., 2018). We used functions of the Bayes Factor R package (Morey et al., 2015) implemented in MATLAB (Teichmann et al., 2021) to run Bayesian *t*-tests at each timepoint, testing whether the data is more consistent with the alternative hypothesis (i.e., above chance decoding) or the null hypothesis (i.e., at chance decoding). We used a half-Cauchy prior with default, medium width of .707. We adjusted the prior range of the alternative hypothesis to .5 to infinity to allow for small effects under the alternative hypothesis (Rouder et al., 2009). This was done to account for potential differences between observed and theoretical chance decoding (cf. Teichmann et al., 2021). Bayes Factors that are larger than 1 represent evidence for above chance decoding, whereas Bayes Factors that are smaller than 1 indicate evidence for at chance decoding. The strength of evidence is directly interpretable (e.g., a Bayes Factor of 10 indicates that the alternative hypothesis is 10 times more likely than the null hypothesis). We did not threshold the Bayes Factors and are interpreting the amount of evidence at face value. No part of the study procedures or analyses was pre-registered prior to the research being conducted.

3. Results

Our main goal was to investigate the temporal dynamics underlying self-generated recall of personally familiar people and places. To do this, we measured the brain activation patterns evoked during cued recall with whole-brain MEG. First, we confirmed that participants were able to vividly recall the stimuli during the task in the scanner as instructed by examining their responses on the pre-scan VVIQ and the post-scan recall vividness questionnaire. Previous investigations of visual imagery have used VVIQ scores above 40 as a conservative threshold for good visual imagery ability (Bainbridge et al., 2021). Eyes-open and eyes-closed VVIQ scores ranged from 40.5 to 76 out of a maximum of 80 ($M = 60.9$, $SD = 8.79$) indicating that all participants fell within the expected range of good visual imagery ability. Similarly, the mean recall vividness of the experimental stimuli was 3.46 ($SD = .69$) out of a maximum of 4, confirming that participants were able to successfully visualize the subject of their personalized recall prompts during the MEG experiment. Places were reported as significantly more vivid during recall when compared to people (places: $M = 3.57$, $SD = .68$; people: $M = 3.34$, $SD = .69$; $t\ (30) = -2.17$, $p = .0009$; $d = .33$). Overall, these results suggest that participants were able to vividly recall personally familiar people and places during the MEG experiment as instructed.

Our first aim was to determine whether self-generated representations of familiar people and places contained category-specific information that could be decoded from whole-brain MEG signals. To do this, for each participant and time point, we trained an LDA classifier to discriminate between the patterns of neural signals evoked by recalling and visualizing their personally familiar "people" versus "places." This produced a plot showing when category-selective information could be decoded from the representation (Fig. 2a). As expected, classifier performance was at chance in the early stages of the trial when the cues and retro-cue were presented, as the participant was not yet aware of which stimulus to recall and visualize. During the recall period, differentiation of people versus places emerged ~1000 msec after retro-cue onset, and was then sustained for the remainder of the 4 sec recall period. In a cluster from ~1500 to 3000 msec there was only support for above chance and not at-chance decoding. Notably, there was not a discrete peak in classifier performance during the recall period as is typically found for discriminating visual stimuli (Bankson et al., 2018; Contini et al., 2021; Hebart et al., 2018; Wardle et al., 2020). Instead, maximal decoding performance was sustained throughout several seconds of the recall period. Additionally, control analyses described in Supplementary Material A indicate little evidence that eye movements impacted decoding accuracy. These results show that distinct category-specific representations of recalled personally familiar items are relatively slow

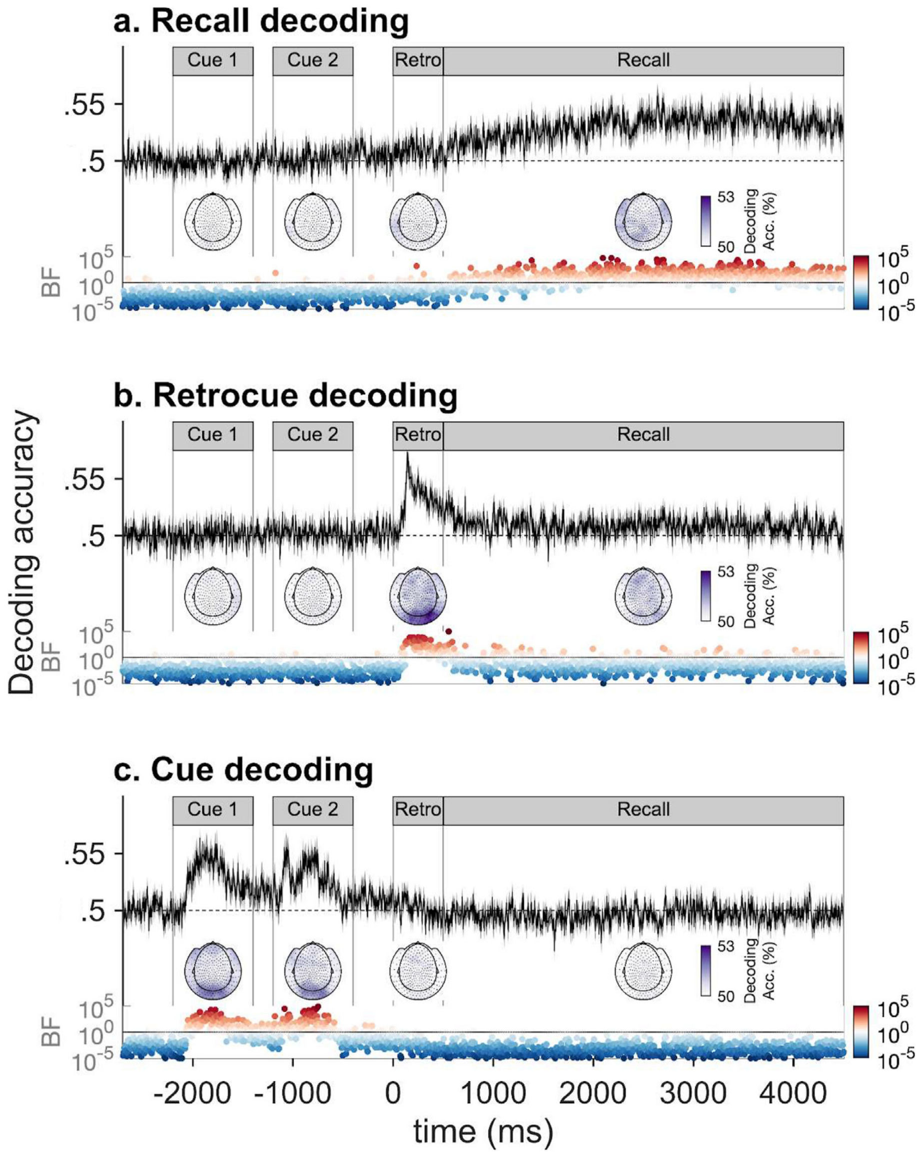


Fig. 2 – Mean decoding accuracy from time-varying MEG activation patterns across the entire trial duration for decoding (a) the category of the personally familiar item (people vs places) visualized during the recall period, (b) the identity of the presented retro-cue as the written number "1" or "2," and (c) the category (person or place) of the two written cues. In all plots, colored dots beneath the time course indicate Bayes Factors (log scale) for each timepoint and the shaded area represents standard error of the mean. Inset scalp topographies show multivariate searchlight decoding results in sensor space (radius = 9) averaged across all timepoints in the four time periods of interest (cue 1, cue 2, retrocue, and recall). The sensor searchlight analyses for the cue and retrocue decoding indicate that these effects are primarily driven by posterior sensors. For the recall analysis, we do not find a particular sensor cluster drove the effect.

to develop, yet once formed they are maintained even over several seconds of active free recall.

For comparison with the time course of recall decoding, we also decoded the identity of the retro-cue (Fig. 2b) and the category corresponding to the two cued stimuli on each trial (Fig. 2c). Above-chance decoding of the identity of the retro-cue as a "1" or a "2" was mostly confined to the retro-cue period, beginning ~100 msec after onset of the retro-cue on the screen, with a distinct peak at 145 msec (Fig. 2b). Following this peak, decoding accuracy for the retro-cue rapidly declined, returning to chance around the time of the onset of the recall period. Similarly, category decoding of "person" vs "place" for the individualized word cues was confined to the corresponding cue periods early in the experimental trial when they were displayed on the screen (Fig. 2c). As expected, category decoding of the word cues was not possible in the recall period because of our counterbalanced design in which the category information cued for recall was presented in each cue period exactly 50% of the time. Together, these control analyses show that, as expected, the word cues and numeric retro-cue were only decodable from the MEG activation patterns during the corresponding periods of the experimental trial in which they were presented. In both cases, the onset of decoding for these visual cues was relatively rapid with a clear peak, in contrast to the recall decoding which exhibited a gradual onset with sustained maximal decoding for several seconds.

The above analyses demonstrate above-chance decoding of recalled visualizations of personally familiar people and places at the category level. Next, we explored the distinctiveness of the recalled representations for the individual stimuli within each category. To achieve this, we repeated the decoding analysis at the exemplar level by training a separate linear classifier for each pair of stimuli (e.g., "Ellie" and "Metro Station"). Since stimuli were individualized for each participant, we grouped them as "people" or "places" and plotted each within-category or between-category decoding time course separately (Fig. 3). As expected, decoding for between-category pairs (people vs places) was similar to the category-level decoding analysis in Fig. 2a, with a gradual onset of decoding that was sustained over the recall period (Fig. 3a). In contrast, there was only spotty, inconsistent evidence for above-chance decoding for within-category pairs (i.e., between two places or between two people, Fig. 3b and c).

The lack of strong evidence for above-chance decoding for within-category pairs suggests that the representations of individually recalled familiar people (and places) as reflected in the MEG response are highly similar to each other. To examine this further, we constructed 12 × 12 pairwise decoding matrices at the exemplar level for four 1 sec time periods during recall (Fig. 3d). This visualization confirms that there is high similarity between exemplars of the same category, and that similarity is greater than between exemplars of different categories, which is particularly evident after the first second of the recall period, once the representations have stabilized.

Given that the recalled representations of familiar people versus places were maintained for several seconds after their formation (Figs. 2a and 3a), we were interested in how well these representations generalized over time. One possibility for the sustained decoding during the recall period is that the representations of recalled people and places are relatively stable. Another possibility is that the representations rapidly evolve during active recall but maintain their distinctiveness from each other at the category level. We performed a temporal generalization analysis (training and testing classifiers on MEG data from different time points during the recall period) to distinguish between these possibilities (Fig. 4). Strikingly, there was substantial temporal generalization for decoding familiar people versus places during the recall period, which extended over the majority of the 4 sec (Fig. 4a). This suggests that the MEG activation patterns corresponding to the recalled representations were highly stable, as a classifier trained and tested on MEG data from different time points during the recall period could still successfully distinguish between whether the participant was recalling a familiar person or a familiar place. In contrast, there was limited temporal generalization for decoding the identity of the retro-cue as a "1" or a "2" (Fig. 4b), as might be expected. These results demonstrate that the recall and visualization of self-generated representations involves a period of evolving processing followed by a period of high generalizability.

4. Discussion

Here, we investigated the temporal dynamics of recalled representations of personally familiar people and places using multivariate pattern analysis of whole-brain MEG. We found that above-chance decoding of the category of the recalled item (as a person or a place) took several hundred milliseconds to develop, with category information emerging in the neural signal approximately 1000 ms after the onset of the retro-cue. Notably, these representations were highly stable once developed, with sustained decoding for the remainder of the 4 sec recall period. Additionally, there was temporal generalization of the representations across the majority of the recall period, indicating that these representations were both stable and sustained rather than dynamic and rapidly evolving. Overall, these results demonstrate that the recall of highly familiar people and places is a complex process that takes time to develop. However, once distinct representations at the category level are formed, they are highly robust and sustained even during several seconds of active recall.

The relatively slow latency of recall decoding we observe here with MEG is consistent with the sequence of events thought to underlie cued recall (Staresina & Wimber, 2019), namely that, after pattern completion in the hippocampus, the corresponding signal is projected to visual and parietal cortex ~500–1500 msec after cue presentation to facilitate memory reinstatement. In contrast, the decoding of visual stimuli from whole-brain MEG generally has a much shorter latency, consistent with fast processing of visual input (e.g., Bankson et al., 2018; Contini et al., 2021; Hebart et al., 2018; Jafarpour et al., 2014; Wardle et al., 2020).

Interestingly, much faster latencies than observed in the current study (~500 msec) have been reported for decoding internal representations from MEG in the context of visual imagery (e.g., Dijkstra et al., 2018) and cued associative memory (Jafarpour et al., 2014). A key difference is that these faster latencies occur in an experimental design which is based on comparing perception versus imagery, and participants are forming mental imagery of experimental stimuli that had been perceived moments before. This form of visual recall would require the participants to retrieve and visualize a specific image from working memory, similar perhaps to the notion of "refreshing" the visual image (Johnson et al., 2007; Yi et al., 2008).

In contrast, our free recall paradigm required participants to actively generate representations of personally familiar people and places in the absence of any immediate visual stimuli reflecting those items. This is a more complex cognitive task which likely engages additional neural mechanisms outside of those serving visual working memory. Therefore, it is unsurprising that we found a longer latency before representations distinct enough to support category decoding were formed. Additionally, it is possible that variable representations across participants and instances of recall also contributed to the relatively slow onset of decoding in the recall period. We note that in our paradigm a relatively long recall period (4 sec) was provided to participants to generate internal representations of the cued stimulus. It is possible that representations could develop more rapidly if participants were

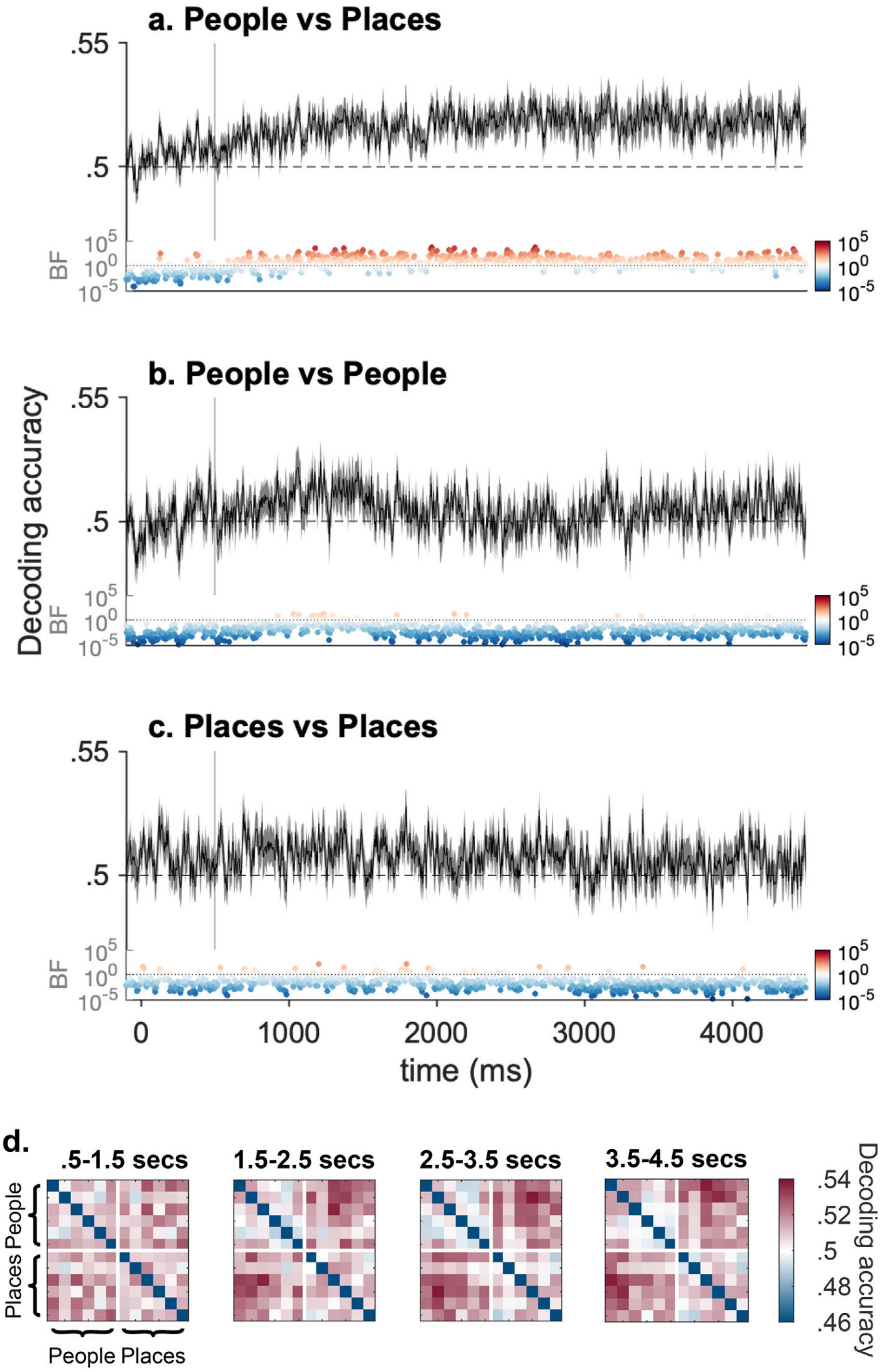
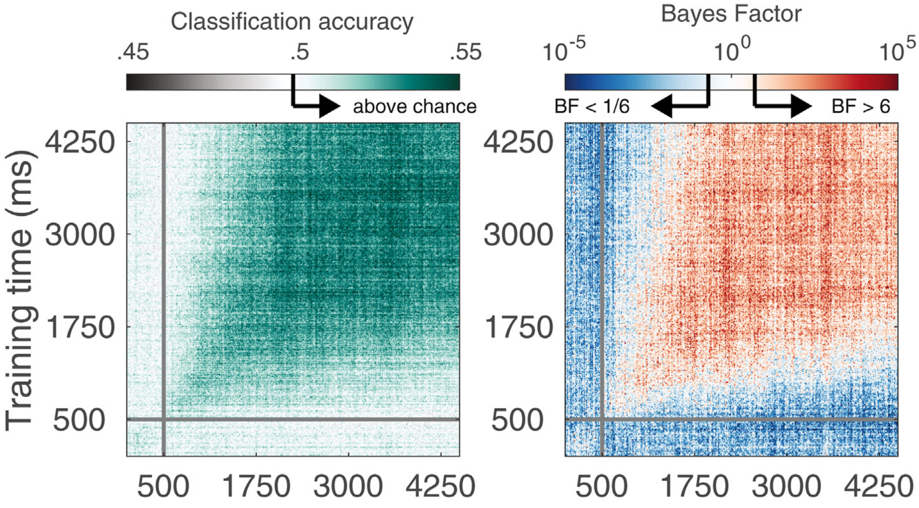
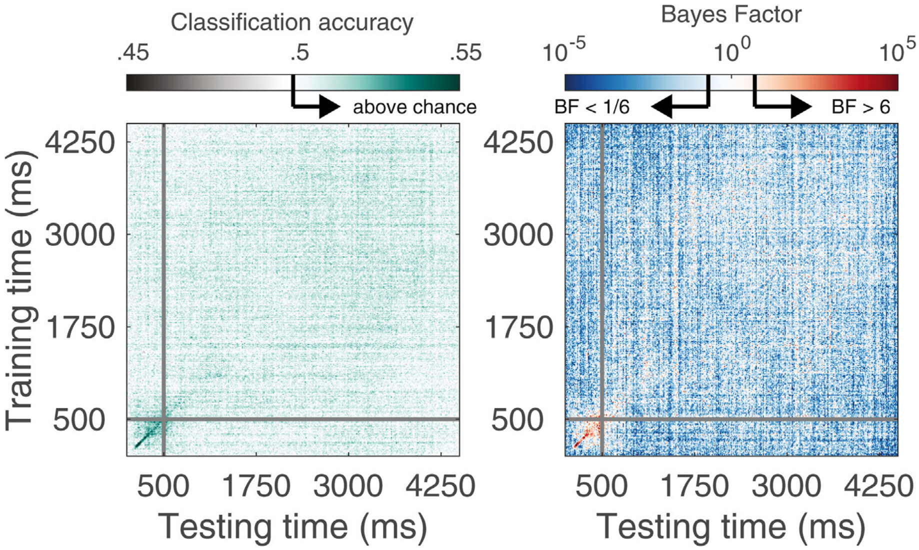


Fig. 3 – Mean pairwise decoding from time-varying MEG activation patterns across the retro-cue and recall period for decoding (a) between-category pairs (people vs places) of the personally familiar item visualized during the recall period, (b) pairs of exemplars in which both stimuli were familiar people, and (c) pairs of exemplars in which both stimuli were familiar places. Colored dots beneath these time courses indicate Bayes Factors (log scale) at each timepoint and the shaded area represents standard error of the mean. (d) Mean pairwise decoding accuracies averaged within 1 sec blocks during the 4 sec recall period. Warm colors indicate higher decoding accuracy between exemplar pairs.

given a more constrained recall period. However, we would still expect the generation of representations from memory to have a longer latency than for recall of recently viewed items in visual working memory if given the same recall period. Finally, although is not possible to entirely rule out some contribution from short-term memory in our paradigm as participants recalled the same items multiple times and may have held such representations in memory during the cue period as the experiment progressed, it is clear that there are important differences in the cognitive processes involved in



a. Recall Generalization



b. Retrocue Generalization

Fig. 4 – Temporal generalization for decoding (a) the category of the recalled personally familiar item (person or place) and (b) the identity of the retro-cue as a written "1" or a "2" from MEG activation patterns. Left panels show decoding accuracies with green hue indicating above chance classification accuracies. Right panels show the Bayes Factors for the decoding time-generalization analyses. Warm colors indicate support for the alternative hypothesis (above chance decoding) and blue colors indicate support for the null hypothesis (at chance decoding). The points on the diagonal represent training and testing the classifier from MEG data at the same time point within the trial; off-diagonal points represent training and testing on different time points (i.e., require generalization across time).

picture recall versus the recall of personally relevant people and places.

Previously, an fMRI study examined the cortical locus of self-generated memory of people and places and found an alternating pattern of selectivity in the medial parietal area for the recall of people and places (Silson et al., 2019). This was the case for both famous and personally familiar faces and places, suggesting that self-generated recall of people and places arises from spatially distinct, yet neighboring, regions of the brain. Additionally, semantic information about famous people and places was reported to be represented in distinct anterior temporal (people) and posterior medial (places) networks, as well as in discrete clusters in the hippocampus (Morton et al., 2021). Our results complement these findings by revealing the temporal dynamics of recalled representations of personally familiar people and places. We reveal a time course for when representations of familiar people and places become reliably distinct and demonstrate that these representations can be sustained stably over time.

The majority of studies investigating high-level visual processing use visual stimuli that are unfamiliar to the participant or rely on famous stimuli (e.g., Tom Cruise, Eiffel Tower) with which the participants are presumed to have experience. Recently, there has been some evidence from fMRI that the representation of visual objects that are personally familiar differs from that for unfamiliar objects, and that personally familiar objects may drive some individual differences in the structure of brain representations (Charest et al., 2014). Similarly, Silson et al. (2019) found stronger activation of areas in the medial parietal area for personally familiar compared with famous people and places. This effect of familiarity is likely to be much stronger for memory-related processes like recall in comparison to more perceptual processes. Together, these results suggest a complex interplay between the role of personal experience and individual differences in the neural processes involved in recall.

While our findings reveal the temporal dynamics of recall, the nature of the underlying representations is unclear. The recall of personally familiar items is likely to be incredibly rich and it is possible that the content (e.g., in terms of emotional and semantic content, visualized features, etc.) and vividness of these internal representations are variable both across individuals and across recall instances. However, while it is possible that participants recalled different details about the same person or place across trials in our experimental paradigm, our results indicate that even if this was the case, there remains a shared representation across these trials that is robust enough to support category-level decoding of recalled personally familiar people and places.

Additionally, our current paradigm may not have been sufficiently powered to detect exemplar-level differences within the same categories of these internal representations. However, to our knowledge, within-category exemplar-level differences in brain activation patterns for recalled visual imagery have not previously been reported, and at least one EEG study did not find any decoding of mental imagery (Shatek et al., 2019). In order to gain a better understanding of the underlying nature of these self-generated representations constructed from memory as well as to increase the likelihood of identifying exemplar-level differences, it may be valuable to give more detailed instructions as to how participants should recall particular stimuli. Future studies may specify whether recalled representations should be static vs dynamic, focus on visual features vs semantic information, etc. to develop a more complete understanding of this complex process. Additionally, future work may seek to measure variability in representation content and vividness across trials using measures such as participant self-report or pupil size, which has been shown to change as a function of imagery vividness (Kay et al., 2022).

In sum, our data show that the representations of familiar people and places can be decoded from whole-brain activation patterns measured with MEG. The relatively slow onset of decoding following conscious initiation of active recall suggests that a complex and multifaceted neural mechanism is engaged in this process. However, once formed, participants are reliably able to keep these representations active and coherent for a sustained period of time. The generalizability of the category-specific activation patterns generated during free recall over time points to a stable representation rather than one that is dynamic and evolving. Taken together, our results begin to disentangle the complexities of personally driven memory and illustrate the stable and sustained nature of these representations during recall.

CRediT author statement

Anna Corriveau & Alexis Kidder: Conceptualization, Methodology, Software, Formal Analysis, Investigation, Writing – Original Draft, Visualization; **Lina Teichmann**: Validation, Formal Analysis, Writing – Review & Editing, Visualization; **Susan G. Wardle**: Conceptualization, Validation, Investigation, Writing – Review & Editing; **Chris I. Baker**: Conceptualization, Methodology, Resources, Writing – Review & Editing; Supervision, Funding Acquisition.

AC and AK contributed equally to the study with shared first authorship. AC, AK, CB and SW designed the research. AC and AK collected the data, AC, AK, SW and LT analyzed the data, AC and AK wrote the manuscript, AC, AK, SW, LT and CB edited the manuscript.

Declaration of competing interest

The authors have declared there are no conflicts of interest in relation to the subject of this study.

Open practices

The study in this article earned an Open Data badge for transparent practices. Data for the study is available at https://osf.io/4wupe/.

Data availability

Preprocessed data is available on OSF (link:https://osf.io/4wupe/).

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Supplementary data

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