Investigating the dual processes underlying human recognition memory

Thesis by

Wenying Zhu

In Partial Fulfillment of the Requirements for

the degree of

Master of Science

CALIFORNIA INSTITUTE OF TECHNOLOGY

Pasadena, California

2024

(Submitted December 12th, 2023)

© 2024

Wenying Zhu
ORCID: 0000-0003-3103-9250

ACKNOWLEDGEMENTS

I would like to thank Professor Ralph Adolphs and Professor Ueli Rutishauser for their mentorship over the past years. I would like to thank them for the freedom they allowed me to explore my topics of interest, and the detailed guidance at each step as the research project progressed. I would like to thank Ueli for the meticulous advice he gave during the formulation of the projects, and Ralph for the trust he gave when propelling the projects onward.

I would like to thank the patients at Cedars Sinai Medical Center for participating in the task that comprises the single-unit part of this thesis. I would like to thank them for their time and effort that they were willing to commit despite the stressful plight they were often in. I would also like to thank the doctors, nurses, technicians and staff of the Cedars Sinai Medical Center for their work and collaboration.

I would like to thank people from both the Adolphs lab and the Rutishauser lab for their support and input to the thesis. I would like to thank Yue Xu, David Kahn and Mike Tyszka especially for their help in conceiving and data collection of the face repetition memory part of the thesis.

I would like to thank my undergraduate mentors, Ryan Brady, Professor Robert Hampton and Professor Dieter Jaeger, for introducing me to the topics of memory study and computational neuroscience.

I would like to thank my parents, Tong Zeng and Jin Zhu, for their support through my toughest time. Last but not least, I would like to thank my grandmother, Xiangyun Wang, to whom I would like to dedicate the thesis.

ABSTRACT

This thesis examines two aspects of human recognition memory by using two separate behavioral paradigms. Given the dual process hypothesis of recognition memory, the first chapter investigates the correlation between encoding and retrieval of recognition and source memory for images by using a cued retrieval paradigm. Participants were shown images in a particular judgment task (source context) and later asked to retrieve them in a cued retrieval task. Recording from the human brain, I found separate cell populations to be responsive to the source context during the encoding and recognition stages of the task, suggesting a lack of single-cell level reactivation during source retrieval. In the second chapter, I examined how recognition memory signals change over time using repeated longitudinal behavioral testing in an fMRI study. Through repetitive presentation and memory tests over a period of three months, face stimuli were introduced to three participants. The behavioral outcome of the task showed that as frequency of exposure to specific faces increases, the memory performance and judged confidence increases correspondingly, supporting the hypothesis of a continuous familiarity signal.

TABLE OF CONTENTS

LIST OF ILLUSTRATIONS AND/OR TABLES

Chapter 1

GENERAL INTRODUCTION

Recognition memory is the cognitive ability to re-identify previously encountered events, individuals, or objects. The processes underpinning recognition memory have long been the subject of ongoing debate (Squire et al., 2007; Wais et al., 2006), with the dual process model being one of the major frameworks that conceptualize our present understanding of how human episodic memory works (Yonelinas, 2002; Wixted, 2007).

The dual process model posits that recognition memory is comprised of two distinct processes acting in parallel: familiarity and recollection. In this framework, familiarity involves a feeling that an item has been seen before, often assessed in tasks that involve rapid new/old judgments, is relatively context-independent, and is associated with bottom-up attention. In contrast, recollection is a slower process involving the deliberate retrieval of specific details and contextual information associated with a familiar stimulus. Both familiarity and recollection often come into play in recognition memory, but the processes can be dissociated to some extent by their distinct properties.

The precise mechanisms underlying familiarity and recollection have been a topic of debate. Familiarity is often modeled using a signal detection model (Yonelinas, 1994), in which it is represented as a continuous memory strength signal. Conversely, theories on the dual process model vary in their characterization of recollection as either an all-or-none memory retrieval event or a continuous signal akin to familiarity (Wixted, 2007; Atkinson & Juola, 1974; Yonelinas, 2002).

Physiological studies have allowed researchers to examine these two processes separately, but the extent of their correlation remains a subject of discussion. Timed-response paradigms have shown that individuals tend to maintain high accuracy in new/old judgments but exhibit diminished accuracy in context retrieval when a rapid response is required, suggesting that recollection is a slower process than familiarity (Grunlund & Ratcliff, 1989; Yonelinas &

Jacoby, 1994; Atkinson & Juola, 1974). Similarly, extending the length of a study list appears to selectively interfere with conscious recollection while leaving familiarity intact, further indicating the independent nature of these processes (Yonelinas & Jacoby, 1994). However, it remains uncertain whether recollection necessarily follows the onset of familiarity and whether it is only engaged when a familiarity signal is present to begin with. Thus, while there are a number of distinguishing psychometric properties for familiarity and recollection, the relationship between familiarity and recollection remain debated and await further clear evidence.

This thesis seeks to investigate the structure of recognition memory using two distinct behavioral paradigms and utilizing rare single-neuron recordings from the human brain. The first part of the thesis employs an encoding/retrieval paradigm together with single-neuron recordings to explore whether recollection of associated context is encoded separately from familiarity of a previously seen stimulus. If a separate recollection process exists at the psychological level, one might expect that the recollection process relies on a reactivation of the memory trace that could be evident at single-unit level. The second part of the thesis utilizes a repetitive, longitudinal new/old reporting paradigm to assess the rate of decay of memory strength, primarily influenced by familiarity, when systematically varying the repetition frequency of stimuli presented. Notably, data from the first part is complemented with simultaneous single-unit recordings, while data from the second part is paired with fMRI recordings, enabling future exploration of the neural correlates underlying the behavioral responses. This thesis describes the data acquired from the behavioral data in both studies, and from the single-unit recordings in the first study. The fMRI data are not presented here.

Both behavioral tasks use faces as stimuli for several reasons. Firstly, recognizing familiar faces is a ubiquitous memory process in daily life. In support of this, one of the most famous analogies illustrating the dual model of memory, the "Butcher in the Bus" example (Yovel and Paller, 2004), involves face recognition. Secondly, regions of the brain known as "face patches" have been identified in both non-human primates and humans through fMRI data

(Kanwisher et al., 1997; Landi and Freiwald, 2017), supporting a large literature that demonstrates neural specializations for face processing, and making faces a particularly attractive type of stimulus since they are known to elicit category-selective responses in many regions of the brain. One of these regions is the amygdala, in which face-selective responses have been studied extensively (Rutishauser et al., 2015). Single-unit studies in both humans and macaques have identified cells with a strong preference for faces over other visual stimuli (Quiroga, 2012; Quiroga et al., 2023; Desimone et al., 1984; She et al., 2021). Moreover, there are regions in the primate brain that link face perception to memory for unique individuals (Landi et al., 2021). Such evidence suggests that faces represent a unique and highly preserved category of stimuli, with both familiarity and recollection likely playing significant roles, making them an ideal choice for controlled memorability studies.

Chapter 2

SINGLE-UNIT CORRELATES OF RECOGNITION MEMORY FOR FACES

2.1 Introduction

Recognition memory encompasses not only the ability to identify familiar items, but also the retrieval of contextual information associated with those items. The primary goal of this chapter is to explore the neural underpinnings of recollection and its relationship with the familiarity process. Specifically, the current chapter examines the existence of reactivation, a potential mechanism supporting memory retrieval.

Evidence from fMRI data suggests that reactivation of representations present at encoding during retrieval underlies the recollection process (Gordon et al., 2014; Khan et al., 2004; Johnson et al., 2009). By using a cued-retrieval paradigm where subjects are asked to report the processing mode associated with target words, reinstatement effects were observed in regions sensitive to the encoding task (Kahn et al., 2004). Similarly, when multi-voxel pattern analysis was applied to recollection of different memory judgments, above-chance transfer decoding performance was observed when the classifier was trained on encoding data, and then used on data from the recognition stage (Johnson et al., 2009).

Convergent evidence of reactivation during memory retrieval has also been found on the cellular level in the rodent literature (Josselyn and Tonegawa, 2020; Tingley and Peyrache, 2020). Observations of early genetic expression in mice have revealed that cell ensembles represent engrams for specific memories through reactivation during memory retrieval tests. Manipulating the activity of these cells optogenetically has demonstrated the ability to induce memory retrieval and dysfunction (Josselyn and Tonegawa, 2020). Electrophysiological recordings further support these findings, showing replay and reactivation of cell firing sequences after the encoding stage. The disruption of these replay sequences similarly impairs later memory retrieval, suggesting a role for replay in consolidation (Tingley and Peyrache, 2020; Wilson and Mcnaughton, 1994; Lee and Wilson, 2002).

To bridge the gap between these findings and human neural activity, we took advantage of the unique opportunity to record data from epilepsy patients undergoing electrophysiological monitoring. Previous studies have identified cells that exhibit selectivity for new/old judgments (Rutishauser et al., 2008) and the task context presented (Minxha et al., 2018) from single cell recordings in epilepsy patients. Our next step was to explore whether recollection of the task type at the single-cell level exhibits similar reactivation patterns as observed in fMRI and rodent studies.

To commence this investigation, we first established the validity of a cued-retrieval task for both new/old and source memory in healthy subjects recruited from Amazon Mechanical Turk (MTurk). During the encoding phase, participants encountered 72 faces presented twice in blocks of 3, 6 or 9 trials, with each block associated with a distinct judgment task (cf. Figure 2.1, all faces were unfamiliar to begin with). Memory retrieval took place five minutes later, during which participants were presented with 36 novel faces and the 72 previously encoded faces as retrieval cues. In the recognition stage, participants were tasked with determining whether each face was new or old and, in the case of faces deemed old, specifying the associated judgment task, which was defined as the source context for each face exhibited during the encoding stage.

Upon confirming that MTurk participants could perform this task well, we extended our investigation to include nine epilepsy patients undergoing monitoring. Paired with behavioral testing, single-unit recordings enabled us to identify cells with selectivity for the source context during either encoding stage (encoding task-selective cells, abbreviated as encoding TS cells) or during the recognition stage (recognition TS cells). We were also able to identify cells selective to the novelty of the faces during recognition (memory selective cells, abbreviated as MS cells) across multiple brain regions. Interestingly, we observed limited overlap between encoding TS and recognition TS cells. This observation suggests that source memory retrieval may not involve an exact replay of neural activity at the single-cell level in human patients.

In summary, our approach encompasses both behavioral paradigm design and single unit recording in epilepsy patients undergoing intracranial monitoring. By using a cued-retrieval

task, we leveraged single-unit recordings from the medial temporal lobe (MTL), the medial Frontal cortex (MFC), and posterior temporal lobe (PT) in human patients to show that familiarity and source memory appear to rely on distinct processes.

2.2 Methods and Results

Stimulus Selection

Images were selected from the FFHQ face data set, a high-quality image dataset of human faces crawled from Flickr (Karras et al., 2019). Manual screening was applied to the faces. Faces of any famous people were excluded. Faces that showed exaggerated facial expressions, excessive facial makeup or looked artificial were excluded. Faces with glasses were also excluded. Backgrounds of the images were then removed using semantic segmentation (Long et al., 2014).

Three versions of face sets were prepared, two of which were used for the current nine patients (Table 2.1). For each version, the gender of the faces used was balanced, both in total and in terms of associated task type and new/old.

Behavioral: MTurk Testing

Prior to administering the cued recall task to patients, we conducted a preliminary behavioral assessment with a sample of 15 participants recruited through MTurk. The primary objective of this phase was to evaluate the feasibility of the task. Each participant engaged with a version of the task implemented with JSpsych (Leeuw et al., 2023) consisting of two key components: the face encoding period and the retrieval period.

In the face encoding period, participants encountered each face twice. This presentation was organized in a pseudo-random sequence, ensuring that the second exposure of each face occurred only after the completion of the initial presentation of all 72 faces. Participants were tasked with making judgments about each face, specifically assessing either its talkativeness or roundness. The trials involving the same judgment type were grouped together, with sequences of 3, 6, or 9 faces. Participants were provided with a reminder before the start of

each block of the trial, indicating the type of judgment required. Participants rated their judgments on a scale of one to five. Notably, each face was associated with only one type of judgment, even though it was presented twice.

Five minutes after completing the encoding judgments, participants transitioned to the retrieval phase. In this stage, the 72 original faces were interspersed with a set of 36 entirely new faces. Participants were tasked with determining whether each face presented in the retrieval phase was old (previously encountered) or new (unfamiliar). Additionally, they were asked to provide their level of confidence using a three-tiered confidence scale. If participants indicated that a face was old, they were subsequently prompted to specify whether the face had originally been associated with the talkativeness task or the roundness task.

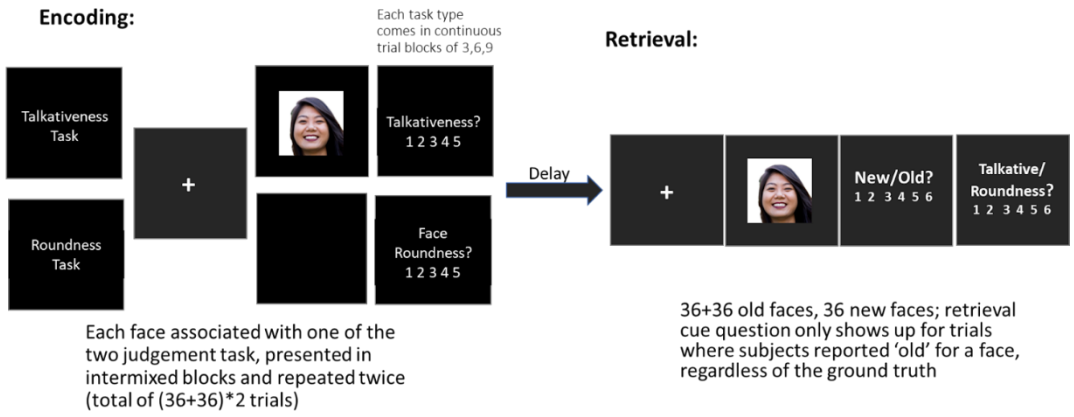

Figure 2.1 Task design of the cued retrieval paradigm used for both MTurk subjects and epilepsy patients undergoing intracranial monitoring

Behavioral results from the MTurk subjects showed an above chance performance of both new/old (one sample t-test, p=3.3e-17; average AUC of 0.95±0.035; Figure 2.2a) judgment and task type recollection (one sample t-test, p=1.80e-10; average AUC of 0.84±0.082; Figure 2.2c). Notably, new/old confidence ratings of correctly recognized new faces and correctly recognized old faces were significantly higher than those for faces with incorrect new/old reporting (Figure 2.3b; two sample t-test, p=0.0029 for old faces; p = 1.1e-7 for new faces), indicating a level of meta-cognition (insight) for the quality of the memory of the faces. Similarly, among correctly recognized faces, task retrieval confidence ratings for

correctly retrieved trials were also significantly higher than those for incorrect trials, indicating meta-cognition for memory of task type contexts (figure 2.3c, two sample t-test, p = 0.0048). Additionally, we found a correlation between the confidence reports for memory itself (the new/old task) and for context (task retrieval; Pearson correlation r=0.69, p=4.0e-5), such that when confidence was high in the new/old task, it was also high in the context task. (figure 2.3d; two sample t-test p=4.0e-5).

When comparing the two source context task types, talkativeness judgment and face roundness judgment, there was no bias shown towards one task over another in terms of recollection accuracy (AUC of 0.84 ± 0.082 and 0.84 ± 0.080, two sample t-test, p= 0.95; Figure 2.2d). Nevertheless, there was a small but significant bias in the ratio of choices, indicating that the MTurk subjects tended to choose talkativeness judgment more than the face roundness judgment (percentage of 53% and 47%, two sample t-test, p = 0.0058; Figure 2.3a).

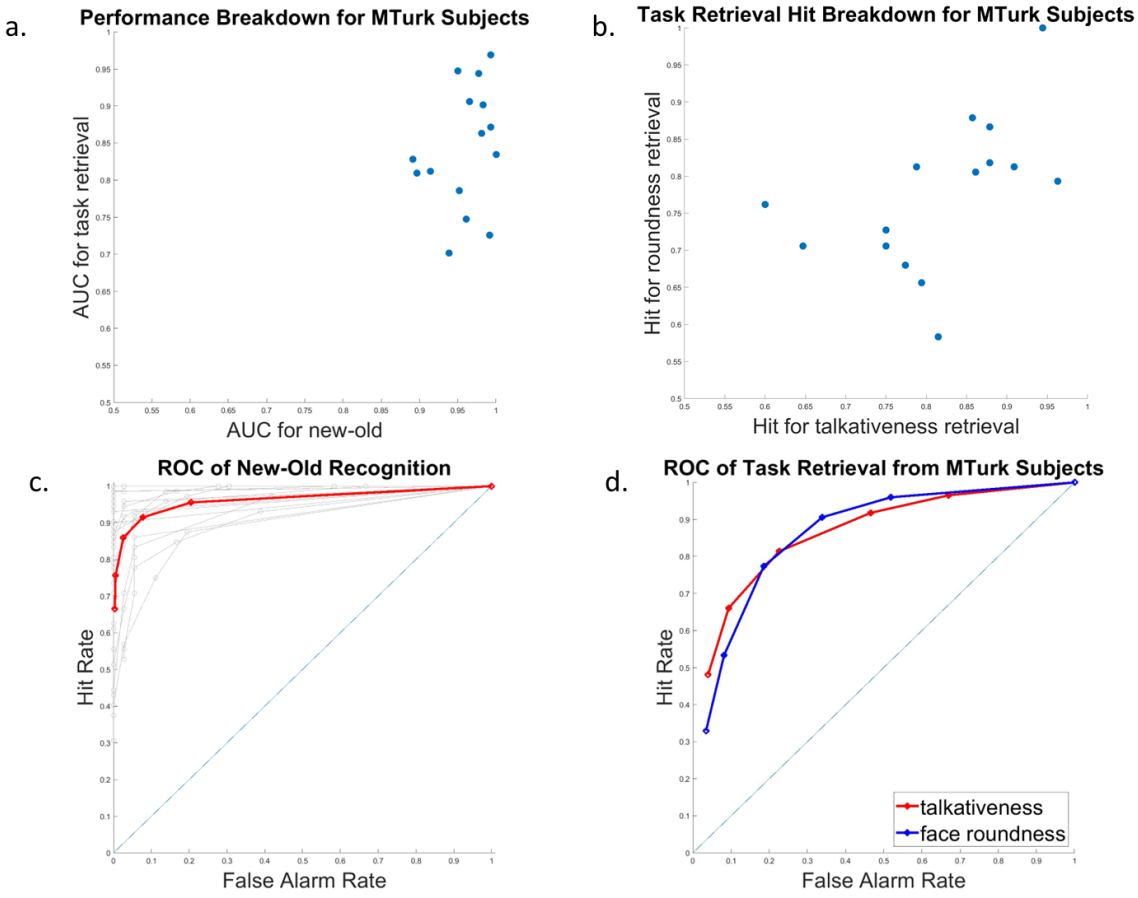

Figure 2.2 Receiver Operating Characteristics (ROC) and Area under the Curve (AUC) for MTurk subjects. a) AUC of new/old recognition and task retrieval performance for MTurk subjects. Each data point represents the performance outcome of one participant. b) Hit rate for correct retrieval of talkativeness judgment versus roundness judgment. Each data point represents the performance outcome of one participant. c) ROC for new/old recognition of MTurk participants. d) ROC for task retrieval for MTurk participants.

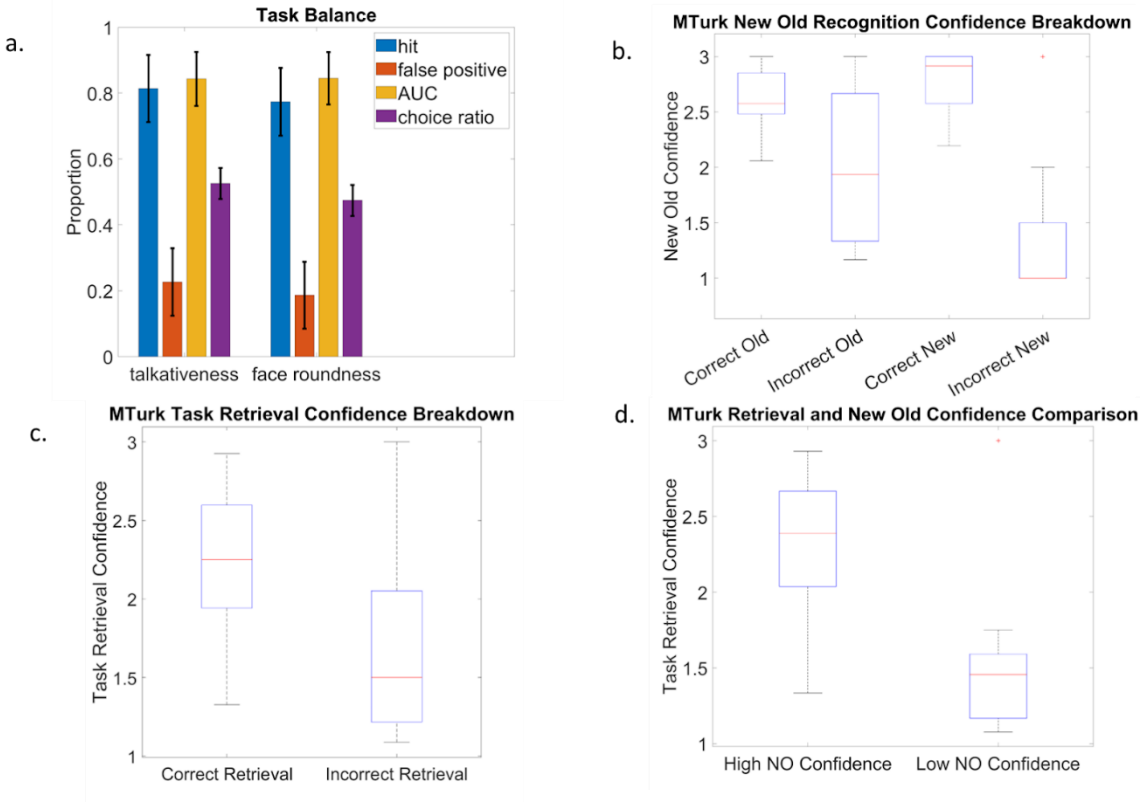

Figure 2.3 Task balance and confidence reporting for MTurk subjects. a) MTurk performance balance for talkativeness and roundness judgment tasks. Error bars indicate standard deviation of each measurement. b) Confidence reporting for new/old recognition split by correctness of trials. c) Confidence reporting for cued source context retrieval split by correctness of trials. d) Confidence reporting of the cued source context retrieval split by high/low new/old confidence trials.

Behavioral: Patient Testing

Once the behavioral feasibility was achieved in the healthy comparison group, the same task was presented to the patients. Stimulus presentation and task were implemented with psychtoolbox (Kleiner et al., 2007), and patients were asked to respond with a Cedrus response box, again from 1 to 5 for the judgment tasks during the encoding stage, and three levels of confidence for the recognition stage. Behaviorally, although slightly lower than the healthy comparison group, patients performed consistently well on both item familiarity and source context memory (one sample t-test, p value of 2.6e-5 and 0.0012 against chance level, average AUC of 0.85±0.14 and 0.72±0.11 for new/old and source retrieval, respectively).

In addition to the cued retrieval task, three patients (Table 2.1) also performed an object screening task (Figure 2.4). The aim of this task was to screen for cells responsive to specific object categories, especially the face images. For the task, patients passively viewed a total of 100 images, belonging to the category of either faces, fruits, landscape, cars or animals. 6 one-back questions were randomly scattered between the images as attention checks, for which subjects answered yes or no accordingly.

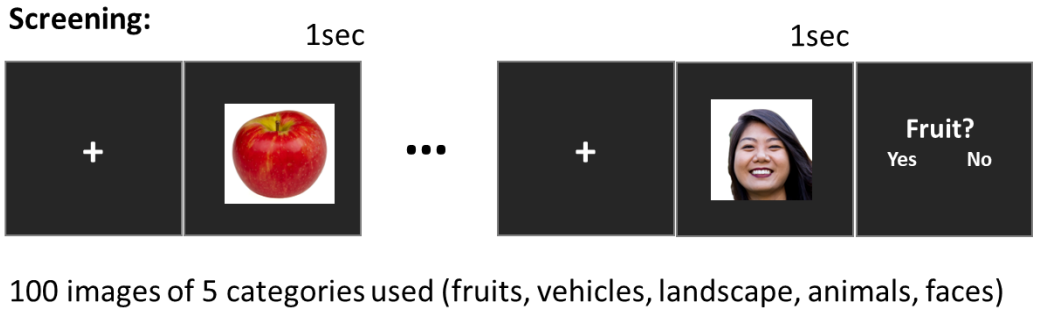

Figure 2.4 Task design of the screening task shown to patients for screening of category-selective cells.

The confidence reporting in our memory task did not show as clear a trend in the patients as in the MTurk participants, possibly due to the relatively smaller patient sample size, or their general lower performance accuracy (Figure 2.5).The average new/old confidence for correctly remembered old trials was still significantly higher than the erroneously identified trials (Figure 2.6b, two sample t-test, p= 0.0071), while the average new/old confidence

difference for correctly rejected new trials was no longer significantly higher than that for incorrectly accepted new trials (Figure 2.6b, two sample t-test, p=0.30). Comparing trials with correctly and incorrectly retrieved context information, their confidence difference was also no longer significantly different (Figure 2.6c, two sample t-test, p = 0.28). Additionally, there is still a correlation between the confidence reports for memory itself and for context (Pearson correlation, r=0.56, p = 0.016), such that when confidence was high in the new/old task, it was also high in the context task (Figure 2.6d, two sample t-test, p = 0.0048).

Also similar to the MTurk outcome, when comparing the two source context task types, there was no bias shown towards one task over another in terms of recollection accuracy (AUC of 0.72 and 0.72, two sample t-test, p=1.0; Figure 2.5d). Different from the MTurk subjects, the ratio of choices during the recognition stage no longer showed a bias (percentage of 51.8% and 48.2%, two sample t-test, p = 0.50 ; Figure 2.6a), either due to the smaller sample size of patients, or indicating less choice bias towards the talkativeness task in the patient sample.

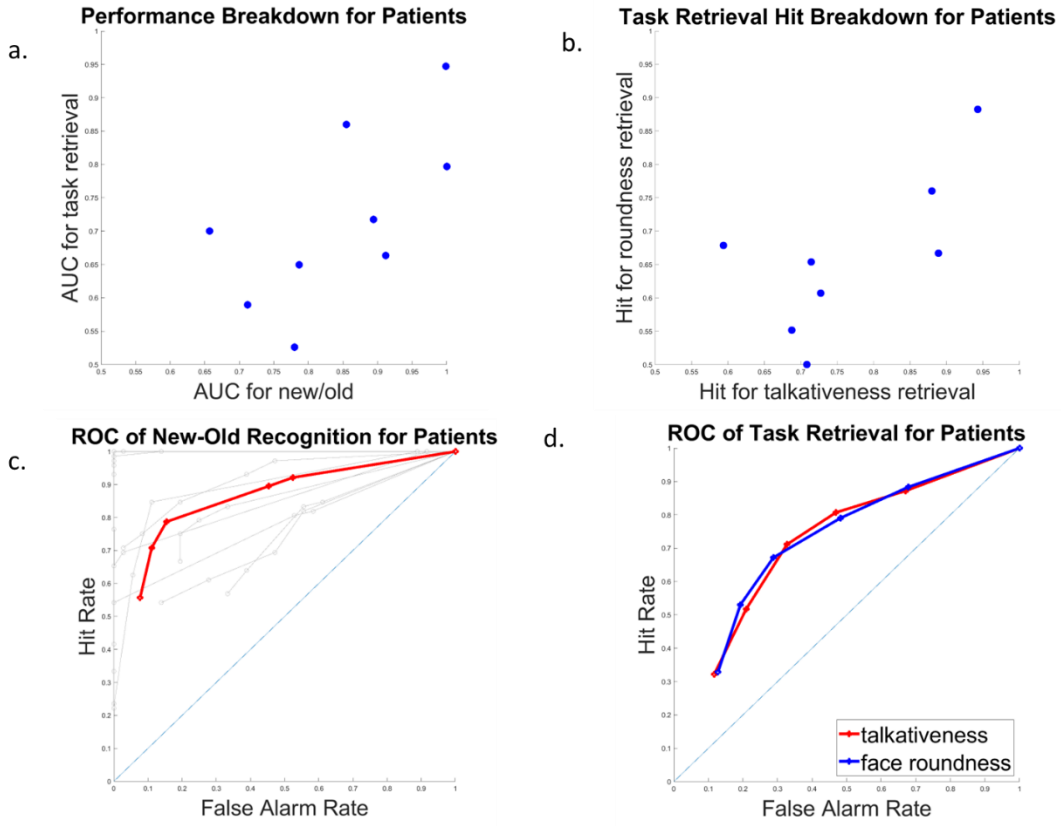

Figure 2.5 ROC and AUC reporting for patients. a) AUC of new/old recognition and task retrieval performance for patients. Each data point represents the performance outcome of one participant. b) Hit rate for correct retrieval of talkativeness judgment versus roundness judgment. Each data point represents the performance outcome of one patient. c) ROC for new/old recognition of patients. d) ROC for task retrieval for patients.

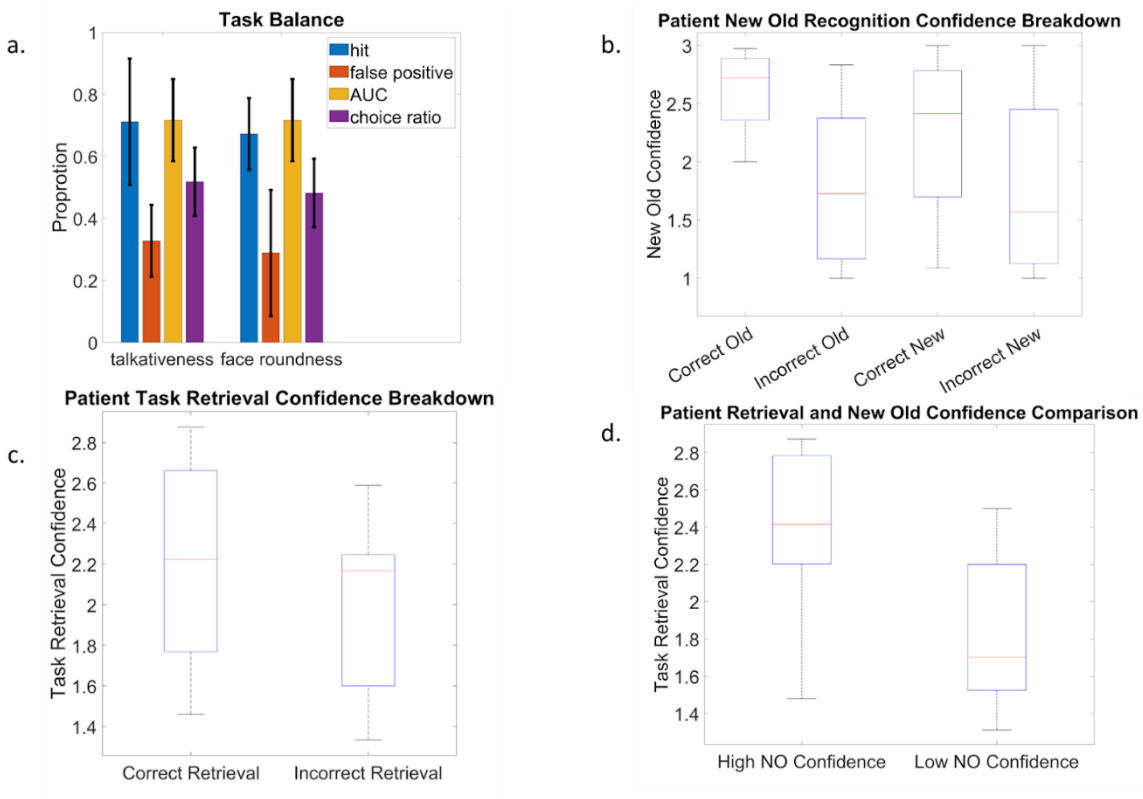

Figure 2.6 Task balance and confidence reporting for patients. a) Patient performance balance for talkativeness and roundness judgment tasks. b) Confidence reporting for new/old recognition split by correctness of trials. c) Confidence reporting for cued source context retrieval split by correctness of trials. d) Confidence reporting of the cued source context retrieval split by high/low new/old confidence trials.

Electrode Placement and Spike Sorting

The subjects of the single unit recording part of the task were adult patients being evaluated for surgical treatment of drug-resistant epilepsy (see table 2.1). The institutional review boards of Cedars-Sinai Medical Center and the California Institute of Technology approved

all protocols. Patients were monitored intracranially via Behnke-Fried depth electrodes with embedded microwires. So far, nine sessions of recordings were performed in the medial temporal lobe (MTL: amygdala, hippocampus), medial frontal cortex (MFC: anterior cingulate, pre-supplementary motor area) and PT (posterior temporal lobe).

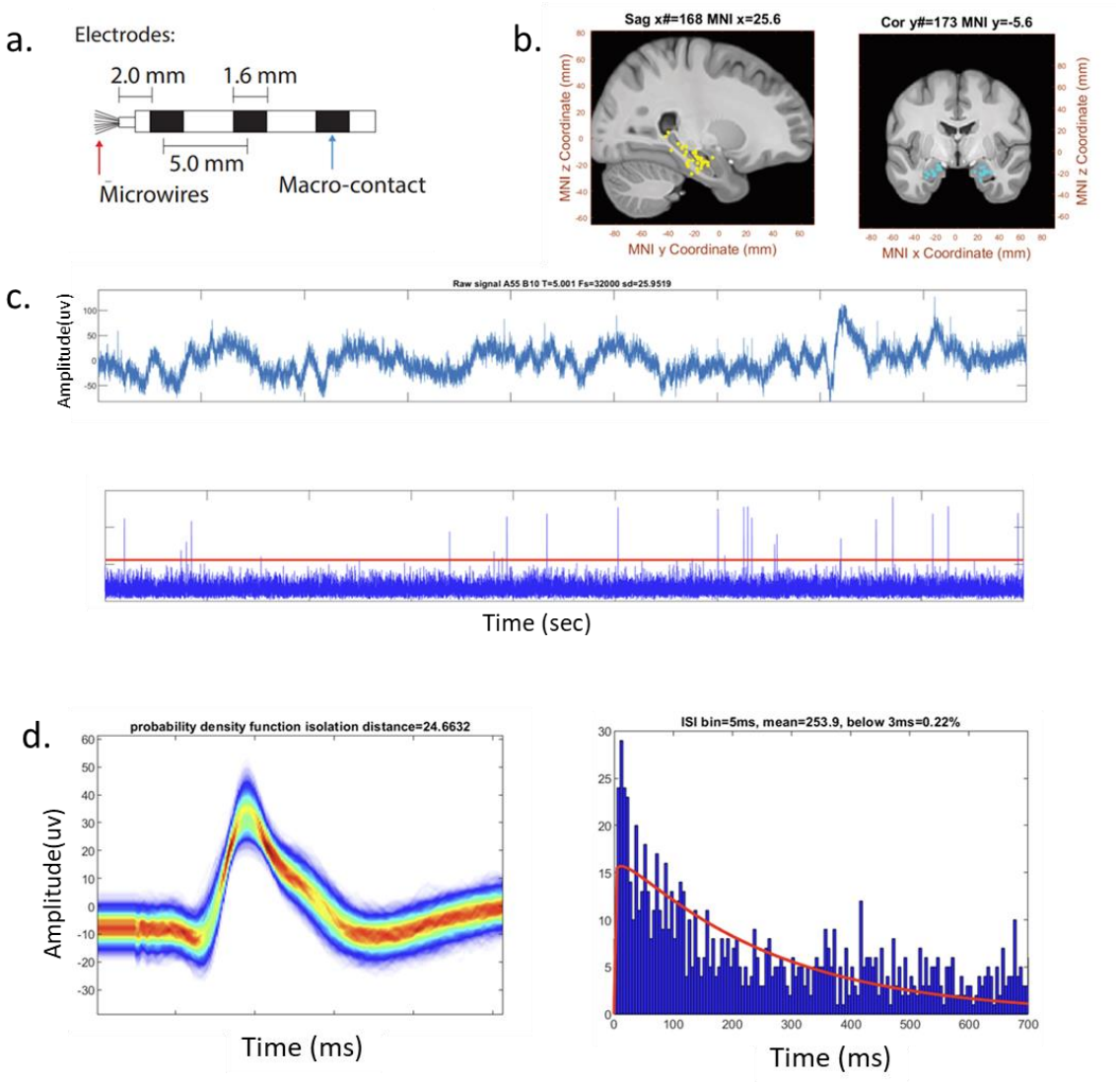

Figure 2.7 Electrode placement and spike sorting. a) Illustration of the design of Benke-Fried depth electrodes used for single cell recording. b) Example of common recording regions in the patients (For illustration purpose only; locations shown are from different patients). c) Example of raw traces of electrophysiological recording and bandpass filtered recording. d) Waveform and inter-spike-interval outcomes of an example cell unit identified using Osort.

Subject ID	Folder Name	Variant used	Screening task	Randomized Encoding Sequence	Region recorded	Total units recorded
P74CS	081921_p74	1	N	N	MTL, MFC, OFC (orbitofrontal cortex), PT	32
P76CS	092021_p76	1	N	N	MTL, MFC, OFC, PT, INS(insula)	57
P78CS	031122_p78	1	N	N	MTL, PHG (parahippocampal gyrus), PT	46
P79CS	040222_p79	1	N	N	MTL, MFC, OFC, PT	127
P80CS	080222_p80	2	N	N	MTL, MFC, OFC, PT	89
P81CS	102822_p81	1	N	N	MTL, MFC, OFC, PT	67
P82CS	011223_p82	1	Y	Y	MTL, MFC, OFC, CM (central medial thalamic nucleus)	46
P85CS	042223_p85	2	Y	Y	MTL, MFC, OFC, CM	58
P87CS	072623_p87	1	Y	Y	MTL, MFC, OFC, PUL (pulvinar)	59

Table 2.1 Patient and task information of the currently recorded nine sessions.

The recorded sessions were band-pass filtered within the range of 300-3000 Hz, and single units were selected using Osort, a semi-automated algorithm that defines potential cell clusters based on their waveforms (Rutishauser et al., 2006). Overall, 581 cells from MTL, MFC and PT were identified across the 9 patients. The patient information is shown in Table 2.1, and the distribution of cells recorded from these patients is shown in Figure 2.8.

Single Cell Selectivity

We focused the single cell selectivity analysis on MTL, MFC and PT, the three regions most related to the encoding of memory, task context and face stimuli. Cells with special selectivity to features of the task were selected with two methods. When the selectivity involved a binary feature, we conducted a bootstrapped test on the mean firing rate over a time window 200 to 2400 msec relative to the face image onset (significance criteria of $p <= 0.05$, B = 10,000, two-tailed; Rutishauser et al., 2008). When the selectivity involved more than two choices, a parametric N-way analysis of variance test was applied, with selection criteria of $p<0.05$. Four types of cells were specifically selected. Firstly, two distinct populations of cells were found to represent source context information during encoding and retrieval periods (encoding and recognition TS cells). Secondly, new old selective cells (MS cells) during the recognition stage were selected, which have significantly different firing rates for new versus old faces during the recognition stage of the task. Thirdly, category selective cells (CS cells) were selected, which responded with significant differences to different types of items presented during the screening task (recorded in only three of the patients).

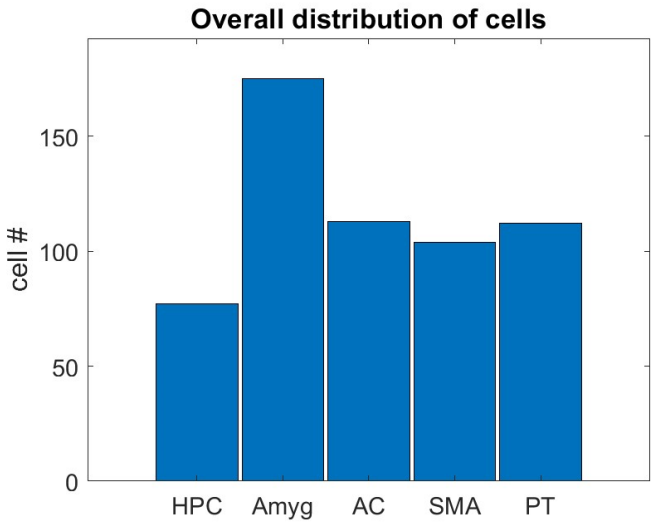

Figure 2.8 Distribution of recorded cell units over MTL (hippocampus, amygdala), MFC (anterior cingulate cortex, supplementary motor area) and PT

The distribution of these cells across different regions were plotted (Figure 2.18). For each region, whether the observed number of cells selected was significantly larger than that expected by chance was calculated based on the binomial distribution, with a significance criterion of alpha = 0.05.

The number of cells that were significantly modulated by task during encoding("encoding TS cells") was larger than expected by chance in all three brain regions examined (Figure 2.18). Overall, 28 encoding TS cells were found in the MTL region (11% out of 252 total cells, see example cell in Figure 2.9). 34 encoding TS cells were found in the MFC region (16% out of 217 total cells, see example cell in Figure 2.10).15 encoding TS cells were found in the PT region (13% out of 112 total cells, see example cell in Figure 2.11).

Only MTL and MFC reached significance in terms of the proportion of MS cells (Figure 2.18). Overall, 40 cells in MTL showed significant new/old selectivity (16%, see example cell in Figure 2.12). 37 cells in MFC showed significant new/old selectivity (17%, see example cell in Figure 2.13). Despite the existence of single cells showing significance for new/old selectivity (see example cell in Figure 2.14), the PT region did not reach an above chance proportion for MS cells (6 cells total, 5.4%).

For recognition TS cells, only amygdala and PT showed above-chance significance in terms of the percentage of cells present (see Figure 2.18). For amygdala, 17 out of 175 cells were source context selective (9.7% see example cell in Figure 2.15). For PT, 10 out of 112 cells were source context selective (8.9%, see example cell in Figure 2.16).

In contrast with MS cells, for CS cells, only MTL and PT reached significant proportions (Figure 2.18). Out of the total sessions that contained a face screening task, 11 out of 39 MTL cells showed selectivity to one of the five categories presented (28%). 16 out of 41 PT cells showed category selectivity (39%, see example cell in Figure 2.17). In contrast, only 6 out of 82 MFC cells showed category selectivity during the face screening task (7.3%).

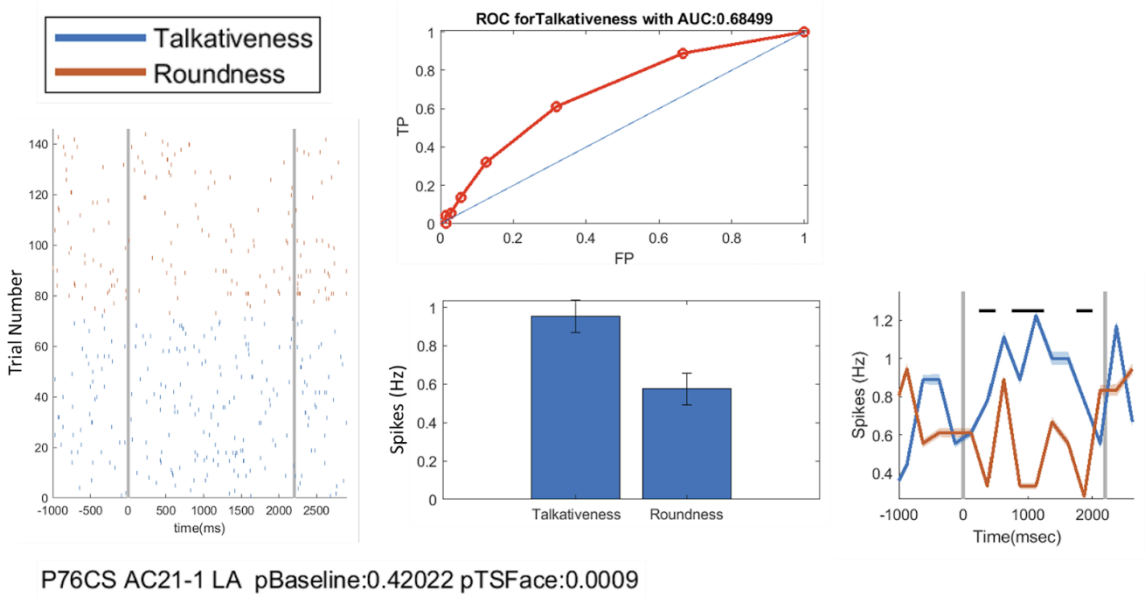

Figure 2.9 Example encoding TS cell from MTL. This cell fired more following stimulus onset during encoding if the task performed was the 'talkativeness' task. Gray lines mark stimulus onset and offset. Firing rate is counted in the time window of 200 to 2400 for the ROC analysis and mean firing rate shown (center of the plot).

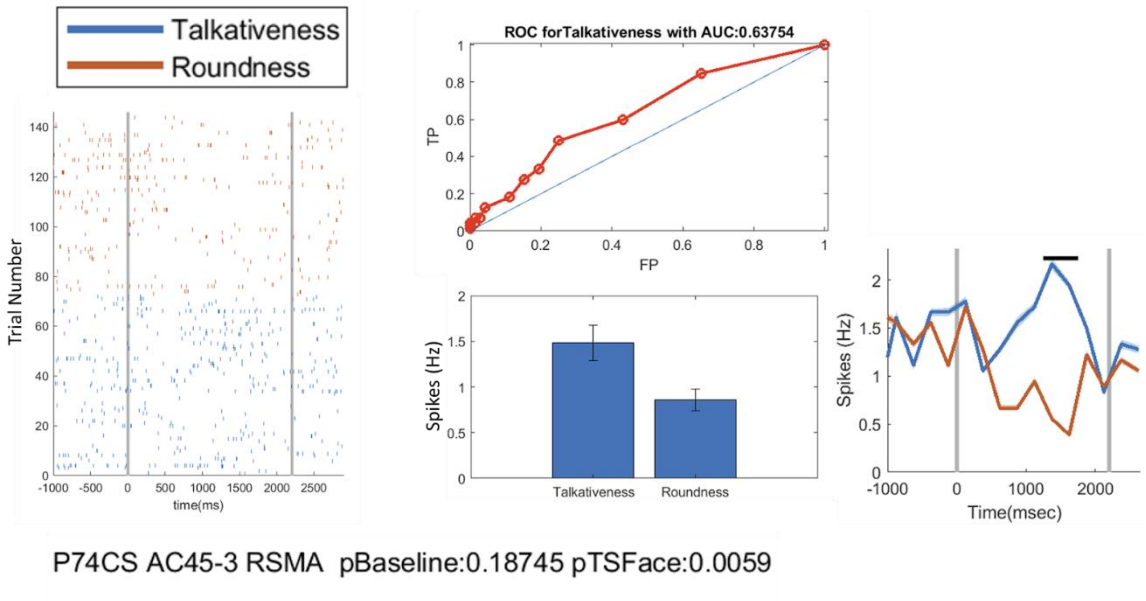

Figure 2.10 Example encoding TS cell from MFC. See Fig 2.9 for notation.

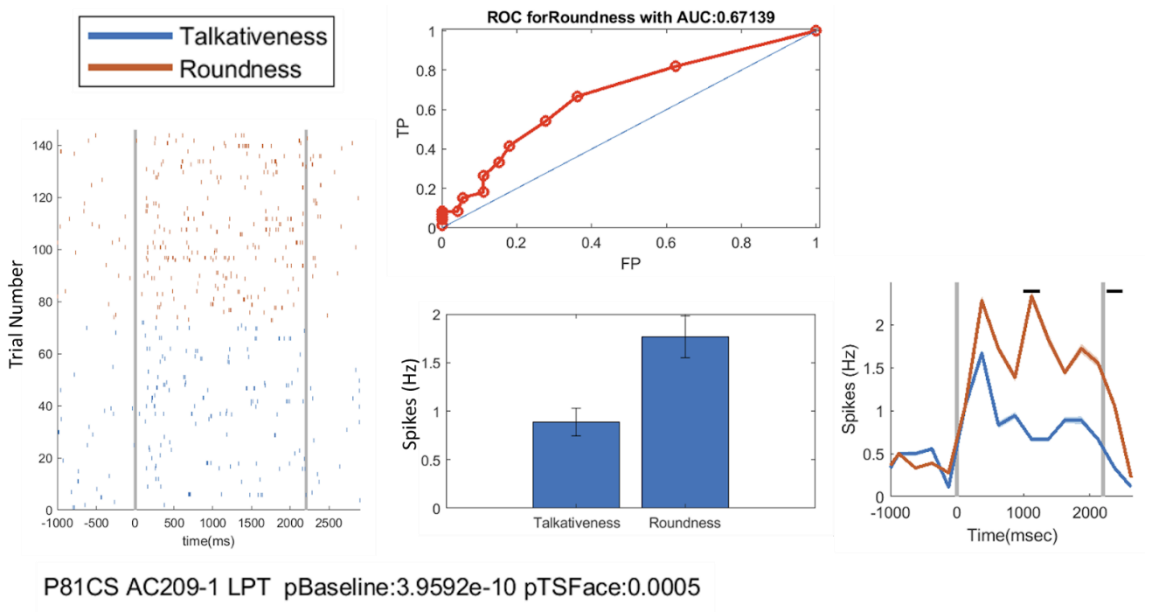

Figure 2.11 Example encoding TS cell from PT. See Fig 2.9 for notation.

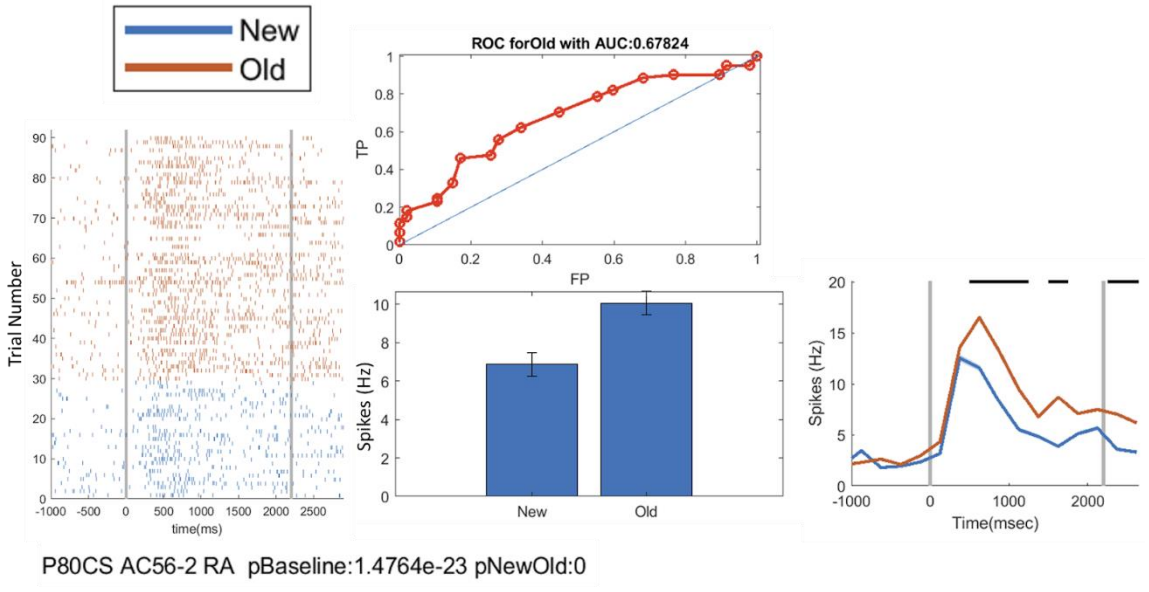

Figure 2.12 Example recognition MS cell from MTL. This cell increased its firing rate more for old compared to new stimuli following stimulus onset. See Fig 2.9 for notation.

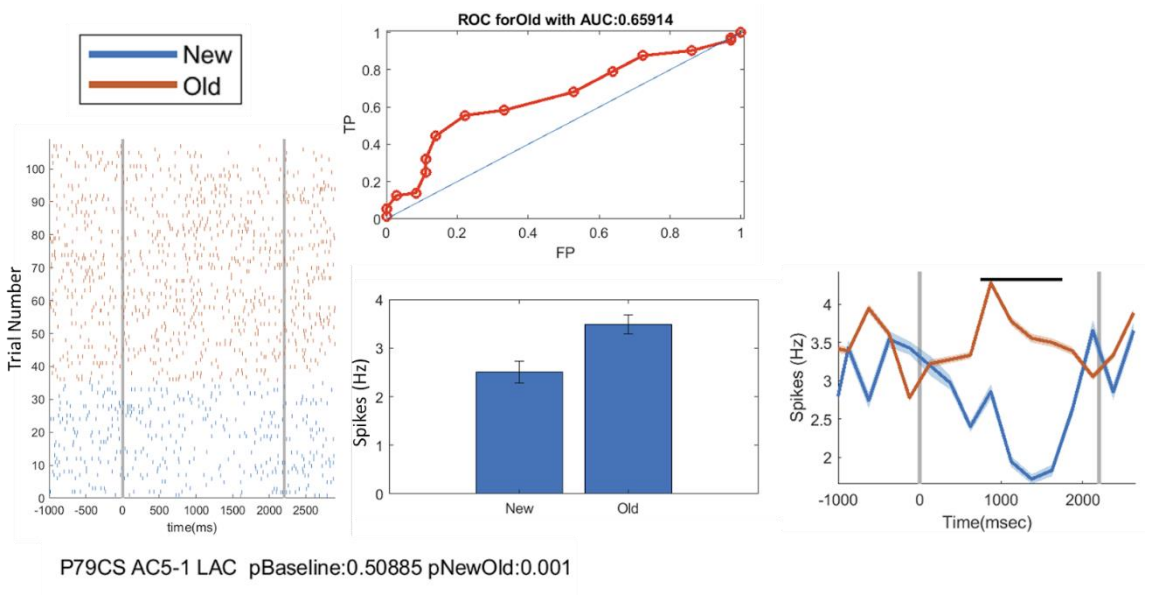

Figure 2.13 Example recognition MS cell from MFC. See Fig. 2.9 for notation.

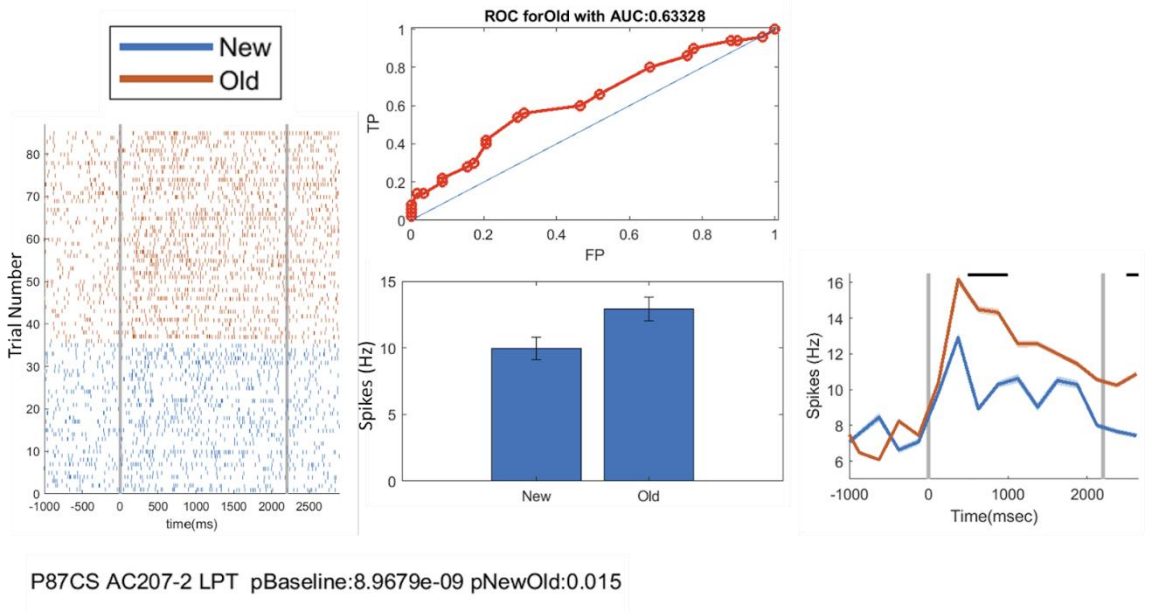

Figure 2.14 Example recognition MS cell from PT. See Fig 2.9 for notation.

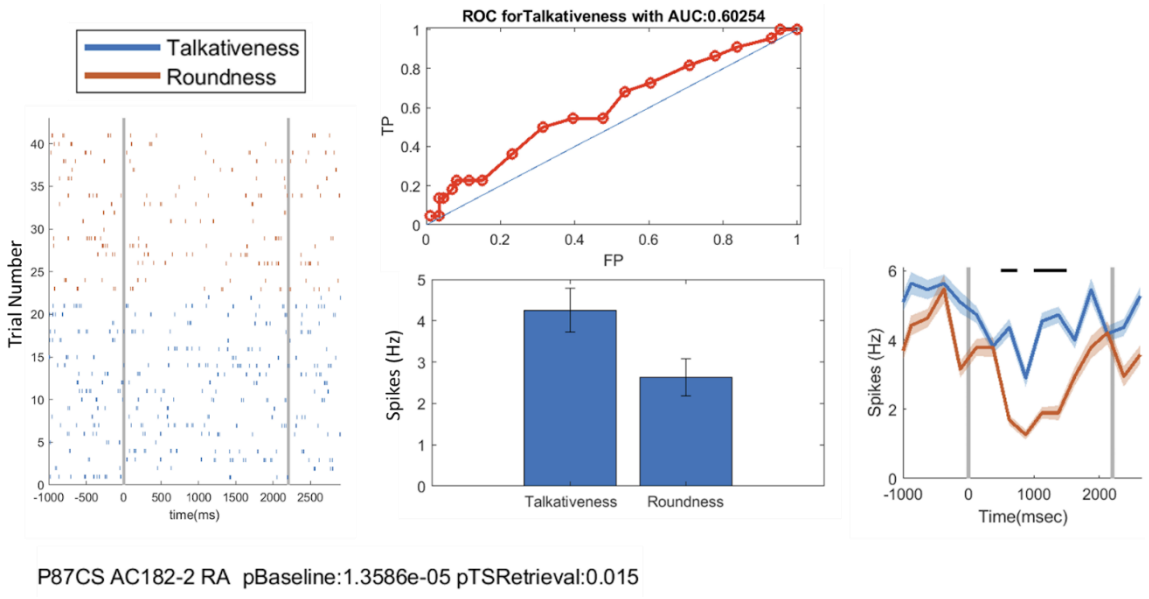

Figure 2.15 Example recognition TS cell from Amygdala. This cell reduced its firing rate more following stimulus onset if an image shown was previously encountered during the roundness task. Data shown here is from the recognition part of the task. See Fig 2.9 for detailed notation.

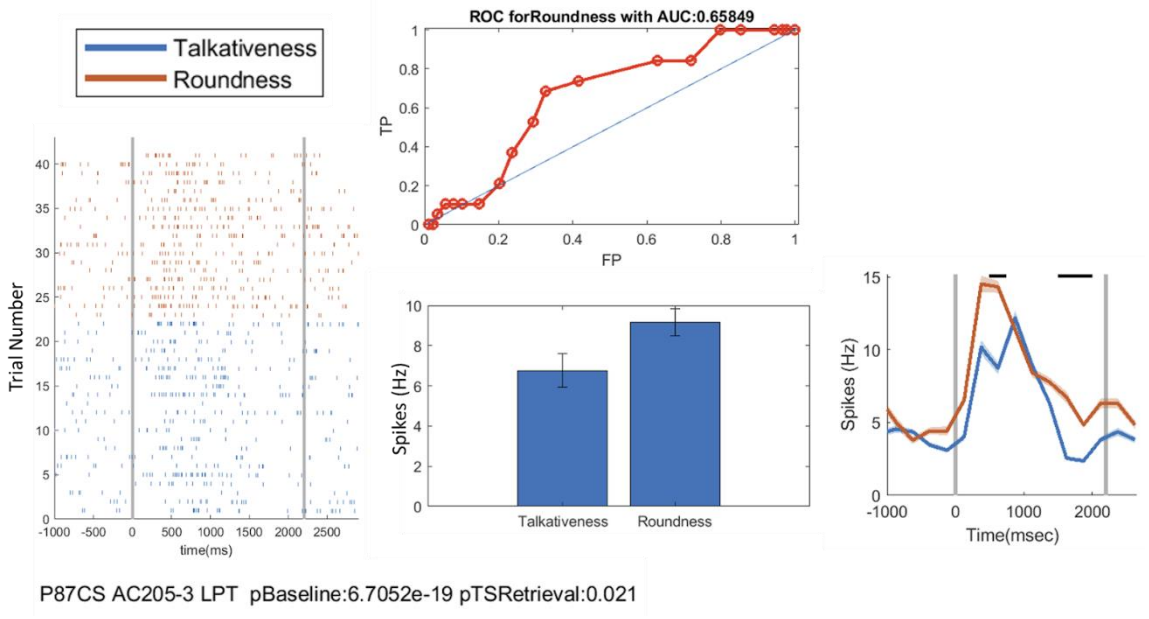

Figure 2.16 Example recognition TS cell from PT. This cell fired more following stimulus onset if an image shown was previously encountered during the roundness task. Data shown here is from the recognition part of the task.

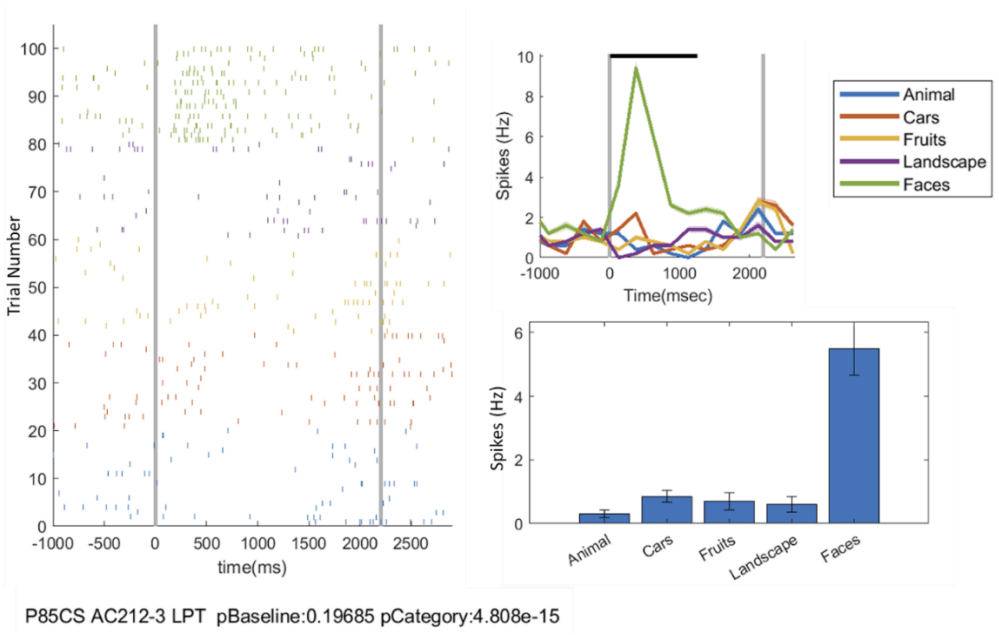

Figure 2.17 Example CS cell from PT. This cell increased its firing rate only if the stimulus shown is that of a face. The gray lines mark stimulus onset and offset. For the mean firing rate, the time window used is 200ms to 1200ms after the stimulus onset. Data shown here is from the additional screening task performed.

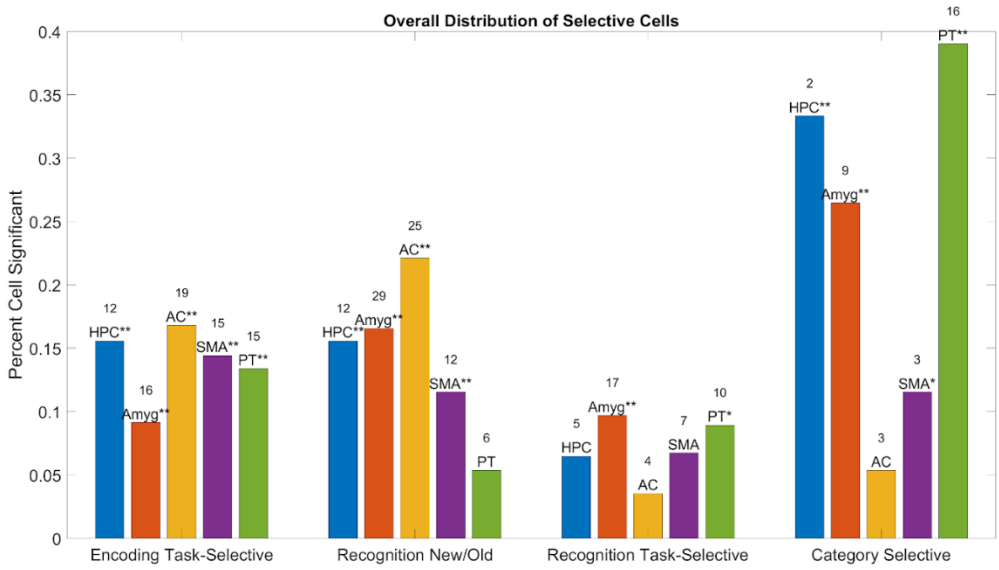

Figure 2.18 Region-wise distribution breakdown of cells with selectivity. Bar plots show the proportion of cells in a given brain area that were significantly modulated by the task during

encoding, new/old during recognition, the ask during recognition, and the visual category during screening. Numbers above the bars are the number of cells that were significant. Asterisks indicate significance of cell concentration within each brain region (*: $p<0.05$; **: $p<0.01$).

Comparison of t-statistics

When plotting the t statistics of cell selectivity for the associated task type of a face, some differential behavior can be observed across MTL, MFC and PT.

Compared to MTL and PT cells, there is a clear difference in the number of cells that qualified as both MS cells and encoding TS cells in MFC. A much higher proportion of MFC cells (7 out of 31 encoding TS cells and 37 MS cells, 23% and 19% respectively; Figure 2.20a) are simultaneously selective to both encoding task type and recognition new/old, while there is almost no such overlap for cells in MTL (1 out of 27 encoding TS cells and 39 MS cells, 3.7% and 2.6% respectively; Figure 2.21a) and PT (0 out of 14 encoding TS cells and 6 MS cells; FIgure 2.22a).

All three regions failed to show a cell-to-cell reactivation pattern, as indicated in Figure 2.20b, 2.21b and 2.22b. Cells with above-chance selectivity (defined here as having a t statistic value greater than 2) for the source context during the encoding stage from all three regions did not exhibit the same selectivity during the recognition stage, and vice versa. However, noticeably, in the PT region, despite a lack of reinstatement of task information, a highly preserved positive correlation can be observed between encoding t statistics and recognition t statistics (Figure 2.22b, Pearson's linear correlation, $p=0.0012$, $r=0.30$), indicating a stable code for the presented stimuli during encoding and recognition. This finding also serves as a control for recording stability, showing that tuning and cells remained stable.

Of the two regions that showed above-chance concentration of encoding TS cells, MTL and MFC, the t-statistics of these cells was also different between the two rounds of repetition during the encoding stage (Figure 2.19). Although encoding TS cells from both regions showed significant drop in t values between encoding and recognition, only the MFC region

showed a significant drop in t value between the first and second round of repetition (Figure 2.19a).

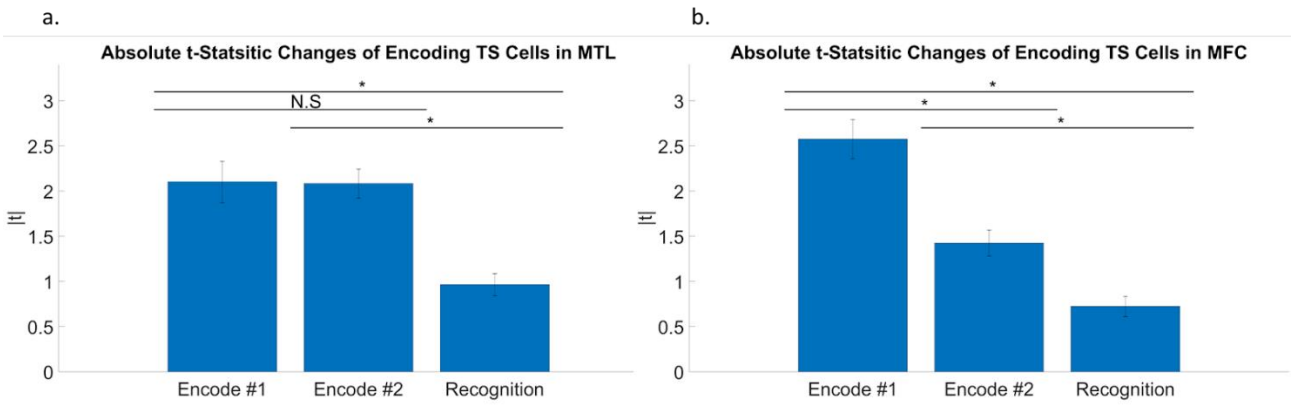

Figure 2.19 Encoding TS cell t-statistic behavior during first, second round of encoding, as well as recognition stage. a) absolute t-statistic changes of encoding TS cells in MFC. b) absolute t-statistic changes of encoding TS cells in MTL.

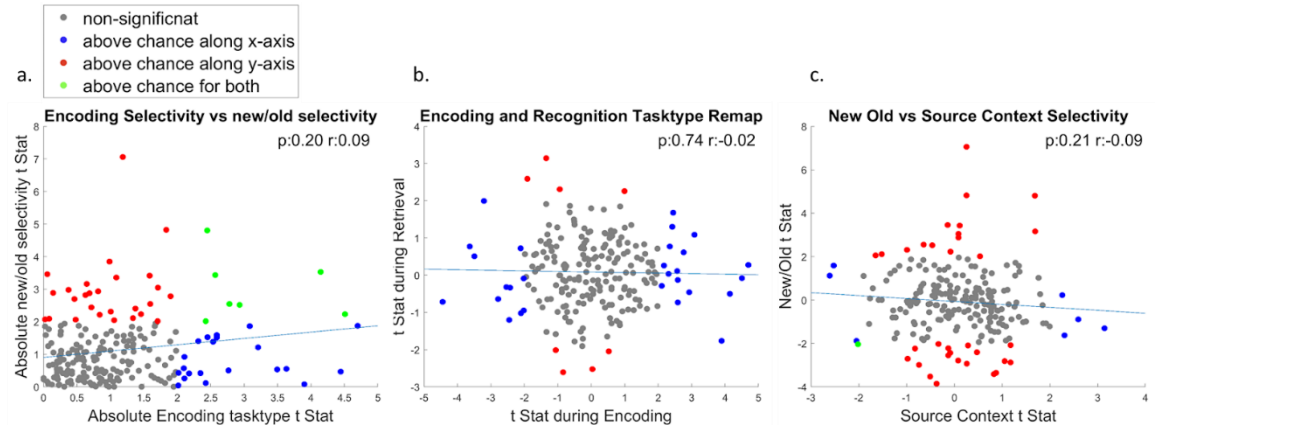

Figure 2.20 t-statistic comparisons of all MFC cells. a) absolute t statistics of new/old selectivity plotted against encoding task type selectivity. b) t statistics of encoding task selectivity plotted against recognition task selectivity. c) t statistics of new/old memory selectivity plotted against recognition task selectivity.

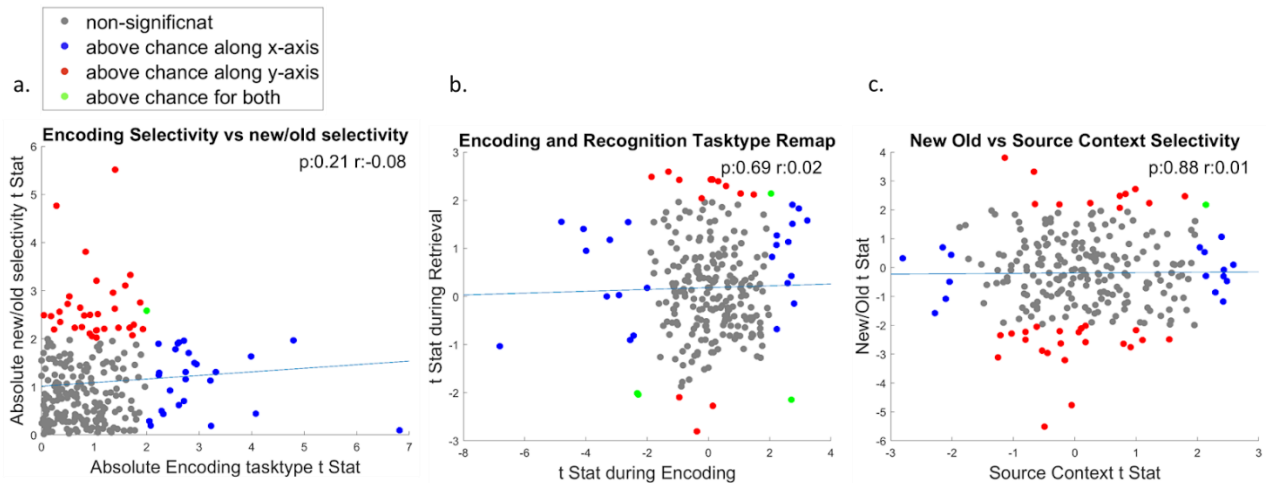

Figure 2.21 t-statistic comparisons of all MTL cells. a) absolute t statistics of new/old selectivity plotted against encoding task type selectivity. b) t statistics of encoding task selectivity plotted against recognition task selectivity. c) t statistics of new/old memory selectivity plotted against recognition task selectivity.

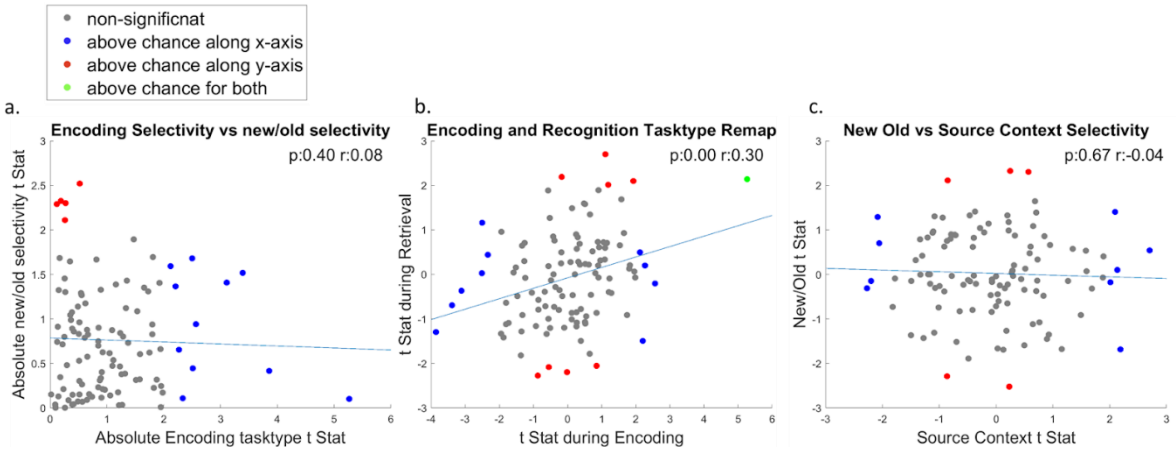

Figure 2.22 t-statistic comparison of all PT cells. a) absolute t statistics of new/old selectivity plotted against encoding task type selectivity. b) t statistics of encoding task selectivity plotted against recognition task selectivity. c) t statistics of new/old memory selectivity plotted against recognition task selectivity.

2.3 Conclusion

In this chapter of the thesis, we leveraged single-unit recordings from epilepsy patients undergoing intracranial electrophysiological monitoring to show that familiarity and source memory appear to rely on distinct processes.

Overall, given the scant overlap found between the MS cells and recognition TS cells (Figure 2.20c, 2.21c, 2.22c), our findings support a dual process theory account of recognition memory. This is because the two types of memory were encoded by different cells. Moreover, our finding also revealed that while source context memory was encoded, there was no clear evidence for reactivation at the single cell level. This is because there was almost no overlap between encoding TS cells, which were found across multiple MTL and MFC regions, and the recognition TS cells, which were found mainly in amygdala and PT (Figure 2.20b, 2.21b, 2.22b). The result suggests that contextual reinstatement and encoding rely on distinct neural processes. Notably, we did find encoding of retrieved context (recognition TS cells), but this information was encoded by different cells than those that were engaged during encoding.

Our current findings are in line with previous human single unit literature on the recollection process. For example, a previous study examining associative memory of images to words in epilepsy patients undergoing intracranial monitoring convergingly found that there was no overlap between cells encoding familiarity and cells encoding the successful retrieval of source information (Derner et al., 2020), indicating the likelihood of a dual memory process. Similar findings were also reported in another study (Staresina et al., 2019), where separate populations of cells distinguished the content of retrieval cues and the successful retrieval itself.

However, our conclusions are limited by the small patient sample and brain regions recorded. The current null finding of reactivation is on a single-cell level, using binned rate code over a range of 200-2400 msec of stimuli presentation. As further trials accumulate, one next step to check is the probability that populational coding and temporal code support recollection of source context of the face stimuli. As more sessions with the category screening task are

collected, another possible next direction would be to examine the roles that the CS cells play in encoding of the source context, and their relationship to the encoding TS and recognition TS cells.

Another aspect to be noted is the sole use of faces as cue stimuli for eliciting the source context retrieval process. Although the t-statistics of PT does not show a significant overlap of encoding and recognition TS cells, a highly preserved correlation exists between the source context task types during encoding and recognition (Figure 2.22b). An immediate next step of the current chapter would be to isolate the effect of face identity versus face context, and check whether the structure of representation in PT is still preserved (Boyle et al., 2022).

Chapter 3

STUDY OF FACE REPETITION MEMORY

3.1 Introduction

This chapter is focused on investigating the long-term consolidation of recognition memory and the effect of repetition, with a specific focus on face recognition memory. This is a situation typically encountered in everyday life: not only do we need to keep track of individuals over long periods of time, but we typically get to know them over repeated social interactions. The major factor that is present in the real world, but omitted in the experiment, is all of the associated context: in the real world, we not only see a face, but a whole body, and we often interact with a person and obtain associated biographical information. Here, we strip away these contextual factors in order to motivate a focus on faces in isolation. Two aspects are associated with this motivation: the consolidation of general recognition memory, and the consolidation of memory specifically related to faces.

The study of consolidation of general recognition memory dates back to the 19th century, when Hermann Ebbinghaus introduced the concept of the forgetting curve (Murre and Dros, 2015; Rubin and Wenzel, 1996). Ebbinghaus's work involved learning artificially created nonsense words and assessing their retention rates over time. His research revealed the rate at which memories decay and emphasized the role of re-exposure in enhancing memory retention. Subsequent studies have not only confirmed the validity of the forgetting curve but also highlighted the importance of repetition in influencing successful later recollection of information (Murre and Dros, 2015). It should be pointed out that repetition does not merely amount to additional instances of encoding, but that repeated presentations of stimuli of course trigger recognition memory as well. Thus repetition amounts to a mixture of additional encoding, and re-consolidation of already familiar items through recognition.

Paired with fMRI recordings, more recent studies have explored how repetition frequency and interval-duration impacts recognition memory. Hippocampal and parahippocampal region activity was examined with a recognition memory task, where the study and test

interval varied between half-hour, 1 day and 1 week (Stark and Squire, 2000). Although a significant new/old difference was found in both regions with a blocked task design, no difference was found for the different interval between encoding and test stages. In comparison, effects of repetition were studied in another study where repetition times of stimuli were manipulated to be either once or three times (Reagh et al., 2017). Repetition was found to evoke a shift in engagement in an anterior CA1-thalamic-medial prefrontal network when comparing true and false recognition, suggesting a change in connectivity of brain circuits caused by repeated experience. Similarly, in a more recent study, engagement of the parietal memory network was found in repetition studies, while the exact repetition suppression and enhancement effect was found to be task-dependent (Gilmore et al., 2015; Gilmore et al., 2019).

Among studies of consolidation via repetition of the stimuli, the studies of face-specific memory have revealed special aspects of face memory consolidation. When contrasting newly familiarized faces with novel faces, the amygdala has been found to exhibit larger fMRI-BOLD signals to novel faces than to familiar faces (Schwartz et al., 2003). In monkeys, personally familiar faces engaged the macaque face-processing network more than unfamiliar faces, revealing two conserved locations within the perirhinal cortex and the temporal pole (Landi and Freiwald, 2017).

Recent discussions have emphasized the need for substantial sample sizes in fMRI studies to ensure the significance of results (Marek et al., 2022). Given this consideration, one alternative approach to take would be dense data acquisition from a small set of subjects over a long period of time (Rosenberg and Finn, 2022; Allen et al., 2022; Gordon et al., 2017). In this chapter, we aim to develop such a dense longitudinal behavioral paradigm to be paired with fMRI recordings to study face repetition memory in humans.

For the current study, three participants were repeatedly scanned over the course of two months while performing face memory judgments. The main task structure was a repeated new/old task with three levels of confidence reporting, with half of the faces used always being new, and another half a mixture of faces that repeat for different amounts of times. To

maintain the level of familiarity, after each memory session, participants also passively viewed all faces from the same session once.

Behaviorally, we anticipated observing above-chance new/old reporting, demonstrating successful long-term memory performance. Over time, especially for highly repeated faces, we expected to see increased accuracy and confidence reporting, along with reduced reaction time. We also predicted a correlation between the number of times an image was repeated and memory accuracy.

3.2 Methods and Results

Stimulus Selection

Images were selected from the FFHQ face data set, a high-quality image dataset of human faces crawled from Flickr (Karras et al., 2019).

Manual screening was applied to the faces. Faces of any famous people were excluded. Faces that looked to be outside of the age range of 18-60 years old were excluded. Faces that showed exaggerated facial expressions or any facial/head movements were excluded. Faces with excessive facial makeup or look artificial were excluded. Last but not least, images with incomplete faces and other image quality issues were excluded from the selection.

Backgrounds of the images were then removed using semantic segmentation method (Long et al., 2014).

In the end, we used 768 images from this set, 252 of which were repeated at least once. For the follow-up scanning session, another 186 completely new images from the same set were selected to be contrasted with the old faces used during longitudinal scanning.

Single Session Procedure

Three participants were recruited from the lab to perform the longitudinal scanning sessions. For each session, two components were presented to the participants: an active memory judgment task, and a passive viewing session.

For the active memory judgment, during each scanning session, a New/Old task with three levels of confidence reporting were presented to the subjects. Within each session, there were always 50% new images and 50% old images.

The task was conducted in an event-related fashion, with faces shown on screen for 1.5 seconds, followed by a question prompt after a jittered short interval (average of 500ms). Participants were asked to respond to the question prompt as fast as possible, with a maximum response time of 2 seconds. After a response was made, there was a jittered inter-trial-interval of 0.5 to 4.5 seconds (average of 2.5sec ITI, making one single trial roughly 6.5 seconds).

Figure 3.1 Task design of the active face memory judgment

The passive viewing stage was similar to the active memory task, except that now the memory reporting screen was removed. During the viewing, we asked subjects to think about the personality of the person whose face was shown on the screen, thus providing a uniform context of relatively "deep" processing of the stimulus.

Longitudinal Session Balance

The whole sequence of scanning sessions happened between March 31st to June 1st, 2022, spanning three months in total. To begin with, the first session was a purely passive viewing session to introduce the faces to be familiarized, in which each face was represented twice to the three participants. Afterwards, the sequence continued with one active face memory judgment session followed by one passive session on each of the days scanned.

Repetition times of images were deterministically assigned. Four repetition schemes for old images were used: faces were either repeated during every single session, during every other session, during every other four sessions, or only one-back. With this strategy, by the end of the 12th session, faces were repeated 12, 6, 3 and 2 times respectively (Figure 3.2).

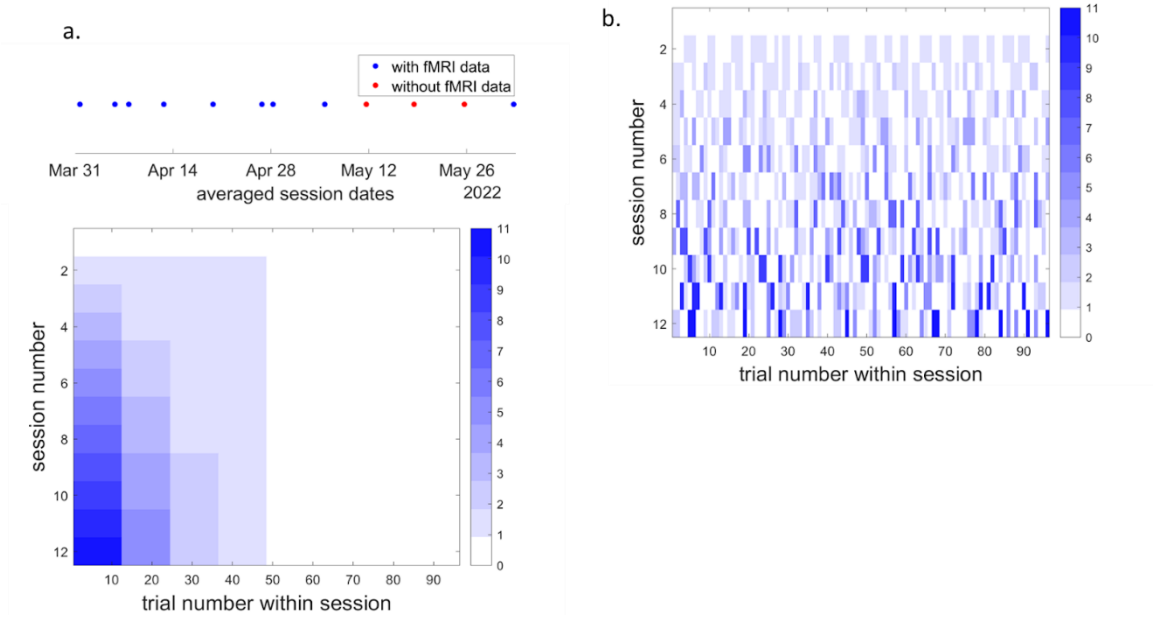

Figure 3.2 Repetition scheme and days of recording for the different groups of face images. a) dates on which the twelve sessions were carried out. Red dots indicate sessions where only behavioral data were collected, excluding fMRI scanning. b) Repetition scheme across sessions in the original sequence. Deeper color indicates higher total number of presentations of a face image. As the number of sessions increased, subgroups of images were repeated more frequently. c) Repetition scheme rearranged by descending order of the total amount of repetition. The color code indicates the number of repetitions a given stimuli was sampled at the moment of presentation.

The task program was implemented using PsychoPy (Peirce et al., 2019). Subjects held a response box with four buttons in each hand to perform confidence reporting. To avoid confounding signals from the button pressing motion, the schematic of the response box was reversed between each active memory rating session.

Percent Retained Test after Four Months

Four months after the last session of the face memory task was obtained, on October 4th, 2022, a retainment task was performed on a subset of the originally used faces. Each subject received three runs of new/old judgment tasks consisting of 124 images, for which they were asked to report familiarity with three levels of confidence.

Out of each run of the 124 faces, half of them were completely new, while the other half were repeated from the previous sessions. For the old faces, within each run, there were 4 faces that had been repeated 12 times, 8 faces that had been repeated 6 times, 16 faces that had been repeated 3 times, 22 faces that had been one-back, and 12 faces that had never been repeated (Figure 3.3).

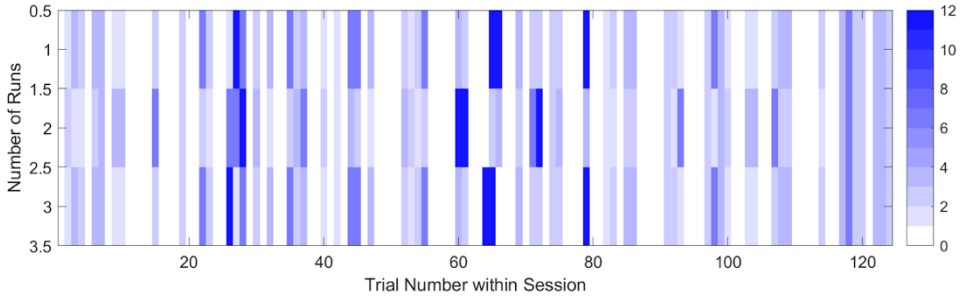

Figure 3.3 Repetition scheme of faces used in the three runs of follow up scanning, on October 4th, 2022. The color code indicates the number of repetitions a given stimuli was sampled at the moment of presentation.

fMRI Acquisition

Structural and functional fMRI data were recorded along with the repeated face familiarization task. For structural scanning, complex-valued T1 weighted images were collected with multi-echo MPRAGE sequence, and a resolution of 0.9 mm. Complex-valued T2 weighted images were collected with SPACE sequence and resolution of 0.9 mm. The functional MRI was acquired with complex multiband T2*w EPI, 1100/30ms, M6, 2.5mm, with a whole brain coverage. Please note that the fMRI data are not presented or analyzed in this thesis; only the behavioral data are.

Preliminary Analysis

Beginning from the second session of the task, all participants performed above chance in the new/old judgment task for faces presented (participant 1: average AUC = 0.85, p = 4.6e-10, one sample t test; participant 2: average AUC = 0.90, p=6.5e-11, one sample t test; participant 3: average AUC = 0.78, p = 2.6e-8, one sample t test). For faces with different repetition frequencies, the session-wise performance of each subject is presented in Figure 3.5a. Notably, for all subjects, the repeat-every-session images reached a saturating new/old judgment accuracy rather quickly. The confidence reporting mirrored the same effect, with the confidence level reaching the maximum of 3 for new/old judgments by the seventh session for each subject (Figure 3.5b). In comparison, response time for the subjects showed no clear differences between different repetition groups, as shown in Figure 3.5c.

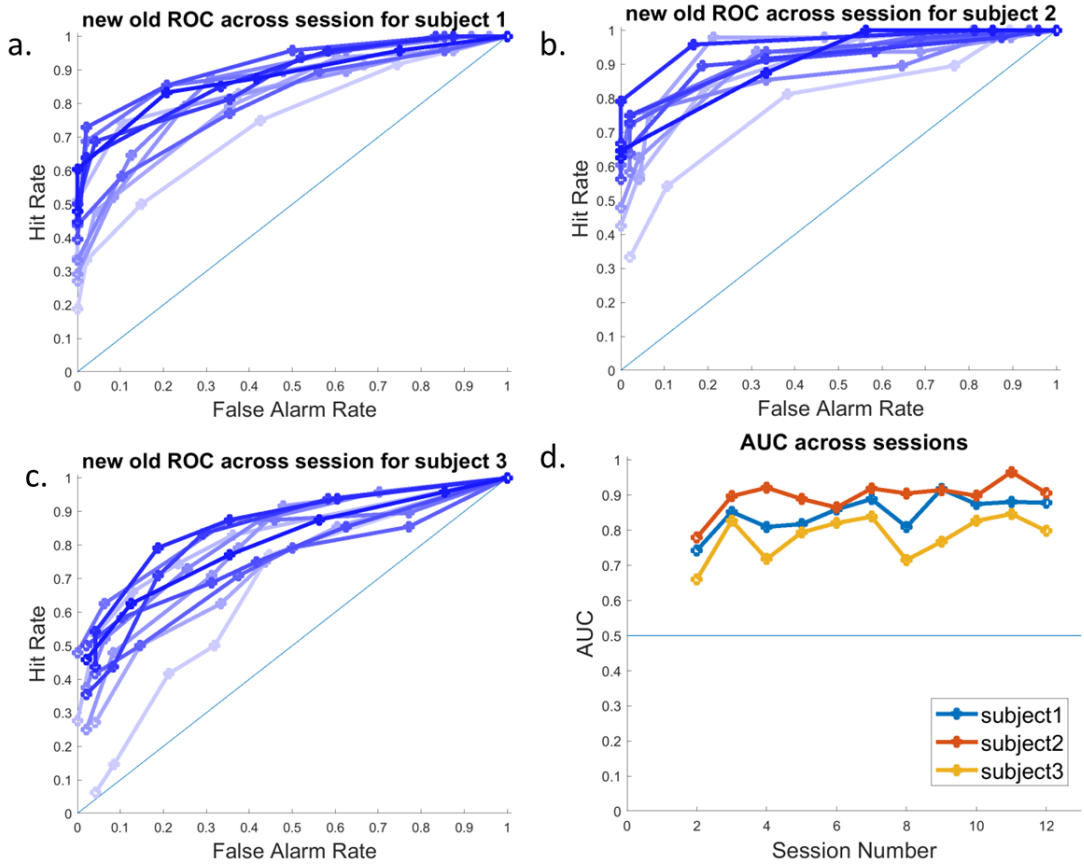

Figure 3.4 Session-wise new/old performance for each participant. a) - c) session-wise ROC curves for participant 1 to 3. Darker lines indicate more recent sessions dating from session 1 to session 12. d) session-wise AUC for participant 1 to 3.

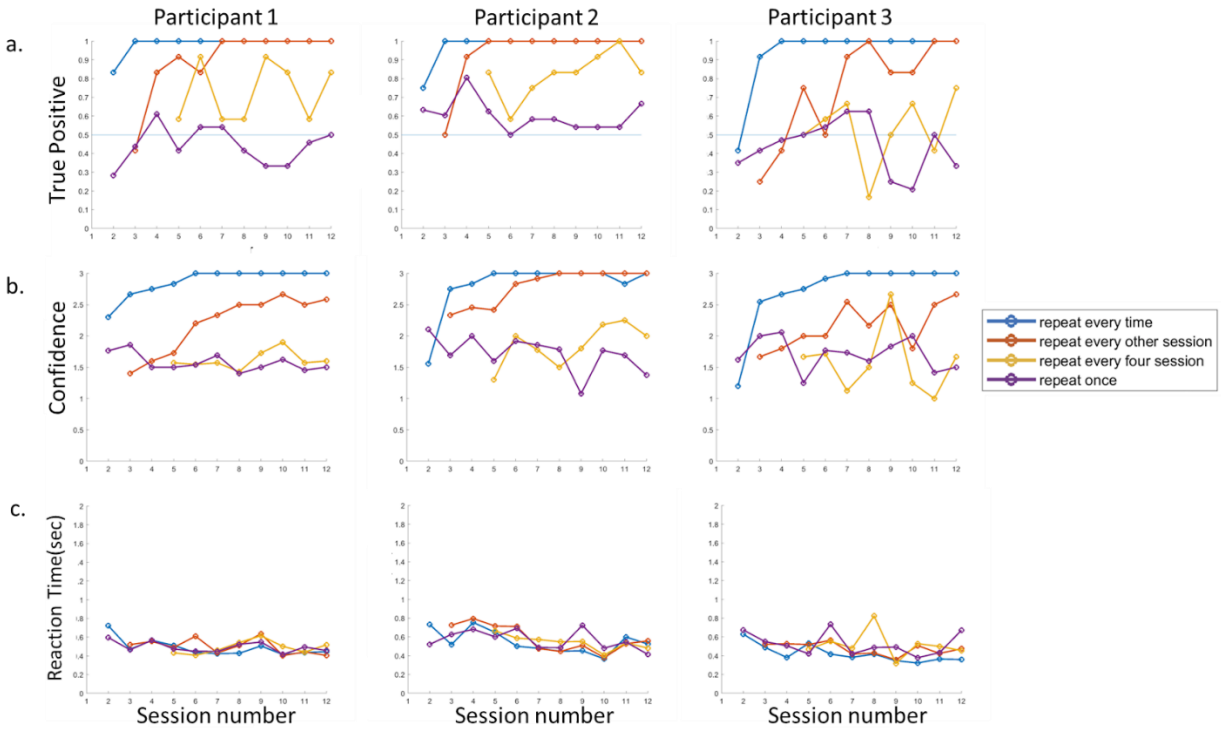

Figure 3.5 Session-wise hit rate, confidence and reaction time of the three participants, split by the image groups assigned to different repetition schemes. a) Session-wise hit rate for different image groups. Each plot represents the result for participant 1 to 3. b) Session-wise confidence rate for different image groups, reported by participant 1 to 3 respectively. c) Session-wise reaction time for different image groups. Each plot represents on participant's behavioral outcome.

Memory Retained after 4 Months

Four months after the initial exposure sequence, the three participants ran through three runs of follow-up new/old testing again. Due to a crash of the PsychoPy program, the behavioral response for the last run of subject 3 was lost. From data that was available, the three participants still performed above chance in recognizing the new/old of most images (AUC: participant 1 = 0.72; participant 2 = 0.74; participant 3 = 0.84; Figure 3.6 a-c).

When the behavioral performance of each subject was split by different repetition schemes, the hit rate for each was still above chance, with the exception of the 12-repetition group from participant 3. This is likely due to small sample size, as the crashing of the program only left 8 out of 12 images on which to perform the hit rate calculation.

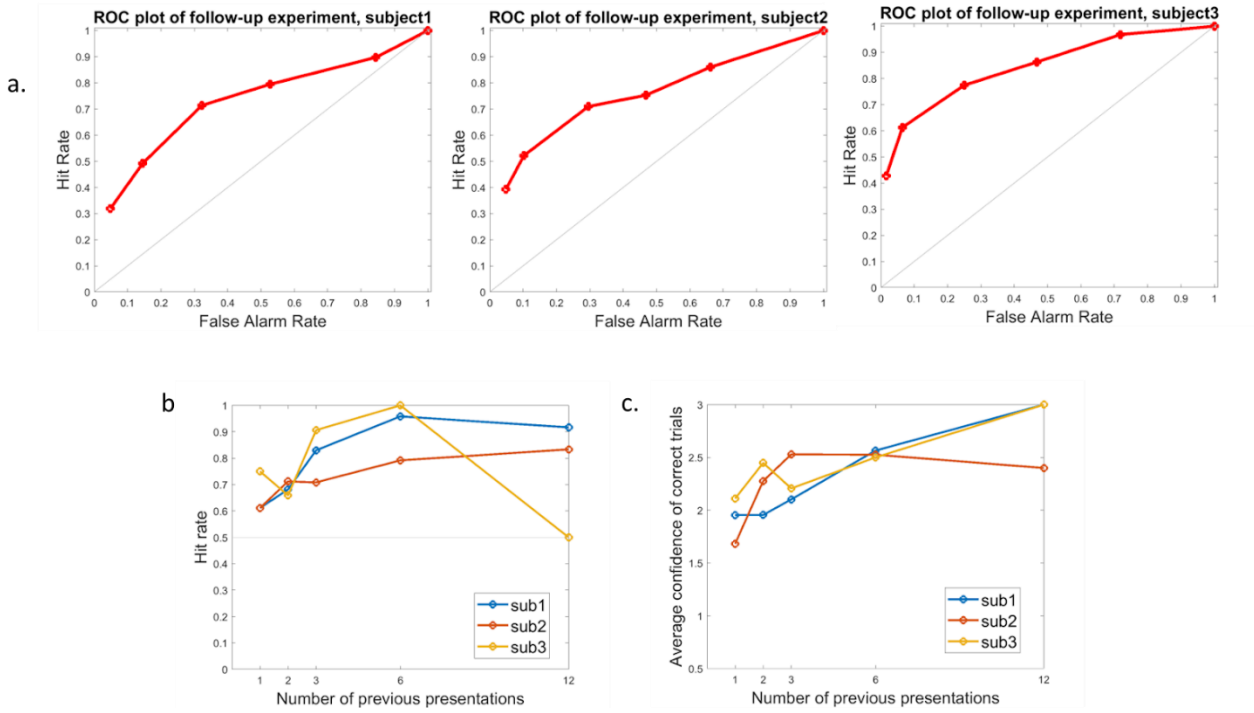

Figure 3.6 Retainment task performance for each participant. a) ROC curve for the general performance of participant 1-3. b) Group-wise hit rate breakdown for each of the three subjects. c) Group-wise confidence reporting breakdown for each of the three participants.

3.3 Conclusion

With the current protocol design, we manipulated two factors that determine familiarity strength of face stimuli, namely, the total amount of repetition of a face, and the frequency with which these repetitions occur.

Behavioral results from the three participants match the hypothesis of the existence of a continuous familiarity signal. Image groups that were systematically manipulated to be more frequently shown were better remembered and showed a higher trend of confidence reporting.

The immediate next step of analysis would be to start examining the fMRI sessions simultaneously acquired with the behavioral data. For fMRI results, we anticipate identifying differential activation patterns for successfully remembered faces compared to false alarms or missed trials, primarily within MTL and cortical regions. New/old faces are likely to elicit distinct responses from the amygdala.

Following examples from the Xue et al., 2010 paper, another thing we may be able to look at is the representational similarity of faces that are repeated for different numbers of times. From this paper, compared with forgotten items, subsequently remembered faces and words showed greater similarity in neural activation across multiple repetitions. This is something that we can also check in the current planned study, with a longer time span and more repetition than the previous study.

Chapter 4

DISCUSSION AND FUTURE DIRECTIONS

In summary, the two chapters of the thesis explored two aspects of recognition memory.

By using a cued retrieval task, the first chapter of the thesis explored single unit correlates of recognition memory for faces. Cells selective to different features of the task were identified. Despite finding an above-chance proportion of cells selective to source context during both encoding stage and recognition stages of the task, the scant overlap between the two indicates a lack of reactivation, at least on the single-cell level, for memory retrieval processes.

As the amount of recording sessions in epilepsy patients accumulates, an immediate next step for the future would be to examine whether population-level encoding exists for the source context information during the recognition stage. If so, whether the three regions of interest play different roles in the encoding of source information also remains to be explored. By using dimensionality reduction methods (for example, Kobak et al., 2016), it may also be possible to isolate the population-level representation of new/old memory from source context information.

By using a repetitive, longitudinal new/old reporting scheme, the second chapter of the thesis explored factors impacting face repetition memory. From the behavioral outcome, the face stimuli that were shown with smaller intervals and more frequently in time were better remembered. The confidence level reporting also follows a similar trend, supporting the hypothesis that more frequent repetition contributes to a higher memory strength signal.

The immediate next step of the second chapter would be to start the analysis of the accompanying fMRI data to the behavioral paradigm. With region-of-interest (ROI) analysis, it could be investigated whether the MTL region and face-related regions in temporal cortex show shifts in activity as memories of the face stimuli consolidate over the duration of the longitudinal task. Within the same session, examining how groups of images with different repetition schemes elicit different reactions in related regions may also offer insights on how long-term memory evolves as time progresses and re-exposure to the stimuli happens.

Overall, preliminary results from the two tasks offer insights to the dual processes underlying human recognition memory. Findings from the first chapter indicates that separate cell groups are in charge of familiarity and recollection processes. Task design from the second chapter established a gradient of familiarity signal in three participants through systematic variation of stimulus exposure frequency, which stayed robust even four months after the test scheme had ended.

BIBLIOGRAPHY

Allen, E. J., St-Yves, G., Wu, Y., Breedlove, J. L., Prince, J. S., Dowdle, L. T., Nau, M., Caron, B., Pestilli, F., Charest, I., Hutchinson, J. B., Naselaris, T., & Kay, K. (2022). A massive 7T fMRI dataset to bridge cognitive neuroscience and artificial intelligence. Nature Neuroscience, 25(1), 116–126. https://doi.org/10.1038/s41593-021-00962-x

Atkinson, R. C., & Juola, J. F. (1974). Search and decision processes in recognition memory. In Contemporary developments in mathematical psychology: I. Learning, memory and thinking (pp. xiii, 299–xiii, 299). W. H. Freeman.

Boyle, L., Posani, L., Irfan, S., Siegelbaum, S. A., & Fusi, S. (2022). The geometry of hippocampal CA2 representations enables abstract coding of social familiarity and identity (p. 2022.01.24.477361). bioRxiv. https://doi.org/10.1101/2022.01.24.477361

Derner, M., Dehnen, G., Chaieb, L., Reber, T. P., Borger, V., Surges, R., Staresina, B. P., Mormann, F., & Fell, J. (2020). Patterns of single-neuron activity during associative recognition memory in the human medial temporal lobe. NeuroImage, 221, 117214. https://doi.org/10.1016/j.neuroimage.2020.117214

Desimone, R., Albright, T. D., Gross, C. G., & Bruce, C. (1984). Stimulus-selective properties of inferior temporal neurons in the macaque. Journal of Neuroscience, 4(8), 2051–2062. https://doi.org/10.1523/JNEUROSCI.04-08-02051.1984

Gilmore, A. W., Nelson, S. M., & McDermott, K. B. (2015). A parietal memory network revealed by multiple MRI methods. Trends in Cognitive Sciences, 19(9), 534–543. https://doi.org/10.1016/j.tics.2015.07.004

Gilmore, A. W., Nelson, S. M., aumann, T. O., Gordon, E. M., Berg, J. J., Greene, D. J., Gratton, C., Nguyen, A. L., Ortega, M., Hoyt, C. R., Coalson, R. S., Schlaggar, B. L., Petersen, S. E., Dosenbach, N. U. F., & McDermott, K. B. (2019). High-fidelity mapping of repetition-related changes in the parietal memory network. NeuroImage, 199, 427–439. https://doi.org/10.1016/j.neuroimage.2019.06.011

Gordon, A. M., Rissman, J., Kiani, R., & Wagner, A. D. (2014). Cortical Reinstatement Mediates the Relationship Between Content-Specific Encoding Activity and Subsequent Recollection Decisions. Cerebral Cortex, 24(12), 3350–3364. https://doi.org/10.1093/cercor/bht194

Gordon, E. M., Laumann, T. O., Gilmore, A. W., Newbold, D. J., Greene, D. J., Berg, J. J., Ortega, M., Hoyt-Drazen, C., Gratton, C., Sun, H., Hampton, J. M., Coalson, R. S., Nguyen, A. L., McDermott, K. B., Shimony, J. S., Snyder, A. Z., Schlaggar, B. L., Petersen, S. E., Nelson, S. M., & Dosenbach, N. U. F. (2017). Precision Functional Mapping of Individual Human Brains. Neuron, 95(4), 791-807.e7. https://doi.org/10.1016/j.neuron.2017.07.011

Gronlund, S., & Ratcliff, R. (1989). Time Course of Item and Associative Information: Implications for Global Memory Models. Journal of Experimental Psychology. Learning, Memory, and Cognition, 15, 846–858. https://doi.org/10.1037//0278-7393.15.5.846

Josselyn, S. A., & Tonegawa, S. (2020). Memory engrams: Recalling the past and imagining the future. Science, 367(6473), eaaw4325. https://doi.org/10.1126/science.aaw4325

Kahn, I., Davachi, L., & Wagner, A. D. (2004). Functional-Neuroanatomic Correlates of Recollection: Implications for Models of Recognition Memory. The Journal of Neuroscience, 24(17), 4172–4180. https://doi.org/10.1523/JNEUROSCI.0624-04.2004

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The Fusiform Face Area: A Module in Human Extrastriate Cortex Specialized for Face Perception. Journal of Neuroscience, 17(11), 4302–4311. https://doi.org/10.1523/JNEUROSCI.17-11-04302.1997

Karras, T., Laine, S., & Aila, T. (2019). A Style-Based Generator Architecture for Generative Adversarial Networks (arXiv:1812.04948). arXiv. https://doi.org/10.48550/arXiv.1812.04948

Kleiner, M., Brainard, D., Pelli, D., Ingling, A., Murray, R., & Broussard, C. (2007). What's new in psychtoolbox-3. Perception, 36(14), 1–16.

Kobak, D., Brendel, W., Constantinidis, C., Feierstein, C. E., Kepecs, A., Mainen, Z. F., Qi, X.-L., Romo, R., Uchida, N., & Machens, C. K. (2016). Demixed principal component analysis of neural population data. eLife, 5, e10989. https://doi.org/10.7554/eLife.10989

Landi, S. M., & Freiwald, W. A. (2017). Two areas for familiar face recognition in the primate brain. Science, 357(6351), 591–595. https://doi.org/10.1126/science.aan1139

Landi, S. M., Viswanathan, P., Serene, S., & Freiwald, W. A. (2021). A fast link between face perception and memory in the temporal pole. Science (New York, N.Y.), 373(6554), 581–585. https://doi.org/10.1126/science.abi6671

Lee, A. K., & Wilson, M. A. (2002). Memory of Sequential Experience in the Hippocampus during Slow Wave Sleep. Neuron, 36(6), 1183–1194. https://doi.org/10.1016/S0896-6273(02)01096-6

Leeuw, J. R. de, Gilbert, R. A., & Luchterhandt, B. (2023). jsPsych: Enabling an Open-Source Collaborative Ecosystem of Behavioral Experiments. Journal of Open Source Software, 8(85), 5351. https://doi.org/10.21105/joss.05351

Long, J., Shelhamer, E., & Darrell, T. (2015). Fully Convolutional Networks for Semantic Segmentation (arXiv:1411.4038). arXiv. https://doi.org/10.48550/arXiv.1411.4038

Marek, S., Tervo-Clemmens, B., Calabro, F. J., Montez, D. F., Kay, B. P., Hatoum, A. S., Donohue, M. R., Foran, W., Miller, R. L., Hendrickson, T. J., Malone, S. M., Kandala, S., Feczko, E., Miranda-Dominguez, O., Graham, A. M., Earl, E. A., Perrone, A. J., Cordova, M., Doyle, O., … Dosenbach, N. U. F. (2022). Reproducible brain-wide association studies require thousands of individuals. Nature, 603(7902), Article 7902. https://doi.org/10.1038/s41586-022-04492-9

Minxha, J., Mamelak, A. N., & Rutishauser, U. (2018). Surgical and Electrophysiological Techniques for Single-Neuron Recordings in Human Epilepsy Patients. In R. V. Sillitoe (Ed.),

Extracellular Recording Approaches (pp. 267–293). Springer. https://doi.org/10.1007/978-1-4939-7549-5_14

Murre, J. M. J., & Dros, J. (2015). Replication and Analysis of Ebbinghaus' Forgetting Curve. PLOS ONE, 10(7), e0120644. https://doi.org/10.1371/journal.pone.0120644

Peirce, J., Gray, J. R., Simpson, S., MacAskill, M., Höchenberger, R., Sogo, H., Kastman, E., & Lindeløv, J. K. (2019). PsychoPy2: Experiments in behavior made easy. Behavior Research Methods, 51(1), 195–203. https://doi.org/10.3758/s13428-018-01193-y

Quiroga, R. Q. (2012). Concept cells: The building blocks of declarative memory functions. Nature Reviews Neuroscience, 13(8), Article 8. https://doi.org/10.1038/nrn3251

Quian Quiroga, R., Boscaglia, M., Jonas, J., Rey, H. G., Yan, X., Maillard, L., Colnat-Coulbois, S., Koessler, L., & Rossion, B. (2023). Single neuron responses underlying face recognition in the human midfusiform face-selective cortex. Nature Communications, 14(1), Article 1. https://doi.org/10.1038/s41467-023-41323-5

Reagh, Z. M., Murray, E. A., & Yassa, M. A. (2017). Repetition reveals ups and downs of hippocampal, thalamic, and neocortical engagement during mnemonic decisions. Hippocampus, 27(2), 169–183. https://doi.org/10.1002/hipo.22681

Rosenberg, M. D., & Finn, E. S. (2022). How to establish robust brain–behavior relationships without thousands of individuals. Nature Neuroscience, 25(7), Article 7. https://doi.org/10.1038/s41593-022-01110-9

Rubin, D. C., & Wenzel, A. E. (1996). One hundred years of forgetting: A quantitative description of retention. Psychological Review, 103(4), 734–760. https://doi.org/10.1037/0033-295X.103.4.734 ‘

Rutishauser, U., Schuman, E. M., & Mamelak, A. N. (2006). Online detection and sorting of extracellularly recorded action potentials in human medial temporal lobe recordings, in vivo. Journal of Neuroscience Methods, 154(1–2), 204–224. https://doi.org/10.1016/j.jneumeth.2005.12.033

Rutishauser, U., Schuman, E. M., & Mamelak, A. N. (2008). Activity of human hippocampal and amygdala neurons during retrieval of declarative memories. Proceedings of the National Academy of Sciences of the United States of America, 105(1), 329–334. https://doi.org/10.1073/pnas.0706015105

Rutishauser, U., Mamelak, A. N., & Adolphs, R. (2015). The primate amygdala in social perception—Insights from electrophysiological recordings and stimulation. Trends in Neurosciences, 38(5), 295–306. https://doi.org/10.1016/j.tins.2015.03.001

Schwartz, C. E., Wright, C. I., Shin, L. M., Kagan, J., Whalen, P. J., McMullin, K. G., & Rauch, S. L. (2003). Differential amygdalar response to novel versus newly familiar neutral faces: A functional MRI probe developed for studying inhibited temperament. Biological Psychiatry, 53(10), 854–862. https://doi.org/10.1016/S0006-3223(02)01906-6

She, L., Benna, M. K., Shi, Y., Fusi, S., & Tsao, D. Y. (2021). The neural code for face memory. bioRxiv, 2021.03.12.435023. https://doi.org/10.1101/2021.03.12.435023

Squire, L. R., Wixted, J. T., & Clark, R. E. (2007). Recognition memory and the medial temporal lobe: A new perspective. Nature Reviews. Neuroscience, 8(11), 872–883. https://doi.org/10.1038/nrn2154

Staresina, B. P., Reber, T. P., Niediek, J., Boström, J., Elger, C. E., & Mormann, F. (2019). Recollection in the human hippocampal-entorhinal cell circuitry. Nature Communications, 10(1), 1503. https://doi.org/10.1038/s41467-019-09558-3

Stark, C. E. L., & Squire, L. R. (2000). FMRI activity in the medial temporal lobe during recognition memory as a function of study-test interval. Hippocampus, 10(3), 329–337. https://doi.org/10.1002/1098-1063(2000)10:3<329::AID-HIPO13>3.0.CO;2-Z

Tingley, D., & Peyrache, A. (2020). On the methods for reactivation and replay analysis. Philosophical Transactions of the Royal Society B: Biological Sciences, 375(1799), 20190231. https://doi.org/10.1098/rstb.2019.0231

Wais, P. E., Wixted, J. T., Hopkins, R. O., & Squire, L. R. (2006). The Hippocampus Supports both the Recollection and the Familiarity Components of Recognition Memory. Neuron, 49(3), 459–466. https://doi.org/10.1016/j.neuron.2005.12.020

Wilson, M., & McNaughton, B. (1994). Reactivation of hippocampal ensemble memories during sleep. Science, 265(5172), 676–679. https://doi.org/10.1126/science.8036517

Wixted, J. T. (2007). Dual-process theory and signal-detection theory of recognition memory. Psychological Review, 114(1), 152–176. https://doi.org/10.1037/0033-295X.114.1.152

Xue, G., Dong, Q., Chen, C., Lu, Z., Mumford, J. A., & Poldrack, R. A. (2010). Greater Neural Pattern Similarity Across Repetitions Is Associated with Better Memory. Science, 330(6000), 97–101. https://doi.org/10.1126/science.1193125

Yonelinas, A. P. (1994). Receiver-operating characteristics in recognition memory: Evidence for a dual-process model. Journal of Experimental Psychology: Learning, Memory, and Cognition, 20(6), 1341–1354. https://doi.org/10.1037/0278-7393.20.6.1341

Yonelinas, A. P., & Jacoby, L. L. (1994). Dissociations of processes in recognition memory: Effects of interference and of response speed. Canadian Journal of Experimental Psychology / Revue Canadienne de Psychologie Expérimentale, 48(4), 516–535. https://doi.org/10.1037/1196-1961.48.4.516

Yonelinas, A. P. (2002). The Nature of Recollection and Familiarity: A Review of 30 Years of Research. Journal of Memory and Language, 46(3), 441–517. https://doi.org/10.1006/jmla.2002.2864

Yovel, G., & Paller, K. A. (2004). The neural basis of the butcher-on-the-bus phenomenon: When a face seems familiar but is not remembered. NeuroImage, 21(2), 789–800. https://doi.org/10.1016/j.neuroimage.2003.09.034