



저작자표시-비영리-변경금지 2.0 대한민국

이용자는 아래의 조건을 따르는 경우에 한하여 자유롭게

- 이 저작물을 복제, 배포, 전송, 전시, 공연 및 방송할 수 있습니다.

다음과 같은 조건을 따라야 합니다:



저작자표시. 귀하는 원저작자를 표시하여야 합니다.



비영리. 귀하는 이 저작물을 영리 목적으로 이용할 수 없습니다.



변경금지. 귀하는 이 저작물을 개작, 변형 또는 가공할 수 없습니다.

- 귀하는, 이 저작물의 재이용이나 배포의 경우, 이 저작물에 적용된 이용허락조건을 명확하게 나타내어야 합니다.
- 저작권자로부터 별도의 허가를 받으면 이러한 조건들은 적용되지 않습니다.

저작권법에 따른 이용자의 권리는 위의 내용에 의하여 영향을 받지 않습니다.

이것은 [이용허락규약\(Legal Code\)](#)을 이해하기 쉽게 요약한 것입니다.

[Disclaimer](#)

Master's Thesis of Science

A study of primate
multi-memory retrieval
and selection process
through gaze patterns

영장류의 눈 움직임 패턴을 통한
다중 기억 인출 및 선택 과정 연구

February Year 2023

Graduate School of Biological Sciences
Seoul National University

Somang Paeng

A study of primate multi-memory retrieval and selection process through gaze patterns

Advised by Professor Hyoung F. Kim

Submitting a master's thesis of
science

February 2023

Graduate School of Biological Sciences
Seoul National University

Somang Paeng

Confirming the master's thesis written by
Somang Paeng
February 2023

Chair	<u>Myunghwan Choi</u>	(Seal)
Vice Chair	<u>Hyoung F. Kim</u>	(Seal)
Examiner	<u>Chanhee Kang</u>	(Seal)

Abstract

Keyword : memory retrieval, memory selection, retrieval selection, primate eye movements, long-term memory

Student Number : 2021-21788

Memory retrieval process often involves the process of selection from multiple associated memories. The aim of this study is to investigate the process of multi-memory retrieval and selection in humans and monkeys. For the human experiments, participants were required to retrieve two long-term spatial memories associated with each visual object and select the context-appropriate memory in the selective location retrieval task. In this task, participants often demonstrated gaze patterns related to multi-memory retrieval in which they gazed at both spatial locations associated with the visual object before the context was given, and then switched to gazing at only the appropriate location. Additionally, this study showed that gaze patterns before context presentation were correlated with different levels of memory accuracy. In the experiments with a monkey, I observed similar gaze patterns during a spatial working memory task requiring selection of spatial memories. The monkey primarily alternated his gaze between the two spatial locations before context presentation and selectively gazed at one of them after context presentation. Overall, gaze patterns showed that multiple spatial memories were retrieved when a cue was given, and the appropriate memory was chosen from those memories. This study suggests that gaze patterns can be used to probe the process of multi-memory retrieval and selection and provide a behavioral task scheme and preliminary results for future studies on retrieval selection in primates.

Table of Contents

List of Tables.....	iii
List of Figures	iii
 Chapter 1. Introduction.....	 1
1.1 Problem Statement and Research Goals	1
1.2 Background	2
1.3 Research Objectives and Proposed Approach	5
 Chapter 2. Results	 7
2.1 Human Experiments	7
2.2 Monkey Experiments	23
 Chapter 3. Methods.....	 27
3.1 Human Experiments	27
3.2 Monkey Experiments	30
 Chapter 4. Discussion	 36
4.1 Expertise effects in the gaze patterns of human participants throughout learning.....	36
4.2 Possibility of external memory use during learning reflected in selective gaze pattern effects on day 2.....	38
4.3 Multi-memory retrieval: sequential vs. simultaneous retrieval?	40
4.4 Possible brain substrates for multi-memory retrieval and selection	41
4.5 Avenues for future research	43
4.6 Conclusion.....	43
 Bibliography	 44
 Abstract in Korean	 49

List of Tables

Table 1. Delay period 1 post-hoc analysis of gaze location comparisons.....	13
Table 2. Delay period 1 post-hoc analysis of retrieval day comparisons.....	14
Table 3. Delay period 2 post-hoc analysis of gaze location comparisons.....	16
Table 4. Delay period 2 post-hoc analysis of retrieval day comparisons.....	17

List of Figures

Figure 1. Selective location retrieval behavioral scheme for humans.....	7
Figure 2. Error distance of the responses in the selective location retrieval task (SLRT)	8
Figure 3. Hypothesized and example gaze patterns in the delay periods of the selective location retrieval task (SLRT).....	10
Figure 4. Gaze time by gaze location reflecting the retrieval of object location memories.....	11
Figure 5. Trial percentage of gaze pattern behavior in the delay period 1.....	20
Figure 6. The error distance of different gaze patterns.....	21
Figure 7. Monkey Experiment Results	25

Chapter 1. Introduction

1.1. Problem Statement and Research Goals

The ability to selectively retrieve the appropriate long-term memory is critical. Across lifetime, multiple memories can be associated with the same cue, making it necessary to select the appropriate memory in a given context. However, despite the importance of this cognitive process, the precise mechanism of retrieval selection has not yet been fully understood. One possible mechanism of retrieval selection is that multiple memories associated with the cue are retrieved in parallel, and the context-relevant memory is selected among the retrieved memories while other context-irrelevant candidates are suppressed. In this study, I aimed to investigate whether this proposed process of "multi-memory retrieval and selection" actually occurs in the brain.

In investigating the underlying cognitive processes, utilizing primates as models can be of advantage. Human and non-human primate (NHP) cross-species studies provide strong means of understanding neural processes. A recent study has shown that functional magnetic resonance imaging (fMRI) in humans and electrophysiology in monkeys can complement each other to provide a more comprehensive understanding of the neural processes (Kang et al., 2021). The basis of these cross-species studies is the assumption that similar behaviors in different species are supported by similar neural mechanisms. Therefore, the first step in human-NHP cross-species studies is to establish a compatible behavioral task scheme and behavioral indices that can be used in both species.

Moreover, establishing an appropriate behavioral index in the study of cognitive processes is important as it can not only provide insight into the internal cognitive process, but also aid in the verification of future neural activity-based studies. In neural activity-based studies utilizing fMRI or neural recordings, behavioral indices can serve as markers for identifying or decoding

the recorded neural activity. With these in mind, my aim was to establish and use primate behavioral indices to study the multi-memory retrieval and selection process.

1.2. Background

1) Previous behavioral index (retrieval-induced forgetting) may be insufficient in capturing the full temporal dynamics of retrieval selection

In literature, one widely-utilized behavioral index of multi-memory retrieval and selection is a phenomenon called “Retrieval-induced forgetting” (RIF). RIF refers to the phenomenon in which the repeated recall of one memory results in the impairment of the related competitor memories later (Anderson et al., 1994; Levy & Anderson, 2002). Many have suggested that RIF is the result of the inhibition of the related memories that are not appropriate to the current context in the process of selecting the appropriate memory.

However, RIF has its limitation in that it is not sufficient in capturing the full temporal dynamics of retrieval selection. The output of retrieval selection is a memory that is relevant to the given context. In other words, the explicit report of the memory is already the product of the internal multi-memory retrieval and selection process that presumably precedes this output memory. As my goal is to probe into the process of retrieval selection, an appropriate behavioral index of retrieval selection should be able to reflect the process preceding the selected memory output in a timely manner. RIF, by definition, is an accumulative behavioral effect of repeated inhibition and cannot fully capture the transient process of the multi-memory retrieval and selection. In this study, I utilized a more online behavioral index to supplement this issue. More specifically, I reasoned that to fully grasp the retrieval selection process, the behavioral index should occur spontaneously at the time of retrieval selection and be independent of explicit reports of memory. As explicit reports of a memory are already the

product of the internal cognitive process that precedes the output, retrieval selection may not be accessed through a report of the subjects. This underlines the importance of a behavioral index that can be acquired without an explicit report of the subjects. Moreover, these criteria are also useful for cross-species studies. A behavioral index independent of explicit reports is useful for the use in non-human primates, where verbal reports of the cognitive processes cannot be used. Also, as the behavioral index should enable trial-by-trial analysis, it can provide a more precise analysis of the neural mechanisms in the unit of individual trials when combined with neuroimaging techniques such as neural recordings.

2) Gaze patterns as a behavioral index of memory

Here I suggest primate gaze patterns as such an index of multi-memory retrieval and selection that meets the criteria mentioned above. Previous literature supports that primate gaze patterns reflect internal memory retrieval processes. It was recently shown that participants' retrieval accuracy was higher when their gaze patterns during memory encoding were reinstated during the retrieval task (Wynn et al., 2020). Another study showed that human participants gaze longer at the picture that was associated with the given context during learning than the non-associated picture, even without explicit memory (Hannula & Ranganath, 2009). A line of studies has also established that both humans and monkeys exhibit a habitual gaze toward higher-value objects based on long-term memory, suggesting the possibility of cross-species behavioral similarities (S.-H. Hwang et al., 2022; Kang et al., 2021; Kim et al., 2015; Kim & Hikosaka, 2013).

Another strong point of using gaze patterns as the behavioral index comes from studies that memory effects on gaze behavior precede explicit responses (Hannula & Ranganath, 2009; Holm et al., 2008) and are expressed even when explicit recollection fails (Beck et al., 2007; Hannula & Ranganath, 2009), implying that gaze

patterns may even reveal implicit cognitive processes (see Hannula et al., 2010 for review). These studies suggest that using gaze behavior as a behavioral index of retrieval selection can reflect more temporally precise process before explicit responses.

Among many properties of gaze behavior, this study focused primarily on the gaze locations. Humans are known to look at locations where visual or verbal information was encoded previously when trying to recall that information later, even when the location is now empty (Richardson & Spivey, 2000; Spivey & Geng, 2001). This widely reported behavior called “looking-at-nothing” (LAN) spontaneously occurs when people try to recall information, even when no visual information is available now. This study makes use of LAN behavior in selective location retrieval task as indications of which associated memory is being retrieved. To utilize LAN, I constructed my task scheme so that subjects have to associate visual objects and their spatial locations. By requiring spatial memory retrieval, I sought to ensure the emergence of LAN to probe into the retrieval selection process. In addition, remembering the location of objects is essential for survival in a diverse range of animals. When animals forage for food, remember where they left food stocks, or remember where a water supply is, these are all demonstrations of spatial memory that are critical for survival. Therefore, the use of spatial memory of objects in my behavioral task scheme is a more naturalistic and intuitive component for both humans and monkeys.

Collectively, these studies provide evidence that gaze patterns may reveal the internal memory retrieval processes. Thus, this study utilizes the participants’ gaze patterns, along with other task-related behavioral responses such as response accuracy and response time, as behavioral indices to verify the multi-memory retrieval and selection process.

1.3. Research Objectives and Proposed Approach

With the goal of probing into multi-memory retrieval and selection process through primate behavioral indices, the objectives are 1) to establish a task scheme designed for multi-memory retrieval and selection, compatible with human and NHP studies, 2) to collect and analyze human gaze patterns and behavioral responses in the designed task scheme to examine the multi-memory retrieval and selection process, and finally, 3) to replicate the gaze patterns related to multi-memory retrieval and selection in a monkey subject, providing a behavioral tool for future human-NHP cross-species neural studies of multi-memory retrieval and selection process.

My research approach to reach these objectives are specified below, divided into two sections for human and monkey experiments.

Human Experiments: Selective location retrieval behavioral scheme

For my study with human participants, I first designed a behavioral task scheme that induces multi-memory retrieval and selection. The task scheme included two tasks, the object-location learning and the selective location retrieval task (SLRT). In the object-location learning task, multiple spatial memories (one on the left and one on the right side of the screen) were associated with visual objects. The participants' ability to selectively retrieve these memories was tested in the SLRT. The SLRT was designed so that the visual object is presented first, prompting multi-memory retrieval of the spatial memories. The contextual boundary box indicating either on the left or right side of the screen is presented later, prompting the selection of these memories. The behavioral task scheme is designed so that all responses during both learning and retrieval tasks are done by joystick manipulation. Participants were not in any way required to fixate on or make a saccade towards anything. Thus, this design ensures full independence and

natural gaze behavior that can be used as an index for the multi-memory retrieval and selection process.

Assuming that the eye movements reflect which spatial memory is being retrieved, the gaze patterns during the retrieval task before and after the contextual boundary box presentation should reveal the memories before and after retrieval selection, respectively. I hypothesized that if multiple memories are retrieved first when a cue is given, the participants would look at both locations associated with the object before the boundary box presentation. This looking at the two locations would converge to one location after the boundary box presentation.

Monkey Experiments: Selective working memory retrieval task

My objective regarding monkey experiments was to present preliminary results of gaze patterns related to multi-memory retrieval and selection. I first designed a selective working memory retrieval task similar to the human SLRT and underwent progressive training with one monkey subject. In the selective working memory retrieval task, two circles were presented in random locations on the touchscreen. The monkey had to retain the two spatial memories and touch one of the two locations that is inside the contextual boundary box after a delay period. Touch responses ensured independence of the gaze behavior, and the similarity in the task scheme to the human task design ensured task compatibility between the two species. I expected similar gaze patterns in which the monkey looks at the two locations in the delay before context reflecting multi-memory retention, and looks at the appropriate location after context reflecting selection among the memories. By confirming similar behaviors are replicated in humans and monkeys, this study provides a foundation for future cross-species retrieval selection research.

Overall, this study implements the use of natural gaze patterns and long-term memory-based behavioral tasks to probe into the multi-memory retrieval and selection process.

Chapter 2. Results

2.1. Human Experiments

1) Establishment of selective location retrieval behavioral scheme for human participants

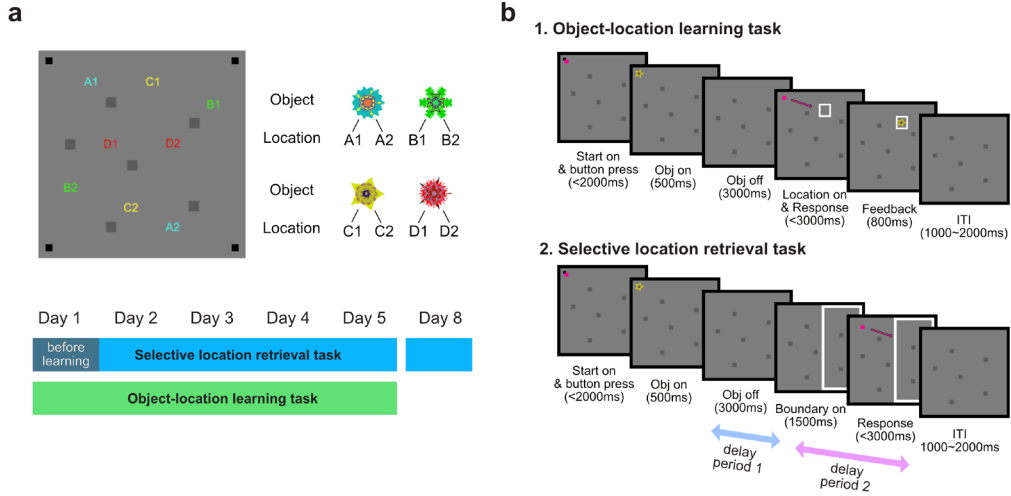


Figure 1. Selective location retrieval behavioral scheme for humans. (a) (Top) All object–location associations are shown. On the left, all locations of object–location associations are shown on the screen. The grey dots were shown as background of the task, and were included to provide a spatial reference to the participants. The black dots on the four corners of the screen indicate the starting point locations. One of them was turned on at the start of each trials in both tasks. (Bottom) A timeline of behavioral task scheme is shown. Note that on day 1, selective location retrieval task was done before object–location learning task. This was included as a control task. **(b)** The object–location learning task and selective location retrieval task (SLRT) are shown. Note that the delay period 1 and 2 is used in future gaze pattern analyses.

I designed a selective location retrieval behavioral scheme (Fig. 1) in which participants had to respond according to the appropriate spatial memory of the object among the two object–associated spatial memories. Each of the four visual objects was associated with two locations, one on the left side and the other on the right side of the screen. These associations were learned through the object–location learning task for five consecutive days. In the task, a visual object and one of the two associated locations was

presented pseudo-randomly in each trial, and the participants were required to move the joystick to the indicated location and respond by pressing a button. Their memory of the object–location associations was tested on the next day, in the SLRT. The SLRT was also performed before learning on day 1 as a control, and on day 8 for the last assessment. In each trial of the SLRT, a visual object was presented first. After a short period, a white boundary box either on the left or the right side of the monitor was presented, which served as a context that indicates which of the two associated locations the participants had to selectively retrieve.

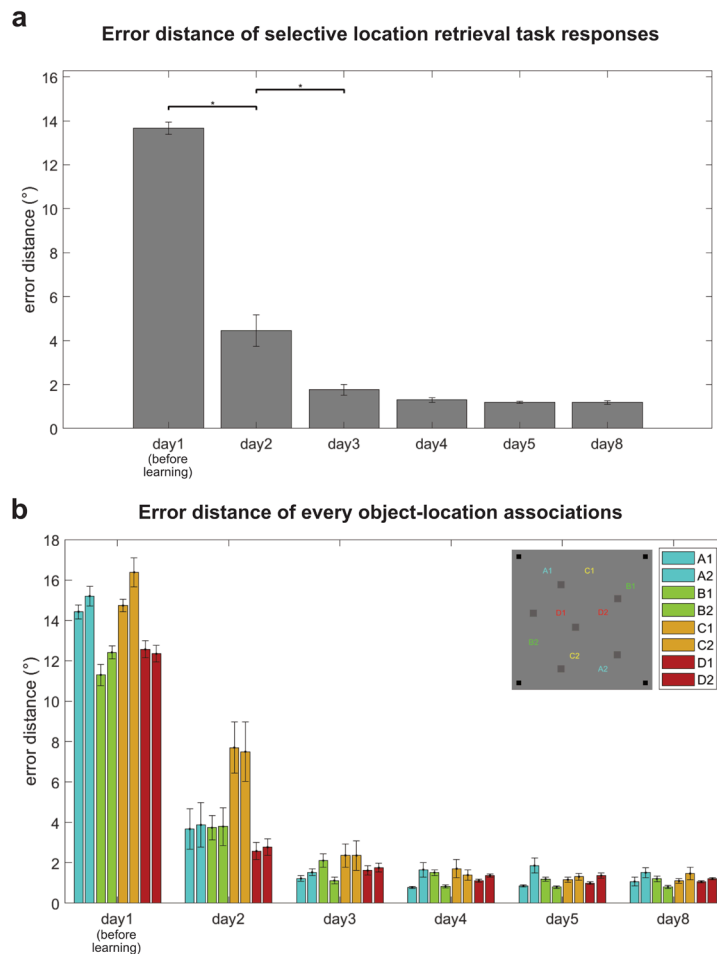


Figure 2. Error distance of the responses in the selective location retrieval task (SLRT). (a) Error distance data of all responses. Error distance is the Euclidian distance from the joystick response location and the answer location of each trial. (b) Error distance of every object–location associations. Error bars indicate between-subjects s.e.m.

The results of the SLRT show that participants successfully learned and retained multi-memory throughout a period of eight days. The decreasing error distance (distance between the joystick response and the answer location; index of response accuracy) in the SLRT reflects the learning occurring throughout the task scheme (Fig. 2). The participants were able to successfully distinguish between the two memories to respond accurately to the boundary that was given, showing that retrieval selection occurred successfully. Repeated measures ANOVA showed a main effect of retrieval days ($F(1.5353, 29.171) = 230.8757, p = 2.1547 \times 10^{-17}$). Post-hoc tests using the Bonferroni method show that learning converged from day 3 (day 1 vs. day 2: $p = 7.7163 \times 10^{-9}$; day 2 vs. day 3: $p = 0.0096$), and participants were able to respond accurately even on day 8. This result shows that the participants were able to successfully learn and selective retrieve the object location memories, the learning being saturated from day 3.

2) Human gaze patterns reflect the retrieval of the object location memory in the selective location retrieval task (SLRT)

I first investigated whether gaze patterns reflect the retrieval of spatial memory of the visual objects as reported in previous studies. I analyzed the participants' gaze patterns during the SLRT, focusing on delay period 1 and 2 (Fig. 3). I defined delay period 1 to be a 3000 ms period from when the visual object is turned off until the boundary box is presented. In delay period 1, the visual object is already given, but the boundary box indicating which of the two associated locations is the to-be-retrieved target location is not given yet. Delay period 2 is defined to be from the boundary box presentation until the participant makes a response. I hypothesized that if the participants' gaze patterns reveal the retrieval of spatial memory of the objects, the participants will look at one of the two locations or both associated with the object during delay period 1, and they will look at the target location during delay period 2 (Fig. 3). I indeed found that participants displayed these hypothesized

gaze patterns, as shown in three example trials in Figure 3.

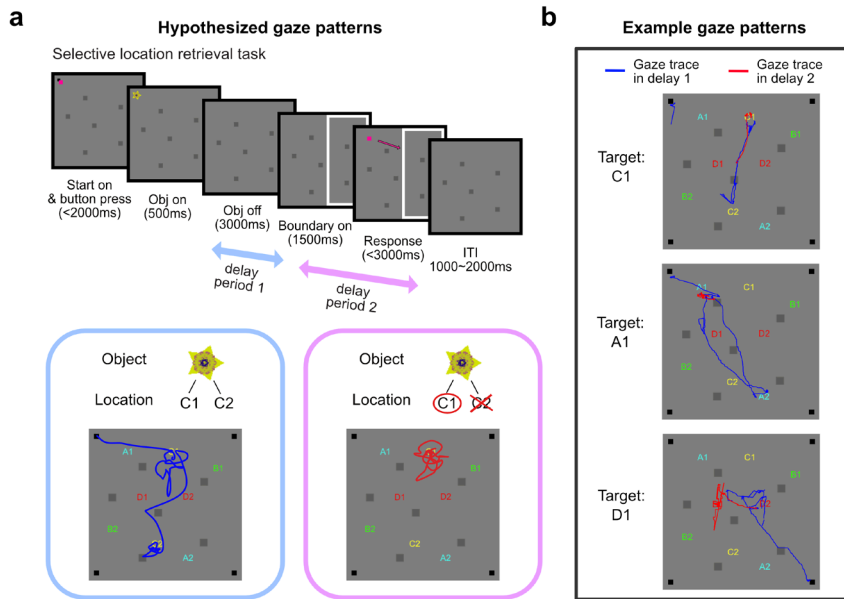


Figure 3. Hypothesized and example gaze patterns in the delay periods of the selective location retrieval task (SLRT). (a) Hypothesized gaze patterns are shown in a diagram. In delay period 1 of the selective location retrieval task (SLRT), I hypothesized the gaze locations to be towards both locations associated with the object. In delay period 2, I hypothesized that there would be selective gaze towards the target location. (b) Three example trials of eye trace data are shown. The target of each trials is indicated on the left. The blue trace represents the eye data obtained from delay period 1, and the red trace represents the eye data obtained from delay period 2.

For quantification of these gaze patterns, I defined the gaze locations as target, competitor, or outside locations for each trial (Fig. 4). The visual object-associated location (radius = 4.5° visual angle from the center of the visual object) that is inside the eventually-given boundary box was defined as the target location, and the visual object-associated location that is outside the boundary box was defined as the competitor location. All other locations outside target or competitor locations were defined as outside. I analyzed how long the participants' gaze stayed in each location type (target, competitor, and outside) across trials during delay period 1 and 2. The results are shown in Figure 4.

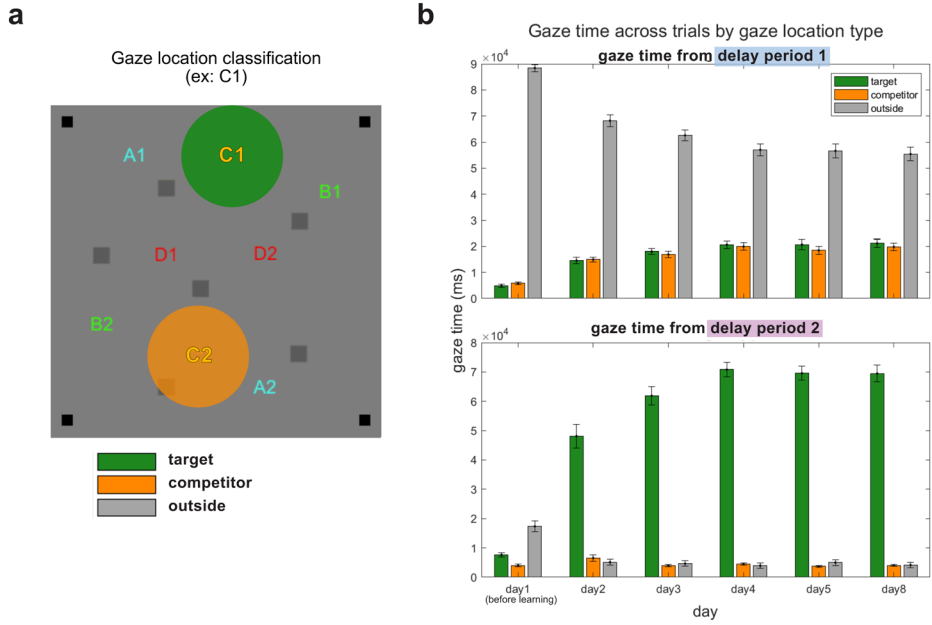


Figure 4. Gaze time by gaze location reflecting the retrieval of object location memories. (a) Diagram of gaze location classification, with the example being a trial where C1 is the target location. The radius of the target and competitor windows is 4.5° visual angle. (b) Gaze time across trials by gaze location type. The above graph shows gaze time from delay period 1, and the bottom graph shows gaze time from delay period 2 of all trials. Error bars indicate between-subjects s.e.m.

Repeated-measures two-way ANOVA revealed that in the delay period 1, there was a significant main effect of gaze locations ($F(0.3053, 5.8016) = 387.164, p = 6.520 \times 10^{-15}$), and a significant interaction between retrieval days and gaze locations ($F(1.5267, 29.0081) = 46.113, p = 2.002 \times 10^{-20}$). Bonferroni post-hoc analyses revealed that throughout day 1 to day 8, gaze time towards competitor and target locations were significantly lower than gaze time towards outside locations (see Table 1 for statistical results). However, there were no significant differences between gaze time towards target or gaze time towards competitor across days. In across-days pairwise comparisons, gaze time of competitor locations generally increased (significant differences in day 1 vs. all other days, day 2 vs. 4,6; see Table 2). Gaze time towards target locations generally increased (significant day 1 vs. all other days, day 2 vs. 4,5,6; see Table 2). Conversely, gaze time

towards outside locations generally decreased (significant differences in day 1 vs. all other days, day 2 vs. 4,5,6, day 3 vs 4; see Table 2).

In delay period 2, there was a significant main effect of days and gaze locations, and significant interaction between the two factors (repeated-measures two-way ANOVA, with days and gaze locations as factors. $F(1.0448, 19.8506) = 73.852$, $p = 4.3078 \times 10^{-20}$ for days effect; $F(0.4179, 7.9402) = 513.479$, $p = 6.1656 \times 10^{-18}$ gaze location effects; $F(2.0895, 39.7012) = 103.293$, $p = 1.951 \times 10^{-23}$ for days x gaze locations). Post-hoc Bonferroni pairwise comparisons revealed that from day 2, gaze time towards target were significantly different from gaze time towards competitor or outside (Fig. 4, Table 3). Pairwise comparisons across days revealed that gaze location towards target increased as retrieval days increased (Table 4).

These results revealed that participants gazed at both locations associated with the cue object before the boundary was presented (delay period 1) across all trials. This gaze behavior switched to gazing at mostly the target location after the boundary box was presented (delay period 2) (Fig. 4). In other words, participants gazed mainly at the locations they had to recall. Thus, the gaze patterns reflect the retrieval of the spatial memory of the objects.

Table 1. Delay period 1 post-hoc analysis of gaze location comparisons

day	Group 1	Group 2	Difference	SE	p Value
Day 1	Comp	Outside	-8.263×10^4	1.578×10^3	1.560×10^{-21}
	Comp	Target	900.650	505.210	0.2719
	Target	Outside	-8.353×10^4	1.731×10^3	7.250×10^{-21}
Day 2	Comp	Outside	-5.327×10^4	3.131×10^3	1.766×10^{-12}
	Comp	Target	353.300	967.736	1
	Target	Outside	-5.362×10^4	3.502×10^3	1.150×10^{-11}
Day 3	Comp	Outside	-4.570×10^4	3.039×10^3	1.575×10^{-11}
	Comp	Target	-1.133×10^3	1.268×10^2	1
	Target	Outside	-4.4571×10^4	3.078×10^3	3.064×10^{-11}
Day 4	Comp	Outside	-3.710×10^4	3.524×10^3	6.879×10^{-9}
	Comp	Target	-697	1.270×10^3	1
	Target	Outside	-36398	3.563×10^3	1.118×10^{-8}
Day 5	Comp	Outside	-3.819×10^4	3.990×10^3	3.174×10^{-8}
	Comp	Target	-2.263×10^3	1.425×10^3	0.386
	Target	Outside	-3.593×10^4	4.393×10^3	3.613×10^{-7}
Day 8	Comp	Outside	-3.563×10^4	3.898×10^3	6.589×10^{-8}
	Comp	Target	-1.346×10^3	1.106×10^3	0.715
	Target	Outside	-3.428×10^4	4.055×10^3	2.189×10^{-7}

Table 2. Delay period 1 post-hoc analysis of retrieval day comparisons

Gaze location	Day (1)	Day (2)	Difference	SE	p Value
Comp	Day 1	Day 2	-9.115×10^3	1.208×10^3	5.947×10^{-6}
	Day 1	Day 3	-1.109×10^4	1.513×10^3	8.994×10^{-6}
	Day 1	Day 4	-1.414×10^4	1.751×10^3	2.195×10^{-6}
	Day 1	Day 5	-1.263×10^4	1.846×10^3	2.367×10^{-5}
	Day 1	Day 8	-1.399×10^4	$1,664 \times 10^3$	1.193×10^{-6}
	Day 2	Day 3	-1.977×10^3	1.282×10^3	1
	Day 2	Day 4	-5.024×10^3	1.490×10^3	0.0480
	Day 2	Day 5	-3.513×10^3	1.591×10^3	0.597
	Day 2	Day 8	-4.877×10^3	1.304×10^3	0.021
	Day 3	Day 4	-3.047×10^3	1.176×10^3	0.269
	Day 3	Day 5	-1.536×10^3	1.353×10^3	1
	Day 3	Day8	-2.900×10^3	1.440×10^3	0.876
	Day 4	Day 5	1.511×10^3	1.218×10^3	1
	Day 4	Day8	147.700	1.349×10^3	1
	Day 5	Day 8	-1.363×10^3	1.243×10^3	1
Outside	Day 1	Day 2	2.025×10^4	2.695×10^3	6.327×10^{-6}
	Day 1	Day 3	2.583×10^4	2.151×10^3	3.843×10^{-9}
	Day 1	Day 4	3.140×10^4	2.284×10^3	3.804×10^{-10}
	Day 1	Day 5	3.181×10^4	3.011×10^3	3.231×10^{-8}
	Day 1	Day 8	3.301×10^4	2.936×10^3	1.158×10^{-8}
	Day 2	Day 3	5.588×10^3	2.161×10^3	0.272
	Day 2	Day 4	1.115×10^4	2.395×10^3	0.003
	Day 2	Day 5	1.156×10^4	2.625×10^3	0.005
	Day 2	Day 8	1.276×10^4	2.270×10^3	3.015×10^{-4}
	Day 3	Day 4	5.562×10^3	1.469×10^3	1.872×10^{-2}
	Day 3	Day 5	5.977×10^3	2.681×10^3	0.570
	Day 3	Day8	7.177×10^3	2.363×10^3	0.102
	Day 4	Day 5	4.152×10^2	2.282×10^3	1

	Day 4	Day8	1.615×10^3	2.108×10^3	1
	Day 5	Day 8	1.200×10^3	1.862×10^3	1
Target	Day 1	Day 2	-9.662×10^3	1.515×10^3	6.088×10^{-5}
	Day 1	Day 3	-1.313×10^4	1.251×10^3	3.64×10^{-8}
	Day 1	Day 4	-1.574×10^4	1.607×10^3	1.104×10^{-7}
	Day 1	Day 5	-1.579×10^4	2.056×10^3	4.588×10^{-6}
	Day 1	Day 8	-1.624×10^4	1.831×10^3	5.272×10^{-7}
	Day 2	Day 3	-3.463×10^3	1477.182252 05608	0.451
	Day 2	Day 4	-6.075×10^3	1.477×10^3	8.879×10^{-3}
	Day 2	Day 5	-6.129×10^3	1.687×10^3	2.660×10^{-2}
	Day 2	Day 8	-6.576×10^3	1.656×10^3	1.227×10^{-2}
	Day 3	Day 4	-2.6112×10^3	1.117×10^3	0.457
	Day 3	Day 5	-2.666×10^3	1.838×10^3	1
	Day 3	Day8	-3.113×10^3	1.434×10^3	0.643
	Day 4	Day 5	-5.455×10^2	1.634×10^3	1
	Day 4	Day8	-5.011×10^2	1.403×10^3	1
	Day 5	Day 8	-4.466×10^2	1.097×10^3	1

Table 3. Delay period 2 post-hoc analysis of gaze location comparisons

day	Group 1	Group 2	Difference	SE	p Value
Day 1	Comp	Outside	-1.332×10^4	1.939×10^3	4.481×10^{-6}
	Comp	Target	-3.632×10^3	8.344×10^2	1.028×10^{-3}
	Target	Outside	-9.686×10^3	2.457×10^3	2.621×10^{-3}
Day 2	Comp	Outside	1.447×10^3	1.236×10^3	7.676×10^{-3}
	Comp	Target	-4.1563×10^4	4.523×10^3	6.049×10^{-8}
	Target	Outside	4.301×10^4	4.4086×10^3	2.347×10^{-8}
Day 3	Comp	Outside	-6.443×10^2	9.198×10^2	1
	Comp	Target	-5.787×10^4	3.158×10^3	4.678×10^{-13}
	Target	Outside	5.723×10^4	3.492×10^3	3.441×10^{-12}
Day 4	Comp	Outside	4.567×10^2	1.073×10^3	1
	Comp	Target	-6.639×10^4	2.511×10^3	5.684×10^{-3}
	Target	Outside	6.6849×10^4	2.961×10^3	1.0428×10^{-14}
Day 5	Comp	Outside	-1.302×10^3	1.058×10^3	0.700
	Comp	Target	-6.587×10^4	2.477×10^3	5.106×10^{-16}
	Target	Outside	6.457×10^4	3.119×10^3	5.112×10^{-14}
Day 8	Comp	Outside	-1.418×10^2	1.019×10^3	1
	Comp	Target	-6.547×10^4	2.929×10^3	1.258×10^{-14}
	Target	Outside	6.532×10^4	3.416×10^3	2.151×10^{-13}

Table 4. Delay period 2 post-hoc analysis of retrieval day comparisons

Gaze location	Day (1)	Day (2)	Difference	SE	p Value
Comp	Day 1	Day 2	-2.532×10^3	1.148×10^3	0.600
	Day 1	Day 3	2.310×10^1	5.813×10^2	1
	Day 1	Day 4	-3.984×10^2	5.981×10^2	1
	Day 1	Day 5	3.216×10^2	5.609×10^2	1
	Day 1	Day 8	2.450	5.206×10^2	1
	Day 2	Day 3	2.555×10^3	1.071×10^3	0.414
	Day 2	Day 4	2.134×10^3	1.082×10^3	0.951
	Day 2	Day 5	2.854×10^3	1.022×10^3	0.175
	Day 2	Day 8	2.535×10^3	1.095×10^3	0.480
	Day 3	Day 4	-4.215×10^2	4.174×10^2	1
	Day 3	Day 5	2.985×10^2	2.879×10^2	1
	Day 3	Day 8	-2.065×10^1	4.663×10^2	1
	Day 4	Day 5	7.200×10^2	4.060×10^2	1
	Day 4	Day 8	4.008×10^2	5.118×10^2	1
	Day 5	Day 8	-3.191×10^2	3.843×10^2	1
Outside	Day 1	Day 2	1.223×10^4	2.266×10^3	4.934×10^{-4}
	Day 1	Day 3	1.270×10^4	1.815×10^3	1.736×10^{-5}
	Day 1	Day 4	1.338×10^4	1.791×10^3	6.869×10^{-6}
	Day 1	Day 5	1.234×10^4	1.908×10^3	5.087×10^{-5}
	Day 1	Day 8	1.318×10^4	1.848×10^3	1.328×10^{-5}
	Day 2	Day 3	4.635×10^2	1.050×10^3	1
	Day 2	Day 4	1.143×10^3	1.123×10^3	1
	Day 2	Day 5	1.045×10^2	1.041×10^3	1
	Day 2	Day 8	9.453×10^2	1.095×10^3	1
	Day 3	Day 4	6.795×10^2	4.412×10^2	1
	Day 3	Day 5	-3.590×10^2	6.107×10^2	1
	Day 3	Day 8	4.818×10^2	6.454×10^2	1
	Day 4	Day 5	-1.038×10^3	6.557×10^2	1

	Day 4	Day 8	-1.976×10^2	5.462×10^2	1
	Day 5	Day 8	8.408×10^2	6.192×10^2	1
Target	Day 1	Day 2	-4.046×10^4	4.422×10^3	3.236×10^{-7}
	Day 1	Day 3	-5.422×10^4	3.260×10^3	1.327×10^{-11}
	Day 1	Day 4	-6.316×10^4	2.459×10^3	4.853×10^{-15}
	Day 1	Day 5	-6.192×10^4	2.546×10^3	1.326×10^{-14}
	Day 1	Day 8	-6.183×10^4	2.998×10^3	2.735×10^{-13}
	Day 2	Day 3	-1.375×10^4	4.367×10^3	7.926×10^{-2}
	Day 2	Day 4	-2.270×10^4	4.428×10^3	9.028×10^{-4}
	Day 2	Day 5	-2.146×10^4	4.334×10^3	1.333×10^{-3}
	Day 2	Day 8	-2.137×10^4	4.687×10^3	3.218×10^{-3}
	Day 3	Day 4	-8.943×10^3	2.445×10^3	2.509×10^{-2}
	Day 3	Day 5	-7.703×10^3	3.035×10^3	0.301
	Day 3	Day 8	-7.616×10^3	2.915×10^3	0.257
	Day 4	Day 5	1.240×10^3	1.830×10^3	1
	Day 4	Day 8	1.327×10^3	1.754×10^3	1
	Day 5	Day 8	8.710×10^1	1.620×10^3	1

3) Participants' gaze patterns to both object-associated locations possibly reflect the multi-memory retrieval process in the brain

Through previous analysis, I established that natural gaze patterns towards the location(s) associated with the visual object arise during delay period 1 and 2, revealing which spatial memory is being retrieved. However, the analysis was done across all trials of the SLRT and so it cannot reveal the gaze patterns on a trial-by-trial basis. I have previously hypothesized that if gaze patterns can reveal multiple memories being retrieved when a cue is given, the participants would look at both locations associated with the visual object before the appropriate context is given. To find out if participants looked at either one of the two associated locations in each trial (look at one), or if they alternated their gaze between the two associated locations (look at both) in each trial. Thus, I next analyzed the portion of trials where participants looked at only one of the locations associated with the given object or alternated their gaze between the two locations during delay period 1. To do so, I divided the trials according to the gaze behavior during delay period 1. If the participant looked at only one of the object-associated locations (either target or competitor locations, defined as in Fig. 4), the trial was classified as a “look at one” trial. If on the other hand, the participant looked at two object-associated locations during delay period 1 of the trial, that trial was classified as a “look at both” trial.

The result revealed that in most of the trials, participants gazed towards at least one of the two object-associated locations during delay period 1 (look at one trials: $46.875 \pm 3.7183\%$, look at both trials: $45.47 \pm 4.87\%$ on day 8) (Fig. 5). To rephrase, gaze patterns to relevant locations based on spatial memory spontaneously occurred in more than 90% of the trials. This result shows that participants retrieved the associated spatial memory after the target object was given, and gaze patterns spontaneously reflected the retrieval.

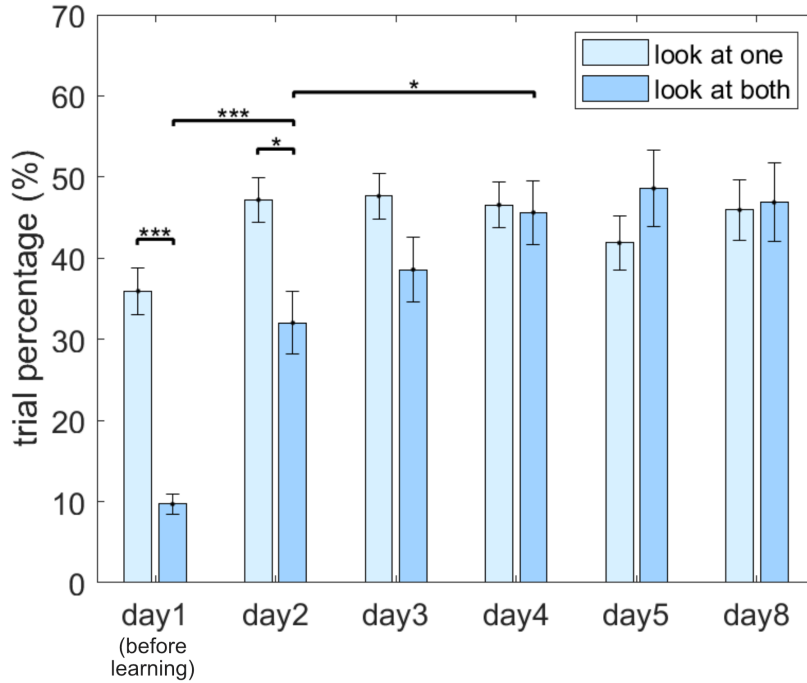


Figure 5. Trial percentage of gaze pattern behavior in the delay period 1.
Error bars indicate between-subjects s.e.m. * $p < 0.05$, *** $p < 0.001$.

Repeated measures two-way ANOVA with day and looking patterns (look at one, look at both) as factors revealed a significant main effect of day, $F(1.4821, 28.16) = 60.958$, $p = 1.871 \times 10^{-15}$. There was no significant main effect of looking patterns $F(0.2964, 5.6320) = 2.832$, $p = 0.109$. However, there was significant interaction between day and looking patterns, $F(1.4821, 28.16) = 5.119$, $p = 0.0017$. Post hoc Bonferroni pairwise comparisons revealed that the proportion of look at both trials significantly differed between day 1 and 2 ($p = 5.295 \times 10^{-4}$), and day 2 and 4 ($p = 0.0158$), with look at both trial percentages increasing as days go on. The percentage of look at both trials did not significantly differ from look at one trials from day 3, showing that look at both gaze patterns emerged as learning progressed, reaching to be similar level as look at one trials from day 3 (day 1: $p = 8.520 \times 10^{-8}$, day 2: $p = 0.0111$). With the assumption that gaze patterns reveal the retrieved spatial memory, these look at both gaze patterns show multiple memories being retrieved before the retrieval selection occurs.

4) Look at both gaze patterns were correlated with higher memory accuracy on day 2

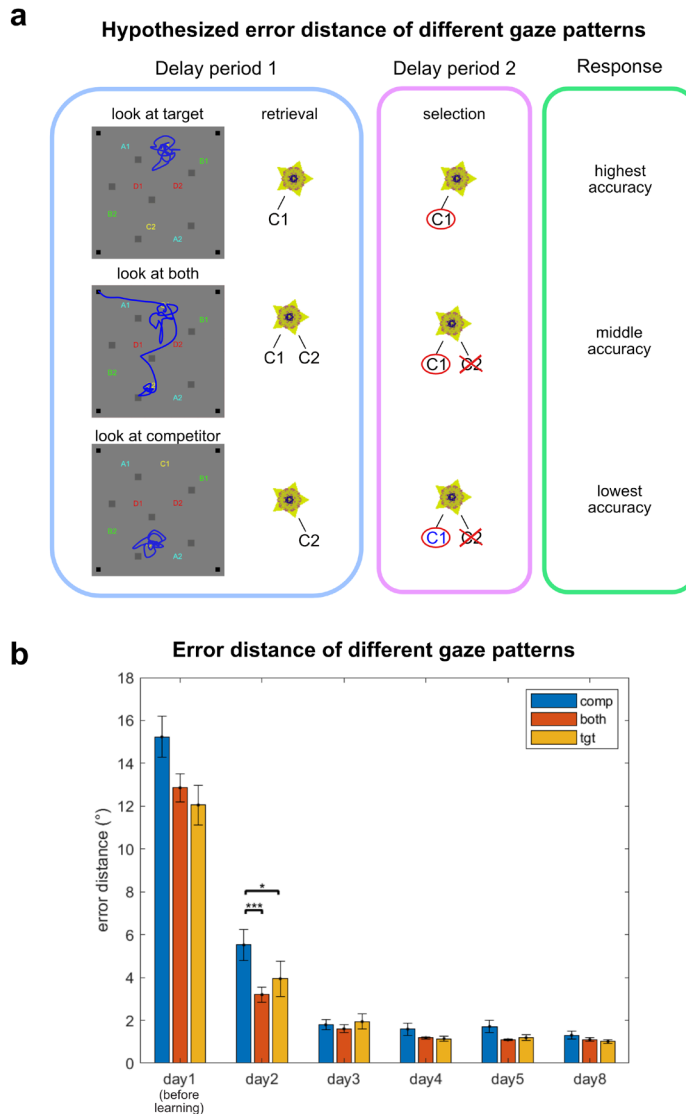


Figure 6. The error distance of different gaze patterns. (a) Hypothesized error distance according to the different gaze patterns displayed in delay period 1. On the left side, the gaze trace of each gaze pattern (look at target, look at both, look at competitor), and the spatial memories that are hypothesized to be reflected in the gaze traces are shown. In the middle, the proposed retrieval selection is shown for each gaze pattern. On the right side, the hypothesized response accuracy according to the three gaze patterns are shown. (b) Observed error distance of the different gaze patterns. Error bars indicate between-subjects s.e.m. * $p < 0.05$, *** $p < 0.001$.

Previous results have established that participants often display looking at both gaze pattern within each trial. To further confirm whether these look at both gaze patterns truly reflect multi-memory retrieval, I looked at whether different gaze patterns can predict response properties such as error distance and/or response times (Fig. 6a). I hypothesized that if gaze patterns reflect memory retrieval, the response accuracy of trials when the participants only looked at competitor–near locations (“look at competitor”) during delay period 1 should be lower than in trials where participants only looked at target–near locations (“look at target”) or when they looked at both locations (“look at both”) (Fig. 6b). When the boundary box is given consecutively, the participant would have to retrieve the memory of the target location and suppress the memory of the already–retrieved competitor location. In contrast, in “look at target” trials, the participant would not need to newly retrieve or suppress anything, and in “look at both” trials, the participant would only need to suppress the competitor memory. Thus, this would result in a relatively inaccurate response in the order of “look at competitor”, “look at both”, and “look at target” trials given the limited time that the participants had to respond in. By analyzing whether these three gaze patterns during delay period 1 can predict response accuracy, I could verify the multi-memory retrieval reflected through alternating gaze patterns.

To test my hypothesis, I first categorized the trials of the SLRT into “look at target”, “look at competitor”, or “look at both” patterns according to the gaze patterns exhibited during delay period 1, and analyzed the error distance of the trial categories. A permutation–based pairwise comparison analysis was performed to determine the differences between the means of three gaze patterns (look at target, look at competitor, and look at both) for each day. The results of the permutation test indicate that on day 2, the error distances in trials when participants looked at only the competitor–near locations were greater than in trials when participants looked at only the target–near locations or when participants alternated their gaze between the two locations (look at competitor vs. look at

both: Bonferroni corrected $p = 3.5999 \times 10^{-4}$, look at competitor vs. look at target: Bonferroni corrected $p = 0.0229$) (Fig. 6a). The error distances were not significantly different on other days. It should be noted that the gaze pattern was related to explicit memory only when learning was still occurring, on day 2.

Overall, the results showing that look at both gaze pattern is beneficial in retrieval selection situations suggest that this gaze pattern reflects multi-memory retrieval.

2.2. Monkey Experiments

1) Preliminary results of NHP gaze patterns related to multi-memory retrieval and selection process in the spatial working memory task

Another objective of this study was to provide a preliminary behavioral task scheme and results that are similar to the human task and results, for future cross-species studies on multi-memory retrieval and selection.

To this end, I first designed a selective working memory retrieval task in which a monkey subject had to remember two spatial locations associated with a visual object and selectively retrieve one of them, similar to the human task scheme (Fig. 7). I trained monkey TG to perform this task by a training paradigm that I developed. As TG performed the selective working memory retrieval task, preliminary data of monkey TG's gaze patterns related to the multi-memory retention in working memory and selection was obtained. An example trial shown in Figure 7b shows a gaze pattern that is similar to the aforementioned gaze pattern obtained in humans. Monkey TG also alternated his gaze between the target and competitor location in delay period 1, and looked at the target location in delay period 2. Analyzing the gaze time sum across all trials in a session according to the gaze location showed that the gaze pattern of looking at both in delay period 1 and selectively looking at target in delay period 2 was replicated in the

monkey subject (Fig. 7c – left) (above: one-way ANOVA of summed gazetime in delay period 1: $F(2, 18) = 53.65$, $p = 2.606 \times 10^{-8}$. Post-hoc Bonferroni pairwise comparisons: target vs. outside $p = 9.95 \times 10^{-7}$; competitor vs. outside: $p = 3.726 \times 10^{-8}$; target vs. competitor: $p = 0.199$; below: one-way ANOVA of summed gazetime in delay period 2: $F(2, 18) = 54.68$, $p = 2.250 \times 10^{-8}$; Bonferroni pairwise comparisons: target vs competitor: $p = 1.822 \times 10^{-8}$; target vs. outside: $p = 5.550 \times 10^{-6}$; competitor vs. outside: $p = 0.0108$).

The percentage of trials where TG looked at one or both locations associated with the visual stimuli during delay period 1 showed that TG alternated his gaze between the two locations in significantly more than just gazing at one of the two locations (paired t-test between look at one vs. look at both trial percentage: $t(12) = -3.125$, $p = 0.0088$) (Fig. 7d). This result also shows that in most trials, TG looked towards at least one of the locations he had to retain in the working memory.

During the analysis of gaze time, I noticed that although not significant, TG seemed to have a spatial preference for the left side of the screen. I split the trials into whether the target was on the left or the right, and analyzed the normalized gaze time according to the gaze locations (Fig. 7c – right). Results revealed that TG had a significant gaze preference towards the left side of the screen in both delay period 1 (one-way ANOVA: $F(4,30) = 33.93$; $p = 9.775 \times 10^{-11}$ for split gaze location effect. Bonferroni pairwise comparisons: left target vs. right target: $p = 5.777 \times 10^{-7}$. left competitor vs. right competitor: $p = 4.458 \times 10^{-4}$). and delay period 2 (one-way ANOVA: $F(4,30) = 38.87$; $p = 1.840 \times 10^{-11}$ for split gaze location effect. Bonferroni pairwise comparisons left target vs. right target: $p = 0.017$; left competitor vs. right competitor: $p = 6.474 \times 10^{-4}$). Within the same side of the screen, the gaze pattern of looking at both locations in delay period 1 (Bonferroni pairwise comparisons. left target vs. left competitor: $p = 0.637$; right target vs. right competitor: $p = 1$) at a similar level and looking selectively at target during delay period 2 (Bonferroni pairwise comparisons.

left target vs. left competitor: $p = 6.628 \times 10^{-7}$; right target vs. right competitor: $p = 2.915 \times 10^{-8}$) remained robust.

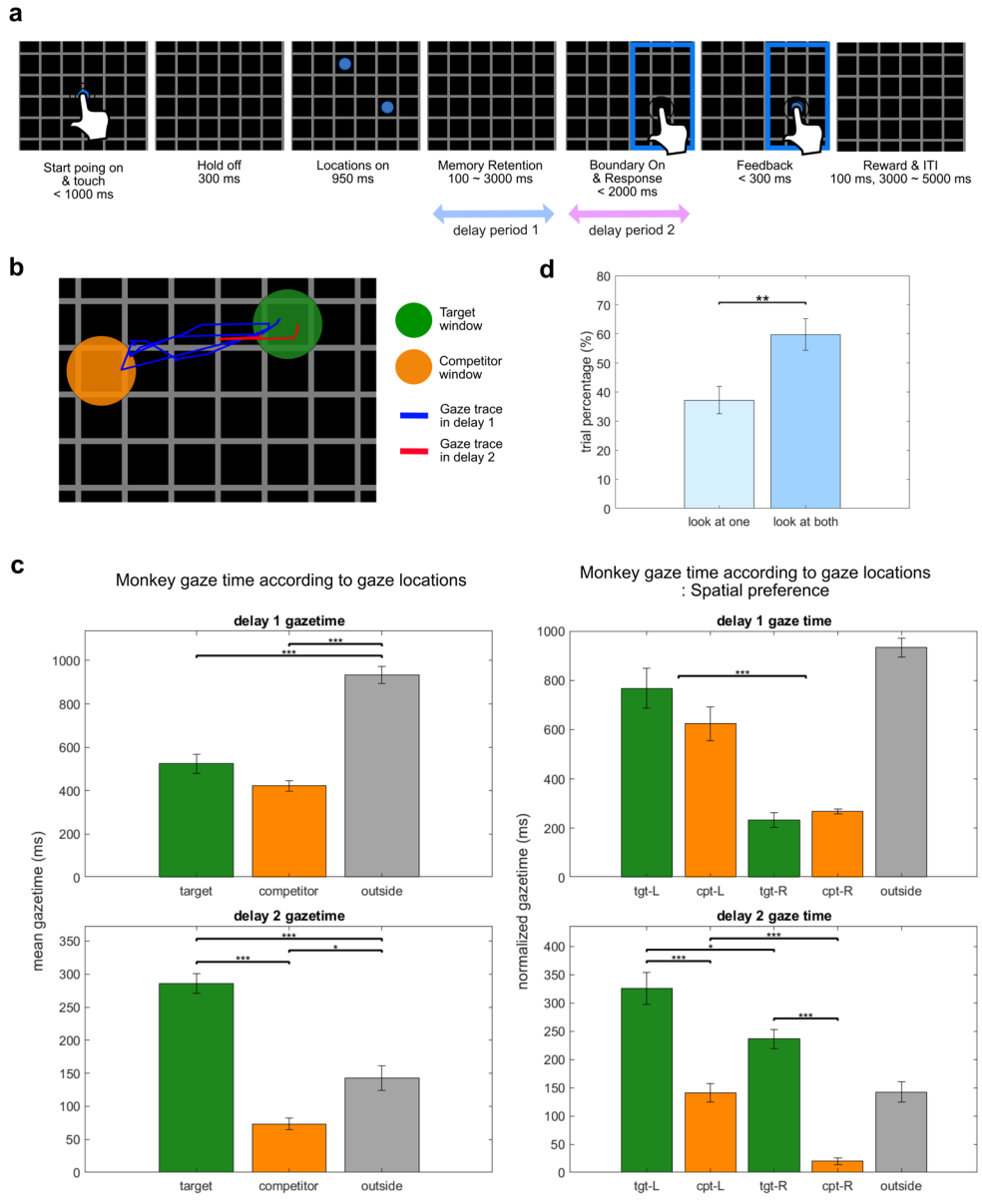


Figure 7. Monkey Experiment Results. (a) Selective working memory task. When a start point was turned on, the monkey was required to touch it. In the locations on period, two blue circle stimuli were presented in random grid locations. The monkey had to retain the memory during memory retention period, and a blue boundary box either on the left or the right of the screen was presented. The monkey made a response, followed by auditory and reward feedback. (b) An example gaze trace of the monkey during delay period 1 and 2. (c) Left: Monkey gaze time according to gaze locations. The mean gaze time across trials are shown in delay period 1

(top) and delay period 2 (bottom). Right: Monkey gaze time according to gaze locations for checking spatial preference. Tgt-L: target location when left stimulus was the target. Cpt-L: competitor location when left stimulus was the competitor. Tgt-R: target location when right stimulus was the target. Cpt-R: competitor location when the right stimulus was the competitor. **(d)** Trial percentage of gaze patterns. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Together, results in the monkey experiment showed that the looking at both patterns in the delay period 1 and selective looking at the to-be-retrieved location in delay period 2 that was first shown in human participants were replicated in non-human primates. This indicates that multi-memory retrieval and selection process can be studied in NHPs with similar approaches as human studies.

Chapter 3. Methods

3.1. Human Experiments

1) Participants

Twenty-one healthy adults (mean age 23.9 years; range 19–34; 13 female) participated in the experiment. Among twenty-one participants, one participant only participated in the study until day 3. Therefore, the data from twenty participants were used for analyses. All participants provided informed consent for the procedure. The experiments received approval from Seoul National University's Institutional Review Board.

2) Stimuli

I used fractal objects for visual stimuli that were created by Fractal Geometry (Kang et al., 2021; Miyashita et al., 1991). The fractals' luminance was equalized with SHINE (Spectrum, Histogram, and Intensity Normalization and Equalization) toolbox written with Matlab (www.mapageweb.umontreal.ca/gosselif/shine).

All fractals used in the experiment and the associated locations are shown in Figure 1.

3) Task Design

Object–location learning task

In the object–location learning task, the participants learned two locations associated with each of the four visual objects. The participants performed this task for five consecutive days. All object–location association are shown in Figure 1. I also included five grey points as the background of the task, so that they were turned on at all times of the task (even on inter–trial intervals). They were included so that they served as reference points to the participants.

In each trial of the task, a black starting point, along with the

magenta cursor indicating the location of the joystick, is pseudorandomly presented in one of the four corners of the screen to indicate the start of the task. The location of the starting point was pseudorandomized so that the participants learned the location and not the appropriate hand movement or direction associated with the object. Upon the presentation of the starting point and the cursor, participants are required to press the button on top of the joystick within 2000 ms of the presentation of the fixation point to start the trial. When the button is pressed, one of the visual objects (size $\sim 2^\circ \times 2^\circ$ visual angle) is presented in the same location as the fixation point for 500 ms and turned off, starting the delay period of 3000 ms. Then, the magenta cursor appears again in the starting location, while one of the two locations associated with the given visual object is indicated with a white boundary box. The participant is required to manipulate the joystick to move the cursor inside the boundary box and press the button within 3000 ms. When the button is pressed, the visual feedback of the object appearing inside the boundary box is given, with appropriate audio feedback (“beep” sound for correct trials that the participants accurately responded inside the boundary box, “boo” sound for incorrect trials in which the participants pressed the button outside the boundary box).

The object–location learning task consisted of 128 trials, with the object–location pair presented 16 times each. The order of the pairs was pseudorandomized.

Selective location retrieval task (SLRT)

In the SLRT, the participants were tested on their memory of the locations associated with the objects. Similar to the object–location learning task, the location of the black starting point was pseudorandomized among the four corners of the screen. In each trial of the task, an object was presented in the starting location after the participant pressed the button upon the presentation of the starting point and the cursor. The object was presented on the screen for 500 ms and turned off for 3000 ms. Then, a boundary of

either left or the right side of the screen indicated with of the two associated locations the participant should respond with. For 1500 ms after the presentation of the boundary, there was no required response from the participants and they were instructed not to move the joystick. After 1500 ms, the cursor reappeared in the starting location, and participants could then move the joystick and press the button to respond with the remembered location until 3000 ms. There was no feedback other than a “beep” sound that indicated that a response had been made, and if the participant did not respond in 3000 ms, a “boo” sound was turned on and the trial was repeated. The participants were instructed to respond within the response period.

The SLRT was conducted on a total of six days, on day 1~5 and day 8. On day 1, the participants performed the SLRT before object–location learning task. This was included to act as a control task, and the participants were instructed to press the button when starting point was turned on, and to move the joystick inside anywhere on the boundary box and press the button to respond. They were told that this task was carried out to get them used to the overall task structure. From day 2 to day 8, the participants received monetary rewards (₩100) according to their performance. They were reminded every day that they will be rewarded for each correct response on each day. However, the trial did not provide any immediate feedback indicating correct or incorrect on each response, and the participants were informed of their performance only at the end of the task.

The SLRT consisted of 32 trials. Each object–location pair was tested in eight trials, and the order of the tested pairs was pseudorandomized.

4) Apparatus

Eye–position data were acquired using the Oculomatic Pro 1000 eye tracker (Bio–Signal, Texas, USA) at a sampling rate of 1,000 Hz. For the joystick, I used the HF22S10 model from APEM.

The output of the eye tracker and joystick was recorded with a data acquisition board (PCIe-6353, National Instruments, USA) interfaced through a shielded I/O connector block (SCB-68, National Instruments, USA). The visual images were presented via a 27-inch monitor (1920 x 1080 resolution, 240 Hz refresh rate). All behavioral tasks were controlled by a custom behavior-controlling system (Blip; available at www.cocila.net/blip).

5) Statistical analysis

To determine the statistical significance of the day and object-location associations on the error distance, and of the day and looking patterns on the trial percentage, repeated-measures ANOVAs were conducted. They were followed by post-hoc Bonferroni pairwise comparisons. For all repeated-measures ANOVAs, sphericity assumptions were checked through Mauchley's test, and corrected using Greenhouse-Geisser correction if they were not met.

For statistical analysis of error distance according to gaze patterns in the SLRT, a permutation-based pairwise comparison analysis was utilized. The permutation test has its advantage in that it is valid for any kind of sample, without the assumption of normalization or random sampling (Edgington, 1987a). Permutation was done 30,000 times. The Bonferroni correction was used to control for the effects of multiple comparisons. All statistical analyses were performed using Matlab.

3.2. Monkey Experiments

1) General procedure

One adult male monkey (*Macaca mulatta*, ~11 kg; monkey TG) was used for monkey experiments. Animal care and experimental procedures were approved by the Seoul National University Institutional Animal Care and Use Committee.

2) Task Design

Selective working memory retrieval task

I designed the selective working memory retrieval task for monkey subjects to mirror the task scheme used for human participants (Fig. 1). In this task, monkeys are required to retain multiple spatial memories during the delay, and a memory among the two was selected when a contextual boundary box is given. As training the monkeys to precisely manipulate the joystick is an arduous process, the task for monkeys was modified to make use of a touch response using a touchscreen. This makes the task design more intuitive to the monkeys, as reaching and touching the target object is a natural behavior, and ensures the independence of the modality of the explicit response (touching by hand) from the uninstructed and natural gaze behavior. Also, a grid background was utilized to be used as spatial references, similar to the reference points of the human task scheme.

In each trial of the task, the monkey touched the presented blue circle in the middle of the monitor to start the trial. When the starting point was turned off, the monkey was required to release its hold. If the monkey successfully released its hold, two blue circles (radius = 4° visual angle) were presented in random grid locations. One of the two locations was turned on in the left side of the screen (one of 12 grid locations left of the center), and the other on the right side of the screen (one of 12 grid locations right of the center). After 950 ms, the two circle stimuli were turned off, and a memory retention period followed. I varied the memory retention period in the training, and the blocks used in analyses used a retention period of 2100 ms. After the retention period, a blue boundary box either on the left or right side of the screen was presented, indicating which of the two previously presented location the monkey had to respond with. The monkey was required to make a response within 2000 ms period after the boundary box. After response, a blue circle was showed in the answer location as a feedback. When the monkey correctly followed through a step in the

task (e.g. touch start point, release start point, and making a response), an auditory feedback (“beep” sound) was given. If the monkey made a correct response, he was given a water reward. If the monkey made an incorrect response, an auditory feedback of the error sound (“boo” sound) was given through a buzzer.

3) Training paradigm

The training paradigm consisted of three phases.

Touch basics phase

The “touch basics phase” is when the monkeys learn the basic rules of response with the touchscreen. It consisted of three tasks. 1) Touch reward task was devised to teach the monkey to precisely touch the presented stimuli (touch reward task) to get a reward. A water reward along with the reward sound was provided when the monkey touched inside the touch window after the stimulus presentation. For shaping, I started off with a large stimulus and window size and gradually decreased the size to be 3° visual angle of radius. 2) Touch release task was designed to teach the monkey to release the stimuli when the stimuli were turned off. A water reward and reward sound were given after the monkey released the stimulus. 3) In the hold box task, the monkey learned to hold on to the presented stimuli until the stimuli is turned off even when another stimulus is presented.

Learning boundary phase

The “learning boundary phase” is when the monkey learned the rules related to the final task scheme. 1) Through the touch inside boundary task, the monkey first learned the meaning of the boundary box (to touch inside of the boundary box instead of the boundary box itself). In the task, a boundary box was presented in a random location of the screen and a blue circle flashed inside of the boundary box, indicating that the monkey should touch inside the box. For shaping, the flash period was decreased, and eventually not used and the monkey was required to touch inside the boundary when it was presented. 2) Selective choice task was designed to

teach the monkey to choose the stimulus inside the boundary box among the simultaneously presented two stimuli. I utilized the grid background in this task for the monkey to grow accustomed to the background. The trial started when the monkey touched a central starting point. After the monkey released the central starting point, two stimuli were presented inside two grid locations, one on the left side of the screen and the other on the right. The monkey had to wait until a boundary box was presented, and had to touch the stimulus inside the boundary box. If the monkey touched the screen before the boundary box presentation, an error sound feedback was given and the trial started again. For shaping, the boundary was initially very small, only to include one grid inside of it, and I gradually increased the boundary until it covered half of the screen (4*3 grids), as in the final selective working memory task. The boundary box always matched the grid outlines and did not cross inside of the grid, as that area was where a target could be presented.

Memory phase

The “memory phase” is when the monkey learns to remember the locations of the presented stimuli and respond via touching the remembered location. 1) In the place working memory task, the monkey first learned that he has to retain the presented location of the stimulus and to touch the retained location after the delay. A grid background was used to provide reference to the monkey. In the task, a stimulus was presented in a random grid location, and the monkey had to touch the stimulus. After a delay period, a blue boundary box was presented. The boundary box had the role of indicating when to respond, and also to hint the location of the answer. The monkey then had to touch the location the stimulus was presented before the delay. For shaping, the delay was initially very short and I gradually increased until the monkey could stably perform even when the delay was 3000 ms. I also gradually increased the size of the boundary box, first to include only one grid and directly indicating the answer location and increased the

boundary until it included all the grids in the screen (4*6 grids).

4) Apparatus

Eye-position data were acquired using the same system as written above for human study. I used a 19-inch touchscreen monitor (IV-190IR model from IVIEWKOREA, 1280 x 1024 resolution, 60 Hz refresh rate). All behavioral tasks were controlled through NIMH Monkeylogic (J. Hwang et al., 2019).

5) Set-Up

During the experiment, monkey TG sat in the primate chair, facing a frontoparallel screen, with head fixed to the chair via a headpost. The primate chair was modified to have two sliding doors in the front to allow the monkey to reach out to touch the monitor during the task. To prevent the monkey from reaching towards the water spout or the hot mirror, an acrylic guard was attached on top of the opening doors of the primate chair. The eye tracker was installed to face downward from an overhead angle of the testing room, and the monkey viewed the screen through a hot mirror attached to the primate chair.

6) Analysis of the gaze pattern behavior

The preliminary gaze behavior analysis of monkey TG was done on 5 sessions performed in a period of two days. Each session consisted of 100 trials.

Due to set up issues, monkey TG's eye calibration was inaccurate when the TG looked at the lower half of the screen. Because of this issue, I only analyzed trials where the blue circles were presented in the upper half of the screen. Also, due to issues in accuracy of the eye calibration, I set the target and competitor window to be of 9° visual angle of radius. I excluded trials in which the target and competitor window overlapped from analysis. This resulted in an average of 17.143 trials per session (range 11–20).

Also, as the analyzed trials were picked with the above

conditions, the number of trials when the target was on the left side of the screen and the right side of the screen were not equal. To account for this in the spatial preference analysis (Fig. 7c –right), I normalized the gaze time based on the occurrence of each conditions (target left or right). Note that in the perspective of monkey TG, the number of trials where the left or the right side is the target is pseudorandomized, as he performed all 100 trials in each session.

Chapter 4. Discussion

The results of this study demonstrate that multiple related memories are typically retrieved first, and the most relevant one is selected based on the context through primate gaze patterns. Human participants often spontaneously looked at both locations associated with a given object before context presentation, based on multiple spatial memories. This looking at both gaze patterns converged to looking at the target location to be retrieved when the context was given, indicating the selection of the appropriate memory. In addition, looking at both locations before context presentation was correlated with higher memory accuracy on day 2 than looking at only the competitor location. This suggests that looking at both eye movement indicates multi-memory retrieval, when learning is occurring. Importantly, these gaze patterns were also replicated in preliminary results obtained from a monkey subject. The monkey's gaze pattern reflected the retention of the locations of the two stimuli before context presentation, and reflected the selection among these two spatial memories after context presentation. To my knowledge, this is the first report of LAN behavior in monkeys. This preliminary data confirms the compatibility of the task scheme in human and monkeys and the similarity of the gaze patterns during the retrieval selection process, suggesting similar underlying neural processes in both species.

4.1. Expertise effects in the gaze patterns of human participants throughout learning

My results can be related to previous studies on gaze patterns and memory retrieval. In previous human studies on the “expertise effect” in the comprehension of visualizations, experts are known to display more fixations on task-relevant areas and fewer fixations on task-irrelevant areas than non-experts (Gegenfurtner et al., 2011). The results on the temporal dynamics of gaze locations shown in Figure 4 replicate these expertise effects. In delay period

1 and 2, human participants increasingly looked at the relevant locations in both delay periods as retrieval day increased. Relevant locations in delay period 1 are both target and competitor location, as the contextual boundary box is not yet presented. On the other hand, only the target location is relevant during delay period 2. Statistical analysis revealed that gaze time towards target and competitor generally increased across retrieval days in delay period 1, and the gaze time towards target location increased across retrieval days in delay period 2. Conversely, gaze time towards irrelevant locations (gaze time towards outside) decreased in delay period 1. Also, gaze time towards competitor locations, which is relevant to the task during delay period 1 but not in delay period 2, decreases significantly from delay period 1 to 2, reflecting the task relevancy of these spatial locations retrieved from memory. These results demonstrate that gaze patterns during the SLRT can reflect the learning process, as participants gain expertise in retrieving the spatial memories associated with the object. Expertise effect in the comprehension of visualizations can be explained through “information–reduction hypothesis” (Haider & Frensch, 1999). The information–reduction hypothesis posits that experts optimize the amount of the processed information by learning to focus only on the task–relevant information. In this context, it can be presumed that participants increasingly looking at the relevant locations as learning occurs is a process of information–reduction, although this is in the modality of internal processing rather than processing of visual information. In the perspective of retrieval selection, this can also be seen as one form of retrieval selection, as the memories of relevant locations are selected to be gazed at, while irrelevant locations are not. This may reflect adaptive gating of memory into the working memory space, a cognitive control mechanism that keeps only the relevant information while keeping irrelevant information out (Scimeca & Badre, 2012). Thus, this top–down selection process may precede the selection among multiple retrieved memories proposed in this study.

4.2 Possibility of external memory use during learning reflected in selective gaze pattern effects on day 2

The results of the human experiments in this study show that looking at both gaze patterns shown before contextual boundary box presentation were correlated with lower error distance in explicit response of the selected memory in the SLRT than looking at competitor gaze patterns (Fig. 6). Interestingly, the significant differences in the error distance between the three gaze patterns (look at competition, look at both, or look at target) were only observed on day 2, while there were no significant differences on other days. What must be noted is that learning also occurred only until day 2, with significant difference not occurring after day 3 (Fig. 2a). This suggests a hint to which can explain this selective phenomenon. Previous studies have shown that participants' behavior of looked at empty locations where the image was located during encoding (LAN) decreased with repeated recalls (Scholz et al., 2011; Wantz et al., 2016). LAN behavior has been suggested to reflect the use of an "external memory", where eye movements function as "spatial indexes" of sparse memory representations of the visual world (Ferreira et al., 2008; O'Regan, 1992; Richardson et al., 2009). Based on this idea, Scholz et al. (2011) and Wantz et al. (2016) suggested that when participants' recall performance increases after practice, there is no longer demand of the use of an "external memory". This is in line with other studies that suggest LAN behavior have a functional role in memory retrieval situations (Johansson & Johansson, 2014; Kinjo et al., 2020). These studies suggest that the emergence of LAN is dependent on the difficulty of the recall task. This argument can explain the selective effects of gaze patterns on memory accuracy on day 2 in the results. Gaze patterns may have a functional role in retrieval as a means of which people access "external memory" as working memory load increases. As people repeatedly practice recall and as their retrieval performance gets better, there is no need of this behavior as participants are able to retrieve memory even without the need

of accessing external memory.

My results differ in that participants maintain LAN behavior even after learning saturation, but the proposed relationship between memory stability and the functional effects of LAN can be applied to explain the selective results of day 2. The functional effect of looking at the location where the object was located during encoding may diminish as participants get better at retrieval. When learning is still actively occurring (as shown through the significant error distance differences until day 3), looking at both gaze patterns can serve as external cues of the two memories, while looking at target patterns serve as external cue of the target memory. When the contextual boundary box is given, then looking at both and looking at target, since they were utilizing the external memory of the target, will result in shorter error distance. Later when the participants are able to accurately retrieve all the associated locations after repeated learning (from day 3 in my experiment), the functional effects of the LAN behavior that serves as external cues of the memories may not have a discernable effect over the saturated retrieval proficiency.

Another point to discuss is that the results shown in Figure 6b are different from the original hypothesis (Fig. 6a) in that look at target error distance was not significantly lower than look at both error distance. One potential explanation for this is that the retrieval of the target location may be the primary factor contributing to differences in memory accuracy during learning. The original hypothesis posited that look at both trials (Fig. 6a) would be correlated with lower memory accuracy than look at target trials, as the selection of one memory among two retrieved locations in delay period 2 would result in a decrease in accuracy. However, it is also possible that this additional selection process may not affect accuracy. Instead, only whether target memory was retrieved in delay period 1 may have an impact on response accuracy. Additionally, these results may be explained by the idea that looking at the associated locations facilitates the use of external memory. If this is the case, looking at both locations in look at both trials may

be beneficial in situations where either memory may need to be retrieved (in delay period 1), if the memory of the spatial index (location where the original memory is encoded) can be accessed. Thus, in look at both trials, it may be that participants are able to access both memories of the associated locations, while in look at target or competitor trials, they are only able to access one. This could suggest that look at both trials reflect more proficiency in general, leading to higher memory accuracy.

4.3 Multi-memory retrieval: sequential vs. simultaneous retrieval?

In this study, gaze patterns towards both object-associated locations in the delay periods in memory tasks in both humans and monkey reflected the retrieval of multiple memories. A question that follows is whether these multiple memories are retrieved simultaneously or sequentially. As fixations can only occur to one location at a time, sequential and simultaneous retrieval of multiple memories cannot be dissociated by utilizing only the gaze pattern data. In literature, the exact mechanism of multiple memory retrieval is still being debated. One study supporting sequential retrieval has showed that when two memories were probed, visual working memory attends to one memory item at a time through alternating visuocortical responses (Thigpen et al., 2019). On the other hand, there are also arguments for simultaneous retrieval of the memories. Competition between visual memories were correlated with more ambiguous neural patterns, suggesting that the memories were activated in parallel (Kuhl et al., 2011; Logan & Delheimer, 2001). Future neuroimaging and electrophysiology studies is needed to clarify the temporal dynamics of multi-memory retrieval.

4.4 Possible brain substrates for multi-memory retrieval and selection

One essential question is where and how the brain implements this process of multi-memory retrieval and selection. A large body of human studies points to regions in the prefrontal cortex to be involved in the selection of memories. In human fMRI studies, it has been demonstrated that activity of ventrolateral prefrontal cortex (VLPFC) and dorsolateral prefrontal cortex (DLPFC) systematically increased as memory competition increased (Sohn et al., 2003), and that DLPFC activations were correlated with the selection of an item from spatial working memory rather than working memory maintenance (Rowe et al., 2000). Another fMRI study with RIF paradigm showed that medial prefrontal cortex (Brodmann area 8) and lateral posterior prefrontal cortex (Brodmann area 9) showed increased BOLD responses during retrieval selection (Wimber et al., 2009). The authors argued that these activations were due to the inhibitory mechanisms during retrieval selection, as the activation levels were correlated with RIF effects but not the strengthening of the practiced items. Supporting the role of these prefrontal areas in memory suppression, DLPFC are repeatedly reported to be activated in memory suppression tasks (Anderson et al., 2004; Benoit & Anderson, 2012). Moreover, the causal role of DLPFC in the suppression of irrelevant memories in retrieval selection was confirmed in another study using transcranial direct current stimulation (tDCS), reporting that the cathodal stimulation to the right DLPFC resulted in no RIF effect in human participants (Penolazzi et al., 2014). The prefrontal cortex is a plausible region for retrieval selection, considering that the selection of relevant memories requires the information of the current context. Single neuron recordings in the primate lateral prefrontal cortex neurons were reported to show different responses according to different task demands (Asaad et al., 2000; Watanabe, 1986, 2013), and human fMRI studies show that prefrontal cortex activity varied under different retrieval contexts (Wagner et al., 1998). Thus, the

DLPFC may use this contextual information to select the relevant memory and suppress irrelevant memories.

If the selection among multiple memories are mediated by prefrontal regions, in what brain regions are these memories retrieved from? In the aforementioned study by Anderson et al. (2004), bilateral hippocampal activity was reduced when the participants were instructed to suppress their memory, compared to when they retrieved the memory. There is a wide agreement that the hippocampus plays a critical role in the conscious retrieval of memory (Eldridge et al., 2000; Squire et al., 2004), and some theories suggest that the hippocampus functions to bind together separate elements in relational memory (Olsen et al., 2012). Thus, the overall reduction in hippocampal activity may reflect the memories being suppressed. Surprisingly, greater hippocampal activity was found for items that were subsequently forgotten in the suppression condition than the items that were not forgotten, which may be seen counterintuitive to the hippocampal functions in memory retrieval. Similar results were found in the study done by Wimber et al. (2009), where greater hippocampal activity was found during retrieval practice. The authors suggest that these activations in the hippocampus may reflect memories being strongly retrieved in the hippocampus, inducing inhibitory control of the DLPFC to be initiated. In support of this argument, DLPFC activations were correlated with right hippocampal activation differences between forgotten and recalled suppression items, suggesting that there may be interaction between the two regions to suppress the intruding memories (Anderson et al., 2004).

Based on these studies, one possible mechanism of retrieval selection in the brain are as follows. When an internal or external cue is given, the multiple associated memories may be retrieved from the medial-temporal lobe (MTL), and DLPFC may incorporate contextual information to suppress irrelevant memories for the selection of relevant memory. Future neuroimaging studies using methods such as fMRI or neural recordings are necessary to further examine the underlying neural mechanisms of retrieval selection.

4.5 Avenues for future research

This study established a common behavioral task scheme and confirmed similar gaze patterns reflecting multi-memory retrieval and selection in both humans and NHP. These results provide further justifications for future cross-species multi-memory retrieval and selection studies. Combination of gaze patterns with neuroimaging techniques will allow future studies to specify the exact neural mechanisms of multi-memory retrieval and selection.

4.6 Conclusion

The results of this study show that in substantial portions of the trials, multiple memories were retrieved when a cue was given, and the context-appropriate memory is selected among the retrieved memories when a context is given through the gaze pattern of human participants. These gaze patterns showed correlations with explicit reports of memory accuracy when learning was still occurring, suggesting that multiple memories are being retrieved when the participants displayed look at both gaze patterns. The gaze pattern related to multi-memory retrieval and selection were robustly replicated in a spatial working memory task in a monkey subject, providing a foundation for future cross-species studies.

Bibliography

- Anderson, M. C., Bjork, R. A., & Bjork, E. L. (1994). Remembering can cause forgetting: Retrieval dynamics in long-term memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 20(5), 1063–1087. <https://doi.org/10.1037/0278-7393.20.5.1063>
- Anderson, M. C., Ochsner, K. N., Kuhl, B., Cooper, J., Robertson, E., Gabrieli, S. W., Glover, G. H., & Gabrieli, J. D. E. (2004). Neural Systems Underlying the Suppression of Unwanted Memories. *Science*, 303(5655), 232–235. <https://doi.org/10.1126/science.1089504>
- Asaad, W. F., Rainer, G., & Miller, E. K. (2000). Task-Specific Neural Activity in the Primate Prefrontal Cortex. *Journal of Neurophysiology*, 84(1), 451–459. <https://doi.org/10.1152/jn.2000.84.1.451>
- Beck, M. R., Peterson, M. S., & Angelone, B. L. (2007). The roles of encoding, retrieval, and awareness. *Memory & Cognition*, 35(4), 610–620. <https://doi.org/10.3758/BF03193299>
- Benoit, R. G., & Anderson, M. C. (2012). Opposing Mechanisms Support the Voluntary Forgetting of Unwanted Memories. *Neuron*, 76(2), 450–460. <https://doi.org/10.1016/j.neuron.2012.07.025>
- Eldridge, L. L., Knowlton, B. J., Furmanski, C. S., Bookheimer, S. Y., & Engel, S. A. (2000). Remembering episodes: A selective role for the hippocampus during retrieval. *Nature Neuroscience*, 3(11), Article 11. <https://doi.org/10.1038/80671>
- Ferreira, F., Apel, J., & Henderson, J. M. (2008). Taking a new look at looking at nothing. *Trends in Cognitive Sciences*, 12(11), 405–410. <https://doi.org/10.1016/j.tics.2008.07.007>
- Gegenfurtner, A., Lehtinen, E., & Säljö, R. (2011). Expertise Differences in the Comprehension of Visualizations: A Meta-Analysis of Eye-Tracking Research in Professional Domains. *Educational Psychology Review*, 23(4), 523–552. <https://doi.org/10.1007/s10648-011-9174-7>

- Haider, H., & Frensch, P. A. (1999). Eye movement during skill acquisition: More evidence for the information-reduction hypothesis. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *25*, 172–190. <https://doi.org/10.1037/0278-7393.25.1.172>
- Hannula, D., Althoff, R., Warren, D., Riggs, L., Cohen, N., & Ryan, J. (2010). Worth a Glance: Using Eye Movements to Investigate the Cognitive Neuroscience of Memory. *Frontiers in Human Neuroscience*, *4*. <https://www.frontiersin.org/articles/10.3389/fnhum.2010.00166>
- Hannula, D. E., & Ranganath, C. (2009). The Eyes Have It: Hippocampal Activity Predicts Expression of Memory in Eye Movements. *Neuron*, *63*(5), 592–599. <https://doi.org/10.1016/j.neuron.2009.08.025>
- Holm, L., Eriksson, J., & Andersson, L. (2008). Looking as if you know: Systematic object inspection precedes object recognition. *Journal of Vision*, *8*(4), 14. <https://doi.org/10.1167/8.4.14>
- Hwang, J., Mitz, A. R., & Murray, E. A. (2019). NIMH MonkeyLogic: Behavioral control and data acquisition in MATLAB. *Journal of Neuroscience Methods*, *323*, 13–21. <https://doi.org/10.1016/j.jneumeth.2019.05.002>
- Hwang, S.-H., Ra, Y., Paeng, S., & Kim, H. F. (2022). Motivational salience drives habitual gazes during value memory retention and facilitates relearning of forgotten value. *iScience*.
- Johansson, R., & Johansson, M. (2014). Look Here, Eye Movements Play a Functional Role in Memory Retrieval. *Psychological Science*, *25*(1), 236–242. <https://doi.org/10.1177/0956797613498260>
- Kang, J., Kim, H., Hwang, S. H., Han, M., Lee, S.-H., & Kim, H. F. (2021). Primate ventral striatum maintains neural representations of the value of previously rewarded objects for habitual seeking. *Nature Communications*, *12*(1), Article 1. <https://doi.org/10.1038/s41467-021-22335-5>

- Kim, H. F., Ghazizadeh, A., & Hikosaka, O. (2015). Dopamine Neurons Encoding Long-Term Memory of Object Value for Habitual Behavior. *Cell*, *163*(5), 1165–1175. <https://doi.org/10.1016/j.cell.2015.10.063>
- Kim, H. F., & Hikosaka, O. (2013). Distinct Basal Ganglia Circuits Controlling Behaviors Guided by Flexible and Stable Values. *Neuron*, *79*(5), 1001–1010. <https://doi.org/10.1016/j.neuron.2013.06.044>
- Kinjo, H., Fookien, J., & Spering, M. (2020). Do eye movements enhance visual memory retrieval? *Vision Research*, *176*, 80–90. <https://doi.org/10.1016/j.visres.2020.07.013>
- Kuhl, B. A., Rissman, J., Chun, M. M., & Wagner, A. D. (2011). Fidelity of neural reactivation reveals competition between memories. *Proceedings of the National Academy of Sciences*, *108*(14), 5903–5908. <https://doi.org/10.1073/pnas.1016939108>
- Levy, B. J., & Anderson, M. C. (2002). Inhibitory processes and the control of memory retrieval. *Trends in Cognitive Sciences*, *6*(7), 299–305. [https://doi.org/10.1016/S1364-6613\(02\)01923-X](https://doi.org/10.1016/S1364-6613(02)01923-X)
- Logan, G. D., & Delheimer, J. A. (2001). Parallel memory retrieval in dual-task situations: II. Episodic memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *27*(3), 668–685. <https://doi.org/10.1037/0278-7393.27.3.668>
- Miyashita, Y., Higuchi, S.-I., Sakai, K., & Masui, N. (1991). Generation of fractal patterns for probing the visual memory. *Neuroscience Research*, *12*(1), 307–311. [https://doi.org/10.1016/0168-0102\(91\)90121-E](https://doi.org/10.1016/0168-0102(91)90121-E)
- Olsen, R., Moses, S., Riggs, L., & Ryan, J. (2012). The hippocampus supports multiple cognitive processes through relational binding and comparison. *Frontiers in Human Neuroscience*, *6*. <https://www.frontiersin.org/articles/10.3389/fnhum.2012.00146>
- O'Regan, J. K. (1992). Solving the “real” mysteries of visual perception: The world as an outside memory. *Canadian Journal of Psychology / Revue Canadienne de Psychologie*, *46*

- 46(3), 461–488. <https://doi.org/10.1037/h0084327>
- Penolazzi, B., Stramaccia, D. F., Braga, M., Mondini, S., & Galfano, G. (2014). Human Memory Retrieval and Inhibitory Control in the Brain: Beyond Correlational Evidence. *Journal of Neuroscience*, 34(19), 6606–6610. <https://doi.org/10.1523/JNEUROSCI.0349-14.2014>
- Richardson, D. C., Altmann, G. T. M., Spivey, M. J., & Hoover, M. A. (2009). Much ado about eye movements to nothing: A response to Ferreira et al.: Taking a new look at looking at nothing. *Trends in Cognitive Sciences*, 13(6), 235–236. <https://doi.org/10.1016/j.tics.2009.02.006>
- Richardson, D. C., & Spivey, M. J. (2000). Representation, space and Hollywood Squares: Looking at things that aren't there anymore. *Cognition*, 76(3), 269–295. [https://doi.org/10.1016/S0010-0277\(00\)00084-6](https://doi.org/10.1016/S0010-0277(00)00084-6)
- Rowe, J. B., Toni, I., Josephs, O., Frackowiak, R. S. J., & Passingham, R. E. (2000). The Prefrontal Cortex: Response Selection or Maintenance Within Working Memory? *Science*, 288(5471), 1656–1660. <https://doi.org/10.1126/science.288.5471.1656>
- Scholz, A., Mehlhorn, K., Bocklisch, F., & Krems, J. F. (2011). Looking at Nothing Diminishes with Practice. *Proceedings of the Annual Meeting of the Cognitive Science Society*, 33, 1070–1075. <https://escholarship.org/content/qt21m7h5xx/qt21m7h5xx.pdf>
- Scimeca, J. M., & Badre, D. (2012). Striatal Contributions to Declarative Memory Retrieval. *Neuron*, 75(3), 380–392. <https://doi.org/10.1016/j.neuron.2012.07.014>
- Sohn, M.-H., Goode, A., Stenger, V. A., Carter, C. S., & Anderson, J. R. (2003). Competition and representation during memory retrieval: Roles of the prefrontal cortex and the posterior parietal cortex. *Proceedings of the National Academy of Sciences*, 100(12), 7412–7417. <https://doi.org/10.1073/pnas.0832374100>
- Spivey, M. J., & Geng, J. J. (2001). Oculomotor mechanisms activated by imagery and memory: Eye movements to absent objects.

- Psychological Research*, 65(4), 235–241.
<https://doi.org/10.1007/s004260100059>
- Squire, L. R., Stark, C. E. L., & Clark, R. E. (2004). The Medial Temporal Lobe. *Annual Review of Neuroscience*, 27(1), 279–306. <https://doi.org/10.1146/annurev.neuro.27.070203.144130>
- Thigpen, N., Petro, N. M., Oschwald, J., Oberauer, K., & Keil, A. (2019). Selection of Visual Objects in Perception and Working Memory One at a Time. *Psychological Science*, 30(9), 1259–1272. <https://doi.org/10.1177/0956797619854067>
- Wagner, A. D., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. (1998). Prefrontal cortex and recognition memory. Functional-MRI evidence for context-dependent retrieval processes. *Brain*, 121(10), 1985–2002.
<https://doi.org/10.1093/brain/121.10.1985>
- Wantz, A. L., Martarelli, C. S., & Mast, F. W. (2016). When looking back to nothing goes back to nothing. *Cognitive Processing*, 17(1), 105–114. <https://doi.org/10.1007/s10339-015-0741-6>
- Watanabe, M. (1986). Prefrontal unit activity during delayed conditional Go/No-go discrimination in the monkey. II. Relation to Go and No-go responses. *Brain Research*, 382(1), 15–27. [https://doi.org/10.1016/0006-8993\(86\)90105-8](https://doi.org/10.1016/0006-8993(86)90105-8)
- Watanabe, M. (2013). How Context Impacts Cognitive and Motivational Control of Behavior in the Primate Prefrontal Cortex. In D. T. Stuss & R. T. Knight (Eds.), *Principles of Frontal Lobe Function* (Second, pp. 211–225). Oxford University Press.
- Wimber, M., Rutschmann, R. M., Greenlee, M. W., & Bäuml, K.-H. (2009). Retrieval from Episodic Memory: Neural Mechanisms of Interference Resolution. *Journal of Cognitive Neuroscience*, 21(3), 538–549. <https://doi.org/10.1162/jocn.2009.21043>
- Wynn, J. S., Ryan, J. D., & Buchsbaum, B. R. (2020). Eye movements support behavioral pattern completion. *Proceedings of the National Academy of Sciences*, 117(11), 6246–6254. <https://doi.org/10.1073/pnas.1917586117>

Abstract

여러 개의 연합된 기억 중, 현재 상황에 적절한 기억을 선택하는 과정은 필수적이다. 본 연구는 사람과 원숭이를 모델로 다중 기억 인출 및 선택 과정을 눈 움직임 패턴을 이용하여 밝히고, 추후 영장류 대상 기억 인출 선택 과정 연구 기반을 마련하고자 한다. 이를 위해 인간 참가자들을 대상으로는 각 물체와 연합된 두 개의 다중적인 위치 기억 중 현재 상황에 적절한 기억을 선택하게 하는 선택적 기억 인출 과제를 진행했다. 이러한 선택적 기억 인출 과제에서 참가자들은 다중 기억 인출과 관련해 두 위치를 모두 보는 눈 움직임을, 그리고 그중에서 적절한 기억의 선택을 보여주는 목표 기억 선택 눈 움직임을 보였다. 또한 특정 상황이 주어지기 전의 눈 움직임 패턴에 따라 참가자들의 명시적인 기억 응답 정확도가 달라지는 결과를 확인하여 눈 움직임 패턴을 어떤 기억이 인출되고 있는지에 대한 지표로 사용할 수 있음을 검증하였다. 또한, 본 연구는 다중 기억 인출 및 선택 과정 관련 원숭이의 선행적인 행동 결과를 제시하고 있다. 원숭이가 사람 실험에 사용된 과제와 유사한 선택적 위치 작업 기억 과제를 진행하는 동안의 눈 움직임은 사람과 유사하게 두 위치를 번갈아 보다가 상황에 적절한 위치를 보는 패턴이 나타났다. 종합적으로, 본 연구는 영장류 눈 움직임 패턴을 통해 자극이 주어지면 여러 기억이 인출되고, 그중 적절한 기억이 선택된다는 것을 보였다. 이를 통해 본 연구는 추후 영장류 대상 기억 선택 과정 연구의 기반을 마련하였다.

주제어: 기억 인출, 기억 선택, 영장류 눈 움직임, 장기 기억