

## Research Article

## Adaptive Memory

## Fitness Relevance and the Hunter-Gatherer Mind

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**ABSTRACT**—Recent studies suggest that human memory systems are “tuned” to remember information that is processed in terms of its fitness value. When people are asked to rate the relevance of words to a survival scenario, performance on subsequent surprise memory tests exceeds that obtained after most other known encoding techniques. The present experiments explored this effect using survival scenarios designed to mimic the division of labor thought to characterize early hunter-gatherer societies. It has been suggested that males and females have different cognitive specializations due to the unique survival tasks (hunting and gathering, respectively) they typically performed during periods of human evolution; the present experiments tested whether such specializations might be apparent in memory for words rated for relevance to these activities. Males and females were asked to rate the relevance of random words to prototypical hunting and gathering scenarios or to matched, non-fitness-relevant control scenarios (gathering food on a scavenger hunt or in a hunting contest). Surprise retention tests revealed superior memory for the words when they were rated for relevance to hunting and gathering scenarios, compared with when they were rated for relevance to the control scenarios, but no sex differences were found in memory performance.

Central to the functionalist agenda in human memory research is the assumption that human memory systems are functionally designed (e.g., Klein, Cosmides, Tooby, & Chance, 2002; Nairne, 2005; Sherry & Schacter, 1987). Like other biological systems, memory likely evolved to enhance fitness (survival and reproduction). Accordingly, memory systems may be specially “tuned” to retain information that is fitness relevant. Studies supporting this proposal have shown that thinking about the relevance of information to a survival situation produces excellent long-term reten-

tion (Kang, McDermott, & Cohen, 2008; Nairne, Thompson, & Pandeirada, 2007; Weinstein, Bugg, & Roediger, 2008). In fact, a few seconds of survival processing produces better free recall than virtually all other known memory-enhancement techniques (Nairne & Pandeirada, 2008a; Nairne, Pandeirada, & Thompson, 2008).

In the prototypical survival experiment, participants are asked to imagine themselves stranded in the grasslands of a foreign land, without any basic survival materials. Participants are told that over the next few months, they will need to find steady supplies of food and water and to protect themselves from predators. Next, randomly selected words are presented, and participants are asked to rate the relevance of each word to the imagined scenario. In a later surprise memory test, participants typically remember the words rated for relevance to this fitness-relevant scenario better than they remember words rated for relevance to matched encoding scenarios that are not fitness relevant (e.g., moving to a foreign land or spending time at a vacation resort). Such “survival-based” retention is also better than retention after traditional “deep”-processing tasks ( Craik & Tulving, 1975), such as thinking about the meaning of an item or forming a visual image.

As a product of natural selection, human memory evolved because it enhanced fitness in specific *environments of evolutionary adaptedness* (Bowlby, 1969; Tooby & Cosmides, 1992), that is, the environments that were present during the extended periods of human evolution. The products of evolution are rooted in the past, by definition, and are likely to reflect the environmentally determined selection pressures faced by human ancestors. Evolutionary psychologists (e.g., Symons, 1992) generally believe that the majority of humans’ cognitive “sculpting” occurred during the Pleistocene era (from approximately 1.8 million to 10,000 years ago), during which the human species lived largely as foragers. Consequently, memory processing should bear the imprint of the selection pressures faced by foragers; memory should be geared toward retaining information that is relevant to the specific adaptive problems faced in hunting-and-gathering environments.<sup>1</sup>

<sup>1</sup>This reasoning is simplistic in some respects. For example, knowledge about ancestral environments is limited; forager “problems” undoubtedly varied across disparate environments. Even so, it is possible to generate hypotheses based on a hunter-gatherer model and attempt resolution in the empirical domain.

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At present, psychologists know little about the evolutionary determinants of human memory, although some relevant research does exist (e.g., Anderson & Schooler, 1991; O’Gorman, Wilson, & Miller, 2008). For example, it has been suggested that sex differences in spatial abilities, including memory for object locations, may have an evolutionary basis (Sherry, Jacobs, & Gaulin, 1992; Silverman & Eals, 1992). Silverman and Eals (1992) suggested that the division of labor typically found in hunter-gatherer societies—men hunt and women gather—may have led to unique foraging-related cognitive specializations of the sexes (for related arguments in a nonhuman domain, see Gaulin & FitzGerald, 1986). Indeed, men generally outperform women on tasks thought to be related to hunting skills (e.g., navigation and orientation), whereas women often show an advantage on tasks requiring memory for objects stored in fixed locales (Voyer, Postma, Brake, & Imperato-McGinley, 2007). The data are somewhat controversial, and subject to alternative explanations, but are broadly consistent with selection-based cognitive tunings.

Participants in the experiments reported here were asked to rate the relevance of words to scenarios that were specifically designed to mimic prototypical hunting and gathering activities. Following the rating task, participants received a surprise recall test on the rated words. Our intent was to design scenarios that were congruent not only with ancestral priorities, but also with the sex-related division of labor thought to exist in the environment of evolutionary adaptedness. Our empirical questions were twofold: First, would hunter or gatherer processing yield enhanced retention relative to appropriate control processing, a finding consistent with the proposal that human memory systems are tuned to remember fitness-relevant information? Second, would males show mnemonic advantages after processing hunter scenarios, and would females show mnemonic advantages after processing gatherer scenarios?

In addition, these experiments offer a significant methodological advance over previous work in this area. Because the activities in the scenarios were specific and focused—hunting and gathering—we were able to design control scenarios that involved the same general activities. In Experiment 1, the control scenario involved collecting food on a scavenger hunt. In Experiment 2, the control scenario involved hunting for food, but as part of a hunting contest. In previous work, control scenarios have involved activities quite different from those included in the survival scenario, such as moving to a foreign land, spending time at a vacation resort, and planning a bank heist. In the current experiments, participants always rated the relevance of the target words to hunting or to gathering food, but under conditions that were either fitness relevant or not. Demonstrating a mnemonic advantage for fitness-relevant processing under these conditions would place the evolutionary account on firmer empirical ground.

## EXPERIMENT 1

In Experiment 1, all participants were asked to rate and recall the same 30 unrelated words. What differed across the conditions was the processing scenario. Participants in the gatherer condition were asked to imagine themselves in charge of gathering edible food for a tribe (collecting fruits, nuts, vegetables, etc.), and participants in the hunter condition were asked to imagine themselves in charge of hunting for food (hunting for big game, trapping small animals, etc.). In the control condition, we asked participants to imagine themselves playing a game (a scavenger hunt) that required searching for and collecting food items. In each condition, the task was to rate the relevance of the presented words to the scenario. Note that the first two scenarios were fitness relevant, because they referred to situations in which participants were contributing to the survival of the group; the scavenger-hunt scenario involved the same behavior of searching for food items, but in a context that was not fitness relevant. The rating task was followed by a short distraction period, during which participants completed a digit-recall task. After the distraction task, all participants were given a surprise free-recall test on the words they had rated.

### Method

#### *Participants and Apparatus*

One hundred fifty people participated in this experiment. Some participated in exchange for partial credit in an introductory psychology course, and others received a small monetary compensation. We tested participants individually in sessions lasting approximately 30 min. Stimuli were presented and controlled by personal computers.

#### *Materials and Design*

Thirty concrete nouns (e.g., *chair, snow, orange*) were used as the target words in this experiment (5 additional concrete nouns were used in a practice phase). The experiment used a simple between-subjects design: All participants were asked to rate the same words, in the same random order, but participants in different conditions rated the words’ relevance to different scenarios ( $n = 50$  in each group). Equal numbers of men and women participated in each group. The rating task was followed immediately by a short digit-recall task and then the unexpected free-recall task. Except for the rating scenario, all aspects of the design, including timing, were held constant across participants.

#### *Procedure*

On arrival at the laboratory, participants were randomly assigned to one of three rating scenarios: gatherer, hunter, or scavenger hunt. The instructions for the gatherer condition read as follows:

In this task we would like you to imagine that you are living long ago in the grasslands of a foreign land. As a part of a small group, you are in charge of gathering food for your tribe. You need to scavenge for edible fruits, nuts, vegetables, etc. Gatherers often have to have knowledge about the locations and seasonal availability of edible foods, but no matter what the conditions (extreme heat, flooding, drought), you must gather edible food successfully for your tribe to eat. We are going to show you a list of words, and we would like you to rate how relevant each of these words would be for your attempt to gather edible food successfully and bring it back to your tribe. Some of the words may be relevant and others may not—it's up to you to decide.

Participants in the hunter condition were told,

In this task we would like you to imagine that you are living long ago in the grasslands of a foreign land. As a part of a small group, you are in charge of contributing meat to the tribe. You could hunt big game, trap small animals, or even fish in a nearby lake or river (if available). Hunters often have to travel great distances in order to find food, but no matter what the conditions (extreme heat, flooding, drought), you must hunt successfully for your tribe. We are going to show you a list of words, and we would like you to rate how relevant each of these words would be in your attempt to hunt successfully for food and bring it back to your tribe. Some of the words may be relevant and others may not—it's up to you to decide.

Finally, the instructions for the scavenger-hunt condition said,

In this task we would like you to imagine that you have been invited to participate in a scavenger hunt. As a part of a team you are in charge of locating food items from the search list for your team (e.g., fruits, meats, etc.). You need to look for clues that might indicate the location of an item, search in various locations, and transport found items to the game center. Members of the team might need to travel great distances to find the items and interpret clues that indicate locations, but no matter what the conditions you must scavenge successfully for your team. We are going to show you a list of words, and we would like you to rate how relevant each of these words would be in your attempt to scavenge successfully for the food items and bring them back to the game center. Some of the words may be relevant and others may not—it's up to you to decide.

The to-be-rated nouns were presented individually (centered on the computer screen) for 5 s each, and participants were asked to rate the words on a 5-point scale ranging from 1 (*totally irrelevant*) to 5 (*extremely relevant*). The rating scale was displayed just below each word, and participants responded by clicking on their value of choice. They were cautioned to respond within the 5-s presentation window, and the retention test that would come later was not mentioned. During a short practice session that preceded the actual rating task, participants

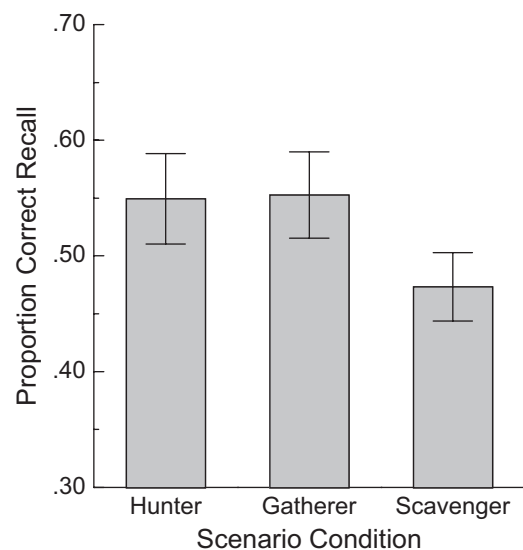
rated five words. After the practice phase, participants were briefly reminded of the main aspects of the assigned scenario.

After participants rated the last word, instructions for the digit-recall task appeared. On each trial of this task, seven digits ranging from 0 to 9 were presented sequentially for 1 s each, and participants were then required to type the digits in order into a text box. The digit-recall task proceeded for approximately 2 min. Instructions for the word-recall test then appeared. Participants were instructed to write down the previously rated words, in any order, on a response sheet. The final, recall phase proceeded for 10 min, and participants were asked to draw a line on the recall sheet, under the last recalled word, after each minute of recall. A clock was displayed on the computer monitor, and a "beep" sounded every minute, signaling participants to draw the line. This procedure allowed for the calculation of cumulative recall curves, but they are not reported here.

## Results and Discussion

The level of significance adopted for all the statistical comparisons reported here was set at  $p < .05$ . Participants had little difficulty rating the relevance of the target words within the allotted time, rating more than 99% of the presented words. The number of unrated words (i.e., no response within 5 s) did not differ significantly across groups.

Figure 1 presents the average proportion of correct recall for the three scenario conditions. An overall analysis of variance (ANOVA) on the data revealed a significant main effect of condition,  $F(2, 144) = 6.05$ ,  $MSE = 0.017$ ,  $\eta_p^2 = .08$ . Post hoc tests (Tukey's honestly significant difference) revealed no significant differences between the gatherer and hunter conditions, but recall was better in both these conditions than in the scavenger-hunt condition. Sex of the participant was also included as



**Fig. 1.** Results from Experiment 1: average proportion of correct recall in each condition ( $n = 50$  per condition). Error bars indicate 95% confidence intervals.

**TABLE 1**  
*Average Relevance Rating and Response Time in Each Condition in Experiment 1*

Condition	Relevance rating	Response time (seconds)
Hunter	2.537 (0.425)	2,389.01 (385.59)
Gatherer	2.806 (0.404)	2,444.34 (368.10)
Scavenger hunt	2.873 (0.426)	2,510.77 (464.19)

**Note.** Standard deviations are given in parentheses.

a factor in the analysis, but did not have a significant main effect,  $F(1, 144) < 1$ . Moreover, the interaction between sex and condition was not significant,  $F(2, 144) < 1$ . The same pattern of results was obtained when we used items, rather than subjects, as the unit of analysis.

We also compared relevance ratings and response times for those ratings across the conditions (see Table 1). It was possible, for example, that the retention advantages in the hunter and gatherer conditions were due to fitness-relevant processing being more effortful than control processing, and analyses of response times provided a test of this hypothesis. The response time analysis indicated no significant differences among the scenario conditions,  $F(2, 144) = 1.10$ ,  $MSE = 168,732.7$ , or between males and females,  $F(1, 144) < 1$ . Significant response time differences among the scenarios were detected in the item analysis,  $F(2, 116) = 4.86$ ,  $MSE = 44,794.3$ ,  $\eta_p^2 = .078$ , but post hoc tests (Tukey's honestly significant difference) revealed that participants took significantly longer to rate words in the scavenger-hunt condition than in the other conditions. According to the effort hypothesis, this pattern would predict better, not worse, performance in the scavenger-hunt condition.<sup>2</sup> Analyses of the ratings also indicated a significant effect of scenario condition,  $F(2, 144) = 8.95$ ,  $MSE = 0.177$ ,  $\eta_p^2 = .11$ ; post hoc tests revealed significantly lower ratings in the hunter condition than in the gatherer and scavenger-hunt conditions, which did not differ from one another. Exactly the same statistically significant pattern of results was obtained in the item analysis. Thus, neither the rating nor the response time data provide insight into the memory differences observed across the scenario conditions. No sex-based rating differences were found in either the subject or the item analyses.

Overall, these data provide strong support for the contention that fitness-relevant processing enhances subsequent retention. Processing information from the perspective of survival-based hunting and gathering activities enhanced subsequent free recall compared with processing information from the perspective of gathering food in a scavenger hunt. It is important to note that although all three scenarios required participants to rate the relevance of words to the same activity—collecting food—

<sup>2</sup>Response times represent only one metric for cognitive effort, and this analysis does not definitively rule out effort as an explanation of fitness-based advantages.

memory was significantly enhanced only when the activity was perceived as relevant to fitness. Experiment 1 produced no sex differences in memory performance; males and females had similar rates of recall regardless of whether the scenario involved hunting (males = .56, females = .54) or gathering (males = .54, females = .56).

## EXPERIMENT 2

Experiment 1 demonstrated mnemonic advantages for fitness-relevant hunting and gathering scenarios relative to a food-gathering scenario involving a scavenger hunt. Given that a scavenger hunt seems more relevant to gathering than to hunting, we designed Experiment 2 to test a survival-based hunting scenario against a virtually identical hunting scenario that was not fitness relevant. In the new control condition, participants were asked to imagine that they were part of a team participating in a hunting contest. All other aspects of the scenarios (e.g., the need to hunt big game, trap small animals, or fish in a nearby lake or river) remained the same in the two conditions.

### Method

#### *Participants and Apparatus*

One hundred people participated in this experiment. They received partial credit in an introductory psychology course and were tested individually in sessions lasting approximately 30 min. Stimuli were presented and controlled by personal computers.

#### *Materials and Design*

The 30 target words from Experiment 1 were also used in Experiment 2. All participants were asked to rate the relevance of the same words, presented in the same random order, but participants in different conditions rated the words' relevance to different scenarios ( $n = 50$  in each group). Equal numbers of men and women were assigned to the two scenario conditions.

#### *Procedure*

The procedure of Experiment 1 was replicated in this experiment, except for changes in the scenarios that were given to participants. In the hunter condition, the rating instructions were as follows:

In this task, please imagine that you are living long ago in the grasslands of a foreign land. As a part of a small group, you are in charge of contributing meat to feed your tribe. You will need to hunt big game, trap small animals, or even fish in a nearby lake or river. Hunters often have to travel great distances, pursue animals through unfamiliar terrain, and successfully return home. Whatever the conditions, you must hunt successfully to feed your tribe. We are going to show you a list of words, and we would like you to rate how relevant each of these words would be in your attempt to hunt successfully for food. Some of the words may be relevant and others may not—it's up to you to decide.

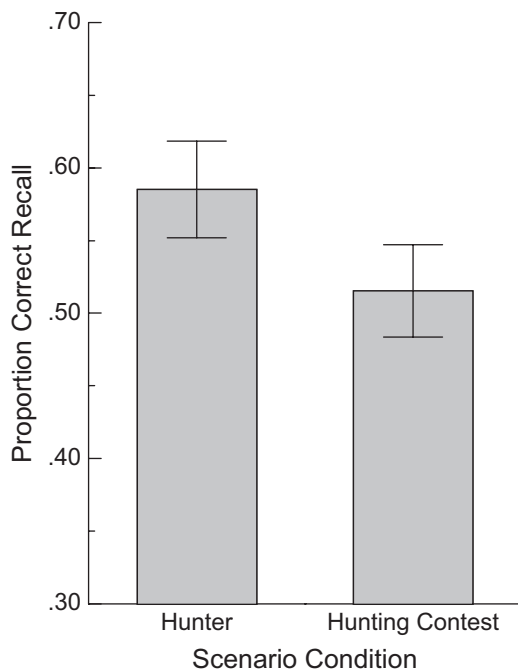
Participants in the hunting-contest condition instead received the following instructions:

In this task, please imagine that you have been invited to participate in a hunting contest. As a part of a team, you are in charge of contributing captured game to the team effort. You will need to hunt big game, trap small animals, or even fish in a nearby lake or river. Members of the team often have to travel great distances, pursue animals through unfamiliar terrain, and successfully return to the contest center. Whatever the conditions, you must hunt successfully to help your team win the contest. We are going to show you a list of words, and we would like you to rate how relevant each of these words would be in your attempt to hunt successfully. Some of the words may be relevant and others may not—it's up to you to decide.

### Results and Discussion

Participants had little difficulty providing ratings within the allotted time. They rated more than 99% of the presented words, and the number of unrated words (i.e., no response within 5 s) did not differ significantly between the groups.

As in Experiment 1, the level of significance adopted for all statistical comparisons was set at  $p < .05$ . Figure 2 presents the average proportion of correct recall for the two scenario conditions. An ANOVA revealed a highly reliable main effect of condition,  $F(1, 96) = 9.04$ ,  $MSE = 0.014$ ,  $\eta_p^2 = .09$ ; a mar-



**Fig. 2.** Results from Experiment 2: average proportion of correct recall in each condition ( $n = 50$  per condition). Error bars indicate 95% confidence intervals.

**TABLE 2**

*Average Relevance Rating and Response Time in Each Condition in Experiment 2*

Condition	Relevance rating	Response time (seconds)
Hunter	2.625 (0.393)	2,387.78 (340.56)
Hunting contest	2.680 (0.310)	2,372.75 (338.04)

**Note.** Standard deviations are given in parentheses.

ginally significant effect of sex,  $F(1, 96) = 3.05$ ,  $MSE = 0.014$ ,  $p < .09$ ,  $\eta_p^2 = .03$ ; and no significant Condition  $\times$  Sex interaction,  $F(1, 96) < 1$ . Females tended to recall slightly more items than males in both scenario conditions (overall averages were .57 and .53 for females and males, respectively), a result that is inconsistent with the pattern predicted by the evolutionary account. The item analysis also revealed a strong main effect of condition,  $F(1, 58) = 18.15$ ,  $MSE = 0.008$ ,  $\eta_p^2 = .24$ , but neither the main effect of sex,  $F(1, 58) < 1$ , nor the interaction of condition and sex,  $F(1, 58) = 1.38$ ,  $MSE = 0.008$ , was significant in this analysis.

Table 2 summarizes the rating and response time data. None of the response time differences approached significance in either the subject or the item analyses. The rating data revealed no significant main effect of condition or sex in either the subject or the item analyses (all  $F$ s  $< 1$ ), although both analyses revealed significant Condition  $\times$  Sex interactions—subject analysis:  $F(1, 96) = 4.70$ ,  $MSE = 0.122$ ,  $\eta_p^2 = .05$ ; item analysis:  $F(1, 58) = 3.14$ ,  $MSE = 0.222$ ,  $\eta_p^2 = .05$ . Men tended to give higher relevance ratings than did women in the hunter condition ( $M$ s = 2.71 and 2.54 for males and females, respectively), whereas women gave higher relevance ratings in the hunting-contest condition ( $M$ s = 2.61 and 2.75 for males and females, respectively). Given that no interaction was found in the recall data, and that the overall recall advantage for the hunter condition was not reflected in the rating data (ratings were equivalent in the two scenario conditions), the interaction provides little insight into the hypothesis of main interest.

### GENERAL DISCUSSION

Most scholars acknowledge that human memory is an evolved adaptation, sculpted by the processes of natural selection (e.g., Paivio, 2007), although the precise nature of that adaptation remains controversial. Psychologists typically assume that there are general memory processes (e.g., encoding, storage, and retrieval) that have similar operating characteristics across materials and domains (e.g., Neath & Surprenant, 2003). In this view, what determines retention is the richness of the initial encoding and, ultimately, the degree of “match” between the conditions present at encoding and those existing at the time of the retrieval query (Tulving, 1983). Although some situations engender more elaborate memory records than others, and thus

create records that are more likely to be matched in later environments, psychologists assume that the memory processes themselves are domain-general, or insensitive to content.

From an evolutionary perspective, though, it seems more reasonable to propose memory mechanisms that are domain-specific, or sensitive to content (Klein et al., 2002; Nairne & Pandeirada, 2008b). Not all events are equivalent from a fitness perspective (e.g., it is usually more important to remember a predator, a food source, or a potential mating partner than other information), and it is easy to imagine that memory is tuned toward helping humans solve adaptive problems related to reproduction and survival. Indeed, processing information in terms of its relevance to survival leads to strikingly good retention, at least compared with processing information using traditional encoding strategies, such as forming a visual image or processing meaning (Nairne et al., 2008).

The experiments reported here provide what is perhaps the strongest evidence yet that human memory systems may be tuned to retain information that is processed for fitness. Rating the relevance of words to ancestrally relevant hunting and gathering activities improved memory compared with rating the relevance of words to essentially the same general activities in a non-fitness-related context. For example, in Experiment 2, both rating scenarios described the same hunting activities—what differed was whether participants imagined themselves hunting for survival or participating in a hunting contest. Activating a context that was fitness relevant led to significantly greater retention. The experimental design we used represents a significant methodological advance over most previous research, in which the control scenarios matched the fitness-related scenarios on numerous dimensions, but involved different activities (e.g., moving to a new home, vacationing at a resort, or planning a bank heist).

The idea that sex-based cognitive specializations might be tapped by our hunter-gatherer scenarios was more speculative. As noted earlier, there is some evidence that men outperform women on tasks involving skills relevant to hunting (e.g., navigation), whereas women excel on tasks requiring skills relevant to gathering (e.g., remembering locations of food resources within a constrained environment). For instance, New, Cosmides, and Tooby (2007) recently showed that women are more accurate than men at pointing to newly learned spatial locations (in an outdoor market) if those locations contain nutritional resources. If men and women have memory systems tuned to hunting and gathering, respectively, they might be expected to show sex-based differences in memory for words rated for relevance to hunting and gathering scenarios. This prediction was not supported by the data; we found no evidence in either experiment for scenario-specific sex differences in recall performance. Although null effects are notoriously difficult to defend, our experiments employed relatively large numbers of participants, and the data offered little, if any, statistical support for the predicted interaction.

The discovery that fitness-relevant processing is a particularly effective form of encoding reinforces the value of adopting a functional-evolutionary perspective on remembering. Memory researchers rarely consider function as an important determinant of the design and operation of memory systems. Even if it turns out that memory performance is shaped primarily by current selection pressures or those operating throughout development, rather than by ancestral priorities, the act of remembering is still goal directed and purposeful. Adopting an agenda driven by a functional perspective can lead to the discovery of new empirical phenomena, and may ultimately provide a clear path toward understanding both how and why people remember.

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