Center for Lifespan Psychology

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Research Project 2: Lifespan Age Differences in Memory Representations (LIME)

LIME investigates mechanisms of memory formation, consolidation, and retrieval, with a focus on the ways in which these mechanisms change across the lifespan (see Sander et al., 2012). The project addresses the fundamental question whether aging-induced decrements in the distinctiveness of neural representations contribute to age-related losses in memory performance during adulthood and old age. Providing answers to this question requires the coordination of concepts and methods from lifespan psychology, cognitive neuroscience, and computational neuroscience. Accordingly, the project relies on experimental research designs, advanced multimodal imaging methods, and computational modeling. The project continues and broadens the work of Myriam Sander's Minerva Group, which was established in 2016.

Research Area 1: Age Differences in Similarity and Distinctiveness of Memory Representations

Are memories represented differently in older than in younger adults? According to the dedifferentiation hypothesis, age-related cognitive decline during adulthood and old age reflects decrements in the distinctiveness of neural representations and processing pathways (Li et al., 2001). In line with this hypothesis, pioneering work by Denise Park and colleagues has shown that differences in the neural representation between items belonging to different categories, such as houses and faces, are less pronounced in older adults than in younger adults. However, most studies thus far have not yet linked differences in the distinctiveness of individual memory representations to adult age differences in cognitive performance. In the LIME project, we systematically probe whether links between neural distinctiveness and performance help to elucidate adult age differences in episodic memory.

In pursuing this research question, the project makes ample use of subsequent memory paradigms, which analyze recall success as a function of neural activity during encoding, such as variations in oscillatory power measured with electroencephalography (EEG). In particular, power increases in the theta band accompanied by power decreases in the alpha/beta bands have been shown to indicate associative binding and elaboration mechanisms in young adults. We were able to show that these oscillatory mechanisms of successful memory formation remain relevant in old age (Sander et al., 2020; see Figure 7).

In addition, multimodal analyses revealed a clear structure–function relationship between the integrity of memory-related brain regions and the strength of the oscillatory subsequent memory effect. In particular, older adults' lower structural integrity of the inferior frontal gyrus (IFG), a region known to be involved in elaboration processes, was accompanied by reduced subsequent memory effects in the alpha frequency. Taken together, these results indicate that memory representations tend to be formed with fewer details with advancing adult age (Sander et al., 2020), with downstream consequences for long-term maintenance and forgetting (see Fandakova et al., 2020).

Recent results from another study support the hypothesis that older adults form less detailed representations than younger adults. Using representational similarity analysis, we compared the similarity of spatiotemporal EEG frequency patterns during initial encoding in relation to subsequent recall performance in younger and older adults (Dissertation Verena Sommer; Sommer et al., 2019). Specifically, we addressed the question whether successful memory is reflected in relatively more distinct or relatively more similar patterns of neural activity in younger and older adults. We found that the association between memory success and pattern similarity differed between young and older adults, suggesting age differences in basic cognitive encoding processes. For older adults, better memory performance was linked to higher similarity during early stages of encoding. For younger adults, lower similarity during later periods of encoding was positively related to memory performance

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Key References

Sander, M. C., Lindenberger, U., & **Werkle-Bergner, M.** (2012). Lifespan age differences in working memory: A two-component framework. *Neuroscience & Biobehavioral Reviews, 36*(9), 2007–2033. https://doi.org/10.1016/j.neubiorev.2012.06.004

Sommer, V. R., Fandakova, Y., Grandy, T. H., Shing, Y. L., Werkle-Bergner, M., & **Sander, M. C.** (2019). Neural pattern similarity differentially relates to memory performance in younger and older adults. *Journal of Neuroscience, 39*(41), 8089–8099. https://doi.org/10.1523/JNEUROSCI.0197-19.2019

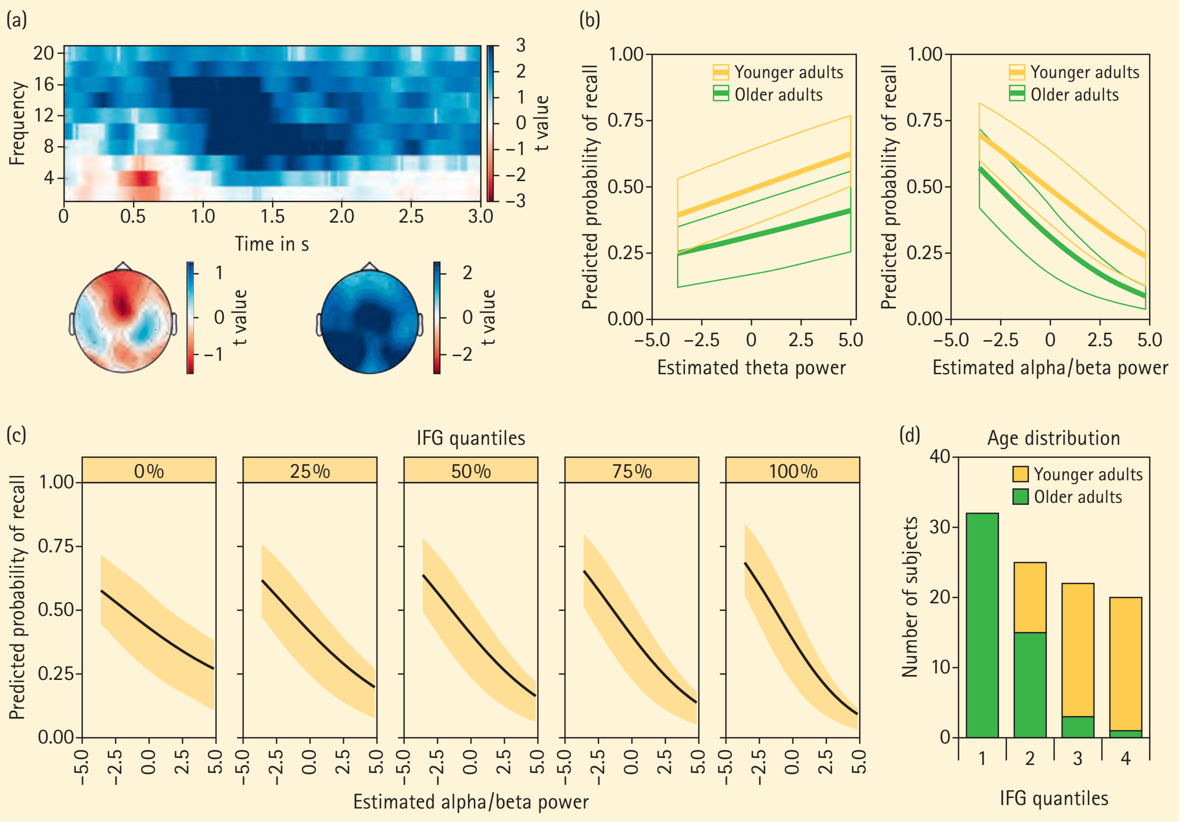

Figure 7. (a) Time-frequency plot of subsequent memory effects (thus, the difference in power of recalled vs. not-recalled word pairs) in theta and alpha/beta power, collapsed across age groups. (b) Power modulations in theta (left) and alpha/beta (right) frequencies predict single trial accuracy in both younger and older adults. (c) Alpha/beta band power is more predictive for memory recall in participants with high cortical thickness of the inferior frontal gyrus (IFG) than in those with lower cortical thickness, as shown by displaying predicted probabilities of varying alpha power for IFG quantiles. (d) Distribution of older and younger adults across different levels of structural integrity of the IFG (represented by quantiles). Most of the participants with low cortical thickness are older, indicating that reduced memory performance in older adults can be attributed to lower structural integrity of the IFG, which is related to smaller subsequent memory effects in alpha/beta power (adapted from Sander et al., 2020).

Key Reference

Sander, M. C., Fandakova, Y., Grandy, T. H., Shing, Y. L., & Werkle-Bergner, M. (2020). Oscillatory mechanisms of successful memory formation in younger and older adults are related to structural integrity. *Cerebral Cortex.* Advance online publication. https://doi.org/10.1093/cercor/bhz339

(see Figure 8). These results suggest that older adults rely more on encoding the general gist of stimuli, reflected in increased early encoding similarity, whereas young adults tend to form and encode mental images with distinct details, reflected in increased dissimilarity during later phases of encoding.

In our ongoing studies, we take a closer look at adult age differences in representational patterns. In a recent functional magnetic resonance imaging (fMRI) paradigm, we went beyond the mass-univariate characterization of neural specificity at the category level, and instead used representational similarity analyses to relate memory performance differences between age groups to neural pattern stability across repeated exposures, and to neural pattern similarity of different exemplars within one semantic category relative to the similarity of objects from different categories. Initial analyses suggest that the stability or self-similarity of neural representations at the item level, relative to their similarity to other items of the same category, is negatively related to adult age and positively related to memory performance.

Adaptation paradigms offer yet another approach to probe the specificity of representations. These paradigms rest on the assumption that neuronal populations reduce their responses (i.e., adapt) when stimulus features to which they are sensitive are repeated.

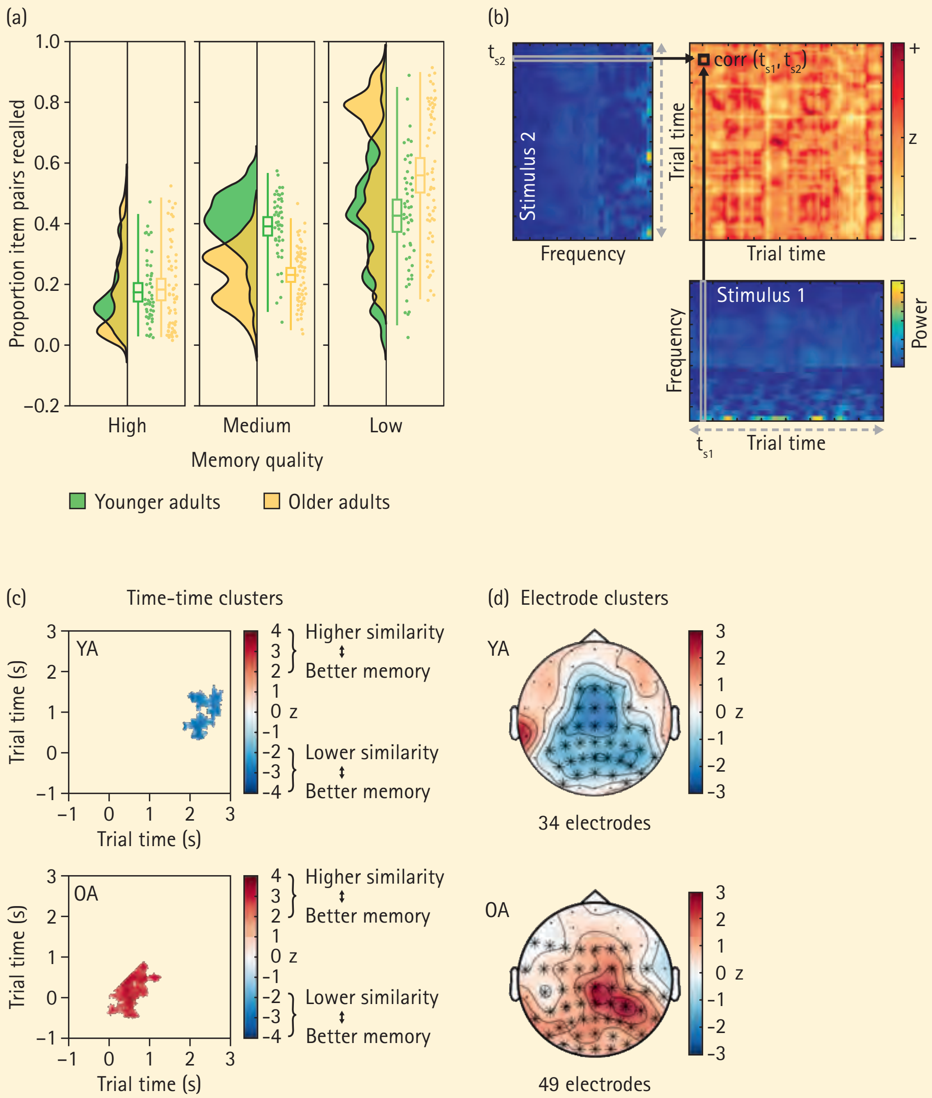

Figure 8. (a) Age differences in the quality of memory representations. In this study, participants repeatedly studied word–scene pairs followed by several rounds of cued recall. The quality of memory representations was defined by the fate of the individual pair across the course of the experiment. The figure shows the proportion items with high, medium, and low memory quality for young adults (YA) and older adults (OA). Older adults have a lower proportion of medium-quality and a higher proportion of lower-quality items than younger adults. (b) Spectral representational similarity analysis methodology. Frequency vectors from every time point of stimulus 1 are Pearson-correlated with frequency vectors from every time point of stimulus 2 (corr(t_{s1}, t_{s2})) resulting in a time-time similarity matrix representing the similarity of the frequency patterns of these two stimuli at all possible time-time combinations at one electrode. (c) Time-time clusters with the corresponding topography (d) in which the stimuli of different memory quality reliably differed from another in each age group. Whereas higher similarity in an early (positive) cluster is related to a higher recall probability in older adults, higher distinctiveness (negative cluster) is beneficial for memory performance in younger adults (adapted from Sommer et al., 2019).

Key Reference

Lindenberger, U., & Mayr, U. (2014). Cognitive aging: Is there a dark side to environmental support? *Trends in Cognitive Sciences, 18*(1), 7–15. https://doi.org/10.1016/j.tics.2013.10.006

The magnitude of adaptation is thus a direct measure of representation specificity. In a lifespan EEG study, we investigated whether differences in adaptation magnitudes predict differences in memory performance between children, young adults, and older adults (Dissertation Verena Sommer). To this end, we varied the number of exposures and the degree of similarity to other stimuli of visually presented objects. Event-related potentials displayed adaptation effects in all age groups and were associated with memory specificity. Our findings demonstrate that adaptation effects reflect encoding mechanisms that facilitate the formation of stimulus-specific memory representations, again highlighting their significance as neural indicators of individual differences in episodic memory across the lifespan. The extension of this investigation to child development was accomplished in collaboration with Sarah Weigelt (formerly Ruhr-Universität Bochum, now Technische Universität Dortmund).

Research Area 2: Effects of Context on Memory Representations

Successful memory is greatly aided by the spatial and temporal settings of an event, commonly referred to as its context. This dependency of memory on context increases with advancing adult age (Lindenberger & Mayr, 2014). At the same time, and somewhat paradoxically, older adults find it particularly difficult to actively retrieve specific object–context associations. Based on these observations, our studies aim at a better understanding of age differences in the contextualization of memories and the precise conditions under which memory performance benefits from context reinstatement.

In a large multimodal study that combined EEG, functional and structural MRI, and eye tracking, we have been investigating how context shapes younger and older adults' memories for objects (Dissertation Anna Karlsson; see Figure 9a). We established a high-resolution multiband fMRI sequence that will allow us to track functional activations at the level of hippocampal subfields. So far, our behavioral results support the well-known observation of lower pair memory performance in older adults compared to younger adults, with no age group differences in object memory. For object memory performance, context reinstatement was beneficial in both age groups, and seeing an object in both a familiar and a new context impaired performance. However, pair memory was only reduced when participants saw an object in a familiar, incorrect context, but not with a new context. These results suggest different contributions of familiarity and novelty detection for object and pair memory (see Figure 9b). Our electrophysiological results suggest that power modulations during encoding, as indicated by subsequent memory effects in alpha/beta band and theta band power measured with EEG, predict single-trial accuracy for both objects and object–context pairs. Interestingly, alpha/beta desynchronization was modulated by both context condition and age group. Larger desynchronization was related to a larger beneficial effect of context for pair memory when the context was old as compared to familiar, and more so in younger than in older adults. This result suggests that younger adults' deeper elaboration during encoding is a way to establish a reliable representation of the object–context pair that comes with a higher probability of recall. We are currently following up on these findings by investigating learning-related changes in neural patterns of object-specific representations in the hippocampus as captured by fMRI.

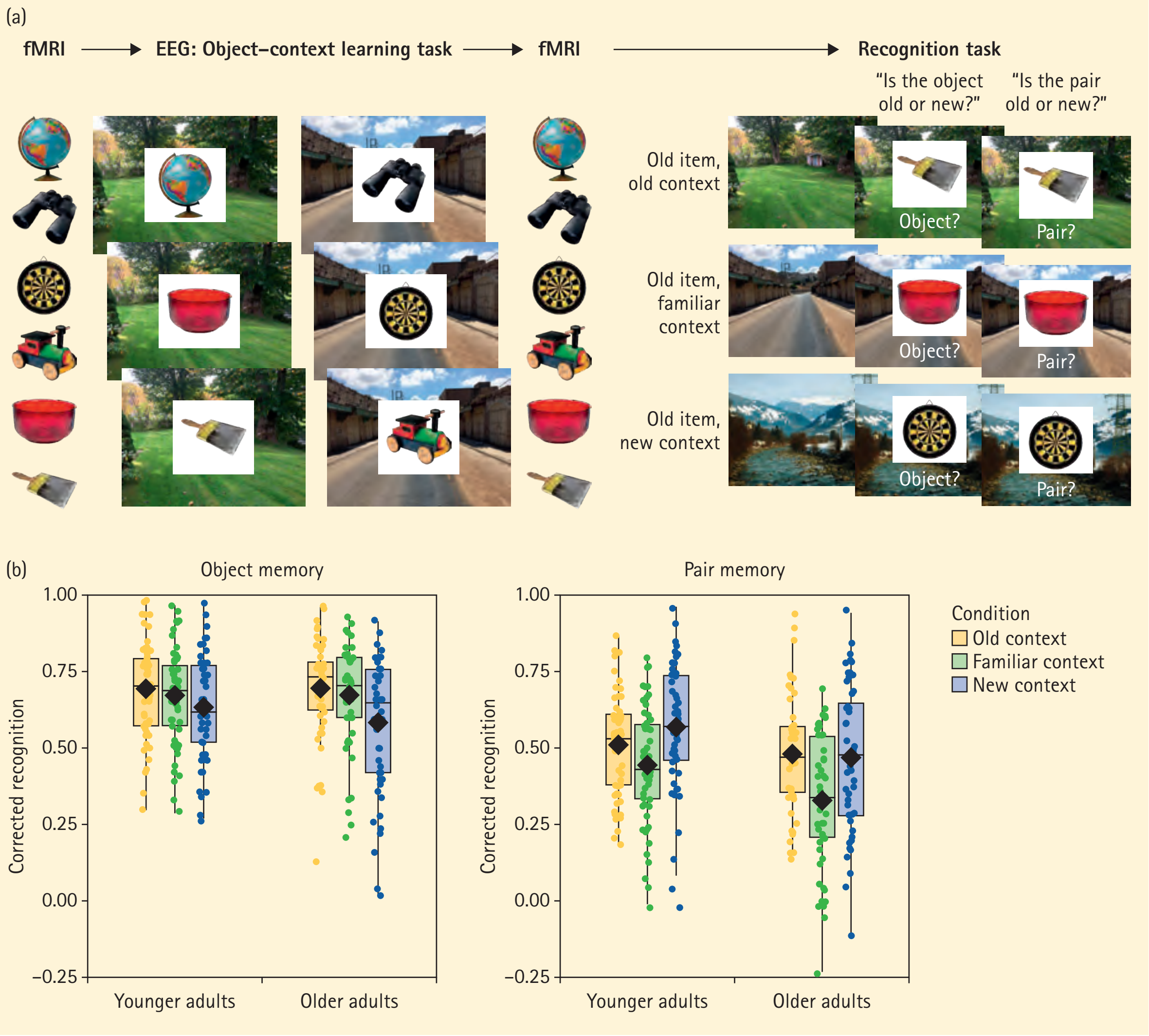

Figure 9. (a) Experimental paradigm of the multimodal study that combined EEG, functional MRI, and structural MRI to investigate the effect of context on memory (Dissertation Anna Karlsson). Participants were first familiarized with pictures of objects in the scanner to measure object-specific activation patterns. The main experiment consisted of an object–context learning paradigm during which EEG was assessed. This was followed by a postlearning fMRI measurement intended to reveal changes in memory representations. Finally, participants took a recognition memory test in which objects were presented with either the original learning context, a familiar context, or a new context. We first tested their memory for the object, followed by the question whether the object–context pair was the same as during learning. (b) First behavioral results: Corrected recognition scores (hits minus false alarms) for the different context conditions (old/familiar/new) as a function of age for object memory (left) and pair memory (right). Age groups differ when the retrieval of object–context pairs is required, but not when only objects need to be recalled. Context reinstatement (original context) benefits performance in both age groups, and seeing an object with a familiar, but incorrect context impairs performance.