Episodic Memory

Elisabeth Wenger and Yee Lee Shing

Introduction

Episodic memory circumscribes the ability to remember events, occurrences, and situations embedded in their temporal and spatial context—in other words, the memory of "what," "where," and "when" (Tulving 2002). It is the unique ability of humans to travel back in time and re-experience past events. To achieve this, elements belonging to the same event need to be associated with each other while being separated from other elements belonging to other events (Tulving 2002).

Throughout the lifespan, episodic memory functioning continuously undergoes extensive change, with rapid increases during childhood, decreases in adulthood, and accelerated decline in very old age (Shing et al. 2010). Given the important role that episodic memory plays in our daily lives, the prospect of potential trainability of episodic memory is a highly attractive idea. This applies to younger adults hoping to optimize their episodic memory ability, but probably even more to older adults, who generally experience a profound decline in episodic memory functioning that can seriously affect their well-being and quality of life. Therefore, it makes sense to incorporate studies of older adults into our consideration of episodic memory and training. In the following, we first provide a brief account of the definition and processes that are involved in episodic memory. We then discuss two theoretical frameworks, one concerning the components of episodic memory across the lifespan

E. Wenger (✉)
Center for Lifespan Psychology, Max Planck Institute for Human Development, Berlin, Germany
e-mail: wenger@mpib-berlin.mpg.de

Y.L. Shing
Center for Lifespan Psychology, Max Planck Institute for Human Development, Berlin, Germany

Division of Psychology, University of Stirling, Stirling, UK
e-mail: yshing@mpib-berlin.mpg.de

T. Strobach, J. Karbach (eds.), *Cognitive Training*,
DOI 10.1007/978-3-319-42662-4_7

and the other concerning the conception of plasticity. These theoretical frameworks help to guide us through the large body of memory training literature. We then summarize and integrate the behavioral literature on memory training and aging, followed by the more recent neuroimaging literature on the topic. Building upon some key points extracted from these sets of literature, we finally discuss the utility of multifactorial types of memory training and potential future work in this direction.

Episodic Memory: Definition and Processes

Following Squire's taxonomy of memory (Squire 1986), long-term memory can be divided into two profoundly different parts: declarative memory and nondeclarative memory. Nondeclarative memory refers to information that is difficult to articulate and does not require conscious awareness. Traditionally, it is thought to comprise procedural memory, classical conditioning, and priming. Declarative memory as our capacity to recollect events and facts, on the other hand, is the umbrella term for both episodic memory and semantic memory. Semantic memories are generalized and encyclopedic and not tied to a specific time or place. In contrast, episodic memories refer to specific episodes or events in a person's life. These memories are tied to the time and place in which the information was acquired. It follows that episodic memory, as a form of explicit memory, involves encoding, consolidation, and retrieval of events. When new declarative information is processed by the brain, it is presumed to be *encoded* by the medial temporal lobe (MTL) and then preserved in different cortical parts in the brain (Paller and Wagner 2002). The *consolidation* of memory traces is a process that stabilizes memory traces so they are preserved and typically takes place during post-learning periods when the brain is not consciously encoding or retrieving a certain memory (McGaugh 2000). *Memory retrieval* is assumed to approximate encoding processes in terms of activated brain regions (Nyberg et al. 2000) and is generally found to be dependent on the MTL as well as prefrontal cortex (PFC).

Two-Component Framework of Episodic Memory

We introduce the two-component framework of lifespan episodic memory here because, as we will demonstrate, the framework helps to orient and organize predictions as well as findings from the large body of literature on memory aging and plasticity. It has been proposed that episodic memory embodies two interacting components:

1. The *strategic* component refers to control processes that assist and coordinate memory processes at both encoding and retrieval. These processes may include elaboration and organization of memory content at encoding and specification,

verification, monitoring, and evaluation of relevant information at retrieval (e.g., Simons and Spiers 2003). On the neural level, the strategic component relies mostly on regions in the PFC and parietal lobes.
2. The *associative* component, on the other hand, refers to mechanisms of binding together different features of a memory item, different memory items, or a given memory episode and its context, into coherent representations, and is mediated by areas of the MTL.

Several behavioral experiments have indicated that these two components develop independently across the lifespan (Brehmer et al. 2007). In short, the associative component has been found to be relatively functional by middle childhood, but exhibits age-related decline in older adults. In contrast, the strategic component has been found to function at a level below that of young adults in children and older adults, most likely due to protracted maturation of PFC regions (and to some extent, of parietal regions as well) across childhood and early age-related decline in PFC regions across later part of adulthood (Shing et al. 2010).

The Concept of Plasticity

Research has shown that the persistent view of an adult brain incapable of change is too pessimistic: the brain remains flexible throughout the lifespan and can adjust to new experiences and challenges, albeit to varying degrees (for a review, see Lövdén et al. 2013). In the conception that we subscribe to, plasticity denotes the capacity for change in brain structure induced by a mismatch between the demands of the environment and the current functional supply the brain can momentarily offer (Lövdén et al. 2010). If the system is capable of a response to altered requirements through previously existing flexibility alone, then no mismatch is experienced, and no plastic change is necessary. On the other hand, if the mismatch is too large, that is, if new requirements are far too high for the momentary functional level of the brain, the system will not be able to assimilate in any way, and plastic changes will also not evolve. In other words, this model emphasizes that the system needs to experience mismatch, which means that the new environmental requirements need to lie between certain boundaries of task difficulty being too high and too low in order to evince experience-dependent plastic changes. Such changes can then help the system to adapt to new circumstances.

Plasticity in Episodic Memory

Behavioral Evidence Demonstrating Plasticity Throughout the Lifespan. Training programs designed to enhance memory performance have proliferated over the past decades, and meta-analytic reviews support the efficacy of at least some of these types of memory training across a broad array of memory tasks (Lustig et al. 2009; Verhaeghen et al. 1992). Episodic memory can be trained by instructing people to use a specific strategy, such as the Method of Loci, name–face mnemonics, number mnemonics, or story and sentence mnemonics, strategies altering the organization of material (categorization, chunking, associations, imagery) or optimizing basic processes like rehearsal or concentration, or even strategies making the best use of external memory cues (for a review, see Gross et al. 2012). In contrast to attempts to train episodic memory via strategy instruction, there have also been endeavors to target the process of memory without strategy instruction, for example, via recollection training (Jennings and Jacoby 2003). In this study, participants were given several trials of a continuous recognition task in which they had to use recollection to identify repeated items. After each trial, the number of intervening items between repetitions increased gradually. This incremented-difficulty approach has been shown to enhance the ability to recollect information across increasing delay intervals and has also been replicated and shown to generalize to at least some working memory tasks. Thus far, a variety of training routes have been shown to improve episodic memory performance in younger as well as older adults.

The next question is whether there are age-related differences in the efficacy of memory training and to which extent memory training may help older adults to reduce age deficits in memory performance. Importantly, cognitively healthy older adults are able to acquire and utilize memory strategies, even up to their 80s and can indeed improve their memory performance through this form of contextual support (for a review, see Brehmer et al. 2014). Older adults often show much improvement in memory performance, bringing them to the initial level of performance of younger adults before training. However, in terms of plasticity, younger adults seem to profit more from strategy-based memory-enhancing interventions than older adults do (e.g., Brehmer et al. 2007; see also Guye et al. this volume). This is clearly visible in the so-called testing-the-limits approach: after extensive training in serial recall word lists with the Method of Loci[1] (i.e., after 17 training sessions distributed over the course of more than 1 year), there is an almost perfect separation of age groups—a magnification of age differences in performance after training (Baltes and Kliegl 1992). Thus, while older adults can clearly benefit from strategy-based memory training, sometimes approaching or even reaching the initial performance level of younger adults, they do not benefit as much as younger adults do, leading to a magnification of age differences after training (see Fig. 1).

There may be several reasons for the above findings. For one, older adults may have difficulties in forming novel associations between landmarks and the to-be-remembered information, for example, due to age-related decline in MTL regions, which are known to be crucial for associative memory formation. They may also have difficulties in the use of mental imagination for memorization and find it

[1] In the Method of Loci, participants are presented with lists of words, which are learned by forming visual associations between the *n*th word and the *n*th place (locus) of a fixed trajectory of places (loci) scanned mentally by the participant. Retrieval occurs by taking a mental walk along the trajectory, retrieving the associated image at each locus, and deriving the original word from it.

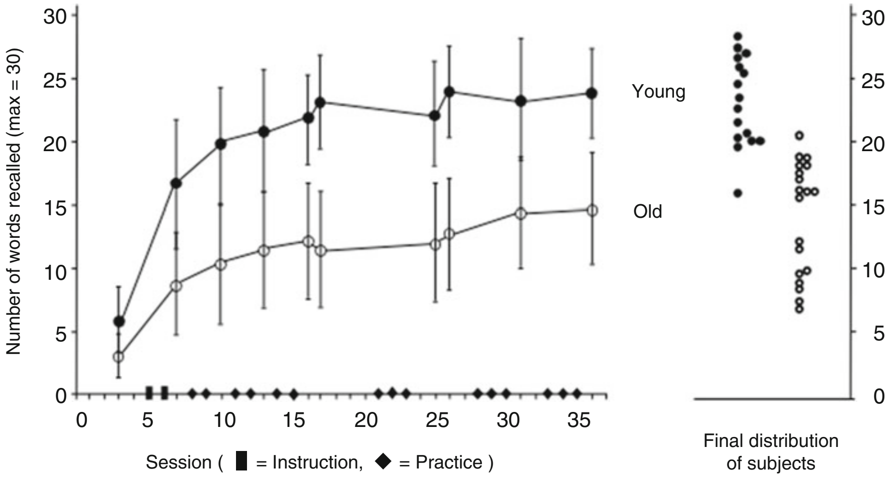

Fig. 1 Training effects and magnification of age differences. Older adults can benefit from memory training, thereby reaching initial performance levels of younger adults. However, younger adults benefit even more, leading to a magnification of age differences after training (Adapted from Baltes and Kliegl 1992)

difficult to form bizarre or unnatural images, which is important for the efficacy of the Method of Loci. Both of these explanations would add up to being a barrier when using rather than acquiring the mnemonic. Age differences in compliance regarding the use of the taught strategy may also play a role. In addition, all of the variables associated with learning in old age (e.g., the speed of mental operations) are characterized by large age differences favoring the young. Age differences in episodic memory performance could then be magnified by training (as in an amplification model) partly because the abilities associated with plasticity are reduced with advancing age (Verhaeghen and Marcoen 1996). While between-person and therefore age differences can be reduced after initial mnemonic instruction (i.e., compensation), age differences are magnified after extensive adaptive practice because baseline performance and general cognitive resources correlate positively with training gains, leading to reduced memory plasticity in older adults (Lövdén et al. 2012).

It is interesting to note that children's episodic memory performance can also be improved through instruction and practice and even more so than older adults: children can advance to the trained level of young adults when they have the chance to practice the newly learned strategy extensively (Brehmer et al. 2007). In this case, instruction gains may primarily reflect developmental and individual differences in the strategic component of memory—that is, the current ability of individuals to make use of the newly learned mnemonic strategy to actively organize (or categorize) the to-be-remembered material. Practice gains on the other hand, which are much stronger in children than in older adults, may then reflect developmental and individual differences in the associative component of episodic memory more than differences in the strategic component—that is, individuals' latent potential in fine-tuning mechanisms involved in the execution of the mnemonic strategy to optimize the formation and retrieval of new associations. Taken together, this evidence reveals that while both children and older adults benefit from memory strategy instruction, only children can improve significantly more through extensive training and practice because they can rely upon the associative component of memory, which is relatively mature. Older adults, on the other hand, show deterioration in the associative component such that even after the strategic deficit has been reduced by strategy instruction, they are limited in their memory improvement.

Training-Related Changes on the Neural Level. Given the improvement in behavioral performance, it is unsurprising that some studies (mostly employing the Method of Loci training) have found associated change in brain activation. A comparison of encoding before and after instruction revealed increased activity in frontal areas and fusiform gyrus, and recall after instruction additionally showed significant activation in parahippocampal gyrus and parietal regions as compared to recall before instruction (Kondo et al. 2005). Maguire and colleagues investigated superior memorizers in contrast to control subjects and found increased activation during encoding in very similar regions, namely, medial parietal cortex, retrosplenial cortex, and right posterior hippocampus (Maguire et al. 2003). Importantly, nearly all of the superior memorizers in this study happened to use a spatial learning strategy like the Method of Loci. In general, the activation of frontal regions in these studies underlines the increased engagement of control processes and thus the strategic component, with more posterior, parietal activation pointing to the specific involvement of imagery due to the nature of the training, while activation in temporal lobe indicates increased engagement of the associative component.

In the context of an aging study, Nyberg and colleagues demonstrated increased activity during memory encoding in occipital-parietal and frontal brain regions after learning the Method of Loci in young adults. Older adults did not show increased frontal activity, and only those older participants who had benefited from the mnemonic exhibited increased occipital-parietal activity (Nyberg et al. 2003). Therefore, age-related differences in memory plasticity may reflect both a frontal processing deficiency (diminished processing resources) and a posterior production deficiency. Interestingly, a study focusing on encoding success (i.e., successful memory formation) instead of encoding processes generally, regardless of outcome (as in the case of Nyberg et al. 2003), found no age differences in neural activation but rather comparable training-induced activation changes across the lifespan (Brehmer et al. 2015). This might speak to the proposition that brain areas supporting successful memory encoding following strategy instruction and practice remain quite stable across the lifespan, particularly in those older adults that have more youth-like brains, such as the positively selected study sample in the Brehmer et al. study (brain maintenance hypothesis of cognitive aging; Nyberg et al. 2012; see also Schmiedek this volume).

Instructions for the use of a new strategy to improve episodic memory performance can be viewed as a case study for the plasticity model introduced above (Lövdén et al. 2010, 2013). Can we regard functional changes as evidence for plasticity when participants show improved performance after instruction for strategy use? Following the theoretical definition laid out above, a more or less immediate change in behavioral performance and its accompanying change in functional activation due to strategy instruction would not be considered as manifested plasticity but rather as flexibility. In the words of Paul Baltes, this improvement following instruction could be termed *baseline reserve capacity*, namely, what an individual is capable of when the conditions of assessment are optimized, in other words, providing for an extended range of possible performances with additional resources (Baltes 1987). *Developmental reserve capacity*, on the other hand, would then be the plasticity as defined in our theoretical model above, namely, a further extension of performance range after conditions have been altered, with the aim of full activation, and possibly expansion, of an individual's task-relevant cognitive or neural resources. The strongest evidence for such developmental reserve capacity or plasticity would then be given if memory performance as such *generally* improved after strategy training, even if the newly acquired strategy was not used at this specific moment. Theoretically, the extensive use of such a mnemonic technique as the Method of Loci may enable an aged individual to rechallenge brain regions important for episodic memory tasks that have become under-challenged due to age-related decline. The heightened recruitment and engagement of these brain regions may then evoke macroscopic changes in brain structure—hence, manifestations of plasticity.

Combination of Training Types to Enhance Generalizability and Maintenance. In general, it seems to be beneficial, if not necessary, for the enhanced magnitude and preservation of behavioral effects to combine training of mnemonic techniques with other important factors affecting memory performance. A crucial limitation of targeted training interventions has been the widespread inability to sustain and generalize (i.e., transfer) the benefits of training in a specific strategy beyond the tasks actually used for training (Noack et al. 2014; see Schmiedek this volume). The most promising results have been provided by multifactorial interventions, in which different memory-enhancing techniques were combined with training of other skills (e.g., attention, relaxation; see Verhaeghen this volume). Under these circumstances, memory performance can improve and can be sustained for up to 3.5 years (Stigsdotter Neely and Bäckman 1993). Stigsdotter Neely and Bäckman provide well-founded arguments for the benefit of involving several critical aspects of memory functioning in memory training programs if they are to be maximally effective. Age-related deficits in episodic memory have an array of different sources (Bäckman 1989). Deficient retrieval mechanisms alone or impaired encoding and retrieval mechanisms could just as well play a role as attentional deficits. Older adults also seem to be disadvantaged with respect to a number of noncognitive factors, such as laboratory anxiety and level of arousal. As memory deficits accompanying the aging process have several origins, efforts to alleviate these deficits should ideally be multifactorial as well, to best target the problems (see Colzato and Hommel this volume). Training of encoding operations to provide effective strategies for organization and visualization of the material could then be combined with training of attentional skills—to improve concentration, focusing of attention, and vigilance, all of which are necessary to meet the attentional demands of remembering—and should additionally be combined with training to reduce levels of situational anxiety. Specific pretraining techniques focusing on image elaboration, verbal judgment, and relaxation have also been shown to enhance the application of a mnemonic technique and helped to maintain its efficacy (Sheikh et al. 1986).

Boosting Memory Training: A Promising Future Training Paradigm

Furthermore, reaching beyond the rationale for multifactorial combined training, we would like to emphasize that physical exercise intervention also needs to be taken into consideration (see Pothier and Bherer this volume). In particular, this applies to older adults whose bodily functioning is also undergoing senescent changes that may have strong implications for cognition. Observational studies continue to suggest that adults who engage in physical activity have a reduced risk of cognitive decline and dementia (for a review, see Duzel et al. 2016). Exercise can exert a protective effect, even if initiated in later life. Although the mechanisms through which physical exercise affects cognition, and especially episodic memory, are not yet fully understood, there is growing evidence that selected aspects of cognition are responsive to increases in physical exercise (Cotman and Berchtold 2002). For example, Erickson and colleagues observed that the hippocampus increased in size after 1 year of moderate exercise and this structural change was correlated with changes in spatial memory performance (Erickson et al. 2011; but note that memory changes did not differ between the experimental and the control group). Another study reported selective increases in cerebral blood volume in dentate gyrus—possibly an indicator for exercise-induced neurogenesis—after 3 months of exercising, which correlated with changes in cognitive performance (Pereira et al. 2007). In an earlier study, a combination of mental and physical training led to greater effects on a memory score than either activity alone (Fabre et al. 2002). The mental training program was multifactorial and comprised tasks involving perception, attention, association, and imagination.

Taken together, we propose that future studies should focus on such multidomain training approaches based on findings from the animal literature. Researchers examining rodents have emphasized both cognitive enrichment and enhanced physical activity as the driving forces behind plastic changes (Kempermann et al. 2010). One can speculate that physical activity may not only enhance cognition directly but also improve plasticity as the capacity for change per se. Physical activity may therefore boost the effects of cognitive enrichment or training on both the behavioral and the neural level. Such an additive effect of physical exercise and environmental enrichment has been shown before in the mouse hippocampus (Fabel et al. 2009). Voluntary physical exercise and environmental enrichment both stimulate adult hippocampal neurogenesis in mice, but via different mechanisms. That is, running in a wheel induces precursor cell proliferation, whereas environmental enrichment exerts a survival-promoting effect on newborn cells. Fabel and colleagues reported an increased potential for neurogenesis in that proliferating precursor cells were activated by running and then received a survival-promoting stimulus due to environmental enrichment following the exercise. Ten days of running followed by 35 days of environmental enrichment were additive such that the combined stimulation resulted in a 30 % greater increase in new neurons as compared to either paradigm alone (see Fig. 2; Fabel et al. 2009). Translated to the human

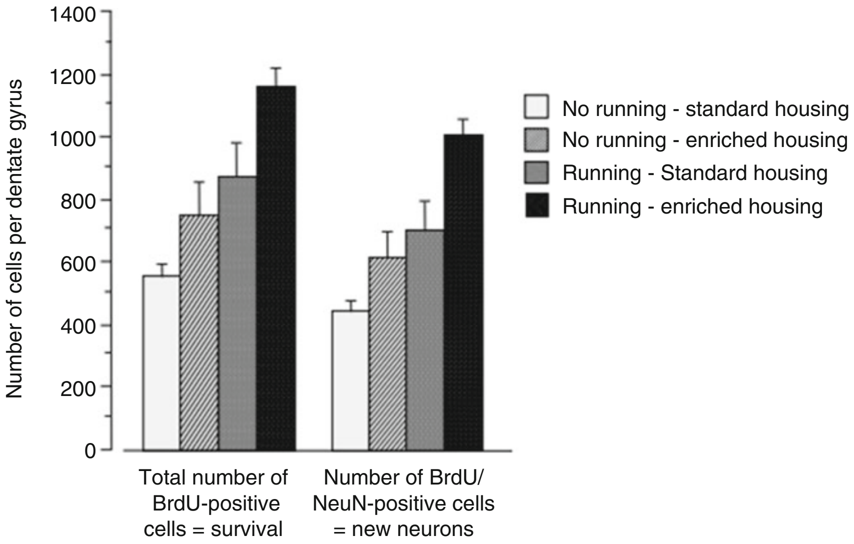

Fig. 2 Additive effect of physical exercise and environmental enrichment in the mouse hippocampus. Voluntary wheel running and enriched housing have each been shown to result in an increased number of cell labels with bromodeoxyuridine (BrdU) and new neurons compared to no running in standard housing. Combined running and enriched housing result in an even greater increase of BrdU-positive cells and newborn neurons. BrdU is commonly used to detect proliferating cells in living tissue (Adapted from Fabel et al. 2009)

hippocampus, this may mean that physical exercise could stimulate proliferating precursor cells that would then be more likely to survive if challenged by appropriate cognitive enrichment relying on the hippocampal structure, as, for example, memory demands. In this way, physical exercise could first "prepare" the aged MTL for increased usage. Hypothetically, any ensuing strategy instruction and specifically the practice of memory strategies could then—and perhaps only then—be successfully and fully exploited. As the associative and strategic components of memory function in intricate ways and are critically important for episodic memory performance, it seems to be a promising route to target both components and the neural regions underlying their functioning, namely, MTL and frontal lobe, in a combined multi-domain training paradigm.

Concluding Remarks

Put simply, episodic memory can be trained. Children as well as younger and older adults profit from strategy instruction, and it is encouraging to see that older adults can reach initial performance levels of younger adults after strategy instruction. Importantly, such performance gains most likely reflect manifestations of flexibility—defined as the adaptive reconfiguration of the exisiting functional and structural repertoire—and, if implemented correctly, rely most heavily on the strategic component of memory, that is, on prefrontal regions of the brain. Further performance gains following extensive practice are then most likely to be manifestations of plasticity. Unlike flexibility, plasticity does not only make use of preexisting neural resources but also changes them fundamentally. Here, older adults show reduced levels of plasticity compared to children and younger adults, as indicated by their lower performance gains following practice. In our view, one promising route for intervention is to provide older adults with memory training in combination with physical exercise to revitalize plasticity and thereby boost training effectiveness. Strategy training alone may be too narrow an intervention to result in substantive transfer and lasting maintenance of acquired skills. Currently, combined memory training types, most promisingly in concert with physical exercise, seem to be the best bet to not only target the strategic but also the associative component of memory, thereby hopefully having a widespread and lasting effect on memory functioning.

References

Bäckman, L. (1989). Varieties of memory compensation by older adults in episodic remembering. In L. W. Poon, D. C. Rubin, & B. A. Wilson (Eds.), *Everyday cognition in adulthood and late life* (pp. 509–544). New York: Cambridge University Press.

Baltes, P. B. (1987). Theoretical propositions of life-span developmental psychology: On the dynamics between growth and decline. *Developmental Psychology, 23*(5), 611–626. doi:10.1037/0012-1649.23.5.611.

Baltes, P. B., & Kliegl, R. (1992). Further testing of limits of cognitive plasticity: Negative age differences in a mnemonic skill are robust. *Developmental Psychology, 28*(1), 121–125. doi:10.1037/0012-1649.28.1.121.

Brehmer, Y., Kalpouzos, G., Wenger, E., & Lövdén, M. (2014). Plasticity of brain and cognition in older adults. *Psychological Research, 78*(6), 790–802. doi:10.1007/s00426-014-0587-z.

Brehmer, Y., Li, S.-C., Müller, V., von Oertzen, T., & Lindenberger, U. (2007). Memory plasticity across the life span: Uncovering children's latent potential. *Developmental Psychology, 43*(2), 465–478. doi:10.1037/0012-1649.43.2.465.

Brehmer, Y., Shing, Y. L., Heekeren, H. R., Lindenberger, U., & Bäckman, L. (2015). Training-induced changes in subsequent memory effects: No major differences among children, younger adults, and older adults. *NeuroImage, 131*, 214–225. doi:10.1016/j.neuroimage.2015.11.074.

Cotman, C. W., & Berchtold, N. C. (2002). Exercise: A behavioral intervention to enhance brain health and plasticity. *Trends in Neurosciences, 25*(6), 295–301. doi:10.1016/S0166-2236(02)02143-4.

Duzel, E., van Praag, H., & Sendtner, M. (2016). Can physical exercise in old age improve memory and hippocampal function? *Brain, 139*(3), 662–673. doi:10.1093/brain/awv407.

Erickson, K. I., Voss, M. W., Prakash, R. S., Basak, C., Szabo, A., Chaddock, L., et al. (2011). Exercise training increases size of hippocampus and improves memory. *Proceedings of the National Academy of Sciences of the United States of America, 108*(7), 3017–3022. doi:10.1073/pnas.1015950108.

Fabel, K., Wolf, S. A., Ehninger, D., Babu, H., Leal-Galicia, P., & Kempermann, G. (2009). Additive effects of physical exercise and environmental enrichment on adult hippocampal neurogenesis in mice. *Frontiers in Neuroscience, 3*, 50. doi:10.3389/neuro.22.002.2009.

Fabre, C., Chamari, K., Mucci, P., Massé-Biron, J., & Préfaut, C. (2002). Improvement of cognitive function by mental and/or individualized aerobic training in healthy elderly subjects. *International Journal of Sports Medicine, 23*(6), 415–421. doi:10.1055/s-2002-33735.

Gross, A. L., Parisi, J. M., Spira, A. P., Kueider, A. M., Ko, J. Y., Saczynski, J. S., et al. (2012). Memory training interventions for older adults: A meta-analysis. *Aging & Mental Health, 16*(6), 722–734. doi:10.1080/13607863.2012.667783.

Jennings, J. M., & Jacoby, L. L. (2003). Improving memory in older adults: Training recollection. *Neuropsychological Rehabilitation, 13*(4), 417–440. doi:10.1080/09602010244000390.

Kempermann, G., Fabel, K., Ehninger, D., Babu, H., Leal-Galicia, P., Garthe, A., & Wolf, S. A. (2010). Why and how physical activity promotes experience-induced brain plasticity. *Frontiers in Neuroscience, 4*, 189. doi:10.3389/fnins.2010.00189.

Kondo, Y., Suzuki, M., Mugikura, S., Abe, N., Takahashi, S., Iijima, T., & Fujii, T. (2005). Changes in brain activation associated with use of a memory strategy: A functional MRI study. *NeuroImage, 24*(4), 1154–1163. doi:10.1016/j.neuroimage.2004.10.033.

Lövdén, M., Bäckman, L., Lindenberger, U., Schaefer, S., & Schmiedek, F. (2010). A theoretical framework for the study of adult cognitive plasticity. *Psychological Bulletin, 136*(4), 659–676. doi:10.1037/a0020080.

Lövdén, M., Brehmer, Y., Li, S.-C., & Lindenberger, U. (2012). Training-induced compensation versus magnification of individual differences in memory performance. *Frontiers in Human Neuroscience, 6*, 141. doi:10.3389/fnhum.2012.00141.

Lövdén, M., Wenger, E., Mårtensson, J., Lindenberger, U., & Bäckman, L. (2013). Structural brain plasticity in adult learning and development. *Neuroscience and Biobehavioral Reviews, 37*(9B), 2296–2310. doi:10.1016/j.neubiorev.2013.02.014.

Lustig, C., Shah, P., Seidler, R., & Reuter-Lorenz, P. A. (2009). Aging, training, and the brain: A review and future directions. *Neuropsychology Review, 19*(4), 504–522. doi:10.1007/s11065-009-9119-9.

Maguire, E. A., Valentine, E. R., Wilding, J. M., & Kapur, N. (2003). Routes to remembering: The brains behind superior memory. *Nature Neuroscience, 6*(1), 90–95. doi:10.1038/nn988.

McGaugh, J. L. (2000). Memory: A century of consolidation. *Science, 287*(5451), 248–251. doi:10.1126/science.287.5451.248.

Noack, H., Lövdén, M., & Schmiedek, F. (2014). On the validity and generality of transfer effects in cognitive training research. *Psychological Research, 78*(6), 773–789. doi:10.1007/s00426-014-0564-6.

Nyberg, L., Habib, R., McIntosh, A. R., & Tulving, E. (2000). Reactivation of encoding-related brain activity during memory retrieval. *Proceedings of the National Academy of Sciences of the United States of America, 97*(20), 11120–11124. doi:10.1073/pnas.97.20.11120.

Nyberg, L., Lövdén, M., Riklund, K., Lindenberger, U., & Bäckman, L. (2012). Memory aging and brain maintenance. *Trends in Cognitive Sciences, 16*(5), 292–305. doi:10.1016/j.tics.2012.04.005.

Nyberg, L., Sandblom, J., Jones, S., Neely, A. S., Petersson, K. M., Ingvar, M., & Bäckman, L. (2003). Neural correlates of training-related memory improvement in adulthood and aging. *Proceedings of the National Academy of Sciences of the United States of America, 100*(23), 13728–13733. doi:10.1073/pnas.1735487100.

Paller, K. A., & Wagner, A. D. (2002). Observing the transformation of experience into memory. *Trends in Cognitive Sciences, 6*(2), 93–102. doi:10.1016/S1364-6613(00)01845-3.

Pereira, A. C., Huddleston, D. E., Brickman, A. M., Sosunov, A. A., Hen, R., McKhann, G. M., et al. (2007). An in vivo correlate of exercise-induced neurogenesis in the adult dentate gyrus. *Proceedings of the National Academy of Sciences of the United States of America, 104*(13), 5638–5643. doi:10.1073/pnas.0611721104.

Sheikh, J. I., Hill, R. D., & Yesavage, J. A. (1986). Long-term efficacy of cognitive training for age-associated memory impairment: A six-month follow-up study. *Developmental Neuropsychology, 2*(4), 413–421. doi:10.1080/87565648609540358.

Shing, Y. L., Werkle-Bergner, M., Brehmer, Y., Müller, V., Li, S.-C., & Lindenberger, U. (2010). Episodic memory across the lifespan: The contributions of associative and strategic components. *Neuroscience & Biobehavioral Reviews, 34*(7), 1080–1091. doi:10.1016/j.neubiorev.2009.11.002.

Simons, J. S., & Spiers, H. J. (2003). Prefrontal and medial temporal lobe interactions in long-term memory. *Nature Reviews. Neuroscience, 4*(8), 637–648. doi:10.1038/nrn1178.

Squire, L. R. (1986). Mechanisms of memory. *Science, 232*(4758), 1612–1619. doi:10.1126/science.3086978.

Stigsdotter Neely, A., & Bäckman, L. (1993). Long-term maintenance of gains from memory training in older adults: Two 3 1/2-year follow-up studies. *Journal of Gerontology, 48*(5), 233–P237. doi:10.1093/geronj/48.5.P233.

Tulving, E. (2002). Episodic memory: From mind to brain. *Annual Review of Psychology, 53*, 1–25. doi:10.1146annurev.psych.53.100901.135114.

Verhaeghen, P., & Marcoen, A. (1996). On the mechanisms of plasticity in young and older adults after instruction in the method of loci: Evidence for an amplification model. *Psychology and Aging, 11*(1), 164–178. doi:10.1037/0882-7974.11.1.164.

Verhaeghen, P., Marcoen, A., & Goossens, L. (1992). Improving memory performance in the aged through mnemonic training: A meta-analytic study. *Psychology and Aging, 7*(2), 242–251. doi:10.1037/0882-7974.7.2.242.