



Cognitive and neural mechanisms of learning and interventions for improvement across the adult lifespan: A systematic review

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ABSTRACT

There continues to be growing interest in the Science of Learning including identifying ways to apply findings. Presently, little is known about learning during healthy adulthood and methods to improve that learning. The main objective of the present systematic review is to identify and synthesize all recent cognitive and brain research investigating learning during healthy aging in adulthood. Searches were performed across Scopus, Web of Science, and ProQuest databases to identify published and unpublished studies conducted in healthy adults. Eligible studies reported measures of learning-related cognition, brain structure or function and their relationship with age, or effects of interventions to improve learning. Risk of bias was assessed using either the Mixed Methods Appraisal Tool or Critical Appraisal Skills Programme checklist. Search and screening were performed by three trained reviewers. Included studies were summarized using narrative synthesis and, for intervention studies, an effect direction plot. A total of 265 relevant studies were identified for inclusion. Studies were primarily lab-based cross-sectional studies conducted in Western contexts. Findings revealed an overall decline in learning-related cognitive and brain outcomes during healthy aging. However, declines were more pronounced in fluid abilities and explicit learning and memory while crystallized abilities and implicit learning and memory showed stability. Generally, higher education and socioeconomic status positively modulated age-related learning trajectories while baseline cognitive function influenced the effectiveness of interventions. Findings from the present systematic review are potentially limited by the exclusive focus on healthy aging and the small number of included studies conducted in non-Western contexts. Implications for policy, practice, and future research are discussed.

1. Introduction

1.1. Rationale

Researchers, practitioners, and the general public have continued to exhibit growing interest in the Science of Learning, the scientific study of the underlying bases of learning with the goal of describing, understanding, or improving learning across developmental stages and diverse contexts (Privitera, Ng, et al., 2023). Recent advances in the cognitive and neural sciences have illuminated our understanding of the principles, processes, and mechanisms of learning across a diverse range

of species, including our own (e.g., Haier, 2023). Findings from these studies support the conclusion that learning is a complex lifelong process involving the interplay of cognitive, neural, and other factors (e.g., Friston, 2003). Furthermore, the experience of learning modifies underlying cognitive processes and brain structure and function in a manner that impacts on future cognition and behavior (Boller et al., 2017). Given the relevance of this work outside the research laboratory, there has been growing interest in the application of findings from the Science of Learning to a number of other fields, including education (e.g., Howard-Jones, 2014; Privitera, 2021; Tokuhamma-Espinosa, 2010).

While there is tremendous interest in understanding human learning,

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previous investigations have generally not been developmentally comprehensive in their focus. Existing studies on the Science of Learning have predominantly investigated samples drawn from developmental stages during early and late life (Goodwill and Chen, 2021), although some notable exceptions do exist (e.g., Archer et al., 2018). This same pattern can be observed across published reviews with most focusing on research in samples of younger children (e.g., Cortés Pascual et al., 2019), or older adults, including clinical populations diagnosed with neurodegenerative diseases (Hopper et al., 2013). Collectively, this has created a gap in our understanding of learning during healthy adulthood as well as effective ways in which that learning can be improved. Given that the human brain retains the capacity for plasticity across the adult lifespan (Lövdén et al., 2013), and that adult learning trajectories can be altered based on the influence of both internal and external factors (Chen and Goodwill, 2022), there is significant value in better understanding learning during this period of development in the interests of maximizing human potential.

Developing a more comprehensive understanding of learning during adulthood, and effective ways of improving that learning, are crucial goals given current global demographic trends. Many nations around the world are continuing to struggle in addressing the significant consequences of a rapidly aging population (Bloom et al., 2011; United Nations, 2022). This issue is further complicated by the dynamic nature of the modern workforce where regular career changes are becoming the norm (Di Battista et al., 2023). Consequently, governments have recently shifted attention and resources toward extending and translating findings from the Science of Learning in order to inform educational policy and intervention strategies. One of the overarching goals of this shift is to support the development of a citizenry that is both productive and agile into late adulthood. Presently, the absence of a comprehensive understanding of learning across adulthood in healthy populations places a significant hurdle on the path to accomplishing this goal. The conduct of an exhaustive review synthesizing existing research on the cognitive and neural mechanisms of learning and interventions to improve learning in healthy adults would contribute significantly to the accomplishment of this goal, with the additional benefit of identifying areas in need of further research.

1.2. Objectives

The main objective of the present systematic review is to identify and synthesize all recent cognitive and brain research investigating learning across the adult lifespan. This review provides an overview of the principles, processes, and mechanisms of learning in healthy adults. Additionally, this review aimed to synthesize all recent findings on interventions to improve learning in adults. Findings from the present review will have implications for our understanding of learning in adulthood, the scoping of funding calls for future Science of Learning research, and for public education and outreach efforts to support life-long learning.

1.2.1. Research questions

The primary research question (RQ) of the present review was “How does learning change across a healthy adult’s lifespan?” The research sub-questions were:

1. What learning-related cognitive changes occur in healthy adults as they age?
 - a. Which specific dimensions of cognitive function have been investigated?
 - b. How do changes in these dimensions influence learning?
 - c. What factors influence these changes?
2. What learning-related brain changes occur in healthy adults as they age?
 - a. Which specific dimensions of brain structure/function have been investigated?

- b. How do changes in these dimensions influence learning?
 - c. What factors influence these changes?
3. What interventions based on evidence from 1 and 2 are most effective in the improvement of learning in healthy adults?
 - a. What are the reported effects of interventions on cognitive function?
 - b. What are the reported effects of interventions on brain structure/function?
 - c. What are the mediating and moderating factors that influence the efficacy of interventions?
4. What are the current knowledge gaps identified in 1–3?

For the purpose of the present review, learning was broadly defined to include traditional measures related to change in achievement or attainment, as well as changes in underlying cognitive and neural processes such as executive function, intelligence, and brain network activation.

2. Methods

2.1. Registration

The protocol for the present review was designed following recommendations provided in the Preferred Reporting Items for Systematic Review and Meta-Analysis Protocols (PRISMA-P) checklist (Page et al., 2021), and was registered with the Centre for Open Science (<https://osf.io/d9yev/>).

2.2. Eligibility criteria

Studies were included if they meet the following criteria:

- Journal articles, theses, dissertations, conference papers, and preprints
- Cross-sectional, longitudinal, and cross-sequential studies or research syntheses
- Published or posted between January 1st, 2012 and September 1st, 2023
- Reported one or more of the following:
 - o RQ1: Relationship between measure(s) of learning-related cognition and age.
 - o RQ2: Relationship between measure(s) of learning-related brain structure or function and age.
 - o RQ3: Impact of any intervention aimed at improving learning.
- Focused on healthy adult humans
- Reported findings (quantitative or qualitative) from participants age ≥ 20 years either exclusively or as a separate analysis from a wider age group.
- Written in English
- Full text available

Studies were excluded if any of the above criteria are not met or if the document was a purely theoretical paper, non-systematic narrative review, magazine article, abstract, protocol, preregistration, blog post, editorial, commentary, corrigendum, book, or book review. For our tabular and narrative syntheses, studies were grouped according to the specific RQ(s) they addressed, with studies relevant to multiple RQs (e.g., study that reported the relationship between age and both cognitive and brain measures associated with learning) included in multiple groups. For narrative synthesis, RQ groups were further organized based on the main themes addressed by studies (e.g., lifestyle interventions).

2.3. Information sources

Searches were conducted using Scopus, Web of Science (Core Collection and Preprints), and ProQuest databases. These databases were selected due to their extensive indexing of relevant published work as well as conference papers, theses, dissertations, and preprints. Searches were limited to research published between January 1st, 2012 and September 1st, 2023. Studies identified across all databases were pooled and filtered for duplicate results prior to screening for inclusion. If the full text for an article could not be located, corresponding authors were contacted. If no reply was received after two weeks, the study in question was excluded.

2.4. Search strategy

For each database used, search strings were written following the database-specific requirements related to Boolean operators and search limiters. Strings for each database contained a combination of terms aimed at identifying all potentially relevant articles including “learning” and “adult”, as well terms related to different measures of interest including “memory”, “intelligence”, “brain”, and “executive function”. Finally, additional terms were included using the “NOT” operator to prevent the inclusion of large numbers of irrelevant articles including “dementia”, “impairment”, and “brain damage”. When appropriate, “wildcard” search terms were included to allow for inclusion of highly similar terms (e.g., “adult*” for “adult”, “adulthood”, “adults”). Full search strategies for each database are presented in [Table 1](#). Searches were limited to title and abstract fields and were run using the “exact search” option or equivalent for each database. Search string performance was evaluated based on the recovery of known sentinel papers ([Archer et al., 2018](#); [Betts et al., 2020](#); [Rabi and Minda, 2017](#)). Final searches were performed on November 16th, 2023 for all databases.

2.5. Selection process

Selection of studies was performed by three trained reviewers. Screening was initially performed at the title and abstract level for articles. Next, full text versions of all candidate articles were retrieved from the Internet, institutional libraries, or corresponding authors. Retrieved studies then underwent full text screening, applying our inclusion and exclusion criteria. During title/abstract and full text screening, agreement between two independent reviewers was required in order for a document to be included in the review. If two reviewers disagreed about the inclusion of a document, the third reviewer settled the conflict. In the event a preprint was later published as a journal article, only the journal article was included.

2.6. Data collection process

Extraction of relevant data was guided by a customized spreadsheet template in Covidence. If relevant data were not reported in an included study, corresponding authors were contacted. If no reply was received after two weeks, all attempts were made to include the study in our analyses. Extraction was completed by three trained reviewers. For each included study, consensus between two independent reviewers was required before extraction was considered finalized. If two reviewers disagreed about any extracted items, the third reviewer settled the disagreement.

2.7. Data items

The primary outcomes of the present review were measures of the relationship between cognition or brain structure/function and age (RQ1 and RQ2), and learning, or learning-related cognitive or brain structure/function difference scores from comparisons between control and experimental groups or pre- and post-intervention timepoints

(RQ3). Cognitive measures could include reaction time (RT) or accuracy rates from behavioral tasks (e.g., Simon task, n-back task), scores from cognitive assessments (e.g., intelligence test score), or self-reported measures (e.g., Behavior Rating Inventory of Executive Function for Adults). Brain measures could include data from any neuroanatomical or neurophysiological instrument related to structure (e.g., magnetic resonance imaging; MRI) or function (e.g., electroencephalogram; EEG). Measures of age could include those that are quantified (e.g., age in years) as well as categorical labels (e.g., young adults and elders). Measures of learning could either be objectively measured (e.g., performance on a memory task, motor skill performance, etc.) or self-reported (e.g., grade point average, educational attainment, etc.). For RQ3, the impact of an intervention could be represented as either a quantitative measurement or qualitative assessment change in reported learning-related outcome.

In total, the following data were extracted from all included studies: 1) publication year; 2) author(s); 3) source format (e.g., journal article); 4) country the study was conducted in; 5) study setting; 6) study design; 7) study duration (if applicable); 8) population of interest 9) number of participants by sex per group; 10) average age of participants per group; 11) sociodemographic background of participants per group; 12) cognitive, brain, or learning outcome(s) reported; 13) additional variables, and; 14) main results. Additionally, 15) intervention format; 16) comparison group, 17) outcome(s) of interest, and; 18) measure of impact of intervention on outcome(s) of interest were extracted from intervention studies. In the event necessary data were not reported in the original articles, corresponding authors were contacted. Authors not responding to a request for data within two weeks were not contacted again and the study in question was included with incomplete details. Additionally, in the case of theses/dissertations reporting results from many separate studies, and studies reporting results from multiple experiments, only data from studies/experiments meeting our inclusion criteria were extracted.

2.8. Risk of bias in individual studies

Risk of bias assessment for each included empirical study was accomplished using relevant checklists from the Mixed Methods Appraisal Tool (MMAT; [Hong et al., 2018](#)). Decisions about which specific checklist to use were made based on the design of the study being assessed. For included systematic reviews and meta-analyses, checklists from the Critical Appraisal Skills Programme (CASP, 2018) were used. A team of three trained reviewers performed this assessment. For each included study, consensus between two independent reviewers was required before risk of bias assessment was considered finalized. If two reviewers disagreed about any items, the third reviewer settled the disagreement. No studies were excluded based on the results of the risk of bias assessment.

2.9. Synthesis methods

Both tabular and narrative synthesis approaches, organized by RQ, were used to summarize characteristics and main findings from all included studies. Additionally, for RQ3, the impact of interventions to improve learning were presented using effect direction analysis ([Boon and Thomson, 2020, 2021](#)). The decision to forego a quantitative synthesis for RQ3 was made based on observed heterogeneity across included studies which differed dramatically in their intervention format, participant age group, and outcome of interest.

3. Results

3.1. Deviation from preregistered protocol

While we aimed to conduct the present systematic review in accordance with our preregistered protocol, a number of unexpected findings

Table 1
Finalized Search Strings for Systematic Review.

Web of Science ¹	ProQuest ²	Scopus	Web of Science (Preprints) ^{1,3}
<p>#1) Domains of Interest (TI=(learn* OR education* OR skill*)) AND TI=(cogniti* OR neur* OR brain OR plasticity OR memory OR intelligence OR "executive function*" OR thinking OR motivation*)OR (AB=(learn* OR education* OR skill*)) AND AB=(cogniti* OR neur* OR brain OR plasticity OR memory OR intelligence OR "executive function*" OR thinking OR motivation*)</p>	<p>#1) Domains of Interest title(learn* OR education* OR skill*) AND title(cogniti* OR neur* OR brain OR plasticity OR memory OR intelligence OR "executive function*" OR thinking OR motivation*) OR abstract(learn* OR education* OR skill*) AND abstract(cogniti* OR neur* OR brain OR plasticity OR memory OR intelligence OR "executive function*" OR thinking OR motivation*)</p>	<p>#1) Domains of Interest (TITLE (learn* OR education* OR skill*) AND TITLE (cogniti* OR neur* OR {brain} OR {plasticity} OR {memory} OR {intelligence} OR "executive function*" OR {thinking} OR motivation*)) OR (ABS (learn* OR education* OR skill*) AND ABS (cogniti* OR neur* OR {brain} OR {plasticity} OR {memory} OR {intelligence} OR "executive function*" OR {thinking} OR motivation*))</p>	<p>#1) Domains of Interest (TI=(learn* OR education* OR skill*)) AND TI=(cogniti* OR neur* OR brain OR plasticity OR memory OR intelligence OR "executive function*" OR thinking OR motivation*)OR (AB=(learn* OR education* OR skill*)) AND AB=(cogniti* OR neur* OR brain OR plasticity OR memory OR intelligence OR "executive function*" OR thinking OR motivation*)</p>
<p>#2) Irrelevant Domains #1 NOT TI=(“artificial intelligence” OR “machine learning” OR “computer science*” OR “learning algorithm*” OR prison* OR disorder* OR disab* OR aphasia OR addiction OR illness* OR impair* OR injury OR trauma* OR patholog* OR autis* OR stroke OR ischemi* OR damage* OR lesion OR cancer* OR suicide OR depress* OR epilep* OR diabet* OR rat OR rats OR mice OR mouse OR rodent* OR monkey* OR drosophila OR bird* OR fish* OR animal* OR dementia OR alzheimer* OR MCI OR disease*) OR AB=(“artificial intelligence” OR “machine learning” OR “computer science*” OR “learning algorithm*” OR prison* OR disorder* OR disab* OR aphasia OR addiction OR illness* OR impair* OR injury OR trauma* OR patholog* OR autis* OR stroke OR ischemi* OR damage* OR lesion OR cancer* OR suicide OR depress* OR epilep* OR diabet* OR rat OR rats OR mice OR mouse OR rodent* OR monkey* OR drosophila OR bird* OR fish*)</p>	<p>#2) Irrelevant Domains #1 NOT title(“artificial intelligence” OR “machine learning” OR “computer science*” OR “learning algorithm*” OR prison* OR disorder* OR disab* OR aphasia OR addiction OR illness* OR impair* OR injury OR trauma* OR patholog* OR autis* OR stroke OR ischemi* OR damage* OR lesion OR cancer* OR suicide OR depress* OR epilep* OR diabet* OR rat OR rats OR mice OR mouse OR rodent* OR monkey* OR drosophila OR bird* OR fish* OR animal* OR dementia OR alzheimer* OR MCI OR disease*) OR abstract(“artificial intelligence” OR “machine learning” OR “computer science*” OR “learning algorithm*” OR prison* OR disorder* OR disab* OR aphasia OR addiction OR illness* OR impair* OR injury OR trauma* OR patholog* OR autis* OR stroke OR ischemi* OR damage* OR lesion OR cancer* OR suicide OR depress* OR epilep* OR diabet* OR rat OR rats OR mice OR mouse OR rodent* OR monkey* OR drosophila OR bird* OR fish*)</p>	<p>#2) Irrelevant Domains #1 AND NOT (TITLE({artificial intelligence} OR {machine learning} OR {computer science*” OR “learning algorithm*” OR prison* OR disorder* OR disab* OR aphasia OR addiction OR illness* OR impair* OR injury OR trauma* OR patholog* OR autis* OR stroke OR ischemi* OR damage* OR lesion OR cancer* OR suicide OR depress* OR epilep* OR diabet* OR rat OR rats OR mice OR mouse OR rodent* OR monkey* OR drosophila OR bird* OR fish* OR animal* OR dementia OR alzheimer* OR MCI OR disease*)) OR (ABS({artificial intelligence} OR {machine learning} OR “computer science*” OR “learning algorithm*” OR prison* OR disorder* OR disab* OR aphasia OR addiction OR illness* OR impair* OR injury OR trauma* OR patholog* OR autis* OR stroke OR ischemi* OR damage* OR lesion OR cancer* OR suicide OR depress* OR epilep* OR diabet* OR rat OR rats OR mice OR mouse OR rodent* OR monkey* OR drosophila OR bird* OR fish*))</p>	<p>#2) Irrelevant Domains #1 NOT TI=(“artificial intelligence” OR “machine learning” OR “computer science*” OR “learning algorithm*” OR prison* OR disorder* OR disab* OR aphasia OR addiction OR illness* OR impair* OR injury OR trauma* OR patholog* OR autis* OR stroke OR ischemi* OR damage* OR lesion OR cancer* OR suicide OR depress* OR epilep* OR diabet* OR rat OR rats OR mice OR mouse OR rodent* OR monkey* OR drosophila OR bird* OR fish*)</p>
<p>#3) Age Limits #2 AND (TI=(adult* OR senior* OR “middle age” OR “middle aged” OR elder* OR lifespan OR “life span” OR lifelong OR “life long” OR age* OR aging) AND AB=(adult* OR senior* OR “middle age” OR “middle aged” OR elder* OR lifespan OR “life span” OR lifelong OR “life long” OR age* OR aging)) NOT (TI=(neonat* OR infant* OR infancy OR child* OR teenage*) OR AB=(neonat* OR infant* OR infancy))</p>	<p>#3) Age Limits #2 AND (title(adult* OR senior* OR “middle age” OR “middle aged” OR elder* OR lifespan OR “life span” OR lifelong OR “life long” OR age* OR aging)) NOT (title (neonat* OR infant* OR infancy OR child* OR teenage*) NOT abstract(neonat* OR infant* OR infancy))</p>	<p>#3) Age Limits #2 AND (TITLE (adult* OR senior* OR {middle age} OR {middle aged} OR elder* OR lifespan OR {life span} OR lifelong OR {life long} OR age* OR aging) OR ABS (adult* OR senior* OR {middle age} OR {middle aged} OR elder* OR lifespan OR {life span} OR lifelong OR {life long} OR age* OR aging)) NOT (TITLE (neonat* OR infant* OR infancy OR child* OR teenage*) OR ABS(neonat* OR infant* OR infancy OR child*))</p>	<p>#3) Age Limits #2 AND (TI=(adult* OR senior* OR “middle age” OR “middle aged” OR elder* OR lifespan OR “life span” OR lifelong OR “life long” OR age* OR aging) AND AB=(adult* OR senior* OR “middle age” OR “middle aged” OR elder* OR lifespan OR “life span” OR lifelong OR “life long” OR age* OR aging)) NOT (TI=(neonat* OR infant* OR infancy OR child* OR teenage*) OR AB=(neonat* OR infant* OR infancy))</p>
<p>#4) Format and Date Limits #3 AND ((LA=(“ENGLISH”)) NOT (DT=(“BOOK REVIEW” OR “CORRECTION” OR “EDITORIAL MATERIAL” OR “BOOK CHAPTER” OR “MEETING ABSTRACT” OR “DATA PAPER” OR “RETRACTED PUBLICATION” OR “LETTER” OR “THEATER REVIEW” OR “RETRACTION” OR “BIOGRAPHICAL ITEM” OR “REPRINT”)))</p>	<p>#4) Format and Date Limits #3 AND (la.exact(“ENG”) NOT stype.exact (“Trade Journals” OR “Wire Feeds” OR “Newspapers” OR “Blogs, Podcasts, & Websites” OR “Magazines” OR “Reports” OR “Working Papers” OR “Other Sources”)) AND pd(20120101–20230901)</p>	<p>#4) Format and Date Limits #3 AND PUBYEAR > 2011 AND PUBYEAR < 2024 AND (EXCLUDE (DOCTYPE, “sh”) OR EXCLUDE (DOCTYPE, “no”) OR EXCLUDE (DOCTYPE, “er”) OR EXCLUDE (DOCTYPE, “ed”) OR EXCLUDE (DOCTYPE, “tb”) OR EXCLUDE (DOCTYPE, “le”) OR EXCLUDE (DOCTYPE, “cr”) OR EXCLUDE (DOCTYPE, “ch”) OR EXCLUDE (DOCTYPE, “bk”) OR EXCLUDE (DOCTYPE, “dp”)) AND (LIMIT-TO (LANGUAGE, “English”))</p>	<p>#4) Format and Date Limits #3 AND ((LA=(“ENGLISH”)) NOT (DT=(“BOOK REVIEW” OR “CORRECTION” OR “EDITORIAL MATERIAL” OR “BOOK CHAPTER” OR “MEETING ABSTRACT” OR “DATA PAPER” OR “RETRACTED PUBLICATION” OR “LETTER” OR “THEATER REVIEW” OR “RETRACTION” OR “BIOGRAPHICAL ITEM” OR “REPRINT”)))</p>

1. Exact search option was used. Additionally, date limits had to be manually entered during final search.

2. The option “Show results outside my library’s subscription” was selected

3. Due to the lack of search flexibility and citation export options in BioRxiv, etc., we used Web of Science to search for preprints.

and further considerations led to slight alterations in our methodology. Our first change related to how studies would be organized. While we proposed to include a “combined studies” section for studies that addressed multiple RQs, the decision was made to simply include relevant details from each of these studies separately for each relevant RQ in order to make the tabular and narrative syntheses more coherent. Additionally, while we originally proposed to use separate checklists from the Joanna Briggs Institute to assess for risk of bias in individual studies (Joanna Briggs Institute, 2017a, 2017b, 2017c), our team later determined that the MMAT (Hong et al., 2018) and CASP (Critical Appraisal Skills Programme, 2018) were more appropriate for our review. Finally, although mentioned as a possible alternative synthesis method in the preregistered protocol, for RQ3 we utilized effect direction analysis (Boon and Thomson, 2020, 2021) due to high levels of heterogeneity encountered across included studies. Consequently, we

were not able to assess for reporting bias or certainty in cumulative evidence as originally planned. Aside from these noted changes, all preregistered steps were followed according to the original protocol.

3.2. Study selection

Searches across all databases returned a total of 23,008 documents. Covidence automatically detected and removed 9,560 duplicate results, with manual screening at the title and abstract level identifying 19 additional duplicates. Initially, 269 unique studies were included in the present review after full text screening. However, additional details identified for four candidate studies during extraction resulted in their later removal. Two studies were excluded because it was revealed they included participants who were below the age range of interest for the present review (Bootsma et al., 2021; Gilson et al., 2023). In another

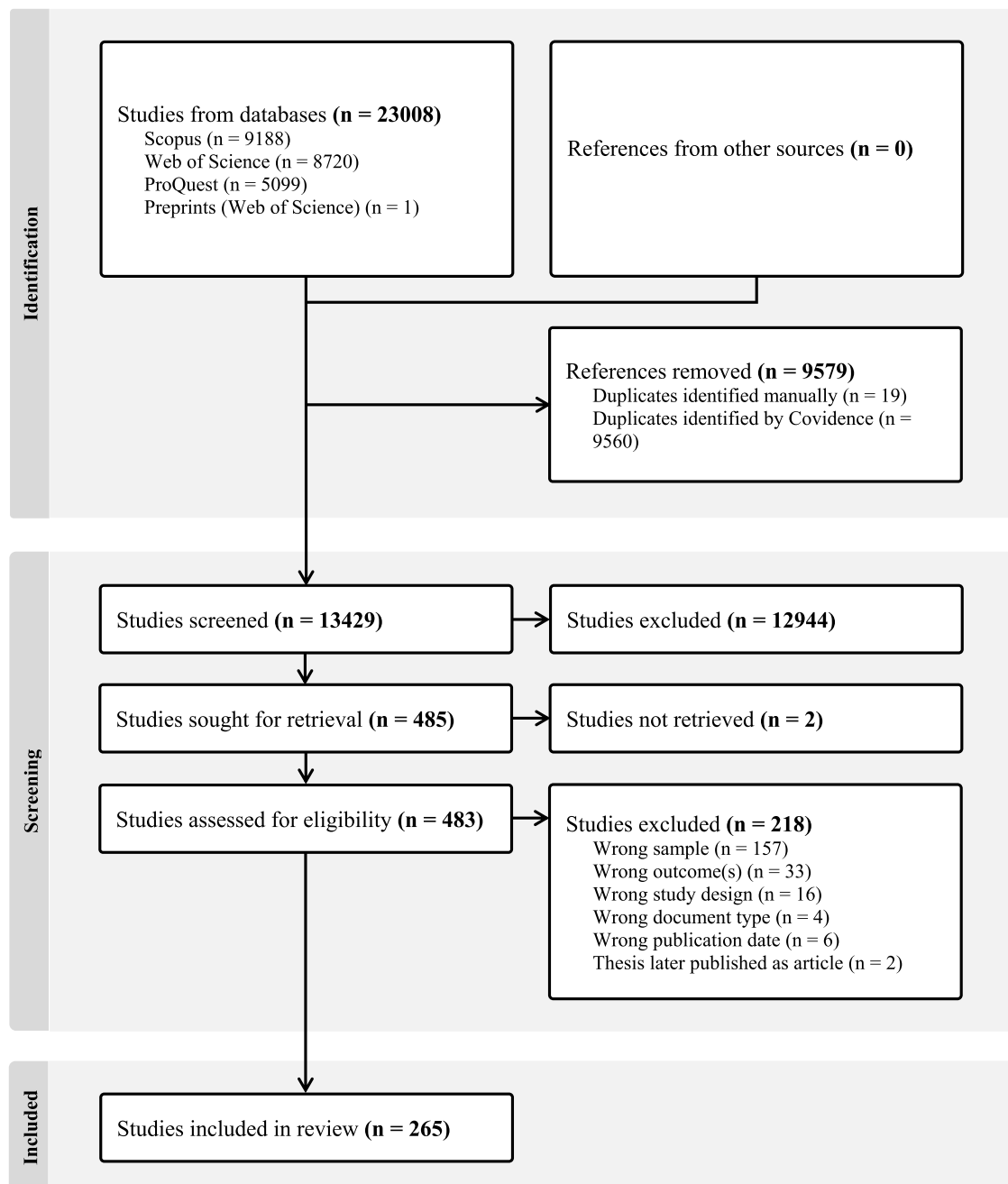


Fig. 1. PRISMA flow diagram.

case, a dissertation originally selected for inclusion (Strickland-Hughes, 2017) was excluded and replaced with a published article presenting the same results (Strickland-Hughes and West, 2022). Finally, one intervention study was removed because during extraction it was identified that participants with mild cognitive impairment (MCI) were included (Small et al., 2018). This resulted in the inclusion of 265 unique studies in the present review. Screening and selection results are summarized in a PRISMA flow diagram (Fig. 1).

3.3. Study characteristics

Characteristics for each included study are presented in Tables 2–4, organized by the specific RQ(s) they contributed findings to. Because studies sometimes contributed relevant findings to multiple RQs, the total number of studies across each RQ in Tables 2–4 exceeds the number of unique studies included in the present review. In total, 82 studies were included for RQ1 (52 contributing exclusively to RQ1), 38 studies for RQ2 (eight contributing exclusively to RQ2), and 177 studies for RQ3 (174 contributing exclusively to RQ3). The majority of studies included for RQ2 (28/38 studies) also reported findings that were relevant for RQ1, while one study reported findings relevant to RQ2 and RQ3 (Abellaneda-Pérez et al., 2019), and another reported findings relevant to all three RQs (Heinzel et al., 2014). One additional study reported findings relevant to both RQ1 and RQ3 (Vance, 2022). Included studies differed in whether they focused exclusively on a single age group (e.g., younger adults) or multiple age groups recruited as either separate samples (e.g., younger adults and older adults) or as part of a wide age range (20–70-year-olds). For this reason, a single study can be counted as investigating multiple age groups, resulting in a total number of studied age groups that exceeds the number of included studies.

3.3.1. RQ1: learning-related cognitive changes during healthy aging

Of the 82 studies relevant for RQ1, 68 (83 %) were conducted exclusively in Western cultural contexts across North America, Europe, and Australia. Nine studies in total (11 %) were conducted in Asian cultural contexts. In one case, data collected from both a Western context (i.e., United Kingdom) and Asian context (i.e., China) were used in the same study to investigate comparative differences in age-related cognitive trajectories (Ruiz et al., 2023). Finally, one study was conducted using a global dataset collected from the Internet across a wide range of cultural contexts (Geyer et al., 2015). Included studies generally adopted an exclusively cross-sectional design (56/82 studies; 68 %), with fewer longitudinal investigations (24/82 studies; 29 %). In two cases, both cross-sectional and longitudinal methodology were used (Hsieh and Chen, 2023; Karlamangla et al., 2017).

The most widely studied age groups were younger adults between 20 and 29 years of age, which were investigated in 39/82 (48 %) of included studies, and older adults between 60 and 69 (39/82 studies; 48 %) and 70–79 (33/82 studies; 40 %) years of age. Comparatively fewer studies included participants between the ages of 30–39 (13/82 studies; 16 %), 40–49 (13/82 studies; 16 %), and 50–59 (20/82 studies; 24 %), with the fewest number of studies investigating older adults 80 years and above (7/82 studies; 9 %). Finally, the majority of included studies were conducted exclusively in a laboratory setting (59/82 studies; 72 %), with the next largest group involving the secondary analysis of previously collected data (15/82 studies; 18 %). In two studies, laboratory components were supplemented with additional data collection in non-laboratory face-to-face settings (Tuokko et al., 2020) or secondary analysis of previously collected data (Nuzum et al., 2021).

RQ1a: Specific dimensions of cognitive function investigated.

Studies included for RQ1 measured a large number of learning-related cognitive functions across a wide range of dimensions. To support a more coherent analysis of findings, studies included for RQ1 were coded and organized based on which dimension(s) of cognitive function was/were the primary outcome(s) of interest. A review of included studies by two independent reviewers resulted in the identification of six domains

of learning-related cognitive outcomes assessed. *Learning and Memory* outcomes were the most commonly studied (present in 53/82 studies; 65 %), and included measures of any form of learning (e.g., California Verbal Learning Task; CVLT) or memory (e.g., episodic memory). This did not include measuring improvement in non-learning task performance as evidence of learning (e.g., improved performance during second administration of a Simon task) nor did it include measures of working memory. *Executive Function and Attention* outcomes included measures of any dimension of executive function including inhibition, updating (working memory), or shifting (switching or cognitive flexibility), or assessment of attention, and were present in 34/82 studies (41 %). This did not include measures of verbal fluency which were categorized as *Language* outcomes along with measures of speech processing or reading comprehension (15/82 studies; 18 %). *Processing Speed* outcomes, present in 19/82 studies (23 %), included any measures that focused on processing or perceptual speed and could include indices derived from tasks used to measure a different cognitive dimension (e.g., neutral trial RT taken from a flanker task). *General Cognition and Intelligence* outcomes, present in 21/82 studies (26 %), included measures of any form of intelligence (excluding emotional intelligence), reasoning, numeracy, global assessment of cognitive function (Mini-Mental State Examination; MMSE), or use of a composite score based on data from multiple measures. Finally, *Socioemotional and Motivation* outcomes included measures of motivational state, emotional intelligence, or other related non-cognitive outcomes and were the least commonly studied, present in 4/82 studies (5 %).

3.3.2. RQ2: learning-related brain changes during healthy aging

Studies conducted in Western contexts accounted for 35 of the 38 studies included for RQ2 (92 %). Only two studies were conducted in Asia cultural contexts, with one study conducted in Taiwan (Chi et al., 2022) and the other in Singapore (Archer et al., 2018). Similar to RQ1, most studies adopted a cross-sectional design (28/38 studies; 74 %), with only nine longitudinal studies identified (24 %). In only one study were both cross-sectional and longitudinal methods were used (Abellaneda-Pérez et al., 2019).

Mirroring the pattern observed with RQ1, included studies disproportionately included younger adults between the ages of 20–29 (21/38 studies; 55 %), and older adults between 60 and 69 (21/38 studies; 55 %) and 70–79 (13/38 studies; 34 %) years of age. Fewer studies included participants between the ages of 30–39 (5/38 studies; 13 %), 40–49 (6/38 studies; 16 %), and 50–59 (6/38 studies; 16 %), with only two studies (5 %) including older adults 80 years and above (Chan et al., 2018; Perry et al., 2017). Likely due to the technical requirements associated with neuroscience research, all included studies were either laboratory-based (32/38 studies; 84 %) or involved the secondary analysis of data previously collected in a laboratory (6/38 studies; 16 %).

RQ2a: Specific dimensions of brain structure/function investigated.

Given the small number of studies included for RQ2, and their exclusive focus on brain structure and/or function, two broad categories were created in order to organize findings from individual studies. The category *Brain Structure* was assigned to studies that focused on physical changes in the brain, and included outcomes such as cortical thickness, grey matter volume, microstructural organization, and white matter integrity. These studies employed the use of fMRI, structural magnetic resonance imaging (sMRI), diffusion tensor imaging (DTI), or other neuroimaging methods that support structural measures. Investigating structural changes in the brain associated with aging was the exclusive focus of 14/38 studies included for RQ2 (37 %). Studies classified under *Brain Function* were those that focused on non-structural changes in brain activity and included outcomes such as functional connectivity, oscillatory activity, event-related potentials (ERPs), and neurochemical synthesis. These studies employed the use of electroencephalography (EEG), functional magnetic resonance imaging (fMRI), positron emission tomography (PET), or other neuroimaging methods that support

Table 2
Summary of Characteristics of Included Studies for Research Question 1.

Study	Source	Location	Setting	Design	Length	Sample(s)	Measure(s)	Main Findings
Bellebaum et al. (2012)	Article	Germany	LAB	CS	NA	S1 (YA): 30, M_{age} : 26.60 (5.30) S1 (OA): 28, M_{age} : 60.70 (9.10) S2 (YA): 30, M_{age} : 27.00 (6.30) S2 (OA): 30, M_{age} : 60.00 (9.00)	S1: observational feedback LRN & declarative associative LRN S2: active LRN from feedback & declarative associative LRN	OA observational learners learned better from positive feedback. No age effect on active feedback LRN
Bielak et al. (2012)	Article	Australia	SEC	LONG	8YR	20 s: 2402, ~1201 M, 20–24 40 s: 2539, ~1270 M, 40–44 60 s: 2551, ~1276 M, 60–64	PS, VerbM, WM, EpM, & VerbINT	↑age associated with ↓scores for nearly all cognitive domains but ↑VerbINT; ↑age associated with ↓PS & VerbM & ↑VerbINT in 60 s but stable WM; ↑age associated with ↑PS, WM, VerbM, VerbINT in 20 s & 40 s but ↓PS in 40 s; gains 20 s > 40 s except in WM; 40 s = 60 s in VerbINT & 20 s = 40 s in WM; Mean activity level related to baseline cognition but no influence on change
Blachstein et al. (2012)	Article	Israel	LAB	CS	NA	528, 257 M, 21–91	Temporal order MEM	Indirect measure changed only at age 70+, while the direct measure did not change between ages 20–39, but did change at 40–59, 60–69, & 70+
Roldán-Tapia et al. (2012)	Article	Spain	LAB	CS	NA	M: 73, M_{age} : 33.42 (13.40) F: 93, M_{age} : 43.52 (18.07)	Reasoning, conceptual problem solving, motor persistence, PS, planning, mental tracking, & mental manipulation.	↑age associated with ↓reasoning, conceptual problem solving, motor persistence, PS, planning, mental tracking, & mental manipulation; ↑CogRes associated with ↑performance on almost all tests
Cansino et al. (2013)	Article	Mexico	LAB	CS	NA	1500, ~750 M, 21–80	Source MEM	↑age associated with ↓source ACC after controlling for EDU; NS impact of sex
Krueger (2013)	Article	USA	LAB	CS	NA	YA: 50, 17 M, M_{age} : 28.40 (5.60) MA: 147, 50 M, M_{age} : 52.40 (5.10) OA: 137, 47 M, M_{age} : 71.50 (7.30)	SpatM	YA & MA had ↑difference between close & far errors while OA had equal rates; ↑age associated with ↑far errors, but repeated LRN trials can ↓far errors; complexity similarly impacted YA & OA; ↑age also associated with ↑VOC, PS, logical MEM
Lam et al. (2013)	Article	Singapore	LAB	CS	NA	833, 434 M, M_{age} : 37.00 (10.84)	VerbM, WM, ATT, MS, semantic MEM, EF, planning, VS ability, & INT	↑age associated with ↓VerbM, WM, MS, INT, semantic MEM, planning, & VS ability (same with composite score); ↑EDU associated with ↑fluency & cognitive processes; ↑ratio between age & EDU associated with WM
Ossher et al. (2013)	Article	USA	LAB	CS	NA	105, 36 M, M_{age} : 75.30 (6.80)	MEM, pattern comprehension, PS, CF, & WM	Age & EDU not associated with everyday MEM but ↑age associated with ↓confidence in MEM; ↑EDU marginally associated with ↑MEM confidence; age not associated with most lab & neuropsychology tests
Chang and Dong (2014)	Article	USA	LAB	CS	NA	3159, 1298 M, M_{age} : 72.80 (8.30)	EpM, WM, PS, ATT, & gCOG	↑age associated with ↓all cognitive measures; ↑EDU had opposite pattern; M associated with ↑gCOG & WM; being married, fewer children, fewer years in the USA & in community, & better self-reported health associated with ↑all cognitive measures
Heinzel et al. (2014)	Article	Germany	LAB	LONG	4WK (OA)	YA: 18, 10 M, M_{age} : 24.06 (2.41) OA: 19, 13 M, M_{age} : 65.95 (3.73)	WM, PS, INH, verbal fluency, & abstract reasoning	YA > OA on all tasks except one WM measure & verbal fluency (null); OA > YA in abstract reasoning
Marcotte and Ansaldo (2014)	Article	Canada	LAB	CS	NA	YA: 10, 5 M, M_{age} : 22.70 (2.00) OA: 10, 4 M, M_{age} : 70.20 (4.00)	VerbL	YA > OA ACC for cognates & non-cognates; no effect on RT or on LRN
Payne et al. (2014)	Article	USA	SEC	LONG	10YR	698, 184 M, M_{age} : 74.05 (6.05)	Spoken discourse MEM, verbal ability, & reasoning	↑age associated with larger decline in spoken discourse MEM; independent of age, decline in spoken discourse MEM + CORR with reasoning but not verbal ability
Samanez-Larkin et al. (2014)	Article	USA	LAB	CS	NA	OA (fMRI): 39, 18 M, M_{age} : 53.00	Probabilistic LRN	Performance not associated with age

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Table 2 (continued)

Study	Source	Location	Setting	Design	Length	Sample(s)	Measure(s)	Main Findings
Todorov et al. (2014)	Article	Sweden	LAB	CS	NA	(16.00) OA (BEH): 27, 17 M, M _{age} : 52.00 (16.00) Overall: 80, 40 M, 20–73 YA: M _{age} : 25.80, 20–38 OA: M _{age} : 67.16, 63–73	Multitasking, spatial ability, & EF	Independent of age, more efficient EF associated with ↑multitasking; ↑age associated with ↓multitasking, spatial ability, & EF; in OA, age & EF but not spatial ability predicted multitasking
Worthy et al. (2014)	Article	USA	LAB	CS	NA	YA: 91, M _{age} : 22.51 OA: 91, M _{age} : 67.63	WM, VerBL, PS, CF, phonemic verbal fluency, & motivational tendencies	OA > YA maximizing rewards across most tasks but OA had ↓model-based strategy use; OA were similar in behavior to YA by adopting simple win-stay-lose-shift heuristic over more complex strategies; In OA, ↑model-based strategy use associated with ↑VerBL
Bhakuni and Mutha (2015)	Article	India	LAB	CS	NA	YA: 15, 11 M, M _{age} : 22.73 OA: 15, 13 M, M _{age} : 63.73	Implicit LRN	No LRN deficits in OA; both YA & OA showed ↓RT with training but no change in switch cost; OA < YA in overall switch cost
Bilodeau-Mercure et al. (2015)	Article	Canada	LAB	CS	NA	YA: 11, 4 M, M _{age} : 25.70 (3.90) OA: 11, 4 M, M _{age} : 68.00 (4.60)	Speech perception	↑age associated with ↓speech perception after controlling for hearing
Cyr (2015)	Thesis	Canada	LAB	CS	NA	S1 (YA CNPT): 32, M _{age} : 22.65 (2.82) S1 (OA CNPT): 32, M _{age} : 72.34 (10.85) S1 (YA LEX): 32, M _{age} : 22.69 (3.37) S1 (OA LEX): 32, M _{age} : 72.69 (10.85) S2A (YA): 56, M _{age} : 22.62 (3.29) S2A (OA): 56, M _{age} : 72.93 (5.39) S2B (YA): 32, M _{age} : 23.66 (3.33) S2B (OA): 32, M _{age} : 72.06 (5.27) S3A (YA): 21, M _{age} : 20.86 (2.46) S3A (OA): 18, M _{age} : 69.64 (4.21) S3B (YA): 19, M _{age} : 21.41 (2.24) S3B (OA): 17, M _{age} : 70.52 (3.27)	All studies: LRN & MEM	S1: YA & OA learn the same from errors S2A: Trial & error LRN was better than errorless LRN in YA & OA with YA benefitting more from errors; YA & OA were better in high vs. low-cloze condition but no effect of condition on MEM benefit of error S2B: YA > OA benefit when errors & targets belong to similar relative to disparate semantic families but not for prior errors S3A: YA & OA showed ↑error correction with ↑initial confidence, but OA had a weaker association S3B: YA & OA showed ↑error correction with ↑initial confidence but avoiding tip-of-tongue states & bypassing explicit confidence ratings eliminated weaker association in OA
Geyer et al. (2015)	Article	Multiple	OL	CS	NA	1890, 578 M, M _{age} : 58.20 (9.50)	WM	↑age associated with ↓baseline scores & LRN rates but not forgetting
Heidemeier and Staudinger (2015)	Article	Germany	F2F	CS	NA	747, 545 M, M _{age} : 38.70 (8.60)	Achievement goals, goal orientations, self-efficacy for LRN, motivational characteristics at work	↑age associated with ↓importance of achievement goals, but this was reduced by ↑affective commitment & intrinsic motivation in older workers; skill level, affective commitment, & intrinsic work satisfaction but not age related to dominance of LRN-approach/avoidance goals; M > F in performance-approach goals but performance-avoidance was more common in older M; ↑age associated with maladaptive impact of performance-goal orientation on self-efficacy & work affect
Hoff et al., 2015a	Article	Germany	LAB	CS	NA	YA: 26, 13 M, M _{age} : 25.65 (0.68) OA: 26, 11 M, M _{age} : 60.69 (1.34)	Motor LRN	YA > OA response speed & more pronounced sequence LRN; OA showed preserved LRN capabilities but ↑switch costs on the first but not second test
Thielgen et al. (2015)	Article	Germany	OL	LONG	15MTH	756, 350 M, M _{age} : 43.59 (10.80)	Implicit/explicit motives; volitional strength; motive-	↑age associated with ↓impact of discrepancies between implicit

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Table 2 (continued)

Study	Source	Location	Setting	Design	Length	Sample(s)	Measure(s)	Main Findings
van Eersel et al. (2015)	Article	Netherlands	LAB	LONG	9YR	2515, 1334 M, M_{age} : 53.00 (10.00)	specific incentives; work motivation Creativity	motives & conscious goals on work motivation ↑age associated with ↓unique designs on each additional test
Deroche et al. (2016)	Article	France	LAB	CS	NA	YA: 43, 21 M, M_{age} : 24.05 (1.91) OA: 43, 23 M, M_{age} : 69.16 (3.12)	INH	Gaze-cueing peaks later in OA vs. YA
Diwadkar et al. (2016)	Article	Italy	LAB	CS	NA	YA: 33, 12 M, <26 OA: 33, 18 M, >26	Associative LRN	↑age associated with ↓LRN, independent of IQ & EDU
Reichert et al. (2016)	Article	Austria	LAB	LONG	2WK	YA: 21, 12 M, M_{age} : 24.80 (2.60) MA: 25, 12 M, M_{age} : 47.80 (5.30) OA: 24, 9 M, M_{age} : 67.50 (5.60)	VSM & VerbM	↑age associated with ↓MEM
Schenk et al. (2016)	Article	Germany	LAB	CS	NA	YA: 17, 3 M, M_{age} : 22.53 (4.16) OA: 10, 2 M, M_{age} : 58.20 (7.48)	Categorization LRN	YA < OA errors in categorization of exceptions; no age effect with prototypical stimuli; OA > YA fixation rates for important stimulus features; YA > OA transition from abstract-based to exemplar-based LRN during task
Adólfssdóttir et al. (2017)	Article	Norway	LAB	LONG	T1-T2: 3.62YR T2-T3: 3.31YR	T1: 122, 40 M, M_{age} : 61.04 (7.56) T2: 123, 41 M, M_{age} : 64.56 (7.51) T3: 100, 31 M, M_{age} : 67.03 (7.29)	INH & CF	↑age associated with ↓INH, CF, & combined INH & CF
Borella et al. (2017)	Article	Italy	LAB	CS	NA	40–49: 30, 12 M, M_{age} : 45.20 (3.03) 50–59: 55, 21 M, M_{age} : 53.98 (2.75) 60–69: 91, 42 M, M_{age} : 63.80 (2.77) 70–79: 55, 26 M, M_{age} : 73.56 (2.80) 80–89: 57, 27 M, M_{age} : 83.63 (2.83)	WM, PS, reasoning, VOC, & reading comprehension	↑age associated with ↓all cognitive variables; ↑EDU ↑all cognitive variables
Corbin (2017)	Thesis	USA	LAB	CS	NA	OA (RM): 15, 4 M, M_{age} : 74.40 (1.88) OA (NRM): 14, 3 M, M_{age} : 76.79 (1.47)	Source MEM	No association between age & MEM intrusions
Giudice et al. (2017)	Article	USA	LAB	CS	NA	Overall: 36, 17 M 20–39: 12, M_{age} : 25.00 (4.70) 40–59: 12, M_{age} : 50.80 (5.80) 60–79: 12, M_{age} : 70.30 (4.60)	Haptic SpatM	↑age associated with ↓haptic MEM & mental rotation ability; difference between 20 and 39 & 60–79 groups significant
Hoefijzers et al. (2017)	Article	Colombia	LAB	CS	NA	YA: 32, 7 M, M_{age} : 33.44 (8.36) OA: 41, 14 M, M_{age} : 70.22 (7.34)	VisWM	↑age not associated with ability to bind intrinsic features in VisWM across delay conditions; OA > YA impact of feature congruency on recognition
Karlamangla et al. (2017)	Article	USA	SEC	CS, LONG	6.5YR	2124, M_{age} : 54.00 (3.00) FMP: 1224, M_{age} : 54.00 (3.00)	PS & verbal EpM	↑age associated with ↓PS, verbal EpM; CS > LONG aging effects
Klencklen et al. (2017)	Article	Switzerland	LAB	CS	NA	YA: 34, 16 M, M_{age} : 24.15 (3.46) OA: 35, 18 M, M_{age} : 69.26 (3.02)	Reference MEM & VSWM	YA > OA on all MEM tasks, especially WM; results suggest a greater age-related decline in allocentric spatial than color WM; however, differences in spatial vs. color WM based on age differ based on measures used
Li et al. (2017)	Article	USA	F2F	LONG	2YR	2713, 1129 M, M_{age} : 72.60	EpM, WM, PS, & gCOG	↑age associated with ↓baseline cognition & ↓decline in gCOG, EpM, & PS; ↑EDU associated with ↑baseline cognition but ↓decline in gCOG & EpM; M > F in most baseline scores but had ↑decline in WM; ↑income

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Table 2 (continued)

Study	Source	Location	Setting	Design	Length	Sample(s)	Measure(s)	Main Findings
Lubitz et al. (2017)	Article	Germany	LAB	CS	NA	YA: 35, 8 M, M_{age} : 22.43 (3.25) OA: 30, 8 M, M_{age} : 68.30 (5.19)	WM, CF & VerbWM	associated with ↑baseline cognition & ↓decline in WM YA > OA ACC in WM
Monteiro et al. (2017)	Article	Belgium	LAB	LONG	2WK SUB: 6MTH	YA: 25, 11 M, M_{age} : 21.50 (2.30) OA: 18, 7 M, M_{age} : 68.60 (6.00)	Motor LRN	YA > OA performance, but similar LRN capability
Perry et al. (2017)	Article	Australia	LAB	CS	NA	101, 44 M, M_{age} : 82.70 (3.80)	ATT, PS, MEM, LANG, VS ability, & EF	↑age associated with ↓all cognitive abilities; ↑EDU associated with ↑VS ability, EF, & LANG
Rhodes and Katz (2017)	Article	Multiple	OL	CS	NA	20–30: 124 30–40: 66 40–50: 34 50–60: 18 60–79: 9	WM	YA > OA task improvement & maximum performance, even when controlling for WM capacity
Tuokko et al. (2017)	Article	Canada	LAB	LONG	20YR	~50,000, 45–85	VerbL, EF, verbal fluency, INH, prospective MEM, & PM speed	↑age associated with ↓performance on all cognitive measures
Zahodne et al. (2017)	Article	USA	SEC	CS	NA	YA (BLK): 246, 87 M, M_{age} : 39.30 (2.90) YA (WH): 964, 439 M, M_{age} : 39.60 (3.20) MA (BLK): 401, 160 M, M_{age} : 53.80 (5.50) MA (WH): 292, 143 M, M_{age} : 54.10 (5.60) OA (BLK): 149, 54 M, M_{age} : 71.70 (5.00) OA (WH): 149, 54 M, M_{age} : 72.20 (5.30)	EpM & EF	↑income associated with ↑EpM & EF independent of age; although daily discrimination was not associated with EpM or EF; minorities had ↓EF
Archer et al. (2018)	Article	Singapore	LAB	CS	NA	189, 83 M	VSWM	↑age associated with ↓speed & ACC
Frøehlich et al. (2018)	Article	Germany	LAB	CS	NA	YA: 20, 7 M, M_{age} : 25.00 (3.46) OA: 38, 22 M, M_{age} : 70.20 (3.15)	Sublexical processing, orthographic processing, phonological processing, lexico-semantic processing, & pattern recognition	↑age associated with ↓speed but no effect on ACC on all tasks
Pflueger et al. (2018)	Article	Switzerland	LAB	CS	NA	YA: 30, 7 M, M_{age} : 27.70 (8.30) OA: 18, 9 M, M_{age} : 69.70 (6.96)	VerbL	YA > OA performance on California VerbL Test but not VR-MEM examination
Berghuis et al. (2019)	Article	Italy	LAB	CS	NA	YA: 15, 6 M, M_{age} : 25.50 (2.50) OA: 15, 9 M, M_{age} : 63.10 (5.20)	Motor LRN	YA > OA motor performance, but practice improved performance similarly
Bertola et al. (2019)	Article	Brazil	LAB	CS	NA	114, 28 M, M_{age} : 72.69 (8.25)	gCOG	↑age associated with ↓gCOG moderated by semantic MEM but not EDU, INT, or occupation
Bowen et al. (2019)	Article	Canada	LAB	CS	NA	YA: 16, 7 M, M_{age} : 25.44 (3.79) OA: 15, 6 M, M_{age} : 68.47 (5.38)	Affective processing & reward LRN	No age difference in reward-size based hit rates, but YA > OA response speed to reward vs. no reward cues; No age differences in response to gain or loss feedback
Dahl et al. (2019)	Article	Germany	LAB	LONG	2YR	YA: 66, 44 M, M_{age} : 32.50 (3.53) OA: 228, 146 M, M_{age} : 72.29 (4.11)	VerbL & MEM	YA > OA LRN & MEM
Fernandez-Baiza et al., 2019	Article	Spain	LAB	CS	NA	28, 12 M, M_{age} : 71.25 (9.50)	SpatM	↑age associated with ↓egocentric & allocentric SpatM; only egocentric SpatM could differentiate between young, middle, & old elderly; only middle old participants did not show LRN effect on allocentric SpatM; no influence of VS ability or gender
Howe et al., 2019	Article	UK	LAB	CS	NA	Overall YA: M_{age} : 26.86 (8.30) Overall OA: M_{age} : 73.43 (8.13)	EpM	OA needed ↑trials to learn A-B & A-C pairings & new associations for reactivated vs. not reactivated pairs

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Table 2 (continued)

Study	Source	Location	Setting	Design	Length	Sample(s)	Measure(s)	Main Findings
Jockwitz et al. (2019)	Article	Germany & Switzerland	SEC	CS	NA	S1 (YA): 89, 26 M S1 (OA): 89, 30 M S2 (YA): 89, 26 M S2 (OA): 86, 28 M 1000BRAINS: 228, 114 M, M_{age} : 70.69 (4.95) LHAB: 228, 114 M, M_{age} : 70.69 (4.89)	PS, CF, reasoning, verbal fluency, & VOC	↑age associated with ↓PS, CF, verbal fluency, & reasoning
Pergher et al. (2019)	Article	Finland & Belgium	LAB	CS	NA	55, 23 M, M_{age} : 62.20 (7.60)	WM & INH	No effect of age on WM & INH
Pliatsikas et al. (2019)	Article	Taiwan	SEC	CS	NA	OA (M): 398, M_{age} : 69.05 (8.79) OA (F): 356, M_{age} : 67.82 (8.25)	WM	↑age associated with ↓WM especially in M; ↑EDU associated with ↑WM especially in F
Tripathi et al. (2019)	Article	India	LAB	CS	NA	258, 189 M, M_{age} : 62.00 (6.44)	WM	↑EDU associated with ↑WM
Zhao et al. (2019)	Article	UK	SEC	CS	NA	8137, 3882 M, M_{age} : 62.69 (7.44)	fINT & VisM	↑age associated with ↓scores on all cognitive tests (fINT & VisM)
Malagurski et al. (2020)	Article	Switzerland	SEC	LONG	4YR	150, 79 M, M_{age} : 69.80, 64–83	PS, Verbl., & Verbm	↑age associated with ↓PS & Verbl. & MEM encoding
Mohammad et al. (2020)	Article	Iran	LAB	CS	NA	415, 123 M, M_{age} : 59.46 (6.59)	EpM	↑age associated with ↓EpM
Perosa et al. (2020)	Article	Germany	LAB	CS	NA	YA: 25, 13 M, M_{age} : 24.16 (2.16) OA: 31, 12 M, M_{age} : 68.58 (4.50)	Probabilistic LRN	YA > OA reward & punishment sensitivity & marginal ↓in LRN & lapse rate
Tuokko et al. (2020)	Article	Canada	LAB, F2F	LONG	~8YR	30097, 15319 M, M_{age} : 62.69 (10.30)	Verbl., EF, verbal fluency, INH, prospective MEM, PM speed	↑age associated with ↓scores on all cognitive measures
Zarantonello et al. (2020)	Article	Italy	LAB	CS	NA	20–29: 29, 15 M, M_{age} : 23.00 (3.00) 30–39: 18, 8 M, M_{age} : 33.00 (2.00) 40–49: 22, 7 M, M_{age} : 44.00 (3.00) 50–59: 23, 7 M, M_{age} : 55.00 (2.00) 60–69: 20, 11 M, M_{age} : 64.00 (2.00) 70–79: 10, 5 M, M_{age} : 76.00 (3.00)	VSWM	↑age associated with ↓speed (at 35) & ACC (at 57); M > F in speed; ↑EDU associated with ↑speed & ACC; ↑CogRes associated with ↑ACC only
Dave et al. (2021)	Article	Canada	SEC	LONG	4YR	YA (T1): 1064, 532 M, 20–21 YA (T2): 1064, 532 M, 24–25	EI	T2 > T1 (moderate) in trait EI (interpersonal & adaptability)
Grasshoff et al. (2021)	Article	Multiple	SEC	LONG	9YR	GER (T1): 1803, 855 M, M_{age} : 64.60 (9.30) GER (T2): 3871, 1812 M, M_{age} : 63.50 (9.80) SPN (T1): 1663, 730 M, M_{age} : 64.70 (9.70) SPN (T2): 2497, 1211 M, M_{age} : 65.60 (10.10) SWD (T1): 2615, 1190 M, M_{age} : 64.60 (9.30) SWD (T2): 2282, 1059 M, M_{age} : 63.50 (9.80)	Verbal fluency & delayed recall	↑age associated with stable ↓in cognitive abilities from 50 years on
Nuzum et al. (2021)	Article	Australia	LAB, SEC	CS	NA	YA: 15, 4 M, M_{age} : 26.20 (3.80) OA: 11, 5 M, M_{age} : 63.70 (15.40)	Sequence LRN	YA & OA improved post-training, no age effect
Woodman (2021)	Thesis	USA	OL	CS	NA	71, 29 M, M_{age} : 65.25 (4.18)	WM, INH, & CF	No significant linear association between age & WM, INH, or CF
Beller et al. (2022)	Article	Germany	SEC	LONG	12YR	MA (T1): 1172, 575 M, M_{age} : 52.70 (7.46) OA (T1): 702,	PS	↑age associated with ↓PS in MA & OA

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Table 2 (continued)

Study	Source	Location	Setting	Design	Length	Sample(s)	Measure(s)	Main Findings
Best et al. (2022)	Article	USA	LAB	LONG	11YR	366 M, M_{age} : 73.96 (4.72) MA (T2): 2158, 993 M, M_{age} : 53.99 (7.06) OA (T2): 1411, 777 M, M_{age} : 73.49 (4.78) 524, 245 M, M_{age} : 53.78 (10.57)	Numeracy	↑age associated with ↓numeracy beginning in later MA; ↓lower in M & those with ↑EDU YA > OA mean performance
Chettouf et al. (2022)	Article	Germany	LAB	CS	NA	YA: 20, 7 M, M_{age} : 22.00, 20–25 OA: 20, 6 M, M_{age} : 63.60, 59–70	Motor LRN	
Chi et al. (2022)	Article	Taiwan	LAB	CS	NA	YA: 30, 17 M, M_{age} : 22.63 (2.34) OA: 30, 12 M, M_{age} : 68.77 (5.95)	Verbal EpM	YA > OA LRN on “when”, “where”, & “what” components & MEM on “when” component
James et al. (2022)	Article	UK	LAB	LONG	26YR	468, 239 M, M_{age} : 70.70 (0.70)	VerbL & visual search speed	↑age associated with ↓visual search speed until ~60 & ↓VerbL after ~50
Neufeld et al. (2022)	Article	Canada	LAB	LONG	4YR	OA (T1): 35, 16 M, M_{age} : 75.02 (6.51) OA (T2): 35, 16 M, M_{age} : 78.76 (6.63)	MEM, EF, LANG, VS skills	↑age associated with ↓EF only
Nooyens et al. (2022)	Article	Netherlands	SEC	LONG	LASA: 6YR DCS: 10YR	LASA-F: 2654, M_{age} : 66.50 (8.70) LASA-M: 2469, M_{age} : 66.70 (8.80) DCS-F: 2482, M_{age} : 55.20 (6.60) DCS-M: 2287, M_{age} : 55.50 (6.60)	LASA: VerbL, CF, fINT, PS, & gCOG DCS: VerbL, CF, INH, & fluency	F > M in MEM, PS, CF, & gCOG (DCS only) but had faster decline than M in all but CF which was slower; LASA F < M in fINT but had slower decline which was larger in later born cohorts; adjusting for EDU increased F advantage
Rojas et al. (2022)	Article	Chile	LAB	LONG	8WK	60–69: 30, M_{age} : 65.73 (2.99) 70–79: 30, M_{age} : 74.00 (2.89) 80–92: 30, M_{age} : 82.53 (3.10)	VerbM	80–92 group had ↑RT on all tasks but good ACC with low cognitive demand; 80–92 < 70–79 group ACC when decisional cognitive factor added to task
Vance (2022)	Thesis	USA	LAB	CS	NA	S1 YA: 28, 9 M, M_{age} : 23.29 (3.04) S1 OA: 26, 8 M, M_{age} : 66.15 (2.59) S2 YA: 17, 6 M, M_{age} : 24.10 (2.80) S2 OA: 16, 4 M, M_{age} : 66.60 (2.00)	S1: EpM & EF S2: VerbL, INH, ATT & SpatWM	YA > OA MEM & EF; ↑physical activity associated with ↑LTM & associative MEM in YA & OA with no difference in benefit between age groups
Wang et al. (2022)	Article	USA	LAB	CS	NA	YA: 36, 21 M, M_{age} : 20.10 (2.10) OA: 45, 33 M, M_{age} : 72.00 (7.10) OA (ST): 15, M_{age} : 71.67 (1.61) OA (DT-CN): 15, M_{age} : 69.93 (1.82) OA (DT-INC): 15, M_{age} : 71.33 (2.02)	VM LRN	YA > OA task performance; OA > YA later stage performance due to reliance on intact implicit processes
Bakhtiari et al. (2023)	Article	Denmark	LAB	LONG	5YR	T1: 124, 124 M, M_{age} : 63.00 (0.66) T2: 88, 88 M, M_{age} : 67.25 (0.58)	gCOG, VerbM, PS, INT, & visual associative MEM	↑age associated with stable cognitive performance over 5 years
Fijałkiewicz et al. (2023)	Article	Poland	LAB	CS	NA	60, 14 M, M_{age} : 63.00 (12.60)	CF	↑age associated with ↑RT on perseveration but not learned irrelevance trials
Hsieh and Chen (2023)	Article	Taiwan	LAB	CS, LONG	1–2YR	CS: 253, 129 M, M_{age} : 46.15 (16.52) LONG (T1): 123, 56 M, M_{age} : 48.87 (16.69) LONG (T2): 123, 65 M, M_{age} : 50.65 (16.73)	ATT, INH, WM, & CF	YA > OA in alerting, stopping, & WM but OA > YA in conflict control & CF. YA = OA in orienting; LONG data show that ↑age associated with ↓alerting & WM but ↑efficiency in conflict control & CF; NS association between age & orienting & stopping

(continued on next page)

Table 2 (continued)

Study	Source	Location	Setting	Design	Length	Sample(s)	Measure(s)	Main Findings
Jin et al. (2023)	Article	Multiple	SEC	LONG	NA	61019, 27764 M, M _{age} : 65.14 (9.67)	EpM, WM, & time orientation	↑age associated with ↓EpM, WM, & time orientation in M & W with rapid ↓ after 70; W tended to have ↑EpM while M had ↑WM; Sex differences ↑ between 50 and 80 & ↓ after; ↑SES associated with ↑cognition, especially in younger women
Montemurro et al. (2023)	Article	Germany	SEC	CS	NA	YA: 137, 93 M, M _{age} : 22.83 (3.42) OA (HE): 30, 18 M, M _{age} : 64.16 (5.88) OA (LE): 30, 12 M, M _{age} : 64.83 (3.59)	VerbL, VerbM, VOC (VerbINT), phonemic fluency, & semantic fluency	YA > OA in all tasks but VOC; YA = OA (HE) in phonemic & semantic fluency
Pauley et al. (2023)	Article	Germany	LAB	CS	NA	YA: 35, 19 M, M _{age} : 22.30 (2.70) OA: 35, 16 M, M _{age} : 70.60 (2.40)	Recognition MEM	YA = OA in recognition MEM; OA > YA indicating they have seen previous & novel stimuli
Ruiz et al. (2023)	Article	UK & China	SEC	LONG	7–9YR	CHARLS-M: 6362, M _{age} : 61.80 (8.00) CHARLS-F: 6470, M _{age} : 61.60 (8.20) ELSA-M: 3974, M _{age} : 67.30 (8.80) ELSA-F: 4901, M _{age} : 67.80 (9.30)	Anterograde MEM & gCOG	↑EDU associated with ↑baseline cognition & ↓age-related cognitive decline; High EDU English > High EDU Chinese in cognitive decline
Tinga et al. (2023)	Article	Netherlands	LAB	CS	NA	YA: 17, 4 M, M _{age} : 27.24 (2.17) OA: 17, 6 M, M _{age} : 58.06 (2.08)	VS LRN	While responses become more accurate over time, OA > YA time in each trial to enhance movement precision

Note: Sample characteristics reported individually only when reported in original study. Standard deviations (in parentheses) or age ranges are reported next to mean age (M_{age}) when available. **Symbols:** ↑: increase or higher levels; ↓: decrease or lower levels; >: greater than; <: less than; =: equal to. **Abbreviations:** 1000BRAINS: 1000 Brains Study; ACC: Accuracy; ATT: Attention; BLK: Black; CF: Cognitive flexibility; CHARLS: China Health & Retirement Longitudinal Study; CN: Consistent; CogRes: Cognitive reserve; CS: Cross-sectional; DCS: Doetinchem Cohort Study; DT: Dual task; EDU: Education; EF: Executive function; EI: Emotional intelligence; ELSA: English Longitudinal Study of Aging; EpM: Episodic memory; F: Female; F2F: In-person outside of lab; fINT: Fluid intelligence; FMP: Final menstrual period subsample; gCOG: Global/general cognition; GER: Germany; HE: High education; INC: Inconsistent; INH: Inhibition; INT: Intelligence; LAB: Laboratory study; LANG: Language; LASA: Longitudinal Aging Study Amsterdam; LE: Low education; LEX: Lexical; LHAB: Longitudinal Healthy Aging Brain; LONG: Longitudinal; LRN: Learning; LTM: Long-term memory; M: Male; MA: Middle adult; Mage: Mean sample age; MEM: Memory; MS: Motor speed; MTH: Month; NRM: No reminder condition; NS: Non-significant; OA: Older adult; OL: Online; PM: Psychomotor; PS: Processing speed; RM: Reminder condition; RT: Reaction time; S: Study; SEC: secondary analysis; SpatM: Spatial memory; SpatWM: Spatial working memory; SPN: Spain; ST: Single task; STM: Short-term memory; SUB: Subset; SWD: Sweden; T: Time; VerbINT: Verbal intelligence; VerbL: Verbal learning; VerbM: Verbal memory; VerbWM: Verbal working memory; VisM: Visual memory; VisWM: Visual working memory; VM: Visuomotor; VOC: Vocabulary; VS: Visuospatial; VSM: Visuospatial memory; VSWM: Visuospatial working memory; WH: White; WK: Week; WM: Working memory; YA: Younger adult; YR: Year

functional measures. A total of 17/38 included studies (45 %) focused exclusively on functional measures with an additional seven studies assessing both brain structure and function (18 %).

3.3.3. RQ3: interventions to improve learning

Similar to both RQ1 and RQ2, studies included for RQ3 were disproportionately conducted in Western contexts (140/177 studies; 79 %), including one study recruiting participants from five different European countries (Carbonell-Hernández et al., 2019). A small number of studies (29/177; 16 %) were conducted in Asian contexts including China, Korea, and Japan. Unlike, RQ1 and RQ2, eight research syntheses were included for RQ3 (Eilat-Adar et al., 2023; Klimova and Pikhart, 2020; Lee et al., 2021; Pan et al., 2018; Roheger et al., 2021; Sala et al., 2019; Viviani and Vallesi, 2021; Zheng et al., 2015). Given the longitudinal nature of intervention studies, we will forego a descriptive analysis of research designs for RQ3. In stark contrast with RQ1 and RQ2, the largest number of studies for RQ3 included older adults between 60 and 69 (107/177; 60 %), and 70–79 (65/177; 37 %) years of age, with only 34/177 studies (19 %) including younger adults between 20 and 29. Included studies were still predominantly conducted exclusively in a laboratory setting (113/177 studies; 64 %). Some additional laboratory-based studies did include non-laboratory face-to-face (17/177; 10 %) or home-based components (25/177; 14 %), including three that employed a combination of all three settings (Engvig et al.,

2012; Merom et al., 2016; Park et al., 2014).

Studies included for RQ3 were coded and organized based on intervention format. A review of included studies by two independent reviewers resulted in the identification of eight categories of intervention studies. *Arts Interventions* involved participants engaging in either learning (e.g., piano training) or appreciating (e.g., music listening) music or visual art, and were used in 12/177 studies (7 %). *Brain Stimulation* interventions, used in 21/177 studies (12 %), included methods that stimulate the brain through the scalp such as transcranial direct current stimulation (tDCS). *Cognitive Based Interventions* included the application of learning or memory strategies, cognitive training, video games, or related interventions, and were the most widely studied interventions (48/177 studies; 27 %). *Food or Drug Interventions* included any study involving food or drugs including supplements, and were used in 16/177 studies (9 %). *Language Learning* interventions, the least studied category (9/177 studies; 5 %), involved participants being trained in a foreign language irrespective of training format (e.g., in-person classes or smartphone-based application). *Lifestyle Interventions*, used in 35/177 studies (20 %), involved changing aspects of daily life related to activity and engagement including exercise and learning how to use new technology; *Other* interventions included those that did not fit into any other category including neurofeedback and AI-based interventions, and were present in 12/177 studies (7 %). Finally, *Combined Interventions* included studies that used a combination of

Table 3
Summary of Characteristics of Included Studies for Research Question 2.

Study	Source	Location	Setting	Design	Length	Sample(s)	Measure (s)	Main Findings
Heinzel et al. (2014)	Article	Germany	LAB	LONG	4WK (OA)	YA: 18, 10 M, M_{age} : 24.06 (2.41) OA: 19, 13 M, M_{age} : 65.95 (3.73)	fMRI	↓WM network GMV & ↑WM network BOLD during 1-back task in OA
Marcotte and Ansaldi (2014)	Article	Canada	LAB	CS	NA	YA: 10, 5 M, M_{age} : 22.70 (2.00) OA: 10, 4 M, M_{age} : 70.20 (4.00)	fMRI	Smaller activation clusters & ↑cortical activation during task in OA
Samanez-Larkin et al. (2014)	Article	USA	LAB	CS	NA	OA (fMRI): 39, 18 M, M_{age} : 53.00 (16.00) OA (BEH): 37, 17 M, M_{age} : 52.00 (16.00)	fMRI	↓frontostriatal representation of prediction errors during probabilistic LRN in OA; stable representation of non-LRN related reward outcome with ↑age
Bilodeau-Mercure et al. (2015)	Article	Canada	LAB	CS	NA	YA: 11, 4 M, M_{age} : 25.70 (3.90) OA: 11, 4 M, M_{age} : 68.00 (4.60)	fMRI	↓core speech network thickness in OA; Left dorsal anterior insula involved in maintaining speech perception with ↑age
Diwadkar et al. (2016)	Article	Italy	LAB	CS	NA	YA: 33, 12 M, <26 OA: 33, 18 M, >26	sMRI	↓GMV in hippocampus & dPFC in OA (associative LRN areas)
Reichert et al. (2016)	Article	Austria	LAB	LONG	2WK	YA: 21, 12 M, M_{age} : 24.80 (2.60) MA: 25, 12 M, M_{age} : 47.80 (5.30) OA: 24, 9 M, M_{age} : 67.50 (5.60)	rsEEG	↓theta & alpha II power with ↑age, associated with ↓verbal & VSM
Rojkova et al. (2016)	Article	France	LAB	CS	NA	47, 24 M, M_{age} : 45.45 (14.79)	MRI	↑age associated with ↓microstructural organization in frontal corpus callosum & integrity in anterior thalamic radiation & ↓integrity of two interlobar tracts in R HEMI & three in L HEMI. No influence of EDU on white matter microstructure in frontal lobe.
Schenk et al. (2016)	Article	Germany	LAB	CS	NA	YA: 17, 3 M, M_{age} : 22.53 (4.16) OA: 10, 2 M, M_{age} : 58.20 (7.48)	EEG	↑P150 AMP in OA, + CORR with categorization LRN
Lubitz et al. (2017)	Article	Germany	LAB	CS	NA	YA: 35, 8 M, M_{age} : 22.43 (3.25) OA: 30, 8 M, M_{age} : 68.30 (5.19)	EEG	In OA: ↓P200 during 2-back task; ↓P300 with ↑frontality; P200 + CORR & P300 - CORR with WM, frontal compensation
Monteiro et al. (2017)	Article	Belgium	LAB	LONG	2WK; 6MTH (Subset)	YA: 25, 11 M, M_{age} : 21.50 (2.30) OA: 18, 7 M, M_{age} : 68.60 (6.00)	fMRI	↑task-related activation in parietofrontal areas & ↓activation in subcortical areas in OA but ↓task planning & execution activity between pre & posttest in temporo-parieto-frontal & subcortical areas in YA & OA
Perry et al. (2017)	Article	Australia	LAB	CS	NA	101, 44 M, M_{age} : 82.70 (3.80)	rsfMRI	↑age associated with ↓function of sensorimotor networks subserving core processes; EDU influences networks insensitive to aging
Archer et al. (2018)	Article	Singapore	LAB	CS	NA	189, 83 M	fMRI-EPI	↑age associated with ↓task area neural activity (NS w/EDU & ACC) but ↑non-task area neural activity.
Chan et al. (2018)	Article	USA	LAB	CS	NA	YA: 44, 18 M, 20–34 ME: 43, 16 M, 35–49 MidL: 85, 29 M, 50–64 OA: 132, 59 M, 65–89	rsfMRI	In ME/MidL ↓SES associated with ↓rs-system segregation & ↓cortical GM thickness when controlling for health, cognitive ability, & demographics, irrespective of childhood SES. No pattern in YA or OA
Frøehlich et al. (2018)	Article	Germany	LAB	CS	NA	YA: 20, 7 M, M_{age} : 25.00 (3.46) OA: 38, 22 M, M_{age} : 70.20 (3.15)	fMRI	Reading network preserved during aging, but ↑activation in subcomponents in OA, most prominent during phonological & orthographic processing. Additional aging effects in frontal midline regions
Abellaneda-Pérez et al. (2019)	Article	Spain	LAB	CS, LONG	3YR (OA)	YA: 24, 5 M, M_{age} : 23.42 (1.60) OA (T1): 27, 5 M, M_{age} : 68.15 (4.60) OA (T2): 14, 0 M, M_{age} : 71.21 (4.70)	rsfMRI sMRI dMRI	iTBS ↑FC in distal DMN in YA & proximal in OA; OA with iTBS response like YA had ↑brain integrity & cognitive performance & ↓cognitive decline over 3YR; EDU made OA response more like YA
Berghuis et al. (2019)	Article	Italy	LAB	CS	NA	YA: 15, 6 M, M_{age} : 25.50 (2.50) OA: 15, 9 M, M_{age} : 63.10 (5.20)	fMRI DTI	OA had ↓GMV & mean white matter anisotropy & showed ↑activity during task performance & ↓frontal cortical deactivations after motor skill consolidation while YA showed ↓parietal, occipital, & temporal deactivations
Bowen et al. (2019)	Article	Canada	LAB	CS	NA	YA: 16, 7 M, M_{age} : 25.44 (3.79)	fMRI	YA & OA engage the same networks to support general feedback processing, but OA engage two additional networks for negative feedback

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Table 3 (continued)

Study	Source	Location	Setting	Design	Length	Sample(s)	Measure (s)	Main Findings
Dahl et al. (2019)	Article	Germany	LAB	LONG	~2YR	OA: 15, 6 M, M_{age} : 68.47 (5.38) YA: 66, 44 M, M_{age} : 32.50 (3.53) OA: 228, 146 M, M_{age} : 72.29 (4.11)	MRI	processing & may show suboptimal decision making following negative feedback. ↑LC integrity associated with ↑LRN & MEM in OA & YA; more youth-like rostral LC associated with ↑MEM in OA
Jockwitz et al. (2019)	Article	Germany & Switzerland	SEC	CS	NA	1000BRAINS: 228, 114 M, M_{age} : 70.69 (4.95) LHAB: 228, 114 M, M_{age} : 70.69 (4.89)	MRI	↑age associated with ↓CTh in both HEMI & L/R medial/lateral posterior DMN; no changes in anterior DMN
Pergher et al. (2019)	Article	Finland & Belgium	LAB	CS	NA	55, 23 M, M_{age} : 62.20 (7.60)	sMRI	↑age associated with ↓GMV & ↑atrophy; ↑EDU associated with ↑GMV & ↓atrophy
Zhao et al. (2019)	Article	UK	SEC	CS	NA	8137, 3882 M, M_{age} : 62.69 (7.44)	MRI	↑age associated with ↓cortical morphology, most clearly in PFC & LTC (all measures), IPC (CTh), ITC & OFC (CVo & CSA), made worse by smoking, alcohol, & sleep issues; Age ~60 was break point for this relationship in AD-prone areas
Malagurski et al. (2020)	Article	Switzerland	LAB	LONG	4YR	150, 79 M, M_{age} : 69.80, 64–83	rsfMRI	↑age associated with ↑global flexibility & network flexibility in DMN, FPN, & SMN, & ↓global network recruitment; overall supports ↑age associated with ↑variability in modular organization
Perosa et al. (2020)	Article	Germany	LAB	CS	NA	YA: 25, 13 M, M_{age} : 24.16 (2.16) OA: 31, 12 M, M_{age} : 68.58 (4.50)	MRI PET	↑age associated with ↓striatal integrity; ↑caudate nucleus volume associated with ↑LRN rate in OA but no influence of dopamine synthesis in the dorsal striatum
Reas et al. (2020)	Article	USA	LAB	CS	NA	F: 90, M_{age} : 76.20 (7.80) M: 57, M_{age} : 77.30 (7.90)	MRI	↑age associated with global ↓GM & white matter microstructure integrity largely independent of atrophy; more profound in F even when controlling for EDU, hypertension, & BMI
Jockwitz et al. (2021)	Article	Germany & Switzerland	SEC	LONG	3–4YR	1000BRAINS (T1): 161, 85 M, M_{age} : 69.20 (4.60) LHAB (T1): 161, 76 M, M_{age} : 69.90 (4.10) 1000BRAINS (T2): 161, 85 M, M_{age} : 72.90 (4.70) LHAB (T2): 161, 76 M, M_{age} : 74.00 (4.10)	MRI	↑age associated with ↓CTh but ↑in anterior cingulate; no relationship between CTh & cognitive performance
Nuzum et al. (2021)	Article	Australia	LAB	CS	NA	YA: 15, 4 M, M_{age} : 26.20 (3.80) OA: 11, 5 M, M_{age} : 63.70 (15.40)	TMS	Only YA showed hemispheric lateralization after unilateral complex finger-tapping training; both YA & OA showed bilateral transfer
Boban et al. (2022)	Article	Serbia	LAB	CS	NA	75, 53 M, M_{age} : 37.32 (11.91)	DTI	↑age associated with ↓FA in PTR but ↑MD in SS, ↑RD in PTR, SS, & retrolenticular internal capsule & ↑axial diffusivity in body of CC. RD had richest correlation with age. FA, MD, & RD showed changes in diffusivity of projection fibers. No association between DTI measures & EDU
Chettouf et al. (2022)	Article	Germany	LAB	CS	NA	YA: 20, 7 M, M_{age} : 22.00, 20–25 OA: 20, 6 M, M_{age} : 63.60, 59–70	EEG fMRI	↓in motor-event-related EEG beta activity more lateralized in contralateral motor region in YA; ↓mean beta-power during task execution in bilateral premotor area in OA
Chi et al. (2022)	Article	Taiwan	LAB	CS	NA	YA: 30, 17 M, M_{age} : 22.63 (2.34) OA: 30, 12 M, M_{age} : 68.77 (5.95)	sMRI	OA had ↓volume in DG, CA1, & subiculum but not in CA2/3, CA4, or entorhinal cortex. ↓DG & CA1 volumes associated with ↓"when" recall while ↓subiculum volume was associated with ↓"when", "where", & "what" recall. ↓volume in subiculum, CA1, CA4, & DG were associated with age-related ↓"when" MEM retention. ↑age & ↓"when" recall relationship mediated by subiculum alone.
James et al. (2022)	Article	UK	LAB	LONG	26YR	468, 239 M, M_{age} : 70.70 (0.70)	PET	↓whole brain & hippocampal volume at age 70 associated with ↑decline in processing search speed over previous 20YR
Neufeld et al. (2022)	Article	Canada	LAB	LONG	4YR	T1: 35, 16 M, M_{age} : 75.02 (6.51) T2: 35, 16 M, M_{age} : 78.76 (6.63)	MRI	↑age associated with ↑GM atrophy
Bakhtiari et al. (2023)	Article	Denmark	LAB	LONG	5YR	T1: 124 M, M_{age} : 63.00 (0.66) T2: 88 M, M_{age} : 67.25 (0.58)	EEG	↑age associated with posterior shift in visually evoked gamma oscillations but stable cognitive performance; ↓frontocentral & ↓parieto-occipital gamma associated with ↑cognitive score

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Table 3 (continued)

Study	Source	Location	Setting	Design	Length	Sample(s)	Measure (s)	Main Findings
Montemurro et al. (2023)	Article	Germany	SEC	CS	NA	YA: 137, 93 M, M_{age} : 22.83 (3.42) OA (LE): 30, 12 M, M_{age} : 64.83 (3.59) OA (HE): 30, 18 M, M_{age} : 64.16 (5.88)	rsfMRI	OA associated with: ↓ in GMV in anterior cingulate, precuneus, superior, middle, & inferior frontal gyri, supramarginal gyrus, insular cortex, temporal, parietal, & lateral occipital regions bilaterally; ↓ total brain volume, white matter, & ↑ CSF. OA had ↓ rs-connectivity in MVN, DAN, L FPN, & DMN but ↑ rs-connectivity in VAN. OA (HE) group showed ↓ rs-connectivity strength in MVN & DMN compared to YA & OA (LE).
Pauley et al. (2023)	Article	Germany	LAB	CS	NA	YA: 35, 19 M, M_{age} : 22.30 (2.70) OA: 35, 16 M, M_{age} : 70.60 (2.40)	fMRI	OA demonstrated less distinctive representations than YA in line with age-related neural dedifferentiation hypothesis
Tinga et al. (2023)	Article	Netherlands	LAB	CS	NA	YA: 17, 4 M, M_{age} : 27.24 (2.17) OA: 17, 6 M, M_{age} : 58.06 (2.08)	EEG	LRN-related EEG changes showed ↑ theta & ↓ gamma power in OA, slight ↑ gamma in YA
Turney et al. (2023)	Article	USA	LAB	CS	NA	OFFSPRING: 497, 173 M, M_{age} : 55.00 (10.70) WHICAP: 970, 381 M, M_{age} : 75.00 (6.50)	MRI	↑ age associated with ↓ CTh & ↑ white matter hyperintensity volume in MA & OA similarly across race & ethnicity
Yang et al. (2023)	Article	Multiple	SEC	CS	NA	552, 0 M, M_{age} : 48.20 (16.00)	MRI	Hippocampus surface is bumpiest between 40 and 50 years
Zhou et al. (2023)	Article	USA & UK	SEC	CS	NA	Overall: 4186, 1837 M, M_{age} : 63.00, 22–97 BLSA: 782, 341 M, M_{age} : 65.99 (14.91) OASIS–3: 824, 364 M, M_{age} : 70.25 (9.45) CARDIA–1: 176, 72 M, M_{age} : 51.27 (4.30) CARDIA–3: 307, 141 M, M_{age} : 51.31 (3.71) CARDIA–4: 252, 112 M, M_{age} : 51.28 (3.94) PENN-ABC: 274, 112 M, M_{age} : 68.30 (13.41) UKBIOBANK: 1571, 695 M, M_{age} : 62.60 (7.38)	rsfMRI	↑ age associated with ↑ functional connectivity in VN-LN, VN-VN, VN-FPN, VAN-FPN, DMN-FPN, & ↓ functional connectivity in: DMN-VN, DMN-DMN, VN-FPN, SMN-DMN, VN-SMN, DAN-FPN, LN-VN, VAN-VN.

Note: Sample characteristics reported individually only when reported in original study. Standard deviations (in parentheses) or age ranges are reported next to mean age (M_{age}) when available. **Symbols:** ↑: increase or higher levels; ↓: decrease or lower levels; >: greater than; <: less than; =: equal to. **Abbreviations:** 1000BRAINS: 1000 Brains; ACC: Accuracy; AD: Alzheimer disease; AMP: Amplitude; BEH: Behavioral; BLSA: Baltimore Longitudinal Study of Aging; BMI: Body mass index; BOLD: Blood oxygenation level dependent; CARDIA: Coronary Artery Risk Development in Young Adults; CC: Corpus callosum; CORR: Correlation; CS: Cross-sectional; CSA: Cortical surface area; CSF: Cerebrospinal fluid; CTh: Cortical thickness; CVo: Cortical volume; d: Diffusion; DAN: Dorsal attention network; DG: Dentate gyrus; DMN: Default mode network; dPFC: Dorsal prefrontal cortex; DTI: Diffusion tensor imaging; EDU: Education; EEG: electroencephalography; EPI: Echo planar imaging; F: Female; FA: Fractional anisotropy; FC: Functional connectivity; fMRI: functional magnetic resonance imaging; FPN: Frontoparietal network; FUN: Function; GM: Grey matter; HE: High education; HEMI: Hemisphere; IPC: Inferior parietal cortex; iTBS: Intermittent theta burst stimulation; ITC: Inferior temporal cortex; L: Left; LAB: Laboratory study; LC: Locus coeruleus; LE: Low education; LHAB: Longitudinal Healthy Aging Brain; LN: Limbic network; LONG: Longitudinal; LTC: Lateral temporal cortex; M: Male; MA: Middle adult; Mage: Mean sample age; MD: Mean diffusivity; ME: Middle early; MidL: Middle late; MRI: magnetic resonance imaging; MTH: Month; MVN: Medial visual network; NS: Non-significant; OA: Older adult; OASIS: Open Access Series of Imaging Studies; OFC: Orbitofrontal cortex; OFFSPRING: Offspring Study of Racial & Ethnic Disparities in Alzheimer Disease; PENN-ABC: University of Pennsylvania Aging Brain Cohort; PET: Positron emission tomography; PFC: Prefrontal cortex; PTR: Posterior thalamic radiation; R: Right; RD: Radial diffusivity; rs: Resting-state; s: Structural; SEC: secondary analysis; SES: Socioeconomic status; SMN: Sensorimotor network; sMRI: structural magnetic resonance imaging; SS: Sagittal striatum; STR: Structure; T: Time; TMS: Transcranial magnetic stimulation; VAN: Salience/ventral attention network; VN: Visual network; WHICAP: Washington Heights–Inwood Columbia Aging Project; WK: Week; WM: Working memory; YA: Younger adult; YR: Year

interventions across two or more categories, and were used in 24/177 studies (14 %).

3.4. Risk of Bias in Studies

For assessing risk of bias, we utilized the MMAT for all empirical

studies (Hong et al., 2018), and the CASP for all research syntheses (CASP, 2018). A summary of results for all included studies is provided in Tables 5 & 6. Overall risk of bias was generally low across most studies (242/265; 91 %), with some concerns identified across a small minority (22/265; 8 %), and only one study assessed as having high risk of bias (Klimova and Pikhart, 2020). Full details and descriptions for

Table 4
Summary of Characteristics of Included Studies for Research Question 3.

Study	Source	Location	Setting	Length	Sample(s)	Intervention	Main Findings
Azevedo et al. (2012)	Conference Paper	USA	LAB	2DY	69, 18 M, M_{age} : 23.00	Intelligent tutor prompt & feedback (PF); prompting only (PO); no prompt or feedback (CON)	PF > PO & CON in LRN efficiency; further supported metacognitive monitoring & regulation during LRN
Berryhill and Jones (2012)	Article	USA	LAB	3DY	25, M_{age} : 63.70, 56–80	tDCS	atDCS improved WM only in OA with \uparrow EDU
Engvig et al. (2012)	Article	Norway	LAB, F2F, HOME	8WK	TRT: 21, 10 M, M_{age} : 61.7 (9.40) CON: 20, 9 M, M_{age} : 60.30 (9.10)	MEM training (method of loci; TRT); no-training (CON)	TRT > CON in FA with \uparrow FA associated with \uparrow MEM, possibly driven by \downarrow RD; TRT > CON source/recognition ratio with \downarrow false alarms
Jackson et al. (2012)	Article	USA	LAB, HOME	30–32WK	Overall: 183, 64 M, M_{age} : 72.90 (7.70) TRT: 85 CON: 98	Inductive reasoning training (TRT); waitlist (CON)	TRT > CON in inductive reasoning
Lin et al. (2012)	Article	USA	LAB	5DY	YA 16, 9 M, M_{age} : 26.40 (3.10) OA: 16, 7 M, M_{age} : 66.20 (4.70)	Interleaved practice	Interleaved > repetitive practice in M1 excitability (\uparrow in OA) & BOLD signal during practice; \uparrow M1 excitability & \uparrow BOLD in dlPFC (YA) or SM & rPFC (OA) associated with \uparrow motor sequence LRN
Maillot et al. (2012)	Article	France	LAB	14WK	TRT: 15, M_{age} : 73.47 (4.10) CON: 15, M_{age} : 73.47 (3.00)	Exergames (TRT); no-training (CON)	TRT > CON on EF & PS but not VS measures
McDougall and House (2012)	Article	UK	LAB, HOME	6WK	TRT: 21, 11 M, M_{age} : 74.81 (7.85) CON: 20, 9 M, M_{age} : 74.40 (9.42)	VG (TRT); no VG (CON)	TRT > CON Digit Span Backwards (WM)
Mortimer et al. (2012)	Article	China	LAB, F2F	40WK	Tai chi: 30, 11 M, M_{age} : 67.30 (5.30) Walking: 30, 11 M, M_{age} : 67.80 (5.00) Social: 30, 9 M, M_{age} : 67.90 (6.50) CON: 30, 9 M, M_{age} : 68.20 (6.50)	Tai chi, walking, social interaction; no intervention (CON)	Tai chi & Social > CON in brain volume; Tai chi > CON on Mattis Dementia Rating Scale, TMT A & B, AVLT, verbal fluency; Social > CON on verbal fluency; no effect of Walking
Szelag and Skolimowska (2012)	Article	Poland	LAB	8WK	TRT: 10, 4 M, M_{age} : 68.08 (2.58) CON (training): 10, 4 M, M_{age} : 69.33 (2.92) CON: 10, 5 M, M_{age} : 71.08 (3.33)	Fast ForWord (temporal) training (TRT); other training (CON training), non-active (CON)	TRT > CON (training) in temporal information processing with amelioration of ATT & MEM resources for up to 18MTH; CON (training) = CON
Alves (2013)	Thesis	Brazil	F2F	4 MTH	Dance: 25, 4 M, M_{age} : 69.36 (7.02) Walking: 15, 0 M, M_{age} : 66.66 (7.78) CON: 25, 1 M, M_{age} : 68.40 (7.56)	Ballroom dancing; walking; no contact (CON)	Dance > Walking & CON in reasoning, visual processing, WM, & psychosocial wellbeing
Bottiroli et al. (2013)	Article	Italy	LAB, HOME	3WK	S1 (Strategy-adaptation): 38, 14 M, M_{age} : 66.00 (0.80) S1 (Strategy): 33, 10 M, M_{age} : 67.40 (1.10) S1 (CON): 36, 13 M, M_{age} : 66.40 (0.90) S2 (Strategy-adaptation): 39, 16 M, M_{age} : 65.90 (0.70) S2 (CON): 33, 8 M, M_{age} : 66.10 (0.80)	S1 strategy-adaptation training, or strategy training; no training (CON) S2 strategy-adaptation; no training (CON)	Both training programs \uparrow LRN & MEM task performance, but transfer was greatest after strategy-adaptation training
Bozoki et al. (2013)	Article	USA	LAB, OL	6WK	TRT: 32, 16 M, M_{age} : 67.20 (6.37) CON: 28, 9 M, M_{age} : 70.80 (6.81)	Online LRN games (TRT); passive content viewing (CON)	TRT improved game performance but not cognition
Chapman et al. (2013)	Article	USA	LAB	12WK	TRT: 18, 5 M, M_{age} : 64.00 (4.30) CON: 18, 5 M, M_{age} : 64.00 (3.60)	AE (TRT); waitlist (CON)	TRT > CON in immediate & delayed MEM from T1 to T3, associated with \uparrow CBF in L & R hippocampus during T2

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Table 4 (continued)

Study	Source	Location	Setting	Length	Sample(s)	Intervention	Main Findings
Maddox (2013)	Thesis	USA	LAB	NA	YA (Short lag): 49, M _{age} : 20.33 (2.46) OA (Short lag): 42, M _{age} : 73.81 (5.20) YA (Long lag): 49, M _{age} : 20.76 (2.89) OA (Long lag): 42, M _{age} : 75.66 (7.49)	Retention interval length	Short lag led to consistent ↑MEM while Long lag resulted in small ↑MEM over time; Final test showed that YA benefitted more from Long lag and OA from Short lag.
McDermott (2013)	Thesis	USA	LAB, HOME	6–7MTH	Brain Game: 15, 4 M, M _{age} : 67.60, 60–83 Action Game: 15, 3 M, M _{age} : 68.90, 60–83	Brain training game	Both groups showed enduring ↑ATT but no change in STM
Moore (2013)	Thesis	UK	LAB	S1: 18WK, S2: 8WK	S1 (Overall): 40, 27 M, M _{age} : 35.40 S1 (MTG): 14, M _{age} : 36.20 (12.40) S1 (WCG): 18, M _{age} : 35.40 (11.10) S2 (MTG): 25, M _{age} : 65.30 (6.00) S2 (BTG): 25, M _{age} : 64.00 (6.70)	Mindfulness training	S1: MTG > WCG in ATT, ERP changes in parallel S2: MTG > BTG in ATT; ERP changes in parallel
Nouchi et al. (2013)	Article	Japan	LAB	4WK	Brain Age: 16, 9 M, M _{age} : 20.50 (1.10) Tetris: 16, 9 M, M _{age} : 20.87 (1.25)	VG	Brain Age led to ↑EF, WM, & PS while Tetris led to ↑ATT & VS ability compared to Brain Age
Petrosyan (2013)	Article	Armenia	LAB	12WK	TRT: 12, M _{age} : 66.70 CON: 12, M _{age} : 67.40	Resistance training (TRT); inactive group (CON)	TRT led to ↑PS & MEM; ↑MEM present after 6MTH
Sathyanarayanan et al. (2013)	Article	India	LAB	12WK	TRT: 33, 10 M, M _{age} : 42.90 (7.50) CON: 33, 11 M, M _{age} : 41.30 (6.30)	Brahmi (TRT); placebo (CON)	No effect of TRT
Schega et al. (2013)	Article	Germany	LAB	6WK	TRT: 17, 4 M, M _{age} : 63.70 (3.40) CON: 17, 4 M, M _{age} : 63.60 (3.20)	Intermittent hypoxic training prior to a strength-endurance exercise program (TRT); placebo (CON)	No effect of TRT
Theill et al. (2013)	Article	Switzerland	LAB	10WK	Overall: 63, 17 M, M _{age} : 71.80 (4.90) Simultaneous Training: 18, M _{age} : 72.39 (4.19) Single WM Training: 12, M _{age} : 73.33 (6.08) CON: 21, M _{age} : 70.90 (4.77)	Simultaneous training, single WM training; no training (CON)	Both TRT > CON in EC; Simultaneous > Single Training in LRN & MEM
Bailey et al. (2014)	Article	USA	LAB	NA	YA (TRT): 41, 10 M, M _{age} : 21.60 (6.50) OA (TRT): 39, 15 M, M _{age} : 68.90 (6.90) YA (CON): 38, 16 M, M _{age} : 20.60 (4.30) OA (CON): 27, 6 M, M _{age} : 71.70 (7.70)	Effective encoding strategy training (TRT); no training (CON)	TRT led to ↑WM in YA & OA; age-related ↓in WM was not greatly affected & no evidence of transfer
Berryman et al. (2014)	Article	Canada	LAB	14WK	LBS-A: 16, 7 M, M _{age} : 69.80 (3.90) UBS-A: 15, 7 M, M _{age} : 69.50 (6.10) GMA: 16, 4 M, M _{age} : 72.70 (6.30)	PE	All TRTs showed comparable ↑ in cognitive function
Chan et al. (2014)	Article	Hong Kong	F2F, HOME	3MTH	44, 22 M, 60–83	Dejian mind-body intervention	TRT led to ↑MEM & CF in OA with ↓baseline MEM
Heinzel et al. (2014)	Article	Germany	LAB	4WK (OA)	YA: 18, 10 M, M _{age} : 24.06 (2.41) OA: 19, 13 M, M _{age} : 65.95 (3.73)	WM training (OA)	TRT led to ↑neural efficiency & capacity in frontal WM network as well as ↑WM, PS, EF, & reasoning; OA with more YA-like brain response had ↑benefit
Kishore et al. (2014)	Article	India	LAB	3WK	YA: 14, M _{age} : 27.60 (3.10) MA: 11, M _{age} : 41.70 (7.00) OA: 12, M _{age} : 60.50 (6.80)	Cerebellar cortical inhibition/PAS L motor cortex; cerebellar cortical excitation / PAS; 25 mg carbidopa & 100 mg levodopa with PAS or cerebellar cortical excitation /	Carbidopa & Levodopa with cerebellar inhibition led to ↑motor cortex response to PAS in OA

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Table 4 (continued)

Study	Source	Location	Setting	Length	Sample(s)	Intervention	Main Findings
Park et al. (2014)	Article	USA	LAB, F2F, HOME	3MTH	Photo: 29, 10 M, M_{age} : 72.83 (6.70) Quilt: 35, 9 M, M_{age} : 71.69 (6.67) Dual: 42, 15 M, M_{age} : 69.74 (7.00) Social: 36, 5 M, M_{age} : 72.14 (8.06) Placebo: 39, 6 M, M_{age} : 70.97 (7.12) CON: 40, 11 M, M_{age} : 73.08 (7.87)	PAS (> 45-year-old with no initial response to PAS) Productive-engagement (photo, quilt, & dual conditions), Receptive-engagement (social, placebo (doing activities at home)) & no treatment (CON)	Photo, Quilt, & Dual > Social, Placebo, & CON in EpM
Sandberg et al. (2014)	Article	Sweden	LAB	5WK	YA (TRT): 16, 5 M, M_{age} : 26.25 (4.01) OA (TRT): 15, 7 M, M_{age} : 69.73 (5.02) YA (CON): 13, 4 M, M_{age} : 24.62 (3.20) OA (CON): 15, 6 M, M_{age} : 68.80 (4.80)	Process training (TRT); no contact (CON)	TRT led to age-equivalent \uparrow performance; near transfer to WM & INH tasks in YA & OA; intermediate transfer to complex WM tasks in YA; no far transfer
Stepankova et al. (2014)	Article	Czech Republic	HOME	5WK	TRT (10 times): 20, 5 M, M_{age} : 67.95 (2.19) TRT (20 times): 20, 6 M, M_{age} : 68.15 (2.62) CON: 25, 7 M, M_{age} : 68.08 (3.01)	WM training (10 vs. 20 times); no contact (CON)	Both TRTs > CON in WM & VS skills with dose-response effect on VS skills despite intervention being in verbal domain
Stine-Morrow et al. (2014)	Article	USA	LAB	30–32WK	Engagement: 188, 55 M, M_{age} : 71.7.0 (8.00) Reasoning: 130, 30 M, M_{age} : 73.40 (7.50) CON: 143. 34 M, M_{age} : 72.90 (7.40)	Team-based competitive program in creative problem solving (engagement, "Odyssey-Troy"); Home-based inductive reasoning training program (reasoning, "Odyssey-Ithaca"); waitlist (CON)	Reasoning TRT led to \uparrow inductive reasoning while Engagement TRT led to \uparrow divergent thinking; \uparrow gains associated with \uparrow baseline cognitive profile
Xiong et al. (2014) ¹	Article	China	LAB	8DY	NF-training: 12, 7 M Behavioral-training: 12, 6 M Sham NF-training: 12, 7 M CON: 12, 5 M	NF; no training (CON)	NF > Others in WM
Duffy and Azevedo (2015)	Article	Canada	LAB	1HR	Overall: 83, 30 M, M_{age} : 21.00 (2.80) Prompt & Feedback: 39 CON: 44	Intelligent tutor prompt & feedback (TRT); no prompt or feedback (CON)	TRT > CON in self-regulated LRN & time viewing science material; adopting performance approach \uparrow benefit
Hoff et al., 2015b	Article	Germany	LAB	2DY	atDCS + MVF: 12, 6 M, M_{age} : 66.17 (1.67) stDCS + MVF: 13, 8 M, M_{age} : 66.77 (1.35) atDCS: 11, 6 M, M_{age} : 66.91 (2.74)	tDCS + MVF	atDCS + MVF > stDCS + MVF & atDCS in performance untrained hand
Reis et al. (2015) ²	Conference Paper	Portugal	LAB	12DY	Overall: 14, 6 M NF: 8 SHAM: 6	NF	NF led to \uparrow WM & \uparrow relative theta & alpha power
Sato et al. (2015)	Article	Japan	LAB, F2F	10WK	Water-based exercise (CON): 11, 2 M, 69–76 Cognitive water-based exercise (TRT): 10, 2 M, 69–86	Cognitive water-based exercise	TRT led to \uparrow pegboard test, choice stepping reaction test, ATT, MEM, LRN, & gCOG
Styron (2015)	Thesis	USA	LAB	NA	Overall: 33, 9 M, M_{age} : 57.91 (6.65) Bookworm: 15 Bejeweled 3: 18 Studies: 9	VG	TRTs led to \uparrow PS & CF
Zheng et al. (2015)	Review Article	China	NA	NA		Tai chi	Tai chi led to \uparrow cognitive performance over regular physical activity
Avellar et al. (2016)	Article	Brazil	LAB	NA	CON/TRT: 25, 7 M, M_{age} : 74.00 (5.20)	D-serine administration (TRT); placebo (CON)	TRT led to \uparrow SpatM, LRN, & problem solving; \uparrow plasma D-

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Table 4 (continued)

Study	Source	Location	Setting	Length	Sample(s)	Intervention	Main Findings
Azevedo et al. (2016)	Conference Paper	USA	LAB	3DY	TRT/CON: 25, 6 M, M_{age} : 72.00 (4.70) 120, 58 M, M_{age} : 20.40	Intelligent tutor with scaffolding (TRT); without scaffolding (CON)	serine associated with \uparrow improvement TRT > CON in LRN, page-level quiz taking, quiz score, note checking, creation, & expansion, summary creation, & metacognitive strategy use; TRT led to \downarrow content reading
Basak and O'Connell (2016)	Article	USA	LAB	2WK	Unpredictable MEM Updating: 27, 8 M, M_{age} : 68.82 (6.00) Predictable MEM Updating: 21, 6 M, M_{age} : 68.81 (4.32)	WM training	Unpredictable MEM updating training led to \uparrow EpM; \uparrow LRN rates associated with \uparrow improvements on EpM & novel WM task
Chan et al. (2016)	Article	USA	LAB	3MTH	Productive Engagement (TRT): 18, 5 M, M_{age} : 74.89 (6.49) Social Engagement (CON): 18, 3 M, M_{age} : 74.89 (6.44) Receptive Engagement (CON): 18, 3 M, M_{age} : 74.50 (5.79)	iPad skills course	TRT > CONs in EpM & PS but no change in mental control or VS processing
Christy (2016)	Thesis	USA	F2F	6WK	Overall: 13, 60+	Interactive Metronome (IM)	\uparrow performance on IM associated with \uparrow cognitive & motor performance
Dumel et al. (2016)	Article	Canada	LAB	5DY	TRT: 12, 6 M, M_{age} : 61.25 (5.08) CON: 11, 5 M, M_{age} : 60.73 (5.82)	tDCS (TRT); stDCS (CON)	atDCS > CON in motor LRN
Külzow et al. (2016)	Article	Germany	LAB, HOME	26WK	TRT: 22, 12 M, M_{age} : 63.00 (6.00) CON: 20, 12 M, M_{age} : 61.00 (6.00)	Fish oil capsules (TRT); placebo (CON)	TRT > CON in MEM; no effect on AVLT
Lin et al. (2016)	Article	USA	LAB	5DY	YA: 16, 9 M, M_{age} : 26.40 (3.10) OA: 16, 7 M, M_{age} : 66.20 (4.70)	Interleaved practice	Interleaved practice led to \uparrow motor LRN; YA > OA in benefit, associated with YA \uparrow brain network efficiency; in YA only \uparrow network centrality associated with \uparrow LRN
Marra (2016) ³	Thesis	USA	LAB	6WK	Art Academy: 14, 4 M, M_{age} : 65.29 (10.42) Tetris: 11, 2 M, M_{age} : ~65.00 (3.52) Brain Age: 21, 6 M, M_{age} : 65.33 (10.80) Virtual Poker: 21, 5 M, M_{age} : 63.71 (8.21)	VG	Art > Tetris in list LRN, VisM, PS, PM ability, mental rotation, & gCOG; Tetris led to \uparrow math fluency; Art & Tetris both led to \uparrow MEM; \uparrow Tetris play associated with \uparrow VisM, VerbM, EF, & gCOG
Merom et al. (2016)	Article	Australia	LAB, F2F, HOME	8MTH	Overall: 79, 12 M, M_{age} : 69.60 (6.40) Dance: 40, 6 M, 60–75+ Walk: 39, 6 M, 60–75+	Mixed dance	Dance > Walk in BVMT total LRN & delayed recall
Nouchi et al. (2016)	Article	Japan	LAB	6MTH	TRT: 32, M_{age} : 72.81 (6.18) CON: 32, M_{age} : 71.38 (4.92)	LRN therapy (TRT); waitlist (CON)	TRT > CON in INH, VerbEpM, ATT, & PS
Reis et al. (2016)	Article	Portugal	LAB	8DY	Overall: 34, 16 M, M_{age} : 65.97 (6.63) NF: 9 NFCT: 8 CT: 7 Sham-NF: 6	NF	NF led to \uparrow alpha & theta relative power & spatial reasoning with \uparrow frontal theta associated with \uparrow alpha & \uparrow spatial reasoning; CT led to moderate \uparrow performance on trained tasks only
Zimmermann et al. (2016)	Article	Switzerland	LAB, HOME	3WK	TRT: 36, 14 M, M_{age} : 66.75 (4.17) CON: 31, 12 M, M_{age} : 68.23 (3.84)	MEM training (TRT); visual perception of same materials (CON)	TRT > CON in spatial EpM & reasoning for 4MTH
Adnan et al. (2017)	Article	USA	LAB	5WK	TRT: 11, 3 M, M_{age} : 65.90 (5.20) CON: 13, 6 M, M_{age} : 69.36 (5.20)	Goal-oriented attentional regulation training (TRT); brain health education program (CON)	TRT led to \uparrow R frontal, parietal, & temporal region activity, associated with \uparrow MEM

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Table 4 (continued)

Study	Source	Location	Setting	Length	Sample(s)	Intervention	Main Findings
Banducci et al. (2017)	Article	USA	LAB	4WK	Overall: 179, 68 M, M_{age} : 69.46 (6.59) TRT: 93 CON: 86	Active experiencing class (TRT); acting class (CON)	TRT > CON in EpM, effects lasted > 4 MTH
Bapka et al. (2017)	Article	Greece	LAB	6WK	VG: 9, 4 M, M_{age} : 71.33 (4.60) VR: 10, 6 M, M_{age} : 70.30 (5.03)	VR	VG & VR \uparrow EF but impact lasted longer with VR
Branscheidt et al. (2017)	Article	Germany	LAB	6–9WK	18, 6 M, M_{age} : 70.60 (5.70)	tDCS	No effect of atDCS; ctDCS impaired LRN of action words
Fujiyama et al. (2017)	Article	Belgium	LAB	2DY	YA (ctDCS-atDCS): 15, 6 M, M_{age} : 25.30 (2.70) OA (ctDCS-atDCS): 15, 7 M, M_{age} : 68.00 (3.20) YA (stDCS-atDCS): 15, 8 M, M_{age} : 25.50 (3.30) OA (stDCS-atDCS): 15, 8 M, M_{age} : 68.00 (5.70)	tDCS	ctDCS before atDCS during training led to \uparrow motor skill improvement & corticospinal excitability vs. YA & OA in stDCS-atDCS group
Hong (2017)	Thesis	Canada	LAB	14DY	9, 5 M, M_{age} : 66.78 (2.91)	Digital MEM augmentation device	Device led to \uparrow autobiographical EpM (effect \uparrow with \downarrow MoCA) & \uparrow immediate MEM recall; no effect on non-autobiographical EpM
Lussier et al. (2017)	Article	Canada	LAB	13–14WK	Heterogeneous training: 14, 2 M, M_{age} : 73.50 (6.54) Homogeneous training: 13, 5 M, M_{age} : 73.92 (6.23) CON: 31, 9 M, M_{age} : 70.42 (6.15)	Dual-task trainings; computer lessons (CON)	TRTs > CON in near-modality transfer; heterogeneous TRT led to \uparrow improvement of dual-task LRN
Müller et al. (2017)	Article	Germany	LAB, F2F	18MTH	Dancing: 12, 6 M, M_{age} : 68.25 (3.91) CON: 10, 6 M, M_{age} : 68.60 (2.79)	Dance; sport (CON)	Dance > CON in GMV in L precentral gyrus & BDNF after 6MTH; both groups showed \uparrow ATT after 6MTH & \uparrow VerbM after 18MTH; Dance led to \uparrow parahippocampal volume after 18MTH
Ordnung et al. (2017)	Article	Germany	LAB	6WK	TRT: 14, 7 M, M_{age} : 69.79 (6.34) CON: 15, 7 M, M_{age} : 68.33 (4.67)	Exergame (TRT); no training (CON)	TRT led to \uparrow game performance but no effect on cognition
Payne and Stine-Morrow (2017)	Article	USA	LAB, HOME	3WK	TRT: 22, 6 M, M_{age} : 67.68 (2.77) CON: 18, 4 M, M_{age} : 68.11 (6.24)	iPad WM training; TRT without recall (CON)	TRT led to \uparrow VerbWM on trained & novel tasks & \uparrow sentence MEM, verbal fluency & comprehension of syntactically ambiguous sentences
Pettersen (2017)	Article	Canada	LAB	18WK	High Dose: 42, 13 M, M_{age} : 56.70 (11.70) Low Dose: 40, 14 M, M_{age} : 52.60 (13.40)	Vitamin D	Only High Dose led to \uparrow VisM & LRN; \uparrow VisM effect \uparrow in those with \downarrow serum vitamin D
Ramos et al. (2017)	Article	Spain	LAB, F2F	8MTH	TRT: 26, 14 M, M_{age} : 67.42, 60–80 CON: 17, 8 M, M_{age} : 69.18, 70–78	LANG LRN (TRT); no training (CON)	No effect of TRT
Souders et al. (2017)	Article	USA	LAB, HOME	1MTH	TRT: 30, 13 M, M_{age} : 72.27 (4.88) CON: 30, 13 M, M_{age} : 72.43 (5.58)	Gamified CT (TRT); puzzle games (CON)	No effect of TRT
Tao et al. (2017)	Article	China	LAB	12WK	Tai chi Exercise: 21, 8 M, M_{age} : 62.38 (4.55) Baduanjin Exercise: 15, 6 M, M_{age} : 62.33 (3.88) CON: 25, 6 M, M_{age} : 59.76 (4.83)	Tai chi, baduanjin; basic health education (CON)	TRTs > CON in MEM; Tai chi led to \uparrow fALFF in dlPFC in slow–5 & low-frequency bands; Baduanjin led to \uparrow fALFF in mPFC slow–5 & low-frequency bands; \uparrow fALFF associated with \uparrow MEM
Vaportzis et al. (2017)	Article	UK	LAB	10WK	TRT: 22, 6 M, M_{age} : 68.40 (3.50) CON: 21, 8 M, M_{age} : 69.80 (3.00)	Digital tablet training (TRT); no contact (CON)	TRT > CON in PS

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Table 4 (continued)

Study	Source	Location	Setting	Length	Sample(s)	Intervention	Main Findings
Bapka et al. (2018)	Conference Paper	Greece	LAB	6WK	VR: 10, 6 M, M_{age} : 70.30 (5.03) VG: 9, 4 M, M_{age} : 71.33 (4.60)	VR	TRTs led to \uparrow EF but effect of VG lasted longer & \uparrow positive affect
Dumel et al. (2018a)	Article	Canada	LAB	3MTH	TRT: 18, 9 M, M_{age} : 61.56 (5.85) stDCS: 19, 9 M, M_{age} : 61.26 (6.82)	tDCS	atDCS led to \uparrow trained motor skill; no transfer or effect on M1-disinhibition
Dumel et al. (2018b)	Article	Canada	LAB	9DY	TRT: 16, 8 M, M_{age} : 62.31 (5.70) stDCS: 16, 7 M, M_{age} : 62.63 (6.51)	tDCS	atDCS > CON in motor LRN & disinhibition of long-interval cortical inhibition; \uparrow generalization associated with \uparrow long-interval cortical inhibition
DuPont (2018)	Thesis	USA	LAB, F2F	6WK	8, M_{age} : 59.00 (4.80)	Resistance training	TRT led to \uparrow PS, ATT, LRN, STM, WM, VSM, planning, & \uparrow beta & gamma band task function
Haeger et al. (2018)	Article	Germany	LAB	4WK	TRT: 16, 8 M, M_{age} : 70.25 (3.77) CON: 21, 9 M, M_{age} : 72.38 (4.17)	Driving simulator (TRT); no training (CON)	TRT led to \uparrow divided VisATT
Huhn et al. (2018)	Article	Germany	LAB	26WK	TRT: 27, 13 M, M_{age} : 68.60 (4.92) CON: 26, 12 M, M_{age} : 67.54 (5.07)	Resveratrol (TRT); placebo (CON)	No effect of TRT
Kalbe et al. (2018)	Article	Germany	LAB, HOME	1YR	CT: 17, 7 M, M_{age} : 67.53 (5.88) CPT: 18, 7 M, M_{age} : 68.22 (7.96) CPT+C: 20, 5 M, M_{age} : 68.75 (6.62)	Multi-domain CT; CT with physical activity (CPT); CPT with physical activity counseling (CPT+C)	All TRTs led to improvements, but CPT > CPT+C in gCOG & VerblTM; bigger gains with \downarrow baseline performance, EDU, or BDNF levels & \uparrow IGF-1
Lee et al. (2018)	Article	Taiwan	LAB	8WK	TRT: 23, 7 M, M_{age} : 65.40 (6.00) CON: 19, 1 M, M_{age} : 64.50 (4.90)	PE, word games, & CT (memorization strategies; TRT); PE, word games, & health education (CON)	TRT led to \uparrow list LRN & MEM; TRT > CON in LRN
Lindbergh et al. (2018)	Article	USA	LAB, HOME	1YR	TRT: 30, 14 M, M_{age} : 72.43 (6.48) CON: 14, 4 M, M_{age} : 70.43 (5.43)	Lutein & zeaxanthin (TRT); placebo (CON)	TRT led to \downarrow decline in Verbl & \uparrow BOLD in L dlPFC & anterior cingulate cortex
Ludyga et al. (2018)	Article	Switzerland	LAB	1WK	51, 21 M, M_{age} : 21.80 (1.30)	Moderately intense running (TRT); reading (CON)	TRT > CON in INH & MEM
Pan et al. (2018)	Review Article	USA	NA	NA	Studies: 11	Tai chi	Tai chi led to \uparrow CTH, function connectivity, brain homogeneity, & executive network function
Perry-Deegan (2018)	Thesis	USA	F2F	6WK	Piano: 9 Piano (No pretest): 8 CON: 9	Piano training (TRT); no training (CON)	No effect of TRT
Pfenninger and Polz (2018)	Article	Austria	LAB	4WK	TRT/BL: 6, M_{age} : 84.33 (5.46) CON/ML: 6, M_{age} : 70.80 (7.46)	LANG LRN in BL (TRT); LANG LRN in ML (CON)	TRT led to \uparrow linguistic EF, self-confidence, autonomy, communicative skills, & wellbeing
Rehfeld et al. (2018)	Article	Germany	LAB	6MTH	Dance: 20, 8 M, M_{age} : 68.16 (4.31) Sports: 18, 10 M, M_{age} : 68.72 (2.68)	Dance	Dance > Sports in cingulate, insula, corpus callosum, & SM cortex volume & BDNF levels; both groups had \uparrow ATT & SpatM
Rosi et al. (2018)	Article	Italy	LAB	6WK	44, M_{age} : 68.73 (6.05)	MEM training	TRT led to \uparrow MEM in trained & untrained tasks; \uparrow baseline MEM & cognition associated with \uparrow gains
Shake et al. (2018)	Article	USA	LAB, F2F	10WK	TRT: 60, 9 M, M_{age} : 73.59 (7.89) CON: 45, 6 M, M_{age} : 73.22 (7.79)	Bingocize (PE & health education; TRT); health education (CON)	TRT > CON in WM
Tomporowski and Pendleton (2018)	Article	USA	LAB	S1 & S2: 1WK	S1: 32, 8 M, M_{age} : 22.90 (2.90) S2: 31, 13 M, M_{age} : 22.40 (3.00)	S1: simple stepping (two-step dance sequence which involved side-to-side alternation of foot positions), complex stepping (four-step dance sequence that alternated target positions in unpredictable sequences) after pursuit-rotor task training S2: Same as S1 but before training	TRTs before or after training led to \uparrow PM LRN when measured 24HR & 7DY after
Abellana-Pérez et al. (2019)	Article	Spain	LAB	3YR (OA)	YA: 24, 5 M, M_{age} : 23.42 (1.60) OA: 27, 5 M, M_{age} : 68.15 (4.60)	iTBS	iTBS led to \uparrow FC in distal DMN in YA & proximal DMN in OA; OA with response to iTBS like YA had \uparrow brain integrity & cognitive performance at baseline & 3YR

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Table 4 (continued)

Study	Source	Location	Setting	Length	Sample(s)	Intervention	Main Findings
Aguirre-Loaiza et al. (2019)	Article	Colombia	LAB	NA	OA (3YR after): 14, M _{age} : 71.21 (4.70) S1 (TRT): 25, M _{age} : 20.70 (2.50) S1 (CON): 29 S2 (TRT): 10, M _{age} : 21.60 (1.80) S2 (CON): 26	S1: Indoor cycling in physically active YA (TRT); no cycling (CON) S2: Indoor cycling in physically inactive YA (TRT); no cycling (CON)	later, & ↓decline; ↑EDU associated with YA-like response in OA TRT led to ↑INH in S1 & S2; TRT & CON had ↑PS & CF; CON had ↑verbal fluency; TRT ↓emotional recognition errors in Active & ↑body emotion recognition in Inactive YA
Alain et al. (2019)	Article	Canada	LAB	3 MTH	Music: 17, 3 M, M _{age} : 67.70 (5.80) Visual Art: 19, 2 M, M _{age} : 68.90 (6.00) CON: 17, 3 M, M _{age} : 68.50 (6.00)	Music & visual art training programs; no training (CON)	No effect of TRT on cognitive function; TRTs led to ↑auditory evoked responses to piano tones for 3MTH & ↑visually evoked responses: Visual Art led to ↑N1 (vs. CON & Music) & Music led to ↑frontal INH activity (vs. Visual Art)
Antonenko et al. (2019)	Article	Germany	LAB	1WK	34, 18 M, M _{age} : 63.10 (7.70)	tDCS	atDCS led to ↑MEM & LRN
Belchior et al. (2019)	Article	USA	LAB, HOME	3MTH	Overall: 54, 20 M, M _{age} : 73.20 (5.50) TRT: 17 A-CON: 19 P-CON: 18	VG; Brain fitness program (A-CON); no training (P-CON)	TRT led to ↑ATT & mood 3MTH after; A-CON led to ↑ATT & PS lasting 3MTH; no effects on VS skills or MEM
Berggren (2019)	Thesis	Sweden	LAB	11WK	S2 (Overall): 160, 65–75 S2 (LANG LRN): 90 S2 (Relaxation): 70	LANG LRN	No effect of TRT
Bugos (2019)	Article	USA	LAB	16WK	Fine Motor: 49, 14 M, M _{age} : 67.90 (6.42) Gross Motor: 38, 12 M, M _{age} : 69.13 (7.27) CON: 48, 12 M, M _{age} : 68.83 (7.38)	Piano training (fine motor), percussion training (gross motor); music listening (CON)	Fine & Gross Motor TRT led to ↑bimanual synchronization, PS, & CF vs. CON; Fine Motor TRT led to ↑motor synchronization vs. other groups
Carbonell-Hernández et al. (2019)	Article	Multiple	F2F	2MTH	TRT: 44, M _{age} : 67.60 (5.60) CON: 10, M _{age} : 66.20 (5.40)	Combined dance, athletics, functional exercise, Nordic walking (TRT); cognitive games (CON)	TRT led to ↑INH; no effect on LRN or MEM
Chae et al. (2019)	Article	Germany	LAB	NA	Yohimbine + Placebo: 26, 26 M, M _{age} : 23.19 (3.29) Hydrocortisone + Placebo: 26, 26 M, M _{age} : 24.54 (4.04) Yohimbine + Hydrocortisone: 26, 26 M, M _{age} : 23.81 (3.36)	Yohimbine, hydrocortisone, or combination	No effect of TRT
Cole and Shields (2019)	Article	USA	LAB	1WK	YA: 40, 20–39 OA: 24, 60–80	Cognitive load	Cognitive load led to ↑LRN time in YA & OA but ↓dual-task effect in YA; effects modulated by EF
Fertonani et al. (2019)	Article	Italy	LAB	NA	YA (Overall): 45, 23 M, M _{age} : 22.30 (3.10) OA (Overall): 36, 15 M, M _{age} : 66.10 (3.60) YA (Sham): 15, 7 M, M _{age} : 22.60 (3.20) OA (Sham): 12, 5 M, M _{age} : 66.00 (2.70) YA (tRNS): 15, 8 M, M _{age} : 21.70 (3.20) OA (tRNS): 12, 5 M, M _{age} : 65.80 (4.10) YA (atDCS): 15, 8 M, M _{age} : 22.30 (3.20) OA (atDCS): 12, 5 M, M _{age} : 66.30 (4.10)	tRNS	tRNS led to ↓visual perceptual LRN in YA
Grégoire et al. (2019)	Article	Canada	LAB	8WK	LBS-A: 13, 5 M, M _{age} : 70.45 (4.44) UBS-A: 11, 7 M, M _{age} : 70.62 (6.35)	PE	All TRTs led to ↑cognitive function, but GMA led to ↑plasma BDNF vs. LBS-A; no association between BDNF & cognition

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Table 4 (continued)

Study	Source	Location	Setting	Length	Sample(s)	Intervention	Main Findings
Hering et al. (2019)	Article	Switzerland	LAB	NA	GMA: 10, 3 M, M_{age} : 74.59 (5.18) S1 (TRT): 20, 3 M, M_{age} : 80.00 (3.62) S1 (CON): 19, 3 M, M_{age} : 79.90 (3.57) S2 (TRT): 19, 3 M, M_{age} : 79.00 (5.29) S2 (CON): 20, 5 M, M_{age} : 78.50 (4.59) 30, 18 M, 20–25	Rehearsal instruction	S1: No effect of TRT; S2: TRT > CON in WM
Ke et al. (2019)	Article	China	LAB	5DY		HD-tDCS	HD-tDCS with training led to ↑WM vs. stDCS & transferred to novel WM task
Ljubisavljevic et al. (2019)	Article	UAE	LAB	NA	22, 16 M, M_{age} : 62.60 (3.20)	tDCS: unilateral anode L, unilateral anode R, bilateral anode L, bilateral anode R	Only bilateral anode L tDCS of dlPFC led to ↓dual task cost of manual task during ATT task; anode on the R TRT led to same effect but 30 min after stimulation
Nespollo et al. (2019)	Article	Brazil	LAB	2MTH	TRT: 10, 0 M, M_{age} : 63.70 (3.40) CON: 6, 0 M, M_{age} : 68.33 (6.80)	Taigeiko & cognitive stimulation (TRT); Taigeiko only (CON)	Both TRTs led to ↑LRN & INH
Nouchi et al. (2019)	Article	Japan	LAB, HOME	6WK	CTCD: 27, M_{age} : 71.67 (3.62) ACT: 28, M_{age} : 73.11 (3.90)	CT game for car driving (CTCD); Active control CT game (ACT)	CTCD > ACT in INH & PS
Opie et al. (2019)	Article	Australia	LAB	~3WK	YA: 14, 7 M, M_{age} : 20.40 (2.10) OA: 13, 7 M, M_{age} : 69.00 (5.60)	PAS long term potentiation; PAS long term depression	Both PAS TRTs led to ↓motor LRN in OA
Patan (2019)	Thesis	UK	LAB	26WK	CH3 DHA-rich: 26, 9 M, M_{age} : 35.08 (1.72) CH3 EPA-rich: 26, 15 M, M_{age} : 32.92 (1.31) CH3 CON: 26, 14 M, M_{age} : 33.85 (1.57) CH5 DHA-rich: 57, 11 M, M_{age} : 33.71 (1.05) CH5 EPA-rich: 56, 11 M, M_{age} : 36.20 (1.40) CH5 CON: 56, 16 M, M_{age} : 37.15 (0.87) CH6 DHA-rich: 113, 29 M, M_{age} : 34.95 (0.76) CH6 EPA-rich: 112, 36 M, M_{age} : 35.33 (0.07) CH6 CON: 112, 28 M, M_{age} : 36.15 (0.69)	All studies: DHA or EPA-rich supplements; placebo (CON)	CH3: No effect of TRT CH5: DHA-rich > CON in errors but had ↓word recognition speed CH6: EPA-rich > DHA-rich & CON in global accuracy & ↑global speed & word recognition vs. CON; EPA-rich > DHA-rich in MEM; EPA-rich TRT ↑gCOG, EF, & EpM
Sala et al. (2019)	Review Article	Japan	NA	NA	Studies: 43	WM training	TRT consistently led to ↑WM task performance, but modest to near-zero effects on near & far transfer
Sosa and Lagana (2019)	Article	USA	LAB	5WK	TRT: 20, 4 M, M_{age} : 74.95 (6.53) CON: 15, 5 M, M_{age} : 74.40 (5.62)	VG (TRT); no VG (CON)	TRT > CON in PS & ATT
Wong et al. (2019)	Article	Hong Kong	LAB, F2F	6MTH	LANG LRN: 53, 10 M, M_{age} : 70.81 (5.97) Games: 51, 7 M, M_{age} : 71.06 (6.45) Music Appreciation: 49, 6 M, M_{age} : 71.06 (6.12)	LANG LRN	LANG LRN & Games led to ↑cognitive abilities lasting 3MTH; No effect of Music
Berggren et al. (2020)	Article	Sweden	LAB	11WK	LANG LRN: 90, 38 M, M_{age} : 69.20 (2.70) Relaxation Training: 70, 22 M, M_{age} : 69.50 (2.80)	LANG LRN	No effect of TRT

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Table 4 (continued)

Study	Source	Location	Setting	Length	Sample(s)	Intervention	Main Findings
Čekanauskaitė et al. (2020)	Article	Lithuania	LAB	10WK	Overall: 33, 3 M, M _{age} : 66.90 (6.00) Yoga: 18, 1 M CON: 15, 2 M	Yoga; no yoga (CON)	Yoga > CON in motor LRN; no change in cognition; †motor LRN associated with †BDNF
Delhom et al. (2020)	Article	Spain	LAB	10WK	TRT: 57, 30 M, M _{age} : 67.89 (6.75) CON: 68, 38 M, M _{age} : 67.38 (6.50)	Emotional intelligence intervention program (TRT); waitlist (CON)	TRT led to †ATT to emotions, †clarity, repair, resilience, & life satisfaction
Ferreira (2020)	Thesis	Portugal	LAB	33WK	TRT: 11, 5 M, M _{age} : 68.82 (3.95) CON: 9, 2 M, M _{age} : 66.88 (1.81)	Combined aerobic, strength, stretching & balance exercise (TRT); TRT once a week with less intensity (CON)	TRT & CON had †semantic fluency; TRT < CON in WM
Formica et al. (2020)	Article	Australia	LAB, HOME	24WK	PE & Meat: 77, 29 M, M _{age} : 71.20 (4.00) PE & Carbs: 77, 29 M, M _{age} : 70.30 (4.30)	PE & food	PE + Carbs > PE + Meat group in WM & LRN
Gajewski et al. (2020)	Article	Germany	LAB	16WK	TRT: 32, 12 M, M _{age} : 71.00 (4.20) A-CON: 33, 13 M, M _{age} : 71.00 (4.50) P-CON: 37, 14 M, M _{age} : 70.00 (4.20)	Multidomain CT (TRT); relaxation training (A-CON); no contact (P-CON)	TRT > P-CON in ATT & INH, similar effect vs. A-CON; no transfer observed
Habich et al. (2020)	Article	Switzerland	LAB, HOME	~3WK	YA: 33, 13 M, M _{age} : 24.50 (2.60) OA: 22, 11 M, M _{age} : 67.30 (4.40)	tDCS	No effect of atDCS
Isotalus (2020)	Thesis	UK	LAB	S1: ~5WK S2: 2 X 5DY	S1 (Encoding): 32, 16 M, M _{age} : 71.10 (7.10) S1 (Retrieval): 28, 14 M, M _{age} : 70.90 (6.90) S2: 35, 13 M, M _{age} : 68.90 (3.50)	L-DOPA	L-DOPA at encoding, retrieval, or before LRN did not alter MEM; L-DOPA after LRN but before sleep †MEM after 24 H but effect was gone by 3DY
Jaeggi et al. (2020)	Article	USA	LAB	3MTH	WM Training: 78, 23 M, M _{age} : 72.33 (5.51) Knowledge Training: 77, 17 M, M _{age} : 73.39 (5.33) Studies: 7	WM training	No effect of TRT on WM; some within-domain transfer in WM & INH that lasted 3MTH
Klimova and Pikhart (2020)	Review Article	Czech Republic	NA	NA	Studies: 7	LANG LRN	TRT led to †cognitive abilities, possibly through †social wellbeing
Kolarik et al. (2020)	Article	USA	LAB	4WK	TRT: 25, 5 M, M _{age} : 69.80 (4.10) CON: 23, 5 M, M _{age} : 71.40 (8.40)	Real world exploration (TRT); no contact (CON)	TRT > CON in MEM
Lenze et al. (2020)	Article	USA	LAB, OL, HOME	26WK	Vortioxetine + CT (TRT): 51, 23 M, M _{age} : 71.68 (4.77) Placebo + CT (CON): 49, 26 M, M _{age} : 71.88 (5.30)	CT + vortioxetine	TRT > CON in gCOG at 12WK; both groups improved functional cognition
MacRitchie et al. (2020)	Article	Australia	LAB, F2F	10WK	Overall: 17, 4 M, M _{age} : 70.90 (5.50) TRT: 9 CON: 8	Piano training (TRT); waitlist (CON)	TRT led to †PS but †CF
Nilsson et al. (2020)	Article	Sweden	LAB	12WKS	CT: 21, 9 M, M _{age} : 70.95 (3.04) PE: 27, 12 M, M _{age} : 70.30 (3.00) CT+PE: 24, 13 M, M _{age} : 70.29 (3.11) PE+CT: 25, 12 M, M _{age} : 70.28 (2.70)	PE, CT, or combination	No differences between TRTs, but all led to †WM, EpM, & spatial reasoning
Opie et al. (2020)	Article	Australia	LAB	10DY	PAS LTD: 15, 9 M, M _{age} : 67.90 (5.30) CON: 15, 7 M, M _{age} : 68.50 (5.60)	PAS LTD; PAS non-LTD (CON)	TRT > CON in motor LRN 7DY after training
Roig-Coll et al. (2020)	Article	Spain	LAB, HOME	12WK	AE: 25, 12 M, M _{age} : 58.40 (5.12) CCT: 23, 7 M, M _{age} : 57.91 (5.31) AE+CCT: 19, 5 M,	AE, computerized CT (CCT), or both; waitlist (CON)	AE > CON in WM & ATT; AE+CCT > CON in ATT & PS; CCT = CON

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Table 4 (continued)

Study	Source	Location	Setting	Length	Sample(s)	Intervention	Main Findings
Suominen et al. (2020)	Article	Finland	LAB	8WK	M _{age} : 60.32 (5.54) CON: 15, 7 M, M _{age} : 56.60 (5.97) TRT: 50, 19 M, M _{age} : 69.00 (2.00) CON: 50, 20 M, M _{age} : 68.00 (3.00)	Dark chocolate with 410 mg flavanols (TRT); dark chocolate with 86 mg flavanols (CON)	No effect of TRT
Takeuchi et al. (2020)	Article	Japan	LAB	3MTH	WMT: 30, 11 M, M _{age} : 68.77 (2.94) AE: 22, 12 M, M _{age} : 69.30 (3.37) AE+WMT: 30, 12 M, M _{age} : 68.03 (3.27)	AE, WM training (WMT), or both	Combined TRT led to ↑EF & brain activity in ATT reorientation areas during WM task, & ↓dopamine system MD, but did not affect LRN vs. WMT
Whitmoyer et al. (2020)	Article	USA	LAB	4WK	MBAT: 37, 15 M, M _{age} : 65.92 (3.85) Lifestyle Education: 37, 16 M, M _{age} : 66.89 (4.09)	Mindfulness-based ATT training (MBAT)	No effect of TRT
Abraham et al. (2021)	Article	Argentina	LAB	2WK	S1 (Mu/MI): 10, 1 M, M _{age} : 65.40 (0.65) S1 (NMu/MI): 13, 0 M, M _{age} : 69.38 (1.73) S1: (Mu/RI): 10, 5 M, M _{age} : 70.60 (3.42) S1 (NMu/RI): 19, 2 M, M _{age} : 73.21 (1.51) S1: (Mu/CON): 12, 7 M, M _{age} : 71.25 (2.93) S1 (NMu/CON): 14, 2 M, M _{age} : 69.64 (1.13) S2 (Mu/MI): 13, 1 M, M _{age} : 68.38 (1.51) S2 (NMu/MI): 16, 2 M, M _{age} : 73.25 (1.96) S2 (Mu/RI): 10, 6 M, M _{age} : 69.60 (2.93) S2 (NMu/RI): 21, 2 M, M _{age} : 72.52 (1.78) S2 (Mu/CON): 10, 1 M, M _{age} : 68.90 (3.35) S2 (NMu/CON): 16, 4 M, M _{age} : 76.06 (1.82)	All studies: Music improvisation (MI); rhythmic imitation (RI); rest condition (CON); in musicians (Mu) or non-musicians (NMu)	MI > CON in VerbM, effect ↑in musicians
Dobrowolski et al. (2021)	Article	Poland	LAB	NA	YA: 60, M _{age} : 23.95 (2.71) OA: 58, M _{age} : 59.05 (5.82)	Immersive VR; manual & training video (CON)	TRT > CON in task performance for YA & OA
Etnier et al. (2021)	Article	USA	LAB, HOME	6DY	21, 8 M, M _{age} : 64.71 (5.68)	Stationary recumbent cycle	Exercise prior TRT > Other TRTs in STM, LTM, & LRN; Exercise post TRT > CON
Gómez and Rodríguez (2021)	Article	Spain	LAB, F2F	4YR	TRT: 137, 22 M, M _{age} : 73.89 (6.38) CON: 130, 22 M, M _{age} : 72.99 (6.51)	Everyday cognition training (TRT); conventional CT (CON)	TRT > CON in cognitive function
Hong et al. (2021)	Article	China	LAB	3MTH	TRT: 23, 15 M, M _{age} : 72.80 (1.90) CON: 16, 10 M, M _{age} : 73.20 (1.20) Studies: 31	Multidomain CT (TRT); no training (CON)	TRT > CON in WM & P3 amplitude
Lee et al. (2021)	Review Article	Korea	NA	NA		tDCS	Only online tDCS led to ↑EF, LRN, MEM with ↑age associated with ↑impact
Nilsson et al. (2021)	Article	Sweden	LAB	11WK	LANG (All): 90, 38 M, M _{age} : 69.24 (2.70) LANG (MR): 40,	LANG LRN	No effect of TRT

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Table 4 (continued)

Study	Source	Location	Setting	Length	Sample(s)	Intervention	Main Findings
Puri et al. (2021)	Article	Australia	LAB	1WK	17 M, M _{age} : 69.35 (2.68) Relaxation (All): 70, 22 M, M _{age} : 69.49 (2.85) Relaxation (MR): 35, 12 M, M _{age} : 69.89 (2.94) Before: 16, 5 M, M _{age} : 65.60 (3.20) During: 16, 10 M, M _{age} : 64.40 (3.90) After: 16, 7 M, M _{age} : 66.90 (6.00)	tDCS	No immediate effect of atDCS; atDCS during training led to ↓motor LRN at 24HR
Roheger et al. (2021)	Review Article	Germany	NA	NA	Studies: 12	MEM training	↓age & ↑EDU associated with ↑MEM improvement
Rutledge et al. (2021)	Article	USA	LAB	90DY	TRT: 19, 5 M, M _{age} : 67.80 (4.60) CON: 19, 7 M, M _{age} : 67.30 (4.80)	Freeze-dried blueberry powder (TRT); blueberry flavored drink (CON)	↑phenolic compounds after TRT associated with ↑CF & LRN
Santos et al. (2020)	Article	Brazil	LAB	8WK	TRT: 15, 5 M, M _{age} : 68.40 (5.98) CON: 13, 1 M, M _{age} : 67.31 (5.79)	Musical improvisation training (TRT); choir training (CON)	TRT > CON in EF; TRT & CON both led to ↑PS
Satler et al. (2021)	Article	Brazil	LAB	9WK	Group A: 13, 5 M, M _{age} : 67.69 (1.06) Group B: 14, 3 M, M _{age} : 70.64 (1.33)	INH training; groups differed by test form to control for LRN	TRT led to ↑INH
Sloan et al. (2021)	Article	USA	LAB	20WK	TRT (Low): 53, 23 M, M _{age} : 61.88 (6.10) TRT (Middle): 53, 23 M, M _{age} : 61.65 (6.69) TRT (High): 53, 23 M, M _{age} : 62.07 (6.41) CON: 53, 22 M, M _{age} : 62.35 (6.70) Studies: 20	Flavanol dose (TRT); placebo (CON)	TRT led to ↑hippocampal-dependent LRN with biggest ↑in those with ↓ healthy eating habits; suggested that flavanols target dentate gyrus
Viviani and Vallesi (2021)	Review Article	Italy	NA	NA	Studies: 20	NF for EF	TRT led to ↑EF
Whyte et al. (2021)	Article	USA	LAB	7DY	35, 12 M, M _{age} : 51.00 (8.00)	Wild blueberry beverage	TRT led to ↑Verbl & EF
Wu et al. (2021)	Article	Taiwan	SEC	12WK	TRT: 19, 4 M, M _{age} : 63.60 (4.00) CON: 19, 1 M, M _{age} : 63.20 (4.40)	Tai chi (TRT); no training (CON)	TRT led to ↑CF with ↑prefronto-striato-thalamo-prefrontal loop fiber integrity associated with ↑effect
Yang et al. (2021)	Article	USA	LAB, F2F	1MTH	25, 4 M, M _{age} : 72.40 (6.45)	Outdoor mindful walking	TRT led to immediate ↑PS; ↑PS & EF after 1MTH
Zuber et al. (2021)	Article	Switzerland	LAB, HOME	18WKS	MB: 32, 11 M, M _{age} : 64.50 (8.80) MB+: 29, 12 M, M _{age} : 64.30 (8.40) CON: 29, 8 M, M _{age} : 63.50 (8.10) Dual n-back training: 33, 14 M, M _{age} : 64.00 (8.20)	Model-based WM training (MB) with distractor inhibition (MB+); CT (CON)	MB+ > MB in WM; MB+ led to ↑WM & VS LRN; MB led to ↑PS & WM; Dual n-back led to ↑WM
Au et al. (2022)	Article	USA	LAB	1–2WK	Overall: 55, 15 M, M _{age} : 71.32, 65–85 Active tDCS (Daily): 12 Active tDCS (Alternate Day): 12 Sham (Daily): 13 Sham (Alternate Day): 15	tDCS	TRT led to ↑LTM but mixed for WM, only emerged in those with lower baseline WM
Baklouti et al. (2022)	Article	Tunisia	LAB, F2F	2YR	TRT: 15, 15 M, M _{age} : 64.00 (3.02) CON: 15, 15 M, M _{age} : 66.00 (5.11)	Yoga (TRT); no training (CON)	TRT led to ↑EF but no effect on EpM & ATT
Bidelman et al. (2022)	Article	Canada	LAB	NA	14, 3 M, M _{age} : 72.60 (5.03)	tDCS + Music/ tDCS	tDCS+Music > tDCS in WM & modulated early cortical encoding of speech (↑ERP)

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Table 4 (continued)

Study	Source	Location	Setting	Length	Sample(s)	Intervention	Main Findings
Bugos and Wang (2022)	Article	USA	LAB, F2F	16WK	Piano: 30, 10 M, M_{age} : 67.20 (4.09) Computer CT: 35, 13 M, M_{age} : 69.29 (5.57) CON 50, 15 M, M_{age} : 67.64 (6.28)	Piano training; computer-assisted CT; no training (CON)	Piano & Computer > CON in WM & PS; Piano > Computer & CON in verbal fluency
Cogan et al. (2022)	Article	USA	LAB, F2F	4WK	TRT: 21, 7 M, M_{age} : 59.00 (1.00) CON: 20, 6 M, M_{age} : 59.00 (1.00)	Pecans (TRT); avoid nuts (CON)	No effect of TRT
Dever et al. (2022)	Conference Paper	USA	LAB	2DY	Overall: 105, 48 M, M_{age} : 20.50 (3.31) Prompt & Feedback: 58 CON: 47	Intelligent tutor prompt & feedback (TRT); no prompt or feedback (CON)	TRT led to \uparrow LRN & \uparrow use of self-regulated LRN strategies
Draaisma et al. (2022)	Article	Switzerland	LAB	NA	21, 10 M, M_{age} : 69.60 (4.40) Overall: 230, 97 M, M_{age} : 71.35 (5.33) Brain Training: 45 VG Training: 38 Directed IADL Training: 42 Puzzle Training (Control): 47	tACS	tACS led to \uparrow WM & \uparrow LRN during \uparrow but not \downarrow WM load No effect of TRTs
Gray et al. (2022)	Article	USA	LAB, F2F	4WK T2: 1YR	30, 13 M, M_{age} : 67.33 (3.57)	Brain training; VG; or directed instrumental activities of daily living training (IADL)	
Johnson et al. (2022)	Article	USA	LAB	4DY	TRT: 59, 27 M, M_{age} : 69.49 (3.22) CON: 62, 25 M, M_{age} : 69.42 (3.79)	tDCS	TRT led to \uparrow WM, theta network synchrony, & theta-gamma phase-amplitude coupling in OA with \uparrow EDU TRT prevented age-related \downarrow in fornix fiber density, with \uparrow density associated with \uparrow EpM
Jünemann et al. (2022)	Article	Germany & Switzerland	LAB, F2F	6MTH	TRT: 23, 20–50 CON: 19, 20–50 TRT: 28, 14 M, M_{age} : 68.50 (2.83) A-CON: 17, 10 M, M_{age} : 67.80 (2.86) P-CON: 16, 11 M, M_{age} : 68.90 (3.19)	Fermented laminaria japonica (TRT); Placebo (CON) LANG LRN (TRT); VG (A-CON); social component of class (P-CON)	TRT led to \uparrow BNDF, HGH, IGF-1, gCOG, LRN, & SpatM No effect of TRT
Kim et al. (2022)	Article	Korea	LAB, HOME	6WK	S2 (Novice): 37, 18 M, M_{age} : 64.43 (3.93) S2 (Experienced): 45, 10 M, M_{age} : 64.38 (4.25)	Tai chi	TRT led to \uparrow INH in Novices only
Kliesch et al. (2022)	Article	Switzerland	LAB, F2F	30WK	1.5 oz almonds: 19, 10 M, M_{age} : 61.60 (6.30) 3 oz almonds: 24, 14 M, M_{age} : 60.40 (6.80) 3.5 oz snack mix: 17, 9 M, M_{age} : 63.00 (5.60)	Almonds	3 oz almonds led to \uparrow VSWM, VisM, VisL, spatial planning, & WM after 6MTH vs. Snack group
Lv et al. (2022)	Article	China	LAB, F2F	S2: 12MTH	MBAT: 37, 15 M, M_{age} : 65.92 (3.81) CON: 37, 16 M, M_{age} : 66.78 (4.12)	mindfulness-based ATT training (MBAT); lifestyle education (CON)	No effect of TRT on cognition; only OA with \uparrow baseline WM showed \downarrow in emotion dysregulation
Rakic et al. (2022)	Article	USA	LAB	6MTH	atDCS: 16, 8 M, M_{age} : 69.80 (3.40) stDCS: 15, 7 M, M_{age} : 70.13 (4.70)	tDCS; stDCS	atDCS > stDCS in WM & LRN
Samimy et al. (2022)	Article	USA	SEC	4WK	S1 (YA SRP): 30, 5 M, M_{age} : 23.10 (2.40) S1 (OA SRP): 30, 4 M, M_{age} : 68.90 (8.20) S1 (YA CON): 30, 9 M, M_{age} : 23.60 (1.70) S1 (OA CON): 30, 8 M, M_{age} : 69.00	Selective retrieval practice (SRP); no SRP (CON)	SRP \uparrow MEM in YA & OA

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Table 4 (continued)

Study	Source	Location	Setting	Length	Sample(s)	Intervention	Main Findings
					(6.70) S2 (YA SRP): 30, 12 M, M_{age} : 24.60 (3.60) S2 (OA SRP): 30, 9 M, M_{age} : 68.10 (6.00) S2 (YA CON): 30, 10 M, M_{age} : 24.00 (3.40) S2 (OA CON): 30, 12 M, M_{age} : 68.10 (6.00)		
Strickland-Hughes and West (2022)	Article	USA	LAB	3WK	SO: 46, 11 M, M_{age} : 71.51 (7.34) SB: 38, 7 M, M_{age} : 76.08 (8.83) CON: 38, 8 M, M_{age} : 72.51 (8.34)	Strategy training (SO); strategy training & self-regulatory boost (SB); waitlist (CON)	TRTs > CON in MEM, MEM self-efficacy, & effective strategy use; near-transfer to novel task
Vance (2022)	Thesis	USA	LAB	S2: 9DY	S1 YA: 28, 9 M, M_{age} : 23.29 (3.04) S1 OA: 26, 8 M, M_{age} : 66.15 (2.59) S2 YA: 17, 6 M, M_{age} : 24.10 (2.80) S2 OA: 16, 4 M, M_{age} : 66.60 (2.00)	Stationary recumbent cycle exercise while watching an educational video with closed captioning; Video only (CON)	Exercise led to \uparrow LTM & associative MEM in YA & OA
Worschech et al. (2022)	Article	Germany & Switzerland	F2F	6MTH	TRT: 67, 28 M, M_{age} : 69.54 (3.13) CON: 67, 28 M, M_{age} : 69.62 (3.90)	Piano training (TRT); music listening/culture (CON)	TRT > CON in L Heschl's gyrus, planum temporale, bilateral superior temporal sulcus, & R Heschl's sulcus CTh
Yang et al. (2022)	Article	Japan	LAB, HOME	4WK	TRT: 20, 12 M, M_{age} : 69.70 (4.20) CON: 20, 10 M, M_{age} : 70.30 (3.60)	Verbal articulation training (TRT); no training (CON)	TRT > CON in frontotemporal FC associated with LANG & MEM function
Zhang et al. (2022)	Article	USA	F2F, HOME	12MTH	300, 66 M, M_{age} : 76.15 (7.40)	Computer training	No effect of TRT
Alescio-Lautier et al. (2023)	Article	France	LAB	S2: 12WK	S2 TRT: 16, 6 M, M_{age} : 25.25 (1.61) S2 (CON): 15, 5 M, M_{age} : 28.42 (0.21) S3 TRT (from S2): 15, 6 M, M_{age} : 25.25 (1.61)	S2: Problem solving training (TRT); Crossword (CON) S3: Post training vs Pre	S2: Problem solving training led to \uparrow innovative thinking influenced by CF S3: Training led to \uparrow FC in AN & VN
Dever et al. (2023)	Article	USA	LAB	2DY	Overall: 117, 56 M, M_{age} : 24.40 (3.20) Prompt & Feedback: 59 CON: 58	Intelligent tutor prompt & feedback (TRT); no prompt or feedback (CON)	TRT led to \uparrow LRN & use of self-regulated LRN strategies
Eilat-Adar et al. (2023)	Review Article	Israel	NA	NA	Studies: 5	Yoga	TRT led to mixed outcomes in brain & cognition
Ferguson et al. (2023)	Article	USA	LAB, F2F	1YR	S1: 6, 2 M, M_{age} : 66.33 (6.41) S2: 27, 9 M, M_{age} : 66.44 (7.12)	S1: LANG LRN, iPad class, painting class, S2: LANG LRN, iPad class, drawing class, photography class, music comp class	TRT led to \uparrow EF after 1YR
Ghasemian-Shirvan et al. (2023)	Article	Germany & Belgium	LAB	4WK	25, 11 M, M_{age} : 72.13 (5.91)	tDCS	atDCS led to motor LRN maintenance
Lee et al. (2023)	Article	Korea	LAB	2DY	Before TRT: 15, 9 M, M_{age} : 69.70 (5.10) After TRT: 15, 8 M, M_{age} : 71.30 (6.37) CON: 15, 7 M, M_{age} : 71.10 (4.87)	Deep slow breathing (TRT); no deep slow breathing (CON)	Deep & slow breathing led to \uparrow cognitive skills & function in short & long term
Liu et al. (2023)	Article	China	LAB	12WK	MICT: 21, 12 M, M_{age} : 25.44 (1.58) HIIT: 26, 11 M, M_{age} : 24.83 (2.35) CON: 20, 10 M, M_{age} : 25.42 (2.61)	High-intensity interval training (HIIT); Moderate-intensity continuous training (MICT); healthy education (CON)	MICT > CON in PS & CF & showed improvements in CBF
Marie et al. (2023)	Article	Germany & Switzerland	LAB, HOME	18MTH	TRT: 66, 28 M, M_{age} : 69.20 (3.20) CON: 66, 27 M, M_{age} : 69.20 (3.80)	Piano training (TRT); Musical culture (CON)	TRT & CON both led to \uparrow GMV in whole brain, caudate nucleus, Rolandic operculum, & inferior cerebellum & \uparrow WM; CON led to \downarrow R primary auditory cortex GMV

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Table 4 (continued)

Study	Source	Location	Setting	Length	Sample(s)	Intervention	Main Findings
Meltzer et al. (2023)	Article	Canada	LAB, HOME	16WK	TRT: 28, 10 M, M _{age} : 69.57 (2.97) BrainHQ: 24, 7 M, M _{age} : 70.08 (2.89) CON: 24, 8 M, M _{age} : 70.00 (2.62)	LANG LRN (TRT); BrainHQ; waitlist (CON)	TRTs > CON in INH & WM; BrainHQ was more likely to ↑PS compared to Duolingo & CON
Moret et al. (2023)	Article	Italy	LAB	4–5WK	ATT-CCT: 27, 8 M, M _{age} : 70.89 (4.33) EXERG-T: 28, 6 M, M _{age} : 70.75 (3.89) CON: 28, 10 M, M _{age} : 69.03 (5.97)	ATT computerized CT (ATT-CCT); Exergame training (EXERG-T); no training (CON)	ATT-CCT led to ↑ATT, PS, Verbl, & MEM
Ramadas et al. (2023)	Article	India	LAB	3WK	8, 4 M, M _{age} : 63.87, 56–79	Short-term computerized music-based intervention (Carnatic classical music)	TRT led to ↑performance on all auditory processing & cognitive tasks
Ro et al. (2023)	Article	Korea	LAB	4WK	ICI: 16, 10 M, M _{age} : 73.94 (4.65) TCI: 16, 3 M, M _{age} : 75.00 (3.98)	Interactive multitouch game-based cognitive intervention (ICI); Pen paper cognitive intervention (TCI)	TRTs led to ↑MEM; ICI led to ↑INH & Verbl
Sheffler et al. (2023)	Article	USA	LAB	S1: 15WK S2: 12WK	S1 (TRT): 6, 2 M, M _{age} : 66.33 (6.41) S1 (CON): 9, 3 M, M _{age} : 70.22 (9.97) S2 (TRT): 27, 9 M, M _{age} : 69.44 (7.12)	S1: combined LANG LRN, painting, & iPad training (TRT); no training (CON) S2: three of five potential classes (LANG LRN, photography, music composition, drawing, & iPad training) (TRT)	S1: TRT > CON in growth mindset; S2: OA with ↑initial growth mindset showed ↑cognitive gains
Worschech et al. (2023)	Article	Germany & Switzerland	SEC	12MTH	Overall: 156, 64 M, M _{age} : 69.7 (3.50) TRT: 82 CON: 74	Piano training (TRT); music listening/culture (CON)	TRT led to ↑fine motor skills, WM, GMV in contralateral M1, putamen & thalamus & coupling between motor & cognitive domains

Note: Sample characteristics reported individually only when reported in original study. Standard deviations (in parentheses) or age ranges are reported next to mean age (M_{age}) when available. Studies that do not list an explicit control group (CON) are within-subjects designs. **Symbols:** ↑: increase or higher levels; ↓: decrease or lower levels; >: greater than; <: less than; =: equal to. **Abbreviations:** A-CON: Active control; AE: Aerobic exercise; AN: Attention network; atDCS: anodal transcranial direct current stimulation; ATT: Attention; AVL: Auditory verbal learning test; BDNF: Brain-derived neurotrophic factor; BL: Bilingual; BTG: Brain training group; BVMT: Brief visuospatial memory test; CBF: Cerebral blood flow; CH: Chapter; CS: Cross-sectional; CT: Cognitive training; ctDCS: Cathodal transcranial direct current stimulation; CTh: Cortical thickness; dlPFC: Dorsolateral prefrontal cortex; DMN: Default mode network; DY: Day; EC: Executive control; EF: Executive function; EpM: Episodic memory; ERP: Event-related potential; F2F: In-person outside of lab; FA: Fractional anisotropy; fALFF: Fractional amplitude of low-frequency fluctuation; FC: Functional connectivity; gCOG: Global/general cognition; GMA: gross motor activities; GMV: Grey matter volume; HD-tDCS: High-definition transcranial direct current stimulation; HGH: Human growth hormone; HR: Hour; IGF-1: Insulin-like growth factor; INH: Inhibition; iTBS: Intermittent theta burst stimulation; LAB: Laboratory study; LBS-A: lower body strength & aerobic training; LONG: Longitudinal; LRN: Learning; MA: Middle adult; Mage: Mean sample age; MB: model-based working memory training without distractor inhibition; MB+: model-based working memory training with distractor inhibition; MD: Mean diffusivity; MEM: Memory; ML: Monolingual; MoCA: Montreal Cognitive Assessment; mPFC: Medial prefrontal cortex; MR: Magnetic resonance; MTG: Mindfulness training group; MTH: Month; MVF: Mirror visual feedback; NF: Neurofeedback; OA: Older adult; OL: Online; P-CON: Passive control; PAS: Paired associative stimulation; PE: Physical exercise; PM: Psychomotor; PS: Processing speed; RD: Radial diffusivity; rPFC: Rostral prefrontal cortex; S: Study; SEC: secondary analysis; SM: Sensorimotor; SpatM: Spatial memory; stDCS: Sham transcranial direct current stimulation; STM: Short-term memory; tACS: Transcranial alternating current stimulation; tDCS: Transcranial direct current stimulation tRNS: Transcranial random noise stimulation; TRT: Treatment/experimental/intervention group; UBS-A: upper body strength & aerobic training; VerbEpM: Verbal episodic memory; Verbl: Verbal learning; VerblTM: Verbal long-term memory; VerblM: Verbal memory; VG: Video game; VisATT: Visual attention; VisL: Visual learning; VisM: Visual memory; VN: Visual network; VR: Virtual reality; VS: Visuospatial; VSWM: Visuospatial working memory; WCG: Waitlist control group; WK: Week; WM: Working memory; YA: Younger adult; YR: Year

¹Participants were either undergraduate or graduate students

²Participants were all over 55 years old

³Table in study contained an error for Tetris group, so mean age was estimated based on characteristics of other groups

each of the individual MMAT and CASP criteria can be found in their respective original articles.

3.5. Results of individual studies

To provide a more coherent narrative synthesis of findings, results of individual studies were organized based on the specific research sub-question they most directly addressed. Additionally, results were further organized following the same conventions used in our coverage of study characteristics. Under each RQ and sub-question, results were presented separately for each dimension of cognitive function (RQ1), or brain structure or function (RQ2). Given the large number of studies included for RQ3, and the summary of their results in both an effect direction plot organized by intervention format (Table 7) and tabular synthesis (Table 4), findings related to the effects of interventions were

presented separately based on whether they investigated effects on cognitive (RQ3a) or brain outcomes (RQ3b). Mediating and moderating factors influencing the efficacy of interventions (RQ3c) were presented separately under cognitive and brain outcome sections. Coverage of results for studies addressing RQ1 and RQ2 represent either comparisons between samples of younger and older adults or reported associations between age and the outcome(s) of interest. Coverage of results for RQ3 represent comparisons between either experimental and control groups or pre- and post-test conditions depending on a given study's design. For included studies reporting findings that were relevant to either multiple organizational dimensions under a single RQ or to multiple RQs, coverage of relevant findings was sub-divided and presented under each respective section. Finally, narrative coverage of individual study results will be limited to main patterns overserved and should not be considered exhaustive. Full details of relevant findings for all included studies can

Table 5

Summary of Risk of Bias Analysis for All Primary Studies (MMAT Criteria).

Study	RQ	Are there clear research questions?	Do the collected data allow the address of the research questions?	Are the participants representative of the target population?	Are measurements appropriate regarding both the outcome and intervention (or exposure)?	Are there complete outcome data?	Are the confounders accounted for in the design and analysis?	During the study period, is the intervention administered (or exposure occurred) as intended?	Overall Rating
Azevedo et al. (2012)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Bellebaum et al. (2012)	1	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Berryhill and Jones (2012)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Bielak et al. (2012)	1	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Blachstein et al. (2012)	1	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Engvig et al. (2012)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Jackson et al. (2012)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Lin et al. (2012)	3	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Maillot et al. (2012)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
McDougall and House (2012)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Mortimer et al. (2012)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Roldán-Tapia et al. (2012)	1	Yes	Yes	Yes	Yes	Can't Tell	Can't Tell	Yes	Low Risk
Szelag and Skolimowska (2012)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Alves (2013)	3	Yes	Yes	Can't Tell	Yes	Yes	Yes	Yes	Low Risk
Bottiroli et al. (2013)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Bozoki et al. (2013)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Cansino et al. (2013)	1	Yes	Yes	Yes	Yes	Can't Tell	Yes	Yes	Low Risk
Chapman et al. (2013)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Krueger (2013)	1	Yes	Yes	Yes	Yes	Can't Tell	Can't Tell	Yes	Low Risk
Lam et al. (2013)	1	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Maddox (2013)	3	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
McDermott (2013)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Moore (2013)	3	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Nouchi et al. (2013)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Ossher et al. (2013)	1	Yes	Yes	Yes	Yes	Can't Tell	Can't Tell	Yes	Low Risk
Petrosyan (2013)	3	Yes	Yes	Can't Tell	Yes	Yes	Can't Tell	Yes	Low Risk
Sathyanarayanan et al. (2013)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Schega et al. (2013)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Theill et al. (2013)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Bailey et al. (2014)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Berryman et al. (2014)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Chan et al. (2014)	3	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Chang and Dong (2014)	1	Yes	Yes	Yes	Yes	Yes	No	Yes	Low Risk
Heinzel et al. (2014)	1, 2, 3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Kishore et al. (2014)	3	Yes	Yes	Yes	Yes	Can't Tell	Can't Tell	Yes	Low Risk
Marcotte and Ansaldo (2014)	1, 2	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Park et al. (2014)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Payne et al. (2014)	1	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Samanez-Larkin et al. (2014)	1, 2	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Sandberg et al. (2014)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Stepankova et al. (2014)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Stine-Morrow et al. (2014)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Todorov et al. (2014)	1	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Worthy et al. (2014)	1	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Xiong et al. (2014)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Bhankuni & Mutha, 2015	1	Yes	Yes	Yes	Yes	Can't Tell	No	Yes	Some Concerns
Bilodeau-Mercure et al. (2015)	1, 2	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Cyr (2015)	1	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Duffy and Azevedo (2015)	3	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Geyer et al. (2015)	1	Yes	Yes	Yes	Yes	Can't Tell	Yes	Yes	Low Risk

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Table 5 (continued)

Study	RQ	Are there clear research questions?	Do the collected data allow the address of the research questions?	Are the participants representative of the target population?	Are measurements appropriate regarding both the outcome and intervention (or exposure)?	Are there complete outcome data?	Are the confounders accounted for in the design and analysis?	During the study period, is the intervention administered (or exposure occurred) as intended?	Overall Rating
Heidemeier and Staudinger (2015)	1	Yes	Yes	Can't Tell	Yes	Yes	Yes	Yes	Low Risk
Hoff et al., 2015a	1	Yes	Yes	Yes	Yes	No	Yes	Yes	Low Risk
Hoff et al., 2015b	3	Yes	Yes	Yes	Yes	Yes	No	Yes	Low Risk
Reis et al. (2015)	3	Yes	Yes	Yes	Yes	Can't Tell	Yes	Yes	Low Risk
Sato et al. (2015)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Styron (2015)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Thielgen et al. (2015)	1	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
van Eersel et al. (2015)	1	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Avellar et al. (2016)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Azevedo et al. (2016)	3	Yes	Yes	Yes	Can't Tell	Yes	Can't Tell	Yes	Low Risk
Basak and O'Connell (2016)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Chan et al. (2016)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Christy (2016)	3	Yes	Yes	Yes	Yes	No	Can't Tell	Yes	Some Concerns
Deroche et al. (2016)	1	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Diwadkar et al. (2016)	1, 2	Yes	Yes	Yes	Yes	Can't Tell	Can't Tell	Yes	Low Risk
Dumel et al. (2016)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Külzow et al. (2016)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Lin et al. (2016)	3	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Marra (2016)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Merom et al. (2016)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Nouchi et al. (2016)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Reichert et al. (2016)	1, 2	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Reis et al. (2016)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Rojkova et al. (2016)	2	Yes	Yes	Yes	Yes	Can't Tell	Can't Tell	Yes	Low Risk
Schenk et al. (2016)	1, 2	Yes	Yes	Yes	Yes	Can't Tell	No	Yes	Some Concerns
Zimmermann et al. (2016)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Adnan et al. (2017)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Adólfssdóttir et al. (2017)	1	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Banducci et al. (2017)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Bapka et al. (2017)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Borella et al. (2017)	1	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Branscheidt et al. (2017)	3	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Corbin (2017)	1	Yes	Yes	Yes	Yes	Can't Tell	No	Yes	Some Concerns
Fujiyama et al. (2017)	3	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Giudice et al. (2017)	1	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Hoefelijzers et al. (2017)	1	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Hong (2017)	3	Yes	Yes	No	Yes	Yes	Can't Tell	Yes	Some Concerns
Karlamangla et al. (2017)	1	Yes	Yes	Yes	Yes	Can't Tell	Yes	Yes	Low Risk
Klencklen et al. (2017)	1	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Li et al. (2017)	1	Yes	Yes	Yes	Yes	Can't Tell	Yes	Yes	Low Risk
Lubitz et al. (2017)	1, 2	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Lussier et al. (2017)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Monteiro et al. (2017)	1, 2	Yes	Yes	Can't Tell	Yes	Yes	Can't Tell	Yes	Low Risk
Müller et al. (2017)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Ordnung et al. (2017)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Payne and Stine-Morrow (2017)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Perry et al. (2017)	1, 2	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Pettersen (2017)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Ramos et al. (2017)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Rhodes and Katz (2017)	1	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk

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Table 5 (continued)

Study	RQ	Are there clear research questions?	Do the collected data allow the address of the research questions?	Are the participants representative of the target population?	Are measurements appropriate regarding both the outcome and intervention (or exposure)?	Are there complete outcome data?	Are the confounders accounted for in the design and analysis?	During the study period, is the intervention administered (or exposure occurred) as intended?	Overall Rating
Souders et al. (2017)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Tao et al. (2017)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Tuokko et al. (2017)	1	Yes	Yes	Can't Tell	Can't Tell	Can't Tell	Can't Tell	Can't Tell	Some Concerns
Vaportzis et al. (2017)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Zahodne et al. (2017)	1	Yes	Yes	No	Yes	Can't Tell	Yes	Yes	Some Concerns
Archer et al. (2018)	1, 2	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Bapka et al. (2018)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Chan et al. (2018)	2	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Dumel et al. (2018a)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Dumel et al. (2018b)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
DuPont (2018)	3	Yes	Yes	No	Yes	Can't Tell	Can't Tell	Yes	Some Concerns
Frøehlich et al. (2018)	1, 2	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Haeger et al. (2018)	3	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Huhn et al. (2018)	3	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Kalbe et al. (2018)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Lee et al. (2018)	3	Yes	Yes	Can't Tell	Yes	Can't Tell	Can't Tell	Can't Tell	Some Concerns
Lindbergh et al. (2018)	3	Yes	Yes	Yes	Yes	Can't Tell	Can't Tell	Yes	Low Risk
Ludyga et al. (2018)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Perry-Deegan (2018)	3	Yes	Yes	No	Yes	Yes	Yes	Yes	Low Risk
Pfenninger and Polz (2018)	3	Yes	Yes	Can't Tell	Yes	Yes	Can't Tell	Yes	Low Risk
Pflueger et al. (2018)	1	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Rehfeld et al. (2018)	3	Yes	Yes	Can't Tell	Yes	Yes	Yes	Yes	Low Risk
Rosi et al. (2018)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Shake et al. (2018)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Tomporowski and Pendleton (2018)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Abellana-Pérez et al. (2019)	2, 3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Aguirre-Loaiza et al. (2019)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Alain et al. (2019)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Antonenko et al. (2019)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Belchior et al. (2019)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Berggren (2019)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Berghuis et al. (2019)	1, 2	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Bertola et al. (2019)	1	Yes	Yes	Yes	Can't Tell	Can't Tell	Yes	Yes	Low Risk
Bowen et al. (2019)	1, 2	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Bugos (2019)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Carbonell-Hernández et al. (2019)	3	Yes	Yes	Can't Tell	Yes	Yes	Can't Tell	Can't Tell	Some Concerns
Chae et al. (2019)	3	Yes	Yes	No	Yes	Yes	Yes	Yes	Low Risk
Cole and Shields (2019)	3	Yes	Yes	Yes	Can't Tell	Yes	Yes	Yes	Low Risk
Dahl et al. (2019)	1, 2	Yes	Yes	Yes	Yes	Can't Tell	Can't Tell	Yes	Low Risk
Fernandez-Baiza et al., 2019	1	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Fertonani et al. (2019)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Grégoire et al. (2019)	3	Yes	Yes	Yes	Yes	Can't Tell	Can't Tell	Yes	Low Risk
Hering et al. (2019)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Howe et al., 2019	1	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Isotalus (2020)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Jockwitz et al. (2019)	1, 2	Yes	Yes	Yes	Yes	Can't Tell	Yes	Yes	Low Risk
Ke et al. (2019)	3	Yes	Yes	Yes	Yes	Can't Tell	Yes	Yes	Low Risk
Ljubisavljevic et al. (2019)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Nespollo et al. (2019)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Nouchi et al. (2019)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk

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Table 5 (continued)

Study	RQ	Are there clear research questions?	Do the collected data allow the address of the research questions?	Are the participants representative of the target population?	Are measurements appropriate regarding both the outcome and intervention (or exposure)?	Are there complete outcome data?	Are the confounders accounted for in the design and analysis?	During the study period, is the intervention administered (or exposure occurred) as intended?	Overall Rating
Opie et al. (2019)	3	Yes	Yes	Yes	Yes	Yes	Can't tell	Yes	Low Risk
Patan (2019)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Pergher et al. (2019)	1, 2	Yes	Yes	Yes	Yes	No	Can't Tell	Yes	Some Concerns
Pliatsikas et al. (2019)	1	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Sosa and Lagana (2019)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Tripathi et al. (2019)	1	Yes	Yes	Yes	Yes	No	Yes	Yes	Low Risk
Wong et al. (2019)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Zhao et al. (2019)	1, 2	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Berggren et al. (2020)	3	Yes	Yes	Yes	Yes	No	Yes	Yes	Low Risk
Čekanauskaitė et al. (2020)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Delhom et al. (2020)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Ferreira (2020)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Formica et al. (2020)	3	Yes	Yes	Yes	Yes	Yes	Yes	Can't Tell	Low Risk
Gajewski et al. (2020)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Habich et al. (2020)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Jaeggi et al. (2020)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Kolarik et al. (2020)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Lenze et al. (2020)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
MacRitchie et al. (2020)	3	Yes	Yes	Can't Tell	Yes	Yes	Yes	Yes	Low Risk
Malagurski et al. (2020)	1, 2	Yes	Yes	Yes	Yes	Can't Tell	Yes	Yes	Low Risk
Mohammad et al. (2020)	1	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Nilsson et al. (2020)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Opie et al. (2020)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Perosa et al. (2020)	1, 2	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Reas et al. (2020)	2	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Roig-Coll et al. (2020)	3	Yes	Yes	Yes	Yes	Can't Tell	Yes	Yes	Low Risk
Suominen et al. (2020)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Takeuchi et al. (2020)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Tuokko et al. (2020)	1	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Whitmoyer et al. (2020)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Zarantonello et al. (2020)	1	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Abrahan et al. (2021)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Dave et al. (2021)	1	Yes	Yes	Yes	Yes	No	Can't Tell	Yes	Some Concerns
Dobrowolski et al. (2021)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Etnier et al. (2021)	3	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Gómez and Rodríguez (2021)	3	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Grasshoff et al. (2021)	1	Yes	Yes	Yes	Yes	Can't Tell	No	Yes	Some Concerns
Hong et al. (2021)	3	Yes	Yes	Yes	Yes	Can't Tell	Yes	Yes	Low Risk
Jockwitz et al. (2021)	2	Yes	Yes	Yes	Yes	Can't Tell	Yes	Yes	Low Risk
Nilsson et al. (2021)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Nuzum et al. (2021)	1, 2	Yes	Yes	Yes	Yes	Can't Tell	Yes	Yes	Low Risk
Puri et al. (2021)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Rutledge et al. (2021)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Santos et al. (2020)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Satler et al. (2021)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Sloan et al. (2021)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Whyte et al. (2021)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Woodman (2021)	1	Yes	Yes	Can't Tell	Can't Tell	Can't Tell	Can't Tell	Can't Tell	Some Concerns
Wu et al. (2021)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Yang et al. (2021)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Zuber et al. (2021)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Au et al. (2022)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Baklouti et al. (2022)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk

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Table 5 (continued)

Study	RQ	Are there clear research questions?	Do the collected data allow the address of the research questions?	Are the participants representative of the target population?	Are measurements appropriate regarding both the outcome and intervention (or exposure)?	Are there complete outcome data?	Are the confounders accounted for in the design and analysis?	During the study period, is the intervention administered (or exposure occurred) as intended?	Overall Rating
Beller et al. (2022)	1	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Best et al. (2022)	1	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Bidelman et al. (2022)	3	Yes	Yes	Yes	Can't Tell	Can't Tell	Can't Tell	Yes	Some Concerns
Boban et al. (2022)	2	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Bugos and Wang (2022)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Chettouf et al. (2022)	1, 2	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Chi et al. (2022)	1, 2	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Cogan et al. (2022)	3	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Dever et al. (2022)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Draaisma et al. (2022)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Gray et al. (2022)	3	Yes	Yes	Yes	Yes	Can't Tell	Can't Tell	Yes	Low Risk
James et al. (2022)	1, 2	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Johnson et al. (2022)	3	Yes	Yes	Can't Tell	Yes	Yes	Yes	Yes	Low Risk
Jünemann et al. (2022)	3	Yes	Yes	Yes	Can't Tell	No	Yes	Yes	Some Concerns
Kim et al. (2022)	3	Yes	Yes	Yes	Yes	Can't Tell	No	Yes	Some Concerns
Kliesch et al. (2022)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Lv et al. (2022)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Neufeld et al. (2022)	1, 2	Yes	Yes	Yes	Yes	No	Can't Tell	Yes	Some Concerns
Nooyens et al. (2022)	1	Yes	Yes	Yes	Yes	No	Yes	Yes	Low Risk
Rakic et al. (2022)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Rojas et al. (2022)	1	Yes	Yes	Can't Tell	Yes	Yes	Can't Tell	Yes	Low Risk
Samimy et al. (2022)	3	Yes	Yes	Can't Tell	Yes	Can't Tell	Yes	Yes	Low Risk
Satorres et al. (2022)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Stamate et al. (2022)	3	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Strickland-Hughes and West (2022)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Vance (2022)	1, 3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Wang et al. (2022)	1	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Worschech et al. (2022)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Yang et al. (2022)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Zhang et al. (2022)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Alescio-Lautier et al. (2023)	3	Yes	Yes	No	Yes	Yes	Can't Tell	Yes	Some Concerns
Bakhtiari et al. (2023)	1, 2	Yes	Yes	No	Yes	Yes	Can't Tell	Yes	Some Concerns
Dever et al. (2023)	3	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Ferguson et al. (2023)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Fijalkiewicz et al. (2023)	1	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Ghasemian-Shirvan et al. (2023)	3	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Hsieh and Chen (2023)	1	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Jin et al. (2023)	1	Yes	Yes	Yes	Yes	Can't Tell	Yes	Yes	Low Risk
Lee et al. (2023)	3	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Liu et al. (2023)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Marie et al. (2023)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Meltzer et al. (2023)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Montemurro et al. (2023)	1, 2	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Moret et al. (2023)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Pauley et al. (2023)	1, 2	Yes	Yes	Yes	Yes	Can't Tell	Can't Tell	Yes	Low Risk
Ramadas et al. (2023)	3	Yes	Yes	Can't Tell	Yes	Yes	Can't Tell	Yes	Low Risk
Ro et al. (2023)	3	Yes	Yes	Can't Tell	Yes	Yes	Yes	Yes	Low Risk
Ruiz et al. (2023)	1	Yes	Yes	Yes	Yes	Can't Tell	Yes	Yes	Low Risk
Sheffler et al. (2023)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Tinga et al. (2023)	1, 2	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Turney et al. (2023)	2	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk

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Table 5 (continued)

Study	RQ	Are there clear research questions?	Do the collected data allow the address of the research questions?	Are the participants representative of the target population?	Are measurements appropriate regarding both the outcome and intervention (or exposure)?	Are there complete outcome data?	Are the confounders accounted for in the design and analysis?	During the study period, is the intervention administered (or exposure occurred) as intended?	Overall Rating
Worschech et al. (2023)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Yang et al. (2023)	2	Yes	Yes	Yes	Yes	Yes	Can't Tell	Yes	Low Risk
Zhou et al. (2023)	2	Yes	Yes	Yes	Yes	No	Can't Tell	Yes	Some Concerns

Note: A set of seven questions from the Mixed Methods Appraisal Tool (MMAT) were used to assess the risk of bias of all included primary research studies. Possible responses to each of the criterion questions were either “Yes”, “Can’t Tell”, or “No”. To determine the overall risk of bias for a study, a score of 1 point was assigned for a “Yes” response, 0.5 point for “Can’t Tell”, and 0 for “No”. Studies with a total score of 6 and above were classified as “Low Risk”, 3.5–5.5 as “Some Concerns”, and 0–3 as “High Risk”.

Table 6

Summary of Risk of Bias Analysis for Included Systematic Reviews and Meta-analyses (CASP Criteria).

Study	RQ	Did the review address a clearly focused question?	Did the authors look for the right type of papers?	Do you think all the important, relevant studies were included?	Did the review's authors do enough to assess quality of the included studies?	If the results of the review have been combined, was it reasonable to do so?	Can the results be applied to the local population?	Were all important outcomes considered?	Overall Rating
Zheng et al. (2015)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Pan et al. (2018)	3	Can't Tell	Can't Tell	Can't Tell	Yes	Yes	Yes	Yes	Some Concerns
Sala et al. (2019)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Klimova and Pikhart (2020)	3	No	Yes	Can't Tell	No	Can't Tell	Can't Tell	Can't Tell	High Risk
Lee et al. (2021)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Roheger et al. (2021)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Viviani and Vallesi (2021)	3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Low Risk
Eilat-Adar et al. (2023)	3	Yes	Yes	Yes	No	Yes	Yes	Yes	Low Risk

Note: A set of seven questions from the Critical Appraisal Skills Programme (CASP) were used to assess the risk of bias of all included systematic reviews and meta-analyses. Possible responses to each of the criterion questions were either “Yes”, “Can’t Tell”, or “No”. To determine the overall risk of bias for a study, a score of 1 point was assigned for a “Yes” response, 0.5 point for “Can’t Tell”, and 0 for “No”. Studies with a total score of 6 and above were classified as “Low Risk”, 3.5–5.5 as “Some Concerns”, and 0–3 as “High Risk”.

be found in our tabular synthesis (Tables 2–4), and in our effect direction plot for RQ3 (Table 7).

3.5.1. RQ1b-c: learning-related cognitive changes during healthy aging and factors influencing changes

Learning and memory. Across studies reporting learning and memory outcomes, results generally either supported decreased ability or no change associated with increased age. Negative associations between age and learning were reported in associative learning (Diwadkar et al., 2016), verbal learning (Dahl et al., 2019; James et al., 2022; Montemurro et al., 2023; Tuokko et al., 2017, 2020), probabilistic learning (Perosa et al., 2020), motor learning (Chettouf et al., 2022), and visuospatial learning (Tinga et al., 2023). While the majority of studies reported general age-related declines across different forms of learning, study design impacted on the ability to fully characterize the time course of these declines. In one exception, a longitudinal study by James and colleagues (2022) identified the time course of age-related decline in verbal learning, observing a decline in task performance starting around 50 years of age. Interestingly, despite considerable evidence reported in

other dimensions of cognitive function, no studies reported a significant modulatory influence of any factor on age-related declines in learning, although null associations with IQ and education level were reported (Diwadkar et al., 2016).

Despite strong evidence of age-related decline in learning, there was also considerable evidence in support of sustained learning capacity in older adults. Specifically, older adults showed sustained learning capacity in reward (including probabilistic) learning (Bowen et al., 2019; Samanez-Larkin et al., 2014), implicit learning (Bhakuni and Mutha, 2015; Nuzum et al., 2021), learning from errors (Cyr, 2015), motor learning (Berghuis et al., 2019; Hoff, Trapp, et al., 2015; Monteiro et al., 2017), active feedback learning (Bellebaum et al., 2012), and visuospatial learning (Tinga et al., 2023). Results from many studies, most clearly those that conflict in their reporting of decreased versus null associations between age and learning, highlight a wider trend of inconsistent results in a given dimension of learning. In the case of verbal learning, Marcotte and colleagues (2014) reported an age effect on accuracy, but a null effect on RT. The likelihood of a given study identifying age-related declines in verbal learning may also depend on

Table 7
Effect Direction Results for Research Question 3.

Arts Interventions			
Study	Intervention	Effect Direction	Risk of Bias
Perry-Deegan, 2018	Piano training	◀▶	
Alain et al., 2019	Music & visual art training programs	◀▶	
Bugos, 2019	Piano or percussion training	▲	
MacRitchie et al., 2020	Piano training	◀▶	
Abrahan et al., 2021	Music improvisation	▲	
Santos et al., 2021	Musical improvisation training	▲	
Bugos & Wang, 2022	Piano training	▲	
Jünemann et al., 2022	Piano training	▲	
Worschech et al., 2022	Piano training	▲	
Marie et al., 2023	Piano training	◀▶	
Ramadas et al., 2023	Short-term computerized music-based intervention (Carnatic classical music)	▲	
Worschech et al., 2023	Piano training	▲	
Brain Stimulation			
Study	Intervention	Effect Direction	Risk of Bias
Berryhill & Jones, 2012	tDCS	◀▶	
Dumel et al., 2016	tDCS	▲	
Branscheidt et al., 2017	tDCS	◀▶	
Fujiyama et al., 2017	tDCS	▲	
Dumel et al., 2018a	tDCS	▲	
Dumel et al., 2018b	tDCS	▲	
Abellana-Pérez et al., 2019	iTBS	▲	
Antonenko et al., 2019	tDCS	▲	
Fertonani et al., 2019	tRNS	YA: ▼ OA: ▲	
Ke et al., 2019	HD-tDCS	▲	
Ljubisavljevic et al., 2019	tDCS	▲	
Opie et al., 2019	PAS long term potentiation; PAS long term depression	YA: ◀▶ OA: ▼	
Habich et al., 2020	tDCS	◀▶	
Opie et al., 2020	PAS long term depression	▲	
Lee et al., 2021 ^{REV}	tDCS	◀▶	
Puri et al., 2021	tDCS	◀▶	

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Table 7 (continued)

Au et al., 2022	tDCS	◀▶	
Draaisma et al., 2022	tACS	▲	
Johnson et al., 2022	tDCS	▲	
Satorres et al., 2022	tDCS	◀▶	
Ghasemian-Shirvan et al., 2023	tDCS	▲	
Cognitive Based Interventions			
Study	Intervention	Effect Direction	Risk of Bias
Engvig et al., 2012	Memory training	▲	
Jackson et al., 2012	Inductive reasoning training	▲	
Lin et al., 2012	Interleaved practice	▲	
McDougall & House, 2012	Video game	◀▶	
Szelag & Skolimowska, 2012	Temporal training	◀▶	
Bottiroli et al., 2013	Strategy or strategy-adaptation training	▲	
Bozoki et al., 2013	Online learning games	◀▶	
Maddox, 2013	Long retention interval	▲	
McDermott, 2013	Brain training game	◀▶	
Nouchi et al., 2013	Video game	▲	
Theill et al., 2013	Simultaneous training, single working memory training	▲	
Bailey et al., 2014	Effective encoding strategy training	▲	
Heinzel et al., 2014	Working memory training (Older adults)	▲	
Sandberg et al., 2014	Process training	YA: ▲ OA: ◀▶	
Stepankova et al., 2014	Working memory training	▲	
Stine-Morrow et al., 2014	Team-based competitive program in creative problem solving or home-based inductive reasoning training program	▲	
Styron, 2015	Video game	▲	
Basak & O'Connell, 2016	Working memory training	▲	
Christy, 2016	Interactive Metronome	▲	
Lin et al., 2016	Interleaved practice	▲	
Marra, 2016	Video game	▲	
Zimmermann et al., 2016	Memory training	▲	
Adnan et al., 2017	Goal-oriented attentional regulation training (GOALS)	▲	
Lussier et al., 2017	Dual-task training	▲	
Payne & Stine-Morrow, 2017	Working memory training on iPad	▲	

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Table 7 (continued)

Souders et al., 2017	Gamified CT	◀▶	
Haeger et al., 2018	Driving simulator	◀▶	
Rosi et al., 2018	Memory training	▲	
Belchior et al., 2019	Video game; brain fitness program	▲	
Cole & Shields, 2019	Cognitive load	◀▶	
Hering et al., 2019	Rehearsal instruction	▲	
Nouchi et al., 2019	CT game for car driving	▲	
Sala et al., 2019 ^{REV}	Working memory training	◀▶	
Sosa & Lagana, 2019	Video game	◀▶	
Delhom et al., 2020	Emotional intelligence intervention program	▲	
Gajewski et al., 2020	Multidomain CT	◀▶	
Jaeggi et al., 2020	Working memory training	◀▶	
Gómez & Rodríguez, 2021	Everyday cognition training	▲	
Hong et al., 2021	Multidomain CT	▲	
Roheger et al., 2021 ^{REV}	Memory training	◀▶	
Satler et al., 2021	Inhibition training	◀▶	
Zuber et al., 2021	Model-based working memory training with or without distractor inhibition	◀▶	
Samimy et al., 2022	Mindfulness-based attention training	◀▶	
Stamate et al., 2022	Selective retrieval practice	▲	
Strickland-Hughes & West, 2022	Strategy training with or without self-regulatory boost	▲	
Alescio-Lautier et al., 2023	Problem solving training	▲	
Ro et al., 2023	Interactive multitouch game-based cognitive intervention or pen paper cognitive intervention	▲	
Nouchi et al., 2016	Learning therapy	▲	
Food or Drug Interventions			
Study	Intervention	Effect Direction	Risk of Bias
Sathyanarayanan et al., 2013	Brahmi	◀▶	
Avellar et al., 2016	D-serine administration	◀▶	
Külzow et al., 2016	Fish oil capsules	▲	
Pettersen, 2017	Vitamin D	Low: ◀▶ High: ▲	
Huhn et al., 2018	Resveratrol	◀▶	
Lindbergh et al., 2018	Lutein & Zeaxanthin	▼	
Chae et al., 2019	Yohimbine, Hydrocortisone, or both	◀▶	
Isotalus, 2019	L-DOPA	◀▶	

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Table 7 (continued)

Patan, 2019	DHA or EPA-rich supplements	◄◄	
Suominen et al., 2020	Dark chocolate	◄◄	
Rutledge et al., 2021	Freeze-dried blueberry powder	▲	
Sloan et al., 2021	Flavanol	◄◄	
Whyte et al., 2021	Wild blueberry beverage	▲	
Cogan et al., 2022	Pecans	◄◄	
Kim et al., 2022	Fermented laminaria japonica	▲	
Rakic et al., 2022	Almonds	1.5oz: ◄◄ 3oz: ▲	
Language Learning			
Study	Intervention	Effect Direction	Risk of Bias
Ramos et al., 2017	Basque learning in Spanish speakers	◄◄	
Pfenninger & Polz, 2018	English learning in German/Slovenian speakers	▲	
Berggren, 2019	Italian learning in Swedish speakers	◄◄	
Wong et al., 2019	English learning in Cantonese speakers	▲	
Berggren et al., 2020	Italian learning in Swedish speakers	◄◄	
Klimova & Pikhart, 2020 ^{REV}	Multiple language conditions	▲	
Nilsson et al., 2021	Italian learning in Swedish speakers	◄◄	
Kliesch et al., 2022	Spanish learning in German speakers	◄◄	
Meltzer et al., 2023	Spanish learning in English speakers	▲	
Lifestyle Interventions			
Study	Intervention	Effect Direction	Risk of Bias
Mortimer et al., 2012	Tai chi, walking, social interaction	All: ▲	
Alves, 2013	Ballroom dancing	▲	
Chapman et al., 2013	Aerobic exercise	▲	
Moore, 2013	Mindfulness training	▲	
Petrosyan, 2013	Resistance training	▲	
Berryman et al., 2014	Physical exercise	▲	
Chan et al., 2014	Dejian mind body intervention	▲	
Park et al., 2014	Productive-engagement (Photo, quilt, & dual conditions)	▲	
Zheng et al., 2015 ^{REV}	Tai chi	▲	
Chan et al., 2016	iPad skills course	◄◄	
Merom et al., 2016	Mixed dance	▲	
Banducci et al., 2017	Active experiencing class	▲	
Müller et al., 2017	Dance	▲	

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Table 7 (continued)

Tao et al., 2017	Tai chi or Baduanjin	▲	
Vaportzis et al., 2017	Digital tablet training	◄►	
DuPont, 2018	Resistance training	▲	
Ludyga et al., 2018	Moderately intense running	▲	
Pan et al., 2018 ^{REV}	Tai chi	▲	
Rehfeld et al., 2018	Dance	▲	
Tomporowski & Pendleton, 2018	Stepping task	▲	
Aguirre-Loaiza et al., 2019	Indoor cycling	◄►	
Carbonell-Hernández et al., 2019	Combined dance, athletics, functional exercise, Nordic walking	◄►	
Grégoire et al., 2019	Physical exercise	▲	
Čekanauskaitė et al., 2020	Yoga	◄►	
Whitmoyer et al., 2020	Mindfulness-based attention training	◄►	
Etmier et al., 2021	Stationary recumbent cycle	▲	
Wu et al., 2021	Tai chi	▲	
Yang et al., 2021	Outdoor mindful walking	◄►	
Baklouti et al., 2022	Yoga	◄►	
Lv et al., 2022	Tai chi	Novice: ▲ Experienced: ◄►	
Zhang et al., 2022	Computer training	◄►	
Eilat-Adar et al., 2023 ^{REV}	Yoga	◄►	
Lee et al., 2023	Deep slow breathing	▲	
Liu et al., 2023	High-intensity interval training or moderate-intensity continuous training	▲	
Ferreira, 2020	Combined aerobic, strength, stretching, & balance exercise	▼	
Other Interventions			
Study	Intervention	Effect Direction	Risk of Bias
Azevedo et al., 2012	Intelligent tutor	▲	
Xiong et al., 2014	Neurofeedback	▲	
Duffy & Azevedo, 2015	Intelligent tutor	▲	
Reis et al., 2015	Neurofeedback	◄►	
Azevedo et al., 2016	Intelligent tutor	▲	
Reis et al., 2016	Neurofeedback	▲	
Hong, 2017	Digital memory augmentation device	▲	
Kolarik et al., 2020	Real world exploration	◄►	
Dobrowolski et al., 2021	Immersive virtual reality	▲	

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Table 7 (continued)

Dever et al., 2022	Intelligent tutor	▲	
Yang et al., 2022	Verbal articulation training	▲	
Dever et al., 2023	Intelligent tutor	▲	
Combined Interventions			
Study	Intervention	Effect Direction	Risk of Bias
Maillot et al., 2012	Exergame (video game with exercise)	◄►	
Schega et al., 2013	Intermittent hypoxic training prior to a strength-endurance exercise program	▲	
Kishore et al., 2014	Cerebellar cortical inhibition/PAS with or without carbidopa & levodopa	▲	
Hoff et al., 2015b	tDCS with mirror visual feedback	▲	
Sato et al., 2015	Cognitive water-based exercise	▲	
Bapka et al., 2017	Video game and virtual reality	▲	
Ordnung et al., 2017	Exergame (video game with exercise)	◄►	
Bapka et al., 2018	Video game and virtual reality	▲	
Kalbe et al., 2018	Multi-domain CT; CT with physical exercise; CT with physical exercise & counseling	▲	
Lee et al., 2018	Physical exercise, CT (memorization strategies) & word games	▲	
Shake et al., 2018	Bingocize (exercise & health education)	▲	
Nespolo et al., 2019	Taigeiko & cognitive stimulation	◄►	
Formica et al., 2020	Physical exercise & carbohydrates	▲	
Lenze et al., 2020	CT & vortioxetine	▲	
Nilsson et al., 2020	Physical exercise, CT, or both	▲	
Roig-Coll et al., 2020	Aerobic exercise, computerized CT, or both	AE: ▲ CCT: ◄► AE+CCT: ▲	
Takeuchi et al., 2020	Working memory training with or without aerobic exercise	WM Training: ◄► Dual: ▲	
Viviani & Vallesi, 2021 ^{REV}	Neurofeedback for executive function	▲	
Bidelman et al., 2022	tDCS + Music	▲	
Gray et al., 2022	Brain training, video game; or directed instrumental activities of daily living training	◄►	
Vance, 2022	Stationary recumbent cycle exercise while watching an educational video with closed captioning	▲	
Ferguson et al., 2023	S1: Spanish learning, iPad class, painting class S2: Spanish learning, iPad class, drawing class, photography class, music comp class	S1: ▲ S2: ▲	
Moret et al., 2023	Attention computerized CT	▲	
Sheffler et al., 2023	S1: Combined Spanish learning, painting, & iPad training S2: Three of five classes: Spanish learning, photography, music composition, drawing, iPad training	S1: ▲ S2: ▲	

Note: **Arts Interventions:** involved participants engaging in either learning or appreciating music or visual art; **Brain Stimulation:** included interventions that stimulate the brain through the scalp; **Cognitive Based Interventions:** included the application of strategies to improve aspects of learning, cognitive training, video games, or related interventions; **Food or Drug Interventions:** included any study involving food or drugs, including supplements; **Language Learning:** involved participants being trained in a foreign language; **Lifestyle Intervention:** involved changing aspects of daily life related to activity and engagement; **Other:** included interventions that did not fit into any other category including neurofeedback and AI-based interventions; **Combined:** included studies that used a combination of interventions across two or more categories. Size of effect direction arrows was determined through a median split and corresponds to the number of participants included in each study with small arrows used for studies containing 51 or less participants and large arrows for studies containing over 51. Large arrows were used for all review studies. Effect direction: upward arrow ▲ = positive impact; downward arrow ▼ = negative impact; sideways arrows ◄► = null/mixed/conflicting findings.

Risk of bias scores were assigned based on the number of questions from each respective checklist (7 questions total) receiving ratings of “Yes” (1 point), “Can’t Tell” (.5 points), and “No” (0 points). Studies receiving 6–7 points were coded as green (low risk of bias), 3.5–5.5 points coded as orange (some concerns), and 3 or less coded as red (high risk of bias). Abbreviations: CT: Cognitive training; HD-tDCS: High-definition transcranial direct current stimulation; iTBS: Intermittent theta burst stimulation; PAS: Paired associative stimulation; REV: Review; tACS: Transcranial alternating current stimulation; tDCS: Transcranial direct current stimulation; tRNS: Transcranial random noise stimulation.

the method of assessment used, with traditional lab-based assessments (e.g., CVLT) showing age effects but tasks that appear more ecologically valid (e.g., virtual reality assessment) not showing them (Pflueger et al., 2018). In the case of visuospatial learning, while older adults needed more time to enhance precision on a task, they were still capable of demonstrating learning when compared to younger adults (Tinga et al., 2023).

Age-related declines were also observed across investigations focused on memory. Negative associations between age and memory were reported in source memory (Cansino et al., 2013), episodic memory (Bielak et al., 2012; Chang and Dong, 2014; Chi et al., 2022; Howe et al., 2020; Jin et al., 2023; Karlamangla et al., 2017; Li et al., 2017; Mohammad et al., 2020; Vance, 2022; Zahodne et al., 2017), temporal order memory (Blachstein et al., 2012), spatial memory (Fernandez-Baizan et al., 2019; Giudice et al., 2017; Krueger, 2013), verbal memory (Bielak et al., 2012; Lam et al., 2013; Malagurski et al., 2020; Montemurro et al., 2023; Reichert et al., 2016; Rojas et al., 2022), semantic memory (Lam et al., 2013), spoken discourse memory (Payne et al., 2014), prospective memory (Tuokko et al., 2017, 2020), visual memory (Zhao et al., 2019), and multidomain memory composite scores (Dahl et al., 2019; Perry et al., 2017; Ruiz et al., 2023). The time course of these declines differed based on the specific form of memory under investigation. Significant declines in haptic spatial memory were reported from 60 years and beyond after earlier stability. Delayed recalled ability also showed stability until age 50 after which point there was a steady decline (Grasshoff et al., 2021). Episodic memory, which was consistently reported to have a negative association with age in older adults, showed evidence of a rapid decline after age 70 (Jin et al., 2023). The method of measurement also impacted on reported time courses of decline, with direct measures of temporal order memory declining from age 40 and beyond but indirect measures declining only after the age of 70 (Blachstein et al., 2012).

Significant modulatory factors on memory were reported across a number of studies. Bielak and colleagues (2012) reported a significant positive association between activity level and baseline levels of verbal and episodic memory across younger, middle, and older adults. Similar positive associations with activity level were identified for long term and associative memory in both younger and older adults (Vance, 2022). Education level has been cited as a significant modulator, with positive associations reported with verbal and semantic memory in younger and middle-aged adults (Lam et al., 2013), as well as both episodic memory (Chang and Dong, 2014; Li et al., 2017) and anterograde memory in older adults (Ruiz et al., 2023). Related to education level, socioeconomic status (SES) has been found to have positive associations with episodic memory in older adults (Jin et al., 2023; Li et al., 2017; Zahodne et al., 2017). Sex influences on memory have also been reported, with older females demonstrating superior episodic (Jin et al., 2023) and verbal memory (Nooyens et al., 2022) relative to males, although females also showed a faster subsequent decline in verbal memory. Null findings related to sex have also been reported, specifically in the dimension of source memory (Cansino et al., 2013). Less frequently investigated factors have also been shown to modulate memory. In a sample of older Chinese adults living in the USA, Chang and Dong (2014) identified that being married, having fewer children, living for fewer years in the USA, and higher levels of self-reported health were all positively associated with episodic memory. Additionally, race has also been shown to impact on different forms of memory. In a study of older English and Chinese adults, higher levels of education were associated with higher levels of anterograde memory, but rates of decline were higher in highly educated English relative to Chinese older

adults (Ruiz et al., 2023).

In contrast with studies focused on learning, fewer memory-focused results supported that older adult had sustained function. Exceptions were reported in the dimensions of recognition memory in one cross-sectional study (Pauley et al., 2023), and visual associative memory over five years in a longitudinal study (Fijalkiewicz et al., 2023). Additionally, while age-related declines in source memory were reported in a sample of adults ranging from 21 to 80 (Cansino et al., 2013), no association between age and memory intrusions in source memory was reported in one study conducted exclusively in older adults (Corbin, 2017). In one case, sustained everyday memory capabilities in older adults were accompanied by decreased confidence in that memory (Ossher et al., 2013). Similar to learning-based measures, there is limited evidence of compensatory mechanisms to sustain levels of memory similar to younger adults. While no single study reported overall age-related improvements in memory, Krueger (2013) reported a positive association between age and logical memory, although this was accompanied by age-related increases in far errors on a spatial memory task. Finally, while a negative age-related decrease in visuospatial memory was identified, older adults outperformed younger adults during later stage measures due to reliance on intact implicit processes (Wang et al., 2022).

Executive function and attention. Studies investigating age-related changes in executive function and attention generally reported decreased ability associated with increased age. Age-related declines were reported in the dimensions of working memory (Archer et al., 2018; Borella et al., 2017; Chang and Dong, 2014; Geyer et al., 2015; Heinzel et al., 2014; Jin et al., 2023; Klencklen et al., 2017; Lam et al., 2013; Lubitz et al., 2017; Pliatsikas et al., 2019; Rhodes and Katz, 2017), inhibition (Adólfssdóttir et al., 2017; Deroche et al., 2016; Heinzel et al., 2014; Tuokko et al., 2017, 2020), cognitive flexibility (Adólfssdóttir et al., 2017; Jockwitz et al., 2019), attention (Chang and Dong, 2014; Perry et al., 2017), and composite measures of executive function (Neufeld et al., 2022; Perry et al., 2017; Todorov et al., 2014; Tuokko et al., 2017, 2020; Vance, 2022). The time course of age-related changes in executive function was only investigated by a small number of studies. In a secondary analysis of longitudinal data, Jin and colleagues (2023) identified a negative association between age and working memory in older adults with ability declining rapidly after age 70. In contrast, a cross-sequential study by Zarantonello and colleagues (2020) reported earlier declines in visuospatial working memory with speed declining after age 35 and accuracy declining after age 57.

Few studies explored the modulation of age-related changes in executive function, with positive associations identified between education level and working memory (Bielak et al., 2012; Borella et al., 2017; Chang and Dong, 2014; Lam et al., 2013; Li et al., 2017; Pliatsikas et al., 2019; Tripathi et al., 2019; Zarantonello et al., 2020), as well as attention and a composite measure of executive function (Perry et al., 2017). Higher SES was also positively associated with a composite score of executive function (Zahodne et al., 2017) and working memory (Jin et al., 2023). Sex differences have also been reported, with superior cognitive flexibility and slower age-related decline identified in older females relative to males (Nooyens et al., 2022). However, conflicting results have also been reported in both cross-sectional (Chang and Dong, 2014; Zarantonello et al., 2020) and longitudinal studies (Jin et al., 2023), supporting superior working memory in males relative to females. Specifically, findings from Jin and colleagues (2023) support that sex differences in working memory increase between 50 and 80 years of age and then decrease thereafter. It is also worth noting that this study identified that observed benefits of SES on working memory were more

pronounced in women. Higher levels of activity were positively associated with working memory, but did not influence rate of age-related decline over time (Bielak et al., 2012). Additionally, Chang and Dong (2014) identified the same positive association between being married, having fewer children, living for fewer years in the USA, and higher levels of self-reported health with working memory and attention. Finally, higher levels of cognitive reserve were associated with improved accuracy on a working memory task (Zarantonello et al., 2020).

Limited evidence of age-related improvement and stability in executive function has been reported. Bielak and colleagues (2012) observed working memory improvements from 20 s to 40 s, with stable ability during the 60 s. Identification of age-related improvements in executive function may also be influenced by research designs. In a study by Hsieh and Chen (2023), cross-sectional data showed decline in alerting (attention), stopping (inhibition), and working memory, but improved cognitive flexibility and conflict control in older adults, with null effects on orienting. However, while longitudinal data show similar patterns for alerting, working memory, cognitive flexibility, conflict control, and orienting, null findings were reported for stopping. Stability in different dimensions of executive function was reported more often than improvements, with stability in working memory, inhibition, and cognitive flexibility identified in older adults in their 60 s (Pergher et al., 2019; Woodman, 2021). Stability has also been reported in more limited contexts, with declines in cognitive flexibility reported on perseveration trials but not learned irrelevance trials (Fijałkiewicz et al., 2023).

Language. A smaller number of age-related changes in language ability have been reported across included studies. Negative associations between age and verbal fluency (Grasshoff et al., 2021; Jockwitz et al., 2019; Tuokko et al., 2017, 2020), speech perception when controlling for hearing (Bilodeau-Mercure et al., 2015), and a composite language score (Perry et al., 2017) have been reported. Details on the time course of these age-related changes are sparse, with one study reporting a stable decline in verbal fluency from 50 years on (Grasshoff et al., 2021). Modulatory factors on age-related changes in language ability have also been identified, with education level positively associated with verbal fluency (Lam et al., 2013) and a composite language score (Perry et al., 2017). In one study, higher levels of education were associated with comparable performance in phonemic and semantic fluency when comparing younger and older adults (Montemurro et al., 2023). Age-related declines in more specific aspects of language ability have been reported, with slower sublexical, orthographic, phonological, and lexico-semantic processing independent of a decrease in accuracy (Froehlich et al., 2018). There is also limited evidence of age-related improvement and stability in language ability, with age positively associated with vocabulary (Krueger, 2013) and a composite language score (Neufeld et al., 2022), but not verbal fluency (Heinzel et al., 2014).

Processing speed. Nearly all included studies reported a negative association between age and processing speed (Beller et al., 2022; Borella et al., 2017; Chang and Dong, 2014; Jockwitz et al., 2019; Karlamangla et al., 2017; Malagurski et al., 2020; Perry et al., 2017; Roldán-Tapia et al., 2012; Tuokko et al., 2017, 2020). Regarding the time course of these age-related changes, processing speed continued to decline until around 60 years in one older adult longitudinal study from the United Kingdom (James et al., 2022), while an earlier decline beginning after age 40 after initial improvements in the 20 s was identified in a secondary analysis of cross-sequential data from Australia (Bielak et al., 2012). Processing speed appears to be modulated by factors also shown to influence other learning-related cognitive abilities, with positive associations identified with activity level (Bielak et al., 2012), education level (Borella et al., 2017; Li et al., 2017), SES (Li et al., 2017), and cognitive reserve (Roldán-Tapia et al., 2012). Few studies reported age-related improvements and stability in processing speed. Only one study observed a positive association between age (continuous variable) and processing speed as measured by the Digit Symbol Substitution Test (Krueger, 2013). However, this improvement may be

attributable to higher levels of education which were also positively associated with age within their sample. Stable processing speed during aging has also been reported in older adults with a mean age in the 60 s (Bakhtiari et al., 2023) and 70 s (Ossher et al., 2013).

General cognition and intelligence. Findings reported across included studies related to general cognition and intelligence varied considerably. Negative associations were identified between age and reasoning (Borella et al., 2017; Jockwitz et al., 2019; Roldán-Tapia et al., 2012), problem solving (Roldán-Tapia et al., 2012), creativity (van Eersel et al., 2015), fluid intelligence (Zhao et al., 2019), and composite general cognition scores (Bertola et al., 2019; Chang and Dong, 2014; Li et al., 2017). The time course of age-related declines varied based on the specific dimension of general cognition or intelligence investigated. Numeracy was found to decline steadily after later middle adulthood (Best et al., 2022), while a rapid decline in time orientation was observed after age 70 (Jin et al., 2023). Findings also support that age-related changes in general cognition and intelligence can be modulated, with positive associations identified between activity level and verbal intelligence (Bielak et al., 2012), cognitive reserve and reasoning and problem solving (Roldán-Tapia et al., 2012), and SES and both general cognition and time orientation (Jin et al., 2023; Li et al., 2017). Sex also plays a modulatory role, with males exhibiting higher general cognition (Chang and Dong, 2014; Li et al., 2017), and fluid intelligence (Nooyens et al., 2022), although this same study also reported faster general cognition and slower fluid intelligence declines in females relative to males. Modulatory influences of education on general cognition and intelligence were generally beneficial, but the pattern of reported findings varied based on the specific dimension investigated. Higher levels of education were associated with improved reasoning (Borella et al., 2017), higher baseline general cognition with slower age-related decline (Ruiz et al., 2023), and slower numeracy decline in older adults, which was significantly slower in males relative to females (Best et al., 2022). Conflicting reports have also identified faster decline in general cognition associated with higher levels of education (Li et al., 2017), as well as null associations (Bertola et al., 2019). Finally, age related improvements in general cognition and intelligence were also identified, with a positive association between age and verbal intelligence (Bielak et al., 2012) and abstract reasoning (Heinzel et al., 2014) observed in older (~60 s) relative to younger (~20 s) adults. Stability in general cognition and intelligence over a five year period has also been reported in older adults with a mean age in the mid-60s (Bakhtiari et al., 2023).

Socioemotional and motivation. The fewest number of included studies investigated age-related changes in socioemotional and motivation outcomes. Additionally, these studies each investigated very different aspects of socioemotional and motivation outcomes that preclude narrative generalizations. Consequently, key findings from included studies are presented separately. In one of the only studies conducted in a sample of working adults, Heidemeier and Staudinger (2015) identified a negative association between age and importance of achievement goals which was reduced by higher affective commitment and intrinsic motivation in older workers. In contrast, a positive association between age and maladaptive impact of performance-goal orientation on self-efficacy and work affect was also observed. The authors also reported that skill level, affective commitment, intrinsic work satisfaction, but not age, were positively associated with the dominance of learning approach goals relative to avoidance goals. Sex-related differences were also identified, with males having higher levels of performance-approach goals with a shift toward performance-avoidance goals as they got older. In another study in working adults, Thielgen and colleagues (2015) identified a negative association between age and the impact of discrepancies between implicit motives and explicit goals on work motivation, suggesting that older workers are potentially more capable of staying motivated at work despite the misalignment between implicit and explicit motives. Finally, Dave and colleagues (2021) identified a moderate increase in trait emotional intelligence in young

adults over four years. These increases were specifically observed in the domains of interpersonal emotional intelligence and adaptability.

3.5.2. RQ2b-c: learning-related brain changes during healthy aging and factors influencing changes

Brain structure. Included studies consistently reported age-related declines across a range of different measures of grey matter structure, a component essential for processing and interpreting information in the nervous system. Findings included age-related decreases in total brain (James et al., 2022; Montemurro et al., 2023) and total grey matter volumes (Berghuis et al., 2019), regional grey matter volume (Bilodeau-Mercure et al., 2015; Chi et al., 2022; Dahl et al., 2019; Heinzl et al., 2014; James et al., 2022; Neufeld et al., 2022; Pergher et al., 2019; Perosa et al., 2020) and cortical thickness (Bilodeau-Mercure et al., 2015; Chan et al., 2018; Jockwitz et al., 2019, 2021; Reas et al., 2020; Turney et al., 2023), as well as cortical volume and surface area (Zhao et al., 2019), and grey matter microstructure (Reas et al., 2020). Cortical and subcortical grey matter decreases associated with age were identified broadly across frontal, temporal, and subcortical regions (Neufeld et al., 2022; Zhao et al., 2019), in the networks underlying working memory (Heinzl et al., 2014; Pergher et al., 2019) and speech processing (Bilodeau-Mercure et al., 2015), in memory related structures including the locus coeruleus (Dahl et al., 2019) and hippocampus (James et al., 2022), with more specific decreases identified in the dentate gyrus, CA1, and subiculum hippocampal subregions (Chi et al., 2022), and in learning related structures including the caudate nucleus of the striatum (Perosa et al., 2020). The time course of these age-related changes was not widely investigated. Limited evidence suggests that decreases in cortical thickness are apparent from the mid-30s and beyond (Chan et al., 2018), and that hippocampal neurogenesis may peak between the ages of 40 and 50 (Yang et al., 2023). There was also limited evidence of modulatory factors on these changes, with lower current SES (Chan et al., 2018) or education level (Pergher et al., 2019), female sex (Reas et al., 2020), smoking, alcohol use, or sleep issues (Zhao et al., 2019) all associated with poorer outcomes. Interestingly, in only one study were age-related increases in cortical thickness reported, specific to the learning-related anterior cingulate (Jockwitz et al., 2021).

Comparatively fewer studies investigated age-related changes in white matter, a component which is crucial for communication within the nervous system. Age was negatively associated with total white matter volume (Montemurro et al., 2023) and integrity (Berghuis et al., 2019; Boban et al., 2022; Reas et al., 2020; Rojkova et al., 2016; Turney et al., 2023). Specifically, age-related decreases in white matter integrity have been identified in the executive function and memory-related anterior and posterior thalamic radiations (Boban et al., 2022; Rojkova et al., 2016). While no included studies specifically investigated the time course of age-related white matter changes, factors that modulate these changes were reported. While higher levels of education were associated with improved white matter integrity in older adults (Abellana-Pérez et al., 2019), null findings related to education were also reported (Boban et al., 2022; Rojkova et al., 2016). Finally, worse age-related decline in white matter integrity was also reported in female older adults relative to males (Reas et al., 2020).

Brain function. Age-related changes in brain function were most often investigated by measuring differences in fMRI blood-oxygen-level-dependent (BOLD) signal, which is correlated with neural activity. Generally, older age was associated with increased neural activity, with age-related differences observed in the left dorsal anterior insula, related to the maintenance of speech perception (Bilodeau-Mercure et al., 2015), episodic memory circuits during a naming task (Marcotte and Ansaldi, 2014), the working memory network during performance of a working memory task (Heinzl et al., 2014), parieto-frontal (Monteiro et al., 2017) and parieto-occipital areas (Berghuis et al., 2019) during motor learning, and subcomponents of the reading network during a reading task (Froehlich et al., 2018). In the case of the two studies

investigating age-related changes in brain function during motor learning, identified increases in activity were accompanied by decreased activation in subcortical areas during learning (Monteiro et al., 2017) and decreased frontal cortical deactivations after learning (Berghuis et al., 2019). Additionally, conflicting findings have been reported when investigating age-related differences in brain function during working memory tasks, with one study reporting decreased task area activity but increased non-task area activity (Archer et al., 2018). Increased activity in older adults was not always limited to the same brain structures active in younger adults, but included the engagement of two additional networks during negative feedback processing, although the same networks for general feedback were active in both age groups (Bowen et al., 2019). Negative associations between age and brain activity were also reported, specifically, decreased activity in sensorimotor networks that subserve attention and processing speed (Perry et al., 2017). Finally, age-related changes in BOLD signal patterns of activity have also been reported, with older adults exhibiting decreased frontostriatal representation of prediction errors during probabilistic learning but stable representation of non-learning reward-related outcomes (Samanez-Larkin et al., 2014), and less distinctive representations during recognition memory supporting the age-related neural dedifferentiation hypothesis (Pauley et al., 2023). While education level was reported as a positive modulator of cognitive and brain structural outcomes, null influences on BOLD signal were identified in working memory (Archer et al., 2018) and sensorimotor networks (Perry et al., 2017).

The influence of age on resting-state network dynamics was also investigated. Increased age in older adults was associated with increased global and network flexibility in the default mode network (DMN), frontal parietal network (FPN), and sensorimotor network (SMN), and decreased global network recruitment, supporting that increased age was associated with increased variability in modular organization (Malagurski et al., 2020). Older adults also exhibited increased functional connectivity in the salience/ventral attention network (VAN), but decreased resting state functional connectivity in the medial visual network (MVN), dorsal attention network (DAN), left FPN, and DMN (Montemurro et al., 2023), with highly educated older adults having lower resting state functional connectivity strength in the MVN and DMN compared to both lower education older adults and younger adults. Age was also positively associated with functional connectivity in the visual network (VN) - LN, VN - VN, VN - FPN, VAN - FPN, and DMN - FPN, but negatively associated with functional connectivity in the DMN - VN, DMN - DMN, VN - FPN, SMN - DMN, VN - SMN, DAN - FPN, LN - VN, and VAN - VN (Zhou et al., 2023). Modulation of age-related changes in resting state networks was also reported, with a positive association between current SES and resting state system segregation in middle relative to young adulthood identified (Chan et al., 2018). Finally, a positive association between age and functional connectivity in the proximal DMN was identified, with higher levels of education associated with increased distal DMN functional activity, typically observed in younger adults, higher cognitive function, and lower decline over a period of three years (Abellana-Pérez et al., 2019).

Fewer studies utilized EEG and other methods to investigate age-related changes in brain function. Across these studies, increased age was associated with decreased theta and alpha II power with decreased verbal and visuospatial memory (Reichert et al., 2016), decreased mean beta power in bilateral premotor area during motor learning (Chettouf et al., 2022), learning-related increases in theta and decreases in gamma power (Tinga et al., 2023), and a posterior shift in visually evoked gamma oscillations, despite stable cognitive performance across a range of tasks (Bakhtiari et al., 2023). Aside from age-related changes in EEG power, differences in ERPs were investigated with older adults exhibiting higher P150 amplitudes, which were positively correlated with performance on a category learning task (Schenk et al., 2016), and both decreased P200 and P300 amplitudes during a working memory task, which were positively and negatively associated with task performance,

respectively (Lubitz et al., 2017). Only two studies utilized non-fMRI or EEG methods to investigate age-related changes in brain function. In one study, transcranial magnetic stimulation (TMS) revealed the absence of hemispheric lateralization after motor learning in older adults, but still showed transfer ability (Nuzum et al., 2021). Finally, PET was used to investigate age-related changes in dopamine synthesis in the dorsal striatum which, despite decreasing with increasing age, did not influence probabilistic learning (Perosa et al., 2020).

3.5.3. RQ3: most effective interventions to improve learning

Results from included intervention studies are presented in an effect direction plot (Table 7), with further details provided in the tabular synthesis (Table 4). The effectiveness of different categories of interventions varied considerably. Across all eight categories, *Other Interventions* were the most effective, with the majority of included studies reporting positive effects on learning-related outcomes. These interventions included the use of intelligent tutor software (Azevedo et al., 2012), neurofeedback (Xiong et al., 2014), and virtual reality (Dobrowolski et al., 2021). The most widely studied intervention in this category was the MetaTutor intelligent tutor system, investigated across five separate studies (Azevedo et al., 2012, 2016; Dever et al., 2022, 2023; Duffy and Azevedo, 2015). Of the five studies using the MetaTutor system, all reported positive effects on learning. *Combined Interventions* were the second most effective category, which included any combination of two or more categories such as tDCS with mirror visual feedback (Hoff, Kaminski, et al., 2015), cognitive training with water-based exercise (Sato et al., 2015), and working memory training with aerobic exercise (Takeuchi et al., 2020). Of note is the observation that both studies investigating the effects of exergames (i.e., video games combined with exercise) reported null or mixed findings, with one study identifying positive effects on executive function and processing speed but no effect on visuospatial measures (Maillot et al., 2012), and the other only identifying improved game performance in the absence of any effects on cognitive measures (Ordnung et al., 2017).

Food or Drug Interventions were the least effective, with the majority of included studies reported null or mixed findings. Positive effects were only reported in studies investigating the effects of fish oil capsules (Külzow et al., 2016), high doses of vitamin D (Pettersen, 2017) or almonds (Rakic et al., 2022), freeze-dried blueberry powder (Rutledge et al., 2021) or a wild blueberry beverage (Whyte et al., 2021), or fermented seaweed *laminaria japonica* (Kim et al., 2022). Comparable levels of ineffectiveness can also be observed across studies investigating *Language Learning* interventions, which also generally reported null or mixed findings. One conflicting finding can be found in an included systematic review by Klimova and Pikhart (2020), which actually reported a positive impact of language learning across seven included studies. However, eligibility criteria for their review resulted in the inclusion of only studies conducted in healthy adults who were 55+ years old reporting a broader range of outcomes that were not exclusively learning-related. These difference in study eligibility, combined with a high risk of bias assessment, suggest findings from their review should be interpreted with caution.

3.5.4. RQ3a-c: effects of interventions and factors influencing efficacy

Effects on cognitive function. Learning-related cognitive outcomes were the most widely investigated outcomes across included studies. Positive effects were observed across all dimensions of learning-related cognitive outcomes including *Learning and Memory* (e.g., Azevedo et al., 2012; Park et al., 2014), *Executive Function and Attention* (e.g., Berryhill and Jones, 2012; McDougall and House, 2012; Reis et al., 2016; Xiong et al., 2014), *Language* (e.g., Bugos and Wang, 2022; Pfenninger and Polz, 2018), *Processing Speed* (e.g., DuPont, 2018; Yang et al., 2021), *General Cognition and Intelligence* (e.g., Jackson et al., 2012), and *Socio-emotional and Motivation* (e.g., Alves, 2013; Delhom et al., 2020). Specifically, the largest number of included studies reported positive effects of interventions on memory (e.g., spatial memory, episodic memory),

learning (e.g., motor learning, verbal learning), and working memory outcomes. However, the presence of conflicting reports suggests that the effects of any given intervention were not universally positive.

Despite the large number of positive effects on memory, learning, and working memory outcomes reported, null or mixed findings were also identified, often in the presence of positive benefits in other dimensions of cognitive function. In their study investigating the effects of 6 months of brain training or action game experience in older adults (60+ years), McDermott and colleagues (2013) reported that both groups showed improvement on measures of attention in the absence of any improvements in short term memory. Negative effects on learning have been reported in older adults after a one-year treatment regime with lutein and zeaxanthin (Lindbergh et al., 2018), and in younger adults after transcranial random noise stimulation (tRNS; Fertonani et al., 2019). Finally, despite positive reports of benefits associated with working memory training in older adults (Payne and Stine-Morrow, 2017; Stepankova et al., 2014), both empirical studies (e.g., Jaeggi et al., 2020), and systematic reviews (Sala et al., 2019) have identified null effects or limited benefits, which often only manifested on tasks that participants were initially trained on, if improvements emerged at all.

Baseline levels of cognitive function and, to a lesser extent, brain structure or function, were the most widely-reported modulatory factors on the effectiveness of interventions to improve learning-related cognitive function. Improved effectiveness of interventions was associated with both higher and lower baseline cognitive function. Stine-Morrow and colleagues (2014) reported that inductive reasoning training improved inductive reasoning and creative problem-solving training increased divergent thinking in older adults, but larger gains were associated with higher baseline cognition. Similarly, memory training improved performance on trained and untrained tasks, with higher gains in those with higher baseline memory and cognition (Rosi et al., 2018). On the other end of the spectrum, only those older adults with lower baseline working memory or memory showed improved working memory after tDCS (Au et al., 2022), or memory and cognitive flexibility after a Dejian mind-body intervention (Chan et al., 2014), respectively. Finally, older adults with better brain fiber integrity showed increased gains in cognitive flexibility after Tai chi training (Wu et al., 2021), while those with brains that were more similar to younger adults showed improved working memory, processing speed, executive function, and reasoning after working memory training on an n-back task (Heinzel et al., 2014). Interestingly, modulatory influences of baseline cognitive function or brain structure or function were only reported in older adult samples.

Age was also identified as a significant modulatory factor. In one study (Sandberg et al., 2014), process training was found to improve working memory and inhibition in both younger and older adults, but intermediate transfer to more complex working memory tasks was only observed in younger adults. Following a similar pattern, interleaved practice was found to improve motor learning in both younger and older adults, but benefits were larger in younger adults, attributed to their higher brain network efficiency (Lin et al., 2016). One systematic review reported that online tDCS improved executive function, learning, and memory in older adults, but effects were larger with increasing age (Lee et al., 2021). Other studies reported interactions between treatment format and age, with long lag retention intervals more effective in improving memory in younger adults, while short lag intervals were better for older adults (Maddox, 2013). Finally, age was found to negatively modulate the effects of interventions, with tRNS leading to decreased perceptual learning in younger adults but null effects reported in older adults (Fertonani et al., 2019), and paired associative stimulation resulting in decreased motor learning in older adults, but null effects in younger adults (Opie et al., 2019).

An intervention's duration or dose was also found to modulate its effectiveness. While working memory improvements were reported in older adults after both 10 and 20 sessions of working memory training, larger improvements in visuospatial skills were associated with a larger

number of sessions, showing a dose-response effect (Stepankova et al., 2014). Similarly, vitamin D-related improvements in visual memory and learning (Pettersen, 2017), and almond-related improvements in visuospatial working memory, visual memory, visual learning, spatial planning, and working memory (Rakic et al., 2022) were only associated with the highest treatment dose conditions. Additional studies that did not include separate duration or dose conditions also reported positive associations between exposure to the intervention and effectiveness. In one case, participants who received the same amount of freeze-dried blueberries showed differences in cognitive flexibility and learning improvement associated with postprandial levels of plasma phenolic compounds (Rutledge et al., 2021).

Finally, unlike studies investigating age-related cognitive and brain changes, few intervention studies reported a modulatory influence of education level on effectiveness. In two studies, positive effects of tDCS on working memory in older adults only emerged in those with higher levels of education (Berryhill and Jones, 2012; Johnson et al., 2022). Modulatory effects of education level on intervention effectiveness were also identified in combination with other modulatory factors. Kalbe and colleagues (2018) reported that cognitive training with physical activity or both physical activity and counseling led to improved general cognition and verbal long term memory in older adults, with bigger gains associated with lower baseline cognitive function, education level, brain-derived neurotrophic factor (BDNF) levels, and higher insulin-like growth factor 1 (IGF-1) levels. In contrast, one systematic review identified that memory training in adults was more impactful in those who were younger and with higher education level (Roheger et al., 2021).

Effects on brain structure or function. Fewer intervention studies focused on brain-based outcomes compared with cognitive outcomes. Included studies investigated ways of improving both brain structure and function, with a larger proportion of included studies focusing on ways to modify brain function. Of the small number of studies focusing on improving brain structure, all were conducted in samples of older adults who were generally around the age of 60 years or above. The most consistent benefits were obtained from studies investigating the effects of piano training, which was associated with increased grey matter volume in contralateral M1, putamen, and thalamus, accompanied by increased fine motor skills and working memory (Worschech et al., 2023), increased whole brain, caudate nucleus, Rolandic operculum, and inferior cerebellum grey matter volume, associated with improved working memory (Marie et al., 2023), increased cortical thickness in left Heschl's gyrus, left planum temporale, bilateral superior temporal sulcus, & right Heschl's sulcus (Worschech et al., 2022), and reduction of age-related decline in fornix fiber density, associated with improved episodic memory (Jünemann et al., 2022). Beyond piano training interventions, Tai chi exercise was associated with increased total brain volume and performance on a range of cognitive tasks (Mortimer et al., 2012), while participation in dance led to increased volume in the left precentral gyrus (Müller et al., 2017), as well as the cingulate, insula, corpus callosum, and sensorimotor cortex (Rehfeld et al., 2018). While significant differences in brain structure were observed between treatment groups in these two studies, they were not associated with differences across cognitive measures. No included studies reported modulatory factors influencing the efficacy of these interventions.

Interventions to improve brain function investigated a more diverse range of outcomes in comparison with studies focused on brain structure. These outcomes included changes in fMRI-based BOLD signal and functional connectivity, EEG-based measurement of ERPs and frequency band dynamics, and measurement of plasma levels of chemicals that influence learning-related brain function such as BDNF. The most consistently reported finding across interventions to improve brain function was increased levels of plasma BDNF. In two similar studies, participation in a dance intervention by older adults increased plasma BDNF levels, with cognitive improvements observed in attention in both studies, as well as verbal memory (Müller et al., 2017) and spatial memory (Rehfeld et al., 2018). Differences in intervention duration

between these two studies modulated reported cognitive improvements, with improved attention and spatial memory observable at six months, but verbal memory improvements only observable at 18 months. Participation in gross motor activities also led to increased plasma BDNF, although there was no relationship with cognitive function (Grégoire et al., 2019). Finally, older adults taking fermented seaweed *laminaria japonica* showed not only increased plasma BDNF, but other learning and memory-related chemical including human growth hormone (HGH) and IGF-1, as well as improved general cognition, learning, and spatial memory (Kim et al., 2022).

Interventions studies using fMRI-based measures differed considerably in their intervention format and brain regions of interest, precluding the identification of broader patterns of findings related to the function of specific brain regions. Generally, increases in BOLD signal after intervention were associated with improved brain function. Increases in BOLD signal were reported during interleaved practice, with activity positively associated with motor sequence learning (Lin et al., 2012). Participation in goal-oriented attentional regulation training also led to increased BOLD signal in right frontal, parietal, and temporal regions, which was associated with improved memory (Adnan et al., 2017). However, increased BOLD signal has also been associated with negative cognitive outcomes, including decreased verbal learning associated with increased BOLD signal in the left dorsolateral prefrontal cortex and anterior cingulate cortex after treatment with lutein and zeaxanthin in older adults (Lindbergh et al., 2018). In one study, effects of interleaved practice were modulated by participant age, with increased BOLD signal observed in the dorsolateral prefrontal cortex in younger adults, but in the rostral prefrontal cortex and sensorimotor regions in older adults. This finding suggests that older adults may rely on compensatory mechanisms in support of improved learning compared with younger adults (Lin et al., 2012). Additionally, the effects of intermittent theta burst stimulation (iTBS), a form of brain stimulation, on functional connectivity were also modulated by age, with younger adults exhibiting increased functional connectivity in the distal DMN, while increases in older adults were found in the proximal DMN (Abellaneda-Pérez et al., 2019). Older adults who showed functional connectivity changes similar to younger adults after iTBS had improved cognitive performance during baseline and three years later.

Similar to intervention studies utilizing fMRI-based measures, no consistent pattern of results emerged across intervention studies using EEG-based measures. Mindfulness training was associated with increased N2 amplitudes and decreased P3 amplitudes, accompanied by improved attention, suggesting more efficient processing of task stimuli in both younger and older adults (Moore, 2013). In contrast, increased P3 amplitudes and improved working memory were observed after multidomain cognitive training in older adults (Hong et al., 2021). Increased amplitude of ERPs associated with early speech encoding and improved working memory were observed after combined tDCS and music listening in older adults (Bidelman et al., 2022). Measurement of brain function using non-ERP measures also revealed positive effects of interventions. Resistance training led to increased beta and gamma band activity during tasks and improved processing speed, attention, learning, and memory in older adult women (DuPont, 2018), while neurofeedback training led to increased alpha and theta relative power, with increased frontal theta associated with increased alpha power and spatial reasoning in older adults (Reis et al., 2016). Finally, in one study, the effects of tDCS on brain function were modulated by education level, with increased theta network synchrony, theta-gamma phase amplitude coupling, and working memory observed in older adults with higher education level (Johnson et al., 2022).

3.6. RQ4: current knowledge gaps

Notable knowledge gaps were observed for each of the present systematic review's RQs. Across all three RQs, included studies predominantly focused on younger adults (20–40 years) and older adults (60

years or older), with a noticeable lack of research targeting middle-aged adults (40–59 years). Most significant was the lack of studies evaluating the effects of interventions to improve learning in middle-aged adults, which constituted less than 10 % of included studies for RQ3. Interestingly, studies included for RQ3 investigating the effectiveness of interventions aimed at improving brain structure focused exclusively on samples of older adults.

Most studies included across all three RQs were conducted in Western countries, highlighting a significant lack of diversity in cultural context. Studies conducted in Western contexts always constituted the vast majority of included studies, ranging from 79 % to 92 % across the three RQs. Of note is the observation that only one study for RQ1 utilized a worldwide dataset collected using the Internet (Geyer et al., 2015). This latter finding was surprising given the highly-developed data collection capabilities of Internet-based tools introduced in the 2000s (e.g., MTurk, Gorilla).

Methodological decisions led to a disproportionate reliance on exclusively laboratory-based investigation, ranging from 66 % to 81 % across studies included for each RQ. Consequently, there is a significant gap in our understanding of how learning-related cognitive and brain changes associated with healthy aging manifest in the real world. Methodological trends were also behind the high number of cross-sectional studies identified in the present review. The majority of studies included for RQ1 and RQ2 were cross-sectional, providing snapshots of learning at specific points in time but creating a gap in our understanding of how learning abilities change over time in the same person. In contrast, most intervention studies were longitudinal.

Finally, analysis of the aims and measures of studies included for RQ1 revealed a strong focus on assessment of cognitive outcomes including learning, memory, executive function, and processing speed. In contrast, there was limited investigation of the socioemotional aspects of learning, which were only addressed in 5 % of included studies. Studies included across the cognitive dimensions of RQ1 also generally focused exclusively on decline in older adults with little to no attention given to potential areas of cognitive growth or stability. Finally, the majority of intervention studies included for RQ3 investigated either cognitive-based or lifestyle interventions. These studies tended to have a very narrow scope, often focusing on immediate improvements primarily in cognitive outcomes.

4. Discussion

Recent trends in global aging and workforce dynamics necessitate a comprehensive understanding of learning during adulthood. The present systematic review contributes to this goal by synthesizing findings from 265 published and unpublished studies investigating learning-related cognitive and brain changes during healthy aging, and interventions aimed at improving learning. Findings from included studies generally support the conclusion that healthy aging during adulthood is associated with negative outcomes in cognitive function and brain structure and function. These age-related deficits typically manifested as lower speed or accuracy on tasks measuring cognitive function, or decreased measures of structural integrity or functional efficiency on brain-based measures. Despite extensive support for age-related decline in cognition and brain structure and function, stability and, to a lesser extent, improvements were also reported. Importantly, the present review identified a number of interventions, ranging from participation in physical exercise to learning how to play the piano, that positively impacted on this decline, sometimes restoring cognition or brain structure or function to levels comparable to younger adults.

Although some fairly consistent patterns of findings emerged across included studies, notable heterogeneity, some anticipated and some not, was seen in a number of cases. Expectedly, findings differed significantly based on the specific dimension of cognition or brain structure or function under investigation. Age-related changes in learning-related cognition or brain structure or function, as well as the efficacy of

interventions to improve learning, were modulated by a range of participant-level variables. Accordingly, the general interpretation of findings will focus on the most consistent patterns of results across included studies. First, we will discuss patterns of results observed across studies on cognition and brain structure and function. Evidence for decline versus stability or improvement will be discussed separately. Next, we will discuss findings related to the efficacy of interventions to improve learning. The discussion will then focus on the influence of modulatory factors on outcomes of interest. Finally, we will discuss limitations, and implications for the findings of the present systematic review.

4.1. Decline during healthy aging

Aligning with previous systematic reviews, we identified significant evidence in support of age-related cognitive and brain structural and functional decline in healthy adults. This decline was evidenced across all dimensions of learning-related outcomes investigated, but the pattern of findings differed based on the specific dimension. Age-related declines in processing speed were the most consistently reported finding across included studies. These declines generally began during middle adulthood (Bielak et al., 2012), but potentially leveled off in later adulthood (Bakhtiari et al., 2023; Ossher et al., 2013). This observed pattern of results aligns with older theoretical accounts of aging which place an emphasis on declining processing speed (Salthouse, 1996), and findings from more recent systematic reviews (Seblova et al., 2020). From a structural perspective, these declines paralleled identified age-related decreases in both the volume (Montemurro et al., 2023) and integrity (Berghuis et al., 2019; Boban et al., 2022; Reas et al., 2020; Rojkova et al., 2016; Turney et al., 2023) of white matter structures. The morphology of white matter structures impacts significantly on the ability to perform timed behavioral tasks given the crucial role these structures play in transmitting essential task-relevant information throughout the brain (Turken et al., 2008). Functionally, these declines mirrored age-related decreases in brain activity in sensorimotor networks subserving core cognitive functions (Perry et al., 2017). Age-related declines in processing speed are also thought to underlie reported declines in other dimensions of cognitive function. Specifically, reported declines in memory and other fluid abilities associated with increased age parallel processing speed declines (Finkel et al., 2007). Findings from the present review further support the assertion that decreases in processing speed drive age-related declines in fluid but not crystallized abilities as observed declines in language ability were generally limited to verbal fluency (Grasshoff et al., 2021; Jockwitz et al., 2019; Tuokko et al., 2017, 2020). This same pattern is observed across measures of executive function, especially in the dimension of working memory (Archer et al., 2018; Borella et al., 2017; Chang and Dong, 2014; Geyer et al., 2015; Heinzl et al., 2014; Jin et al., 2023; Klencklen et al., 2017; Lam et al., 2013; Lubitz et al., 2017; Pliatsikas et al., 2019; Rhodes and Katz, 2017). It should be noted that the mixed nature of findings observed across most other fluid domains of cognitive function in the present review may reflect reported heterogeneity in the trajectory of age-related white matter morphological changes (Nilsson et al., 2014).

The present review also identified consistent reports of memory decline during healthy aging. Age-related memory declines were generally identified in explicit memory, most often on measures of episodic memory (Bielak et al., 2012; Chang and Dong, 2014; Chi et al., 2022; Howe et al., 2020; Jin et al., 2023; Karlamangla et al., 2017; Li et al., 2017; Mohammad et al., 2020; Vance, 2022; Zahodne et al., 2017), mirroring a similar decline in explicit learning such as verbal learning (Dahl et al., 2019; James et al., 2022; Montemurro et al., 2023; Tuokko et al., 2017, 2020). Similar age-related declines were also observed in both structural (Boban et al., 2022; Chi et al., 2022; Dahl et al., 2019; James et al., 2022; Rojkova et al., 2016) and functional (Marcotte and Ansaldi, 2014; Reichert et al., 2016) measures of brain

regions involved in memory. Memory decline, including explicit memory specifically, has regularly been reported in the literature, with episodic memory thought to be the first form of memory to show decline during healthy aging (Tromp et al., 2015). This decline in episodic memory is thought to parallel morphological and functional changes in frontal structures as opposed to hippocampal changes associated with Alzheimer's disease (Wang et al., 2006). While memory decline is a normal part of healthy aging, there is considerable heterogeneity in memory trajectories across older adults. Interestingly, one included study noted that even those adults who maintain previous levels of memory function still experience declines in their own confidence in that memory (Ossher et al., 2013). Lower memory confidence despite stable function in older adults may represent the influence of negative stereotypes about memory and aging. While not investigated by any included study, previous findings support that memory in older adults is negatively impacted by knowledge of these stereotypes (Armstrong et al., 2017). However, positive influences of these and similar stereotypes have emerged under certain conditions in other domains of cognitive function including working memory (e.g., Barber and Mather, 2013).

4.2. Stability and improvement during healthy aging

While less consistently reported, we identified evidence for stability and improvement in learning-related cognitive and brain outcomes during healthy aging. Similar to evidence supporting decline, the specific pattern of findings differed across dimensions of cognitive function and brain structure and function. Older adults showed evidence of stable implicit cognitive functions including motor learning (Berghuis et al., 2019; Bhakuni and Mutha, 2015; Hoff, Trapp, et al., 2015; Monteiro et al., 2017; Nuzum et al., 2021) and visuomotor memory (Wang et al., 2022). This pattern of results parallels previous findings in support of stable implicit cognitive functions, despite simultaneous decline in explicit abilities (Mitchell and Bruss, 2003). These findings are generally cited in support of distinct systems underlying implicit and explicit functions, although these claims are contentious (Ward et al., 2013). Observed stability in these dimensions of cognitive function, especially in light of considerable evidence supporting decline, suggests that older adults may rely on compensatory mechanisms to maintain function, with evidence observed in measures of cognition (Schenk et al., 2016; Wang et al., 2022; Worthy et al., 2014) and brain function (Lin et al., 2012).

In contrast with age-related declines in fluid abilities, we observed evidence for improved crystallized abilities. This pattern was evidenced in studies investigating age-related differences in language outcomes, although the total number of included studies in this area was extremely limited. Positive associations between age and measures of vocabulary were reported in older adults (Krueger, 2013; Neufeld et al., 2022), aligning with findings reported in a previous meta-analysis (Verhaeghen, 2003). This finding is noteworthy as similarly-aged participants generally demonstrated age-related declines in other language-related outcomes including verbal learning (e.g., Dahl et al., 2019), memory (e.g., Rojas et al., 2022), and fluency (e.g., Grasshoff et al., 2021). One explanation for this dissociation relates to the nature of tasks used to assess these outcomes. Unlike measures of verbal learning and memory, assessments of vocabulary do not require a participant to acquire or recall any new words, a task that would likely be difficult for older adults given age-related declines in explicit learning and memory identified across included studies. Additionally, performance on assessments of verbal fluency is highly influenced by executive function, which also shows strong age-related decline (Amunts et al., 2021; Whiteside et al., 2016). Taken together with evidence of fluid ability decline driven by age-related decreases in processing speed (Finkel et al., 2007) and white matter integrity (Turken et al., 2008), older adults would only be expected to demonstrate stable or improved performance on assessments that measure crystallized aspects of

language. This pattern of results can also explain reports of stable or improved intelligence in older adults as widely-used intelligence tests (e.g., Wechsler Adult Intelligence Scale; Wechsler, 2008) generally rely on language assessments that are not highly sensitive to executive function (Bakhtiari et al., 2023; Bielak et al., 2012).

4.3. Effective interventions

Across all intervention categories, *Other Interventions* and *Combined Interventions* were the most effective. Interventions classified as *Other Interventions* were those that did not fit into any other intervention category. These interventions, with few exceptions, tended to utilize technology including EEG devices (e.g., Xiong et al., 2014) and AI-based software (e.g., Azevedo et al., 2012). While effective, the high costs associated with the technology required to implement these interventions may limit their positive impact in adult populations that would benefit most. This point is especially relevant as SES was identified as a significant modulator of age-related changes in learning across included studies, suggesting that lower SES adults were likely to benefit most from these interventions, but might be least likely to be able to afford them. Additionally, while promising results were observed in studies using AI-based software (Azevedo et al., 2012, 2016; Dever et al., 2022, 2023; Duffy and Azevedo, 2015), effects on learning were limited exclusively to an educational context generally experienced by undergraduate students, calling into question whether such tools could have broader effects for adults across diverse contexts. Promising results were also reported across included *Combined Interventions* studies, with positive effects on learning-related outcomes associated with the combination of interventions that were generally ineffective if used alone. This pattern was most noticeable across *Combined Interventions* studies that included *Language Learning* (Ferguson et al., 2023; Sheffler et al., 2023) or *Food or Drug Interventions* (Formica et al., 2020; Lenze et al., 2020). These findings support that the benefits of combining different interventions may be broader, extending beyond only studies combining cognitive and physical interventions (Zhu et al., 2016).

Less promising results were obtained across studies investigating *Language Learning* and *Food or Drug Interventions*. There is considerable support that bilingualism, the use of more than one language, confers non-linguistic benefits on cognitive function (Antoniou, 2019; Bialystok and Craik, 2022), although conclusions from previous research syntheses differ based on the estimated role of factors such as publication bias (Lehtonen et al., 2018; Van den Noort et al., 2019). While positive benefits of bilingualism on cognitive function have been reported across the developmental spectrum, these effects are most consistently found in older adults (Ware et al., 2020). There is also growing evidence that bilingualism can support the development of cognitive reserve, reducing the prevalence or delaying the age of onset associated with dementia (Alladi et al., 2013; Perani et al., 2017). Null findings across many *Language Learning* intervention studies may relate to the ignorance of how these interventions impacted on separable dimensions of language experience, and the exclusion of these differences when modeling effects on cognitive and brain outcomes. Bilingualism is a complex, multi-dimension experience showing considerable heterogeneity across individuals that cannot be sufficiently captured using categorical labels (Dash et al., 2022; Gullifer et al., 2021; Luk and Bialystok, 2013). Differences in second language proficiency, dominance, and immersion, while generally ignored during analysis (Privitera, Momenian, et al., 2023b), are nontrivial and are associated with variability in executive function (Privitera et al., 2022; Privitera, Momenian, et al., 2023a). Additionally, the impact of bilingualism on cognitive outcomes may be influenced by the pair of languages spoken, with use of two “distant” languages associated with more significant effects on executive function (Carthey-Goulart et al., 2023). As included *Language Learning* intervention studies did not account for these nontrivial differences across participants, it is unclear whether graded benefits of language learning do exist, but could not be identified due to analysis methods used. It may

also be the case that longer durations of experience with a second language are needed before positive benefits emerge in learning-related outcomes. While not investigated by any included studies, the effects of *Language Learning* interventions of shorter duration may be more pronounced in samples of participants who previously experienced language attrition and are regaining proficiency (Kendro, 2019). Similar patterns of null findings were reported across included *Food or Drug Interventions*. While included studies generally had participants self-report levels of adherence to interventions, insuring that self-reports reflect the true behavior of participants is challenging in intervention studies (Vitolins et al., 2000). For this reason, it is unclear whether the high proportion of null findings is due to the ineffectiveness of the intervention being studied, or due to participants not adhering to the intervention. Alternative measures of treatment fidelity could provide stronger support for adherence to a given intervention, and should be taken into considering during analysis.

4.4. Modulatory factors

Education level and SES (sometimes operationalized as income level) were the most consistently reported modulatory factors on learning-related cognition, brain structure, and function. Positive associations between education level and all dimensions of cognitive function were reported with the exception of learning and socioemotional and motivation outcomes. These same positive associations were reported across different measures of brain structure and function, and impacted on the efficacy of inventions to improve learning. Both higher education and SES are associated with higher cognitive reserve, which can explain observed positive effects on cognitive and brain outcomes (Barulli and Stern, 2013; Stern, 2002). While the presence of null reports suggests that higher levels of education and SES are not universally beneficial across all learning-related measures investigated in the present review (e.g., Diwadkar et al., 2016), there is still considerable evidence in support of a positive modulatory influence. This trend aligns with previous reports of a broader modulatory impact of both education level (Cutler and Lleras-Muney, 2012) and SES (Luo and Waite, 2005) on a diverse range of health outcomes. While SES seems to be influential across the lifespan, with both childhood and adult SES showing consistent modulatory influences on learning-related outcomes, the impact of education level might be most important from early life to young adulthood, building a foundation that can positively impact on later life cognitive function (Kremen et al., 2019). It is important to note that, despite strong associations between education level, SES, and learning-related outcomes, there is presently no consistent evidence supporting a causal link (Adams et al., 2003; Albarrán et al., 2020; Clark and Royer, 2013).

Intervention studies showed a different pattern of results, with little evidence supporting a modulatory role of either education level or SES on effectiveness. A participant's level of baseline cognitive function was the most widely-reported modulatory factor on the effectiveness of an intervention. The pattern of modulation differed based on the specific cognitive or brain outcome under investigation and was only reported in older adult samples. While only a small number of studies investigated factors modulating intervention effectiveness, included studies suggest that interventions aimed at improving executive function are perhaps more effective in older adults with lower cognitive function (Au et al., 2022; Chan et al., 2014), while other interventions are more effective in those with higher baseline function (Rosi et al., 2018; Stine-Morrow et al., 2014). This pattern of results may be attributable to ceiling effects on measures of executive function that would preclude the identification of improvements after completing an intervention unless participants demonstrated lower baseline performance. Together, these findings highlight the importance of assessing baseline cognitive function, adopting measures sensitive enough to detect change, and using analysis methods that account for nontrivial individual differences across participants when investigating the effectiveness of an

intervention. These steps are especially important considering that participants in a given age group are likely to show considerable heterogeneity in any cognitive or brain measure, a claim further supported by inconsistent modulatory effects of age on intervention effectiveness observed in the present review (Table 7). Modulatory effects of intervention dose or duration were also identified, with higher doses and longer durations consistently showing larger effects on learning-related outcomes. Taken together with patterns of null and mixed findings reported across included intervention studies, it is possible that the most effective level of exposure to a given intervention was not investigated. While findings from some intervention studies can be interpreted as evidence that higher doses are always more effective (Pettersen, 2017; Rakic et al., 2022; Stepankova et al., 2014), it is likely the case that positive effects plateau after an optimal level of exposure (e.g., Belleville et al., 2022).

4.5. Limitations

The present systematic review's findings should be considered in light of a few limitations. Because our review focused exclusively on research conducted in healthy adult samples, findings may not be generalizable to adults living with psychiatric or neurological conditions that impact on learning. Additionally, heterogeneity in how learning was operationalized across included studies likely prevents the drawing of broad conclusions regarding learning-related cognitive and brain changes during healthy aging. This heterogeneity also precluded the conduct of a quantitative synthesis, preventing the generation of overall effect estimates across studies. On a related note, mechanisms underlying observed changes in learning-related outcomes likely differ considerably across the diverse range of interventions included in this review. Consequently, conclusions drawn from our results should be limited to the effectiveness of a given intervention on learning-related outcomes and factors that modulate that effectiveness. Because the vast majority of included studies were conducted in Western contexts, findings should be applied to other cultural contexts with caution. Finally, excluding documents not written in English may have limited the comprehensiveness of the searches, providing an incomplete picture of existing research.

4.6. Implications for practice and policy

Nations around the world are grappling with the challenge of an aging workforce, prompting governments and corporations to seek ways to extend the productive lives of their workers. People around the world are living longer, resulting in a significant global increase in the proportion of older adults aged 65 and above (United Nations, 2022). The World Bank estimates that in 2022, individuals aged 65 and above constituted 19 % of the population in high-income countries, with projections indicating a surge to 28 % by 2050 (World Bank, n.d). This demographic shift necessitates policies and practices to support organizations in leveraging the potential of mature workers through upskilling and reskilling training to ensure that participation rates among older workers remain high, and that workers stay productive. The present systematic review offers valuable insights to policy makers and training providers looking to optimize adult learning and create a conducive adult learning environment to extend productive years.

Major implications from the present review include better accommodating older workers in light of age-related declines in learning-related abilities. Considering the stable decline in fluid dimensions of cognition including processing speed and executive function, along with parallel declines in white matter integrity, steps should be taken to provide older workers with additional time to process essential information. However, steps should be taken to avoid assigning less cognitively demanding tasks to older workers based on the false expectation that age-related declines in learning-related abilities would negatively impact the quality of their work. Cognitive stimulation in the workplace

is a crucial positive factor and may reduce the age-related declines in cognition (Marqu   et al., 2010). Additionally, work or learning environments should be design in such a way as to avoid distractions in support of preventing the allocation of limited attentional resources to irrelevant stimuli (Rodrigues and Pandeirada, 2015). Finally, due to age-related declines in explicit memory, the use of memory supports that supplement capabilities of older adults should be considered (Tamez, 2012). However, it is absolutely crucial that appropriate training be provided in order for older workers to learn how to best use these tools in support of their work, and to reduce the stress associated with the adoption of new technology (Charness, 2023).

The present review also provides limited insights that may inform the development of workplace training programs. While limited to the context of a tertiary learning environment in samples of young adults, included studies investigating the effects of AI-based tutoring software report promising results (e.g., Dever et al., 2023). Extending these tools into the context of workplace learning has the potential to positively impact not only the learning of relevant content, but on the training of metacognitive and self-regulated learning strategies that may benefit future learning. Training providers may also want to consider ways in which programs can be gamified in order to exploit intact reward-based learning capabilities used in older adults to support the accomplishment of desired learning objectives (Bowen et al., 2019; Samanez-Larkin et al., 2014; Worthy et al., 2014). Additionally, the structure of workplace training programs can potentially be informed by findings from research on effective methods for learning new information during adulthood, including adopting opportunities for interleaved practice (Lin et al., 2012, 2016). Because the format of workplace training programs varies considerably across industries, and the goals of these programs often differ from those examined in the studies included in this review, the insights described above should not be considered universally applicable.

Given the significant positive modulatory influence of education level on learning trajectories, steps should be taken to ensure easy access to high quality education. However, as the positive benefits associated with high levels of education are most impactful prior to the end of young adulthood (Kremen et al., 2019), access during early life and adolescence is of the upmost importance. Relatedly, steps should be taken to increase socioeconomic equity given the positive influence of SES on a number of learning-related outcomes. As most studies focused on current levels of SES, with null findings regarding the impact of childhood SES on adult learning (Chan et al., 2018), identifying initiatives that can reduce income disparities in adults should be a key focus. It must be noted, however, that despite strong support for positive relationships between education level, SES, and learning-related outcomes in adults, there is presently no conclusive evidence for a causal link.

Finally, the prioritization of interventions to improve learning can also be informed based on findings from the present review. The most significant implication is that different categories of interventions should be combined, when possible, in order to maximize the positive effects on learning-related outcomes. Taking the positive results of *Combined Intervention* studies into consideration, developing a model in which participants are free to pick from multiple interventions based on personal interest may be most impactful while simultaneously respecting the preferences of adult learners. A combined approach is especially important given the observation that interventions shown to be ineffective alone had positive effects in combination with other interventions. Importantly, mixed results associated with more resource-intensive interventions such as brain stimulation suggest that funding can be allocated to less costly options without a potentially negative impact on effectiveness. Steps should be taken to ensure that interventions are accessible to all adults irrespective of SES, and that marketing initiatives are aimed not only at older adults experiencing age-related decline, but younger and middle-aged adults who may experience long-lasting benefits into older adulthood. This is especially relevant in the context of *Language Learning* interventions as they likely

contribute to cognitive reserve (Berkes and Bialystok, 2022), but possible only after extended periods of time exceeding those investigated by studies included in the present review.

4.7. Implications for future research

Research gaps reported in the present systematic review can provide guidance for future research. There is a significant need for future research to investigate learning-related cognitive and brain changes associated with healthy aging during middle adulthood. The prevalence of studies conducted in younger and older adults may reflect a strong interest in learning-related outcomes during periods of significant growth and decline, ignoring a period thought to reflect relative stability (Kremen et al., 2014). This trend, especially related to interventions to improve learning, may also reflect a wider interest in developing and testing interventions for older adults as they are more likely to exhibit measurable decline in cognitive or brain outcomes and, consequently, are more likely to show improvement across outcomes in response to interventions. This interpretation is further supported by the small number of intervention studies focused on younger adults who, based on the findings presented in this review, are least likely to exhibit measurable declines across learning-related cognitive and brain outcomes. This gap is significant as middle-aged adults may experience unique cognitive and brain changes that are not adequately characterized by the extant literature. Future research should aim to include a more balanced representation across all age groups to provide a developmentally comprehensive understanding of learning-related cognitive and brain changes during aging, and effective interventions to improve learning.

The overrepresentation of data collected in Western contexts underscores the need for future studies to focus on more diverse cultural and national settings. This lack of diversity may hinder the identification of learning-related cognitive and neural changes during healthy aging that vary across countries or cultures. For example, retirement policies vary significantly across nations, with eligibility ages ranging from the mid-50s to late 60 s depending on the industry, occupation, and gender (Peir   et al., 2012). Crucially, earlier retirement is associated with accelerated cognitive decline, a phenomenon known as the "mental retirement effect" (Rohwedder and Willis, 2010). Retirement is thought to adversely affect both cognitive and neural trajectories due to reduced mental stimulation, changes in social networks, and loss of daily structure following workforce exit (Coe et al., 2012). These effects are likely to be most pronounced among individuals with fewer resources or poorer physical and mental health, who may be forced to withdraw from the workforce prematurely (van den Berg et al., 2010). Such altered trajectories could reduce the effectiveness of upskilling and reskilling interventions, particularly if those interventions are not tailored to account for life-course and structural variation. Future research should therefore investigate how structural, socioeconomic, and cross-national factors shape learning in midlife and beyond, and how interventions can be adapted to meet the needs of diverse populations. These efforts can be supported through open science practices (e.g., Open Science Framework) and global data-sharing initiatives, which enable researchers to access more representative datasets beyond their immediate recruitment networks.

Laboratory-based investigations, while common, are often criticized for lacking ecological validity (e.g., Shamay-Tsoory and Mendelsohn, 2019). As it follows, findings identified in a highly controlled laboratory setting may not generalize to real world contexts. While the high percentage of laboratory-based studies for RQ2 was expected due to the technical requirements associated with studying brain structure or function, advances in mobile neurotechnology support the conduct of similar investigations in real world learning contexts (Babiker et al., 2019; Ko et al., 2017; Poulsen et al., 2017; Privitera and Du, 2022). Advances in other forms of technology, including virtual reality, may allow researchers to simulate real-world learning environments within

the laboratory. Specifically, the patterns of results obtained from conventional and virtual reality cognitive assessments have been shown to differ significantly (e.g., Pflueger et al., 2018). Advances in online data collection can further support moving some aspects of data collection outside of the laboratory (Rodd, 2024), a trend evidenced in a small number of included studies (Geyer et al., 2015; Rhodes and Katz, 2017; Thielgen et al., 2015; Woodman, 2021). Future research should leverage these technological advances in order to validate lab-based findings and further refine our understanding of how adult learning changes during aging in the real world. Finally, intervention studies in understudied real-world contexts—particularly workplace environments—represent a promising area for future translational work, with additional research needed to better understand adult learning and how to enhance it during the most productive years of life. To this end, one potentially fruitful path forward is the extension of AI-based software interventions into real-world work contexts. This allows the scalable personalization required and investigation into multi-dimensional variables present in natural settings. The limited availability of intervention studies conducted in real-world learning contexts prevents strong conclusions about the generalizability of the findings reviewed here. We therefore encourage future studies to examine whether the promising effects of interventions synthesized in this review can be replicated in more ecologically valid settings.

Further longitudinal research is needed to provide a better understanding of how learning changes during healthy age within the same group of participants. This need is especially crucial in light of evidence that study design can impact on the observed pattern of findings (Salthouse, 2014). While evidence was limited, the present review observed that cross-sectional designs were associated with larger ageing effects relative to longitudinal designs (e.g., Karlamangla et al., 2017). Cross-sectional data also showed a decline in alerting (attention), stopping (inhibition), and working memory, but improved cognitive flexibility and conflict control with null effects on orienting in older adults (Hsieh and Chen, 2023). In contrast, longitudinal data from the same study did not support an age-related effect on stopping. Longitudinal studies can address the extent gap in our understanding of the development and decline of learning capabilities and the factors influencing these changes. Future studies should prioritize longitudinal designs, especially using middle-aged adult samples, to best characterize learning development and dynamics. It is also important for these studies to potentially recruit larger samples than previous studies as recent evidence supports that older adults recruited today are more capable than those recruited previously, making age-related differences harder to detect (Badham, 2024).

Investigation of age-related changes in the socioemotional aspects of learning, including emotional regulation and motivation, are critical components of the learning process (e.g., Conti, 2000). These important outcomes, along with interventions aimed at improving these outcomes, were only investigated in a small number of included studies. These non-cognitive outcomes are equally influential on learning not only during early life, but throughout adulthood. Socioemotional factors also impact on the development of cognitive reserve, the maintenance of cognitive function despite age-related changes in brain structure and function (Stern, 2002). While cognitive measures are essential, they do not capture the full spectrum of factors that can significantly modulate learning. For older adults, there is also a need for studies that examine resilience factors, compensatory strategies, and areas where older adults maintain stable function or even improve as opposed to studies focusing on conventional deficit models (Mitnitski and Rockwood, 2015). The importance of investigating areas of potential growth is further underscored by the presence of studies highlighting the beneficial influence of cognitive reserve on learning-related cognitive outcomes (Roldán-Tapia et al., 2012; Zarantonello et al., 2020). Future research should more actively incorporate socioemotional measures to provide a more balanced picture of how individuals learn and develop, highlighting not only areas of decline, but areas of stability and potential growth.

5. Conclusion

The present systematic review synthesized findings from 265 studies on the Science of Learning investigating the cognitive and neural mechanisms of learning, and interventions for improvement of learning across the adult lifespan. Overall, findings support steady decline in learning-related cognitive and brain outcomes during healthy aging, but with noted stability in both crystallized and implicit functions. However, the trajectory of learning-related outcomes during middle adulthood is in need of further investigation. Technology-based and combined interventions showed considerable promise in the improvement of learning, but further work is needed to ensure that results can be replicated in real-world environments. Additionally, steps should be taken to support equitable access to these inventions for adults of lower SES as they are likely to benefit most. There is also a crucial need for future research on adult learning to recruit diverse, non-Western samples in support of better understanding cultural differences in previously reported findings, and for more thorough investigations of modulatory factors on learning trajectories and intervention effectiveness.

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