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Episodic Memory in Childhood and Old Age: The Role of Cortical Coherence

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> The present study has two major goals: (a) to identify age differences in upper limits of episodic memory performance from middle childhood to old age; and (b) to explore age differences in patterns of oscillatory cortical activity that predict later recall performance. To examine these questions, ninety-six individuals equally distributed over four age groups (9-10, 11-12, 20-25, and 65-78 years) participated in a multi-session memory-training program using a variant of the Method of Loci (MoL), a mnemonic technique for the recall of word lists. Based on lifespan theories of cognition, we hypothesize that children aged 11-12 years will profit more from instruction and training in a mnemonic skill and reach higher levels of asymptotic performance than older adults. Informed by the synchronicity hypothesis of binding, we hypothesize that local synchronization and large-scale coherence at encoding predicts subsequent episodic memory performance at the level of items, individuals, and age groups, especially in the theta frequency band. Here, we review parts of the relevant literature, summarize the rationale and design of the study, report the algorithm used for adaptive testing, and present initial results. We also highlight the role of strategic influences during feature binding at encoding, their relation to late maturation and early decline of prefrontal circuitry, and their possible contributions to observed synchrony patterns. For illustration, learning curves and preliminary analyses of subsequent memory effects are reported for one individual in each age group.

Introduction

Human learning and memory consist of separable functions that involve partially overlapping brain circuitry. Implicit memory refers to any change in behavior induced by past experience. In contrast, explicit memory includes, by definition, conscious recollection of previously experienced events or acquired knowledge. Though implicit processes may participate in them, episodic forms of learning and memory are explicit in kind, and refer to the acquisition, maintenance, and retrieval of information about experienced events, event relations, and their contexts by means of binding processes operating at various time scales. Of particular interest are processes (a) that achieve transient binding states during encoding (e.g., Treisman & Kanwisher, 1998), (b) that convert temporarily bound episodes into more permanent forms of memory (e.g., Shors & Matzel, 1997), and (c) that re-transform stored episodes into transient binding states during retrieval (LePage, Ghaffar, Nyberg & Tulving, 2000).

The goal of the present project is to link lifespan changes in episodic learning and memory (henceforth referred to as episodic memory) to maturational, senescence-related, and learning-induced changes in binding processes as assessed by EEG recordings of small-scale and large-scale oscillatory activity of the brain. Episodic memory performance sharply increases during childhood and decreases monotonically during adulthood, with accelerated decline in old age (Baltes & Lindenberger, 1997; Lindenberger & Baltes, 1997). Though portions of these age gradients reflect pre-experimental task-relevant knowledge or cohort effects (Chi & Koeske, 1983; Shae, 1996), the observed lifespan age differences are massive, and mandate a search for maturational and senescent correlates at neuronal levels of analysis.

Episodic Memory Performance Across the Lifespan

With respect to the age periods investigated in the present study, which range from middle childhood to early old age, differences between strategic and nonstrategic components of episodic memory are particularly important. The strategic component of episodic memory refers to the selection, organization, evaluation and elaboration of episodic features during encoding and retrieval. Elaboration and organization may occur spontaneously or can be elicited by instruction and training. The strategic component is generally less pronounced during recognition than during free recall, reflecting differences in the relative importance of (implicit) familiarity and (explicit) recollection. Similarly, retrieval of contextual features such as source memory, list discrimination, frequency judgments and memory for order generally is aided by recollection and open to strategic influence. In the following, we review ontogenetic changes in episodic memory, with special consideration of the strategic component.

Childhood. Learning and memory do not develop unitarily in early ontogeny. Implicit forms develop relatively fast and appear to be fully functional by early childhood. In contrast, explicit forms continue to improve well into adolescence (Kail, 2000; Murphy, McKone & Slee, 2003). Research on memory development during childhood has made relatively little contact to extant neurocognitive models of memory

organization (but see Nelson, Monk, Lin, Carver, Thomas & Truwit, 2000). Rather, the dominant research strategy has been to link age-based improvements in memory performance to general information processing constructs such as short-term memory capacity, domain knowledge, memory strategies (e.g., metamemory), and processing speed (e.g. Fry & Hale, 2000; Murphy et al., 2003). Few attempts have been made to separate these influences, to determine their relative importance and interaction, and to relate them to maturational changes in functional brain circuitry.

At the neural level, anatomical, chemical, and functional evidence suggests that prefrontal cortex and associated neural networks undergo profound age-based changes well into adolescence. Neural plasticity during corticogenesis entails the production and experience-dependent elimination of neuronal connections (Huttenlocher & Dabholkar, 1997). During brain development, the zone of maximum plasticity moves from primary sensory and motor over secondary association to prefrontal areas (Chugani, Phelps & Mazziotta, 1987). Computational models suggest that later maturing areas require input from earlier maturing areas to represent higher-order concepts (Shrager & Johnson, 1996). Thus, the slow and orderly progression of the corticotrophic wave provides a chronotopic constraint for cerebral cortex organization.

Adulthood and old age. With respect to adult development and aging, the strategic component of episodic memory performance appears to be especially impaired, probably reflecting senescent changes in prefrontal areas and associated fronto-striatal dopaminergic processing pathways (Prull, Gabrieli, & Bunge, 2000). For instance, adult age differences in recognition memory are generally smaller than age differences in recall. Within recall, adult age differences increase as a function of between-list similarity, probably reflecting older adults' disproportionate deficits in encoding context (Kliegl & Lindenberger, 1993). In line with this finding, a meta-analysis by Spencer and Raz (1995) confirmed that adult age differences in memory for context are more pronounced than age differences in memory for content.

Senescent changes in the strategic component of episodic memory are consistent with neuroanatomical, neurochemical and neurofunctional evidence demonstrating that prefrontal cortex and functionally connected basal ganglia are more strongly affected by normal aging than most other areas of the brain. In a comprehensive review of the neuroanatomical literature, Raz (2000) reported average linear reductions in brain weight and volume of about 2% per decade during adulthood, which were more pronounced for anterior parts of the brain. At the neurochemical level, changes in the catecholaminergic system, most notably dopamine, play a prominent role (Bäckman & Farde, in press). Finally, neurofunctional studies point to profound age-associated changes in the functional organization of dorsolateral prefrontal cortex (DLPFC) such as a reduction in the asymmetry of hemispheric activation (Cabeza, Anderson, Houlse, Mangels & Nyberg, 2000).

Conclusion. The late maturation of prefrontal cortex parallels the late emergence of strategic components of episodic memory in similar ways as the relatively early deterioration of certain areas of prefrontal cortex during adulthood parallels older adults' disproportionate deficits in strategic aspects of episodic memory performance.

This is consistent with Ribot's "law" (Ribot, 1882), or the empirical observation that cognitive functions appearing late during phylogeny and ontogeny are among the earliest to show signs of decline during adulthood and old age (e.g., last in, first out).

Despite this lifespan parallelism, it needs to be kept in mind that the neuronal contexts of maturation and senescence differ radically. In the present context, two differences seem especially relevant. First, older adults possess a larger repository of biographically acquired world knowledge, or semantic memory, than children, and this difference is likely to influence the ways in which memory episodes are being formed, stored, and retrieved. Second, nonstrategic components of episodic memory supported by medio-temporal brain circuitry may be perfectly functional in middle childhood but impaired in older adults, the latter reflecting senescent changes in hippocampus and entorhinal cortex. In line with this neurobiological evidence, older adults are disproportionately impaired at forming and retrieving associations between several tobe-learned features, such as item-item or item-context associations (Chalfonte & Johnson, 1996; Naveh-Benjamin, 2001). This second set of observations is consistent with the general proposition, advanced by lifespan theories of cognition (Lindenberger, 2001), that children possess greater amounts of behavioral and neuronal plasticity than older adults. Hence, we expect that children will show greater performance gains, more reliable associative binding processes, and a greater degree of functional reorganization after acquisition and training of a mnemonic skill than older adults

EEG Recordings as Indicators of the Brain's Task-related Oscillatory Activity

The synchronicity hypothesis of transient feature binding postulates that neural synchrony in the millisecond range provides a versatile neural code for cortical representation in the context of perception, attention, and action (Engel & Singer, 2001). Neurons fires in synchrony form assemblies that selectively enhance or suppress related neural activity (Engel & Singer, 2001; Salinas & Sejnowski, 2001; Varela, Lachaux, Rodgriguez & Martinerie, 2001). According to Nunez (1995), electrophysiological activity captured by EEG recordings reflects state-dependent mixtures of 'local' and 'global' processes. Local processes, or small-scale synchronization, extend over an area of approximately 1 cm and are transmitted by monosynaptic connections, with conduction delays of about 4-6 milliseconds. Global processes, or large-scale oscillatory activity, refer to networks of neural assemblies separated by more than 1 centimeter connected through polysynaptic pathways. Large-scale networks may connect widely separated regions of the brains, such as occipital and frontal areas.

As a complex dynamic oscillator, the brain needs to constantly segregate and integrate small-scale and large-scale oscillatory activity (Tononi & Edelman, 1998). Spectral analysis of electroencephalographic (EEG) recordings offers a network of methods that allow examining how patterns of functional segregation and integration are related to behavior, and how these relations change as a function of maturation, learning, and senescence. Based on earlier empirical and formal work (e.g., Petsche & Etlinger,

1998; Weiss & Rappelsberger, 2000; for a review, see Varela, Lachaux, Rodgriguez & Martinerie, 2001), we assume: (a) that power spectral analysis indicates small-scale synchronization, (b) that coherence analyses of various types indicate large-scale oscillatory activity, and (c) that additional methods, such as univariate and multivariate estimates of dimensional complexity, may indicate the degree to which small-scale and large-scale oscillatory activity are coordinated within complex (e.g., simultaneously differentiated and integrated) systems.

Oscillatory EEG Activity and Episodic Memory Performance

Attention, vigilance, expectation, and other top-down modulations of on-going perceptual and motor activity are accompanied by oscillatory activity across a large range of spectral frequencies (Bazar, 1999; Gevins, Smith, McEvoy, & Yu, 1997; Gevins, Smith, Leong, McEvoy, Whitfield, et al. 1998; Gundel & Wilson, 1992). With respect to memory-related brain activity, increments in power and coherence have been noted, which supports the hypotheses that transient feature binding during encoding and retrieval is achieved or at least enhanced through oscillatory cortical activity. A commonly employed research strategy has been to identify patterns of local or global oscillatory at encoding that predict later recall probability (e.g., "subsequent memory effects"). Subsequent memory effects in the spectral domain were most frequently observed in the theta frequency range (Doppelmayr, Klimesch, Pachinger & Ripper, 1998; Jensen & Tesche, 2002), and may reflect hippocampal theta activity induced into cortex by reciprocal pathways (Larson, Wong, & Lynch, 1986; Miller, 1989). For instance, Klimesch (1999) found that spectral power and both inter- and intra-hemispheric coherence during encoding were higher for correctly recalled words, especially in the theta band. Similarly, Sarntheim et al. (1998) observed a consistent increase in coherence between prefrontal and posterior association areas in the theta band during a working memory task. At the same time, increments in power and coherence during successful episodic learning and retrieval processing may not be restricted to the theta band. For instance, Fell et al. (2003) reported subsequent memory effects at encoding for both theta and neighboring frequency bands (see also Weiss & Rappelsberger, 2000; Weiss & Müller, 2003).

Though the precise functions played by different forms of oscillatory activity at various frequency bands are unclear, these findings support the general claim that local synchronization and global coherence at encoding predict subsequent memory performance. Based on previous research and theorizing (e.g., Engel & Singer, 2001; Sarntheim et al., 1998), we assume: (a) that participation of prefrontal brain regions in large-scale synchronization at encoding indicates strategic processing during feature selection and feature binding; (b) that participation of hippocampal and entorhinal structures in large-scale synchronization at encoding facilitates association formation and the transition from temporary to permanent forms of binding (e.g., long-time potentiation; e.g., Larson, Wong, & Lynch, 1986).

Empirical data on age differences in subsequent memory effects are scarce. Anokhin et al. (1990) found that long-distance coherence in the theta band predicted intellectual performance among adolescents aged 13-14 years. Klimesch (1999) suggested that

older adults' lower level of episodic memory performance is linked to decrements in task-induced power and coherence (but see Durstman, LaMarche, Cohn, Shearer & Talone, 1985; McEvoy, Pellouchoud, Smith & Gevins, 2001). Müller, Kray, and Lindenberger (2003) investigated adult age differences in power and coherence in the context of a task-set switching task with Stroop stimuli. Older adults showed lower spectral power than young adults at lower frequencies (e.g. theta, alpha), and higher spectral power than young adults at high frequencies (e.g. beta, gamma). Conversely, average coherence was higher in older adults at low frequencies, and lower at high frequencies. Though differences in task and procedures prohibit strong conclusions, these results point to massive changes in cortical processing dynamics during adulthood.

Statement of Problem and Research Hypotheses

The present study has two goals. The first is to uncover lifespan age differences in upper limits of episodic memory performance from childhood to old age. Direct behavioral comparisons in episodic memory performance among children and adults of different ages are close to absent because few experimental studies have covered such a wide age range (e.g. Li, Lindenberger, Hommel, Aschersleben, Prinz, & Baltes, in press; Mayr, Kliegl & Krampe, 1996). Among all prior studies covering the age range from middle childhood to old age, no study so far has used testing-the-limits and adaptive testing procedures to arrive at lifespan gradients of episodic memory near upper limits of performance (for the domain of working memory, see Mayr, Kliegl & Krampe, 1996). In this regard, we make the following interrelated predictions:

- I (1) Individuals in all age groups will improve their episodic memory performance through mnemonic instruction and training, reflecting ample presence of behavioral plasticity in episodic memory in middle childhood, young adulthood, and early old age.
- Behavioral plasticity will be largest among older children and smallest among older adults. Older children will profit most from a research strategy that uses mnemonic instruction and training to decontaminate the assessment of episodic memory performance from age differences in task-relevant pre-experimental knowledge. Specifically, we predict an age group by training crossover interaction in the sense that older children will perform below the level of older adults at pre-instruction baseline but above the level of older adults after mnemonic instruction and training.
- 1(3) Near upper limits of performance (i.e. after mnemonic instruction and training), lifespan age differences in episodic memory will be shifted towards younger ages compared to age differences at baseline (i.e., prior to mnemonic instruction and training). This prediction is consistent with general assumptions made by lifespan theories of cognition (see, for example, Lindenberger, 2000, Figure 1).
- 1(4) Younger children's episodic memory performance will show much fluctuation across lists and sessions, presumably reflecting difficulties in

implementing and maintaining task-relevant strategies as well as the buildup of proactive interference.

The second goal of the study is to explore the contributions of maturation, learning, and senescence to memory-relevant oscillatory activity at encoding in the context of episodic memory performance. Here, central tasks are to identify patterns of local synchronization and large-scale coherence at encoding that predict subsequent recall, to examine whether these predictive patterns differ by age, and to delineate how predictive patterns change in the course of mnemonic skill acquisition. Compared to the first, the second goal of the study is more exploratory in kind, and its empirical treatment will undoubtedly require the refinement of existing as well as the development of new data-analytic methods in the spectral domain. Nevertheless, a few general predictions can be made.

- II (1) As a general rule, we expect differences in small-scale synchronization and large-scale coherence at encoding between correctly recalled and not correctly recalled words.
- II (2) In part, but not necessarily during the entire encoding period, small-scale synchronization and large-scale coherence will be higher for correctly words than for not correctly recalled words. Specifically, we expect that successful encoding will be marked by periods of increased synchronization, perhaps followed by periods of desynchronization (cf. Fell, Klaver, Lehnertz, Grunwald, Schaller, Elger, & Fernàndez, 2001).
- II (3) Subsequent memory effects will include but may not be restricted to the theta frequency band.
- II (4) The spatial distribution, spectral distribution, and timing of subsequent memory effects will vary considerably by age group and degree of mnemonic skill, revealing a large range of ontogenetic and intraindividual variability in brain-behavior mappings (cf. Li & Lindenberger, in press).

Methods

Research Participants

Ninety-six subjects, equally distributed over four age groups (9-10, 11-12, 20-25 and 65-78 years) participated in the present study. Gender was equally distributed within each age group, resulting in a 2x4 design matrix with 12 individuals in each cell. Children were either attending a Gymnasium (e.g., the school type after completion of elementary school with the highest entry requirements), or were still attending elementary school but had received the elementary school's recommendation to attend Gymnasium. Younger adults were students at Saarland University. Older adults were either auditors at Saarland University, participants in other continuing education programs, or both. Thus, an attempt was made to introduce a positive selection bias of about equal magnitude in all age groups to increase the validity of age comparisons in

upper limits of episodic memory, at the cost of reducing generalizability of results to lower performance segments of the overall population.

In addition, individuals with the following characteristics were excluded from the study: (a) left-handed individuals, to enhance interpretability of EEG data; (b) students of psychology and individuals reporting to make use of mnemonic techniques in everyday life, to reduce the likelihood of unwanted cohort differences in pre-experimental familiarity with mnemonic techniques; (c) individuals with a score of 34 or less on the Digit Symbol Substitution (DSS) test of the WAIS (Weehsler, 1958). The DSS is highly predictive of skilled memory performance with the MoL (e.g., Kliegl, Smith, & Baltes, 1990). Earlier studies on memory plasticity in adulthood and old age indicate that individuals with DSS scores below values around 35 are unlikely to fully acquire and appropriately utilize mnemonic techniques (Kliegl, Smith, & Baltes, 1989; Singer, Lindenberger, & Baltes, 2003; Annette Rentz, personal communication, September 2002). Based on the DSS exclusion criterion, 11 younger children, two older children, zero younger adults, and four older adults were excluded from participation in the present experiment, further introducing a positive selection bias among younger children and older adults.

Overview of Study Design

Table 1 summarizes the overall design of the present study. In the first session, participants were administered a demographic questionnaire, followed by a psychometric battery of intellectual ability tests and standard assessments of visual and auditory acuity (for details, see Lindenberger & Baltes, 1994). The psychometric battery assessed four different intellectual abilities – perceptual speed, reasoning, episodic memory, and verbal knowledge (i.e., semantic memory) – with three tests per ability. For a description of individual tests and their psychometric properties, see Li, Lindenberger, Hommel, Aschersleben, Prinz, & Baltes, in press; Lindenberger, Mayr, & Kliegl, 1993.

After covariate assessment, the first of three sessions with EEG recordings took place. First, EEG during resting and during performance on an auditory oddball task was assessed for the purpose of sample description. After that, individuals were asked to encode and later recall four lists of 16 words each. Performance on these lists was used as an estimate of baseline memory performance. With the first two lists, numbers ranging from 1 to 16 were used as cues at encoding and retrieval. With the latter two lists, the 16 generic city locations (see below) used throughout the rest of the experiment served as cues at encoding and retrieval. The main reason for subdividing the pre-instruction session with EEG assessment into two lists with number cues and two lists with location cues was to provide more than one type of pre-instruction baseline when assessing gain in performance after instruction and training. Specifically, we assumed that use of associative imagery, reflecting pre-experimental exposure to mnemonic techniques, was less likely with number than with location cues.

Table 1: Overview of Study Design

Phase of examination	Number of sessions	Duration per session
Demographic questionnaire, psychometric battery of intellectual abilities, visual and auditory acuity	1	~2 hours
EEG assessment #1 (pre-instruction EEG). Resting state; auditory oddball task; cued recall of four word lists	1	~2 hours
Instruction and initial training in the MoL. General introduction to MoL, followed by individualized instruction and initial training	2	~l hour
EEG assessment #2 (post-instruction EEG).	1	~2 hours
Training and practice to asymptote	2-6	~1 hour
EEG assessment #3 (post-training EEG).	1	~2 hours

Note. EEG recordings were obtained at three points in time (a) before instruction and training in the MoL as baseline (pre-instruction EEG), (b) after instruction and initial training (post-instruction EEG), (c) after extended training and practice near asymptotic levels of performance (post-training EEG). The number of sessions needed to approximate asymptotic levels of performance varied across individuals.

Throughout the entire experiment, order of cues during mnemonic testing was separately randomized at encoding and retrieval, and mnemonic cues were present both at encoding and at retrieval. This stands in contrast to the standard MoL that uses an invariant sequence of cue locations to conserve serial order (e.g., Bower, 1970). Modifications to standard MoL were introduced to reduce the contribution of individual differences in the ability to accurately and swiftly retrieve the cue structure from long-term memory to episodic memory performance, and to maximize the contribution of associative processing (e.g., feature binding) at the level of individual location-word pairs to recall probability.

In the next two sessions, participants were introduced to the (MoL). The first MoL practice session took place in age-homogeneous groups of 3-4 individuals. General instructions followed recommendations by Bower (1970). After participants were told about the historical origins of the method, its principles were explained to them using concrete examples. Aspects of the method referring to the invariant sequencing of locations were omitted. Instead, the generation of interactive, dynamic images or thoughts connecting the landmark with the to-be-learned word was highlighted as the central and critical MoL component. Participants then practiced the technique in a self-paced manner with two word lists. In all later sessions, six lists of 16 words each were administered per session. Instruction and training were continued individually in the second session. Training strategies included prompts to verbalize and discuss all

aspects of image formation and image retrieval, collaborative image generation, assistance during recall, repetition and elaboration of instructions, as well as various other forms of encouragement.

The next session again included EEG recordings to document effects on instruction and initial training (post-instruction EEG). The following sessions were practice sessions using adaptive adjustments of presentation time to control task difficulty (see below for details). Practice took place in age-heterogeneous groups of 2-5 individuals seated comfortably in a large room. Training was completed when individuals reached asymptotic levels of performance.

Electrophysiological measures of skilled memory performance with the MoL were assessed in the final session (post-training EEG). In this final session, presentation time was again adjusted to each individual's level of performance, with the goal to obtain an equal split of recalled and not recalled items within individuals to allow for subsequent memory analyses at the level of items, individuals, and age groups.

For each participant, the entire experiment lasted between eight and eleven sessions, depending upon the number of sessions needed to reach asymptotic levels of episodic memory performance during adaptive training and practice. Participants were paid 7.5 Euro for each full hour of testing. In general, individuals participated in one or two sessions per week, with a minimum of two days between sessions. Care was taken to ensure that the time elapsing between sessions, especially with respect to critical parts of the study, did not vary considerably across individuals or age groups. Using similar procedures, Kliegl and Lindenberger (1993) have found that between-session interference effects are negligible when the interval between sessions exceeds two days.

Apparatus

The psychometric battery of intellectual ability covariates was administered using Macintosh SE/30 personal computers equipped with a touch-sensitive screen (Microtouch Systems, Inc.). For mnemonic instruction and training, Apple Macintosh G4 personal computers and 17" Apple Macintosh Studio Display monitors were used for stimulus presentation, timing and response selection. For the three sessions involving acquisition of EEG data, an Apple Macintosh G3 PowerBook and a 15" ACER FP559 monitor were used. A HP (Hewlett Packard) personal computer equipped with a BrainVision recorder (Brain Products GmbH, Munich) was used for EEG data acquisition. In all experimental sessions, auditory signals were presented over six AKG K66 stereo headphones.

Materials

To minimize age differences in location familiarity, 16 generic city locations were used as landmark cues (bakery (Bäckerei), bus stop (Bushaltestelle), cinema (Kino), church (Kirche), fire brigade (Feuerwehr), flower shop (Blumenladen), hairdresser (Frisör), hospital (Krankenhaus), ice cream parlour (Eisdiele), pizzeria (Pizzeria),

playground (Spielplatz), post office (Post), school (Schule), station (Bahnhof), supermarket (Supermarkt), swimming pool (Schwimmbad)).

The generation of word lists was based on a total of 413 highly imaginable, concrete nouns selected from an original pool of 1200 words spoken by a professional radio speaker and used in prior studies with the MoL (e.g. Singer et al., 2003). Selection was based on a pilot rating study with 10 seven to nine year-old children to reduce age differences in word knowledge as a possible confound for age differences in memory performance (Brehmer, Stoll, Bergner, Benoit, von Oertzen, & Lindenberger, 2004). Every word list consisted of 16 nouns. No noun was administered more than once within a given session. Nouns were recycled over sessions with the following constraints: (a) No noun presented at one of the three sessions with EEG recordings had been presented before; (b) a noun presented at a given session did not reappear in the next session; (c) within each list, the first three letters of all 16 words were different from each other to avoid errors during response entry (see below).

Throughout the experiment, the order in which landmark-noun combinations were presented was separately randomized at encoding and retrieval. Random orders were identical across participants to allow for accurate estimates of individual differences in memory performance, thereby enhancing the validity of between-person comparisons, especially at the level of individual items.

Mnemonic Testing Procedures

Cues were presented visually on a monitor, and to-be-learned words were presented auditorily over headphones.

For a given word list, presentation of cues and to-be-learned words during encoding consisted of three phases. First, a blank screen was presented. Second, the location cue was presented visually on the screen. For presentation times longer than 10 s, the empty screen phase was set to one second, and the cue time was set to two seconds. For presentation times at or below 10 s, the empty screen phase was omitted, and the cue time was set to 0.5s. Third, the cue was replaced by a fixation cross, and the to-be-learned word was presented over headphones. The time of the third phase corresponded to the presentation time t_i of the adaptive algorithm (see next).

Participants started the recall phase by pressing the space bar. After that, an empty screen appeared for 500 ms, followed by a location cue, which was presented for 5000 ms. To minimize the presence of motor artifacts during this initial phase of memory retrieval, participants could not respond during this initial period of memory retrieval. After 5000 ms, a blue rectangle appeared on the screen to signal participants that responding was now possible. Participants made their responses by entering the first three letters of the corresponding word. Participants were allowed to correct their responses by using the backspace key. To minimize seemingly false responses due to errors in spelling, the computer always searched for the closest match between a response and all words presented in the list by checking whether the input was exactly the three-letter prefix of a word in the list; if so, the input was interpreted as this word.

If not, the minimal numbers of letter replacement, deletion or insertion steps to turn the three letters in one of the prefixes was computed. The input was then interpreted as the word with the minimal distance. In this way, effects of orthographical knowledge of the participants were avoided. The maximum response time per word was set to 90 second. Participants went to the next location cue by pressing the enter bar.

Adaptive Testing Algorithm

Testing-the-limits and adaptive testing are effective methods to reduce the importance of age differences in task-relevant pre-experimental knowledge, and to arrive at better estimates of age differences in upper limits of performance (Lindenberger & Baltes, 1995). In the present experiment, adjustments in presentation rate were used to individually adapt the difficulty level of the task (cf. Kliegl & Lindenberger, 1993). Presentation times were fixed to 10 seconds per word the first two sessions with EEG assessment and the two instruction sessions.

The adaptive algorithm was started after the second session with EEG recordings. An adaptation algorithm controlled by three variables determined the amount of presentation time per word for the next. The three variables are the presentation time l_i , the current step width $^{\Delta l_i}$ and the last alteration d. The latter variable can assume three values: increased, decreased or equal. The values of all three variables were updated after each list to maximize the likelihood that a given individual would correctly recall 10 out of 16 words in the next list (62.5% correct performance).

Let c_i denote the number of correct items at list i. Then, the above values were adapted as follows:

$$t_{i+1} = t_i + \begin{cases} 0 & c_i = 10 \\ \Delta t_i & c_i < 10 \\ -\Delta t_i & c_i > 10 \end{cases}$$

$$d_{i+1} = \begin{cases} equal & c_i = 10\\ increased & c_i < 10\\ decreased & c_i > 10 \end{cases}$$

$$\Delta t_{i+1} = \begin{cases} \frac{27}{20} \cdot \Delta t_i & d_i = d_{i+1} \neq equal \\ \frac{20}{34} \cdot \Delta t_i & else \end{cases}$$

If $t_i > 16s$, then we set $t_i = 16s$. If $t_i < 1s$, we set $t_i = 1s$ and $d_i = equal$ such that Δt_{i+1} would be decreased nevertheless. We used the initial value $\Delta t_1 = 3s$ and $d_i = equal$. For the initial value of presentation time, we identified the number m of correct items for the best list during the pre-instruction-, instruction- and post-instruction-sessions and set $t_1 = \min\left\{ 6s, \frac{100}{m}s \right\}$; this is the best prediction assuming that the ratio of presentation time over correct answers is constant

At the beginning of adaptive training and practice, performance was aided by repeating instructions and by additional other forms of assistance. This form of help was discontinued when participants reached a presentation time below 10 seconds for three consecutive lists.

The training phase ended when one of the following two conditions were met: (a) the step width for the next list was lower than 0.08s. A step width below this value implies that performance has stabilized at a given presentation time and accuracy level, presumably indicating asymptotic levels of performance; (b) when 6 training sessions were completed.

After the last training session, individuals participated in the final EEG session. The presentation time of that session was computed by

$$t_{EEG} = 8 \cdot \frac{\sum_{i=0}^{5} t_{k-i}}{\sum_{i=0}^{5} c_{k-i}}$$

This equals eight times the average time divided by the average number of correct items for the six lists of the last training session. The aim of this procedure was to maximize the likelihood of obtaining an equal number of correctly remembered and not remembered in the final EEG session.

An example using simulated data may help to illustrate the control structure of the adaptive algorithm (see Table 2): Initially, $t_1 = 10s$, $\Delta t_1 = 3s$ and $d_1 = equal$. We assume that the participant first successfully remembers 5 out of 16 (i.e. $c_1 = 5$). Hence, for computation of t_2 and d_2 , we follow the second case and compute $t_2 = t_1 + \Delta t_1 = 13s$ and $d_2 = increased$. Since $d_1 \neq d_2$, $\Delta t_2 = \frac{20}{34} 3 = 1.765s$, we assume $c_2 = 7$ for the next step, i.e. the participant again failed the criterion of 10 correctly remembered items; therefore, we get $t_3 = t_2 + \Delta t_2 = 14.765s$ and $t_3 = increased$. Since $t_3 = t_3 \neq equal$, we get $t_4 = \frac{1}{20} \Delta t_2 = 2.382$

Mnemonic Performance Feedback

After recall of each list, participants were informed about their level of recall performance at this list. In sessions with EEG recordings, feedback consisted in the number of correctly recalled items and the rate at which words had been presented at encoding (e.g., 7 of 16 items correct in 7500 ms). During instruction and adaptive training and practice, feedback also included a table that allowed participants to judge their recall performance at the level of individual items. Specifically, this table included: (a) the serial position of each word at encoding; (b) the serial position of each word at recall; (c) The corresponding location cue; (d) the correct word; (e) the up to three letters entered by the participant and the word that the program had assigned to these letters; (f) finally, a letter stating whether this word was correctly ('R' for German 'richtig') or incorrectly ('F' for German 'falsch') recalled.

EEG Recordings, Data Reduction, and Initial Analyses

The electroencephalogram (EEG) was recorded from Ag/AgCl electrodes using an elastic cap (Electrocap International) with a digitization rate of 500 Hz in a frequency band ranging from 0.1 to 100 Hz. A total of 63 electrodes was used. The left mastoid was used as reference and the right mastoid was recorded as an active channel. The electrodes were placed according to the international 10-10-electrode system. Vertical and horizontal electrooculogram (EOG) were recorded for control of eye blinks and eye movements. The remaining 58 electrodes were used to record and assess brain activity. The EEG recordings were filtered off-line with a band pass of 0.53 to 50 Hz, and corrected for eye movements. Eye blink artefacts were rejected based on voltage amplitude.

To synchronize EEG recordings with stimulus presentation and behavioral responses, auditory control signals originating from the Apple Macintosh G3 PowerBook were transmitted to the headphones, clamped, reduced in voltage, and recorded by one of the electrode channels of the EEG amplifier.

Time-frequency representations were calculated by means of Morlet wavelets (Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1996; Tallon-Baudry, Bertrand, Peronnet, & Pernier, 1998) using the BrainVision analyser (Brain Products GmbH, Munich). Continuous wavelet transformations were applied to single trials at each electrode in the 1 to 50 Hz range. The absolute amplitude for each frequency at each time point normalized to the whole time internal was averaged across all epochs separately for recalled and not recalled words. For presentation of data, a time interval of 400 ms with highest spectral power in the encoding phase was chosen for each participant, and a difference diagram was created for differences between recalled and not recalled words.

For coherence analysis, complex FFT was used. Coherence was computed for all possible combinations of electrode pairs (n = 1653). For each electrode, frequency, time interval, and experimental condition, averaged coherence relative to all other electrodes was computed (for example, Fp1 to all other, Fp2 to all other, etc.).

Illustration of Initial Results

We now present preliminary behavioral and electrophysiological data based on four individuals, one from each age group. The four selected individuals are typical in the sense that their presentation times during the final EEG session were close to the median of their age group. Nevertheless, we wish to emphasize that the following observations refer to work in progress, and must not be generalized to the four age groups.

Figure 1 displays individual learning curves for a 9-year old child, a 12-year old child, a younger adult (e.g., 20 years of age) and an older adult (e.g., 67 years of age). The plots display the relation between presentation time and recall performance in the

course of mnemonic training and practice. Results from sessions with EEG recordings are highlighted. Presentation times (i.e., black solid line in Figure 1) were held constant during the first three sessions, and then varied as a function of the adaptive algorithm described above. Presentation times were held constant within individuals across the six lists of the final session at a rate deemed to result in an average recall performance of 50 percent.

As indicated by decrements in presentation time during mnemonic training and practice, all individuals were able to acquire and optimize use of the MoL. Also, step width fell below 0.08 seconds in individuals, indicating attainment of asymptotic performance levels. Among the four individuals considered, the younger adult reached the fastest presentation time. At baseline, the older child and the older adult performed at similar levels. However, in the course of mnemonic training and practice, the older child surpassed the older adult, and approximated the performance level of the younger adult. Relative to the older child, the younger child showed lower and more variable levels of performance.

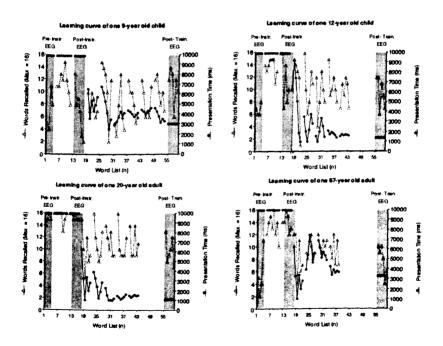


Figure 1. Learning curves of four different subjects are presented (9-year old child, 12-year old child, 20-year old student, 67-year old senior). The interaction between presentation time, measured in milliseconds, (black solid line) and remembered words (gray dotted line) are shown across all word lists. EEG sessions are highlighted gray.

Figure 2 depicts time-frequency amplitudes at encoding for the post-training EGG session based on wavelet transformations. Rows refer to the four individuals displayed in Figure 1, and are arranged by ascending age. The first column refers to time-frequency amplitudes for words that were correctly recalled during retrieval, and the second column refers to words not correctly recalled during retrieval. The third column displays differences between recalled minus not recalled words, and can be regarded as a pictorial rendition of subsequent memory effects at the aggregate level. The x-axis denotes time after onset of the to-be-learned word in milliseconds. The y-axis denotes the frequency in Hz (logarithmic scale).

As expected, all four individuals showed higher synchronization for recalled compared to not-recalled words. In the two children and the young adults, this effect was observed in the theta, and, to a lesser extent, in the delta frequency band. The older adult appeared to show subsequent memory effects at higher alpha and beta frequencies. The temporal location of memory-relevant synchronization and desynchronization patterns varied considerably across individuals. Of course, it remains to be seen whether these findings generalize to each individual's age group.

Outlook

Interest in linking behavioral and cortical correlates of plasticity has increased in recent years (Colcombe, Kramer, Erickson, Scalf, McAuley, et al., in press; Nyberg, Sandblom, Jones, Neely, Petersson, Ingvar, et al., 2003). We hope that the results of the present study will contribute to this endeavor by augmenting our knowledge about lifespan age differences in upper limits of episodic memory performance, and by yielding novel evidence about age-associated as well as learning-related changes in EEG spectral correlates of episodic memory performance.

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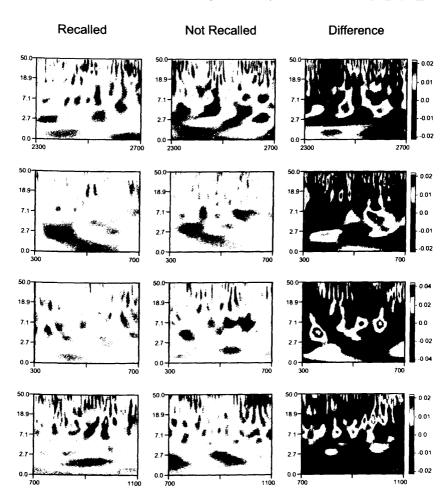


Figure 2. For initial purpose: Time-frequency plots based on EEG recordings during encoding at the final session of the experiment. Rows refer to the four individuals displayed in Figure 1, and are arranged by ascending age. The first column refers to time-frequency amplitudes for words that were correctly recalled during retrieval, and the second column refers to words that were not correctly recalled during retrieval. The third column displays differences in time-frequency amplitudes at encoding between recalled minus not recalled words, and can be regarded as a direct pictorial rendition of subsequent memory effects. The x-axis denotes time after onset of the to-be-learned word in milliseconds. The y-axis denotes the frequency in Hz (logarithmic scale). Time-frequency amplitudes were calculated for single artifact-free trials, normalized and then averaged across all trials and all electrodes separately for recalled and not recalled words.

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