



ERPs and oscillations during encoding predict retrieval of digit memory in superior mnemonists

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ABSTRACT

Previous studies have consistently demonstrated that superior mnemonists (SMs) outperform normal individuals in domain-specific memory tasks. However, the neural correlates of memory-related processes remain unclear. In the current EEG study, SMs and control participants performed a digit memory task during which their brain activity was recorded. Chinese SMs used a digit-image mnemonic for encoding digits, in which they associated 2-digit groups with images immediately after the presentation of each even-position digit in sequences. Behaviorally, SMs' memory of digit sequences was better than the controls'. During encoding in the study phase, SMs showed an increased right central P2 (150–250 ms post onset) and a larger right posterior high-alpha (10–14 Hz, 500–1720 ms) oscillation on digits at even-positions compared with digits at odd-positions. Both P2 and high-alpha oscillations in the study phase co-varied with performance in the recall phase, but only in SMs, indicating that neural dynamics during encoding could predict successful retrieval of digit memory in SMs. Our findings suggest that representation of a digit sequence in SMs using mnemonics may recruit both the early-stage attention allocation process and the sustained information preservation process. This study provides evidence for the role of dynamic and efficient neural encoding processes in mnemonists.

1. Introduction

Superior mnemonists (SMs), who are expert users of particular mnemonics, have remarkable memory capabilities (Ericsson, 2003; Maguire, Valentine, Wilding, & Kapur, 2003; Raz et al., 2009). In the 1980s, two mnemonists obtained the highest digit memory spans ever recorded at the time, namely S.F. (82 digits) (Chase & Ericsson, 1981, 1982) and D.D. (102 digits) (Staszewski, 1988). In 2011, the Chinese mnemonist W.F. set a new record of 5-min numbers (300 digits) in the World Memory Championship (WMC). This record was later broken by a Swedish mnemonist J.E. (392 digits) at the WMC in 2014 and another Swedish mnemonist M.W. (520 digits) at the WMC in 2015 (c.f., www.world-memory-statistics.com). Of particular interest is how these SMs could encode such a large capacity of stimuli.

In the last four decades, there have been increased reports and

laboratory studies of SMs (Chase & Ericsson, 1981, 1982; Konrad, 2014; Staszewski, 1988). These studies demonstrated the important role of mnemonics in SMs' memorization (Biederman, Cooper, Fox, & Mahadevan, 1992; Ericsson, Delaney, Weaver, & Mahadevan, 2004; Hunt & Love, 1972; Hunter, 1977; Thompson, Cowan, & Frieman, 2013; Wilding & Valentine, 1994). These mnemonics have been mostly restricted to well-practiced materials (Chase & Ericsson, 1981, 1982; Thompson et al., 2013; Wilding & Valentine, 1994). With further practice, a few SMs can transfer their commonly used mnemonics to new materials that have not been trained before (Hunter, 1977; Konrad, 2014).

Up to now, only a few studies have explored the neural basis of memory strategies in SMs. A previous fMRI study of SMs from WMC found that the use of the Method of Loci (MOL) evoked brain activations in the medial parietal cortex, the retrosplenial cortex, and the

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right posterior hippocampus in the encoding process (Maguire et al., 2003). Another study showed that the use of MOL in SMs led to enhanced activity in the medial frontal gyrus and dorsolateral prefrontal cortex during the recitation of the first 540 digits of pi (Raz et al., 2009). A recent study on the use of the digit-image mnemonic indicated that, when encoding 2-digit numbers, the bilateral frontal pole, superior parietal cortex, and left premotor cortex were more engaged for an SM (namely C.L.) compared to the controls (Yin, Lou, Fan, Wang, & Hu, 2015). Although results are rather inconsistent, these fMRI studies did implicate a distributed network of brain areas in SMs. However, fMRI is limited in temporal resolution; as a result, the temporal dynamics of superior digit memory are still unclear. According to the skilled memory theory (SMT, Chase & Ericsson, 1981, 1982), by using mnemonics, SMs are able to associate materials with meaningful codes (the meaningful encoding principle), to employ the retrieval cues for recall (the retrieval structure principle), and to encode digit groups quickly (the speed-up principle). The long-term working memory theory (LTWM, Ericsson & Kintsch, 1995) further posits that SMs can rapidly access information in long-term memory to enable high performance. Given that both theories suggest that SMs' brains process information very fast, we anticipated that the neural dynamics during encoding could be demonstrated in the time range measurable by electroencephalography (EEG).

In the current study, sixteen Chinese SMs, mostly Grand Masters of Memory from WMC, were recruited as participants. They all reported that they could skillfully use a particular digit-image mnemonic. For a user of this mnemonic, digits are encoded by mental images; for example S.F. has visual associations with digits (Chase & Ericsson, 1981, 1982). Each sequence of input digits, such as, “21146798257845”, is segmented into pairs of digits in an odd-even way, namely, at positions 1 and 2 (“21”), positions 3 and 4 (“14”), positions 5 and 6 (“67”), and so on. These digit pairs are associated with pre-stored vivid images of objects or living things, such as “crocodile/21/” and “rose/14/”. The associations are generated using visual imagery representations (Higbee, 1979; McCarty, 1980). In general, the digit-image mnemonic shares many properties with the “visual imagery” mnemonic (i.e., use of “mind’s eye” to visualize objects) addressed in previous studies (Bottiroli, Cavallini, Dunlosky, Vecchi, & Hertzog, 2013; Campos, Amor, & González, 2004; Konrad & Dresler, 2010).

There is no common understanding regarding the temporal dynamics underlying the encoding processes of SMs using the digit-image mnemonic. A few previous studies have demonstrated that imagery manipulations, such as object visualization and visual imagery, produce coherent EEG brain signals when materials are processed (Bartsch, Hamuni, Miskovic, Lang, & Keil, 2015; Meyer, Elmer, Baumann, & Jancke, 2007; Villena-González, López, & Rodríguez, 2016; Wegesin, Friedman, Varughese, & Stern, 2002; Wu, Mai, Chan, Zheng, & Luo, 2006). These signals include P2, an attention-related component, for mental imagery (Meyer et al., 2007; Wu et al., 2006; Yamazaki & Katayarria, 2008). For example, in an auditory imagery task, Wu et al. (2006) found that the imagery effect elicited enhanced P2 responses, possibly indexing early top-down allocation of attention in the imagery task. The brain signals also include the posterior alpha-band oscillatory power, which co-varies with mental imagery in tasks involving the representation of visual stimuli. A recent study on oscillatory power during language-driven mental imagery observed increased parieto-occipital alpha when participants were instructed to imagine complex scenes prompted by words (Bartsch et al., 2015). Another study investigating the neural correlates of visual imagery and inner speech with visual stimuli observed stronger alpha power in the visual imagery condition compared to the inner speech condition (Villena-González et al., 2016). The alpha oscillatory activity has also been observed in the mental visuospatial manipulation (Williams, Rippon, Stone, & Annett, 1995) and the auditory imagery task (Cabrera & Dremstrup, 2008; Schaefer, Vlek, & Desain, 2011). ERPs and oscillations thus seem useful measures to study the neural

underpinnings of the use of the digit-image mnemonic prompted by the digit materials, which is related to but still different from imagery manipulations in the aforementioned visual tasks.

In our previous behavioral studies (Hu & Ericsson, 2012; Hu, Ericsson, Yang, & Lu, 2009), Chinese SMs using the digit-image mnemonic demonstrated relatively longer encoding times for even-position digits (e.g., positions 2 and 4) than odd-position digits (e.g., positions 1 and 3). SMs reported that they converted each of the two-digit groups into an image at every even-position in digit sequences. For instance, “79” was converted into “balloon” after the even-position digit (i.e., “9”) was presented following the odd-position digit (i.e., “7”). Given that there is a long line of work on brain activities in tasks with encoding/reaction time differences (e.g., Hanslmayr et al., 2008; Ilan & Polich, 1999; Shen, 2005), we expected differential brain responses to the odd- and even-position digits. The difference is likely due to SMs using a strategy involving generating/associating a mental image immediately at the presentation of each even-position digit. Such a difference, however, should not be observed in control participants who have not received training for this mnemonic. Moreover, given the role of the digit-image mnemonic in superior memory, mnemonic-related neural activities during encoding could be correlated with the retrieval of digit memory. In the current study, we focused our analyses on the early attentional components (e.g., P2) and internal-processing-related dynamics (e.g., posterior alpha oscillation).

2. Methods

2.1. Participants

Sixteen SMs (age 27.4 ± 2.3 years; 5 females; mnemonic training time: 34.0 ± 2.3 months) were recruited as participants. Fifteen of them obtained the title of Grand Master of Memory in the World Memory Championship (WMC). They had demonstrated the ability to perfectly recall 1056–2660 digits in an hour (Hour Numbers), the sequences of 520–1352 playing cards in an hour (Hour Cards), and the sequence of 52 playing cards in 24–115 s (5 min Speed Cards) at WMC (data were drawn from www.world-memory-statistics.com). The last mnemonist was the current holder of the Guinness World Record for reciting digits in pi (67,890 digits). His memory skills have been examined in previous studies (Hu & Ericsson, 2012; Hu et al., 2009). Sixteen undergraduate and graduate students (age 26.6 ± 1.5 years; 6 females) with age and sex matched to SMs formed the control group. One SM failed to complete the EEG session due to poor health. All the fifteen SMs and sixteen controls had normal or corrected-to-normal vision and had no history of neurological, psychiatric, or cognitive disorders. All participants were right-handed with the exception of one mnemonist. This study was carried out in accordance with the Declaration of Helsinki and was approved by the University Committee on Human Research Protection, East China Normal University. All the participants gave their written informed consent and were paid 100 yuan for their participation.

2.2. Stimuli

Twenty 12-digit sequences were used. Digits were randomly selected from “0” to “9”, with the constraint that two consecutive digits were never the same in a sequence. For each studied sequence, six 2-digit probe numbers were arranged to measure memory performance, with 3 for “Yes” responses and 3 for “No” responses to the question “Have you seen these two digits consecutively in the sequence?”.

Since all mnemonists used the digit-image mnemonic with an odd-even strategy (i.e., converting digit-pairs into images at even positions in the sequence) rather than an even-odd strategy (i.e., generating images at odd positions), we only selected 2-digit probes with an odd-even order in the studied sequences in the recall phase (i.e., for “Yes” answers). The other category of probes was new to the studied sequence

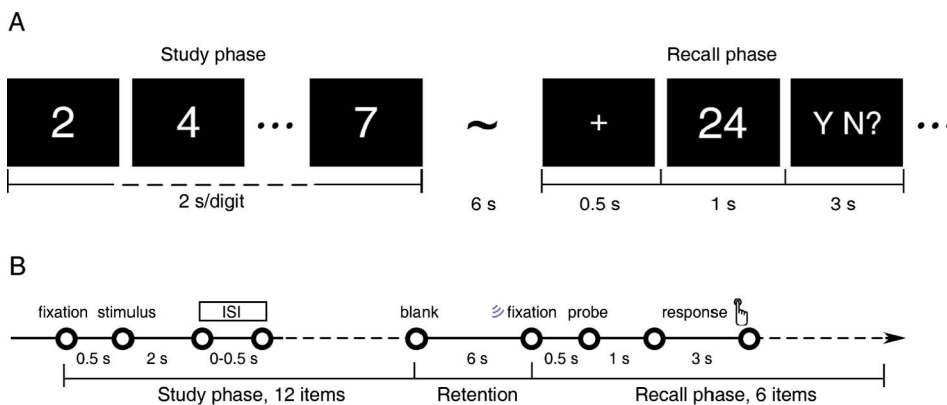


Fig. 1. Experimental design. (A) Screenshots of the study phase and recall phase in a single sequence. (B) Time flow of the task, illustrating an entire single sequence. The experiment consisted of four blocks in total separated by between-block rests. Each block had 5 sequences of digits. ISI = inter-stimulus interval.

(i.e., for “No” answers).

The stimuli were visually presented on a 15-in monitor, controlled by E-prime software (version 2.0; Psychology Software Tools Inc., Pittsburgh).

2.3. Procedure and experimental design

The experimental procedure included four test blocks, each involving five digit sequences to be studied and recalled (Fig. 1).

We instructed participants in both groups to memorize the digit sequence as best as he/she could. For each sequence, participants needed to encode 12 digits. Each digit started with a fixation (“+”, 500 ms). A single digit was then presented (2000 ms), followed by the inter-stimulus interval (ISI, 0 ~ 500 ms). We presented each digit for a relatively long time to allow the control participants to follow the pace of memorization and complete the memory task at a normal level; this time duration was compatible with what has been used in recent neuroimaging studies on superior memory (Dresler et al., 2017; Yin et al., 2015). After the study phase for a sequence, there was a 6000 ms retention period, during which participants were instructed to consolidate their memory. A beep sound then initiated the start of the recall process. A 2-digit probe number was presented for 1000 ms and replaced by the mark of “Yes or No” for 3000 ms. Upon seeing the mark, participants used a response key to indicate whether the 2-digit number had been in the digit sequence just studied (press “F” for “Yes”, press “J” for “No”). For example, if “25” was presented after the sequence of “1 3 2 5 3 7 6 5 4 1 8 9”, the answer should be “Yes”; if “98” was presented, the answer should be “No”.

In total, there were 12 (digits per sequence) × 20 (sequences) = 240 stimuli in the study phase, half of them were either odd- or even-position digits (120 stimuli). Each participant completed 6 (2-digit numbers per sequence) × 20 (sequences) = 120 responses in the recall phase. After the test session, participants were debriefed in detail by the experimenter regarding the strategies they employed in the task. All of SMs reported that they used an odd-even digit-image mnemonic (i.e., generating mental images subsequent to the 2-digit groups), whereas the controls reported that they did not use this mnemonic. Prior to the formal test, a practice block was administered to help familiarize the participants with the experimental procedure. The experiment lasted about 100 min, with rests between blocks.

2.4. EEG data acquisition and preprocessing

2.4.1. EEG acquisition

EEG data were collected with 32-channel electrodes, placed in an elastic cap according to the international 10–20 system. The recording system was from Brain Products (Munich, Germany). Electrode impedance was kept below 10 kΩ for all electrodes. The Electro-Oculogram (EOG) was recorded. Electrodes placed on the orbit muscle above the eyes were used to detect eye blinks, and one electrode (i.e.,

IO site) was placed on the right external canthi to detect horizontal eye movements. Signals were digitized at a sampling rate of 1000 Hz and band-passed through a 0.1–100 Hz band-pass filter. EEG data were recorded against a reference electrode placed at FCz.

2.4.2. EEG preprocessing

Data preprocessing and analyses were carried out with EEGLAB (Delorme & Makeig, 2004) and MATLAB (MathWorks Inc., Natick, MA). Given that our main research question concerned the relationship between the neural dynamics during memory encoding and subsequent performance, we focused on ERP and oscillatory effects in the study phase. The EEG time series were segmented into epochs from –500 to +1720 ms relative to the digit onset. Noisy epochs were removed through visual inspection. Independent components analysis (ICA) was used to further remove artifacts. Bad channels were interpolated using spherical interpolation. On average, 2.6% of the data was interpolated (ranging from 0 to 5.8% across participants). The data were re-referenced to the average reference and baseline-corrected to –500 to 0 ms relative to digit onset. Epochs with deflections exceeding ± 100 μV were also rejected. The EEG signals were low-pass filtered at 30 Hz. Trials were sorted according to condition (even- and odd-position). There were on average 89.6 trials per condition (range: 66–107).

2.5. Statistical analyses

2.5.1. Behavioral data

Memory performance was indexed by five indicators: Accuracy (ACC), discriminability (d'), hit rate, false alarm rate, and reaction time (RT). ACC was calculated by the percentage of correct responses in the recall phases. d' was used to evaluate discrimination performance on the two categories (“yes” vs. “no”) of 2-digit probes. In addition, hit rate and false alarm rate were evaluated. Note that here, $d' = z(\text{hit rate}) - z(\text{false alarm rate})$, and $\text{ACC} = \text{hit rate} + \text{correct rejection rate}$, according to the signal detection metric (Macmillan & Creelman, 2004). RT was defined by the interval from the appearance of the mark (“yes or no”) to the first key response during the recall phase. Using independent-samples t -tests, we calculated differences of ACC, d' , and RT between SMs and the controls. Only RTs for correct trials were included in the RT analysis. All analyses were performed using SPSS software (version 18.0; Chicago, IL, USA).

2.5.2. ERPs

For the ERP data in the study phase (see Supplementary Materials, Fig. S1 for ERP analysis in the recall phase), we identified time windows in which mean voltages showed differences between the odd- and even-positions, as defined by window-by-window t -tests with a criterion of $p < 0.05$ for at least 40 consecutive ms (FDR controlled, Benjamini & Yekutieli, 2001) on at least five electrodes. Adjacent time windows were clustered and were entered into statistical models. Based on these preliminary analyses, we focused on the P2 (mean voltages in

the time window of 150–250 ms post-stimulus). Visual inspection of grand-averaged ERPs revealed that the P2 was distributed over frontocentral sites (Fig. S3), consistent with previous studies on the P2 effect in working memory (e.g., Lijffijt et al., 2009). Mean amplitudes of frontocentral P2 were thus measured at the following four regions of interest (ROIs): left anterior (F3, FC5, FC3), right anterior (F4, FC2, FC6), left central (C3, CP1, CP5), and right central (C4, CP2, CP6). Mixed-design analyses of variance (ANOVAs) were conducted with Group (SM or control) as a between-participant factor, and Position (odd- or even-position) and Region (left anterior, right anterior, left central, or right central) as two within-participant factors.

2.5.3. Oscillatory analysis

To analyze the EEG activity in the time-frequency domain [event-related spectral power (ERSP)], the EEG was convoluted with complex Morlet's wavelet (Kronland-Martinet, Morlet, & Grossmann, 1987) and the ERSPs were computed using EEGLAB (newtimef.m). To model ERSP, power from -500 to 0 ms was used as the reference, and a Morlet wavelet (5 cycles) was applied to decompose signals into the time-frequency plane. Frequencies from 4 to 30 Hz were divided by 27 linear frequency steps. The obtained power values represent percentage increase/decrease of spectral power with respect to the baseline (Pfurtscheller & Aranibar, 1979). An increase referred to event-related synchronization (ERS) and a decrease was expressed as event-related desynchronization (ERD). Visual inspection and previous studies (e.g., Bartsch et al., 2015; Villena-González et al., 2016) disclosed a high-alpha band (10–14 Hz) as the frequency of interest. We identified time windows in which clusters of electrodes showed a significant difference between even- and odd-position conditions, as defined by sample-by-sample t -tests with a criterion of $p < 0.05$ (FDR controlled) for at least 40 ms on at least five electrodes. Such a process led to a large time window from 500 ms to 1720 ms (Fig. S4).

Electrodes were organized into six regions of interest (ROIs, Fig. S5): left anterior (F3, FC5, FC3), left central (C3, CP1, CP5), left posterior (P3, P7, O1), right anterior (F4, FC2, FC6), right central (C4, CP2, CP6), and right posterior (P4, P8, O2). Mixed-design ANOVAs on oscillatory power were performed with respect to Group (SM or control), Position (odd- or even-position), and Region (left anterior, right anterior, left central, right central, left posterior, or right posterior).

All p -values were adjusted with the Greenhouse-Geisser procedure when appropriate. The Bonferroni correction was applied for *post hoc* multiple comparisons.

3. Results

3.1. Behavioral results

The behavioral results for SMs and the controls are illustrated in Fig. 2. Compared with the controls, SMs demonstrated higher accuracy, $t(29) = 4.78$, $p = 0.00004$, Cohen's $d = 1.70$, and higher discriminability, $t(29) = 7.87$, $p = 0.00003$, Cohen's $d = 2.74$. Moreover, SMs displayed a higher hit rate, $t(29) = 4.48$, $p = 0.0003$, Cohen's $d = 1.77$, and a lower false alarm rate, $t(29) = 4.18$, $p = 0.0003$, Cohen's $d = 1.83$, than the controls. They also showed shorter response times than the controls, $t(29) = 2.23$, $p = 0.04$, Cohen's $d = 0.70$. Therefore, SMs' memorization of digit sequences was better than that of the control participants.

3.2. ERP results

A 2 (Group) \times 2 (Position) \times 4 (Region) mixed design ANOVA on P2 revealed a significant main effect of Position, $F(1,29) = 11.39$, $p = 0.002$, $\eta_p^2 = 0.24$, indicating that the even-position digits elicited a more positive-going P2 ($M \pm SD$, $1.93 \pm 0.30 \mu\text{V}$) than the odd-position digits ($0.76 \pm 0.30 \mu\text{V}$). The main effect of Group failed to reach significance, $F(1,29) = 2.82$, $p = 0.11$. The interaction between Group

and Position was significant, $F(1,29) = 4.49$, $p = 0.005$, $\eta_p^2 = 0.11$. Further analyses showed that P2 at the even-position ($1.45 \pm 0.40 \mu\text{V}$) was larger than that at the odd-position ($0.44 \pm 0.36 \mu\text{V}$) in the SM group, $p < 0.05$, but not in the control group, $p > 0.1$. Importantly, there was a three-way interaction, $F(3,87) = 3.15$, $p = 0.04$, $\eta_p^2 = 0.07$. Breaking down the ANOVA based on the factor Region revealed an interaction between Group and Position for the right central region, $F(1,29) = 4.84$, $p = 0.03$, $\eta_p^2 = 0.12$, but not for other regions, $ps > 0.1$. In the right central region, further analyses suggested that P2 was greater at the even-position ($1.92 \pm 0.29 \mu\text{V}$) than at the odd-position ($0.95 \pm 0.22 \mu\text{V}$) for SMs, $p < 0.05$, but not for the controls, $p > 0.1$ (Fig. 3).

It is clear from Fig. 3A that the P2 position effect for SMs was lateralized to the right hemisphere. To confirm this lateralization, we collapsed the position effect (i.e., P2 for the even-position digits minus P2 for the odd-position digits) for the two hemispheres: left side (left anterior, left central) and right side (right anterior, right central). A 2 (Group) \times 2 (Hemisphere) mixed design ANOVA observed a significant main effect of Hemisphere, $F(1,29) = 20.50$, $p = 0.0001$, $\eta_p^2 = 0.44$. This effect interacted with Group, $F(1,29) = 6.66$, $p = 0.02$, $\eta_p^2 = 0.20$. Separate tests showed that only SMs had a significant main effect of Hemisphere, $F(1,14) = 15.01$, $p = 0.004$, $\eta_p^2 = 0.63$, with a larger P2 position effect for the right hemisphere ($1.71 \pm 0.35 \mu\text{V}$) than that for the left hemisphere ($-0.31 \pm 0.27 \mu\text{V}$), $p < 0.05$.

3.3. Neural oscillation results

Fig. 4 illustrates high-alpha (10–14 Hz) oscillations in the time window of 500–1720 ms. A three-way mixed design ANOVA with factors of Group, Position, and Region revealed a significant main effect of Position, $F(1,29) = 14.56$, $p = 0.001$, $\eta_p^2 = 0.37$, indicating that digits at the even-position elicited a greater high-alpha power ($17 \pm 4\%$) than digits at the odd-position ($3 \pm 3\%$). The main effect of Group failed to reach significance, $F(1,29) = 1.64$, $p = 0.21$. The interaction between Group and Position was significant, $F(1, 29) = 4.37$, $p = 0.047$, $\eta_p^2 = 0.15$. Further analyses showed that SMs exhibited a larger alpha power in the even- ($22 \pm 7\%$) than in the odd-position condition ($3 \pm 5\%$), $p < 0.05$, with no such difference in the controls, $p > 0.1$. The three-way interaction also reached significance, $F(5,145) = 3.52$, $p = 0.04$, $\eta_p^2 = 0.12$. Breaking down the ANOVA based on the factor Region revealed an interaction between Group and Position for the right posterior region, $F(1, 29) = 8.66$, $p = 0.007$, $\eta_p^2 = 0.26$, but not for other regions, $ps > 0.1$. Further analyses showed that in this region, only SMs showed significant increased alpha power in the even-position condition ($38 \pm 11\%$) compared to the odd-position condition ($4 \pm 9\%$), $p < 0.05$. No significant effect was found for the control participants (Fig. 4D, $p > 0.1$).

3.4. Neural-behavioral correlations

To investigate whether neural activity during encoding in SMs was related to their behavior performance in the recall phase, we conducted a number of correlational analyses (Fig. 5). The magnitude of P2 and high-alpha power significantly correlated with SMs' performance (response accuracy) for the even-position condition in certain regions: the right central P2: $r_{14} = 0.55$, $p < 0.05$; the right posterior high-alpha: $r_{14} = 0.51$, $p < 0.05$. However, no correlation was found for the odd-position or for the control group ($ps > 0.1$).

4. Discussion

Previous studies have tested non-mnemonists to explore neural correlates of memory strategy use (e.g., Blanchet, Gagnon, & Bastien, 2007; Swick, Senkfor, & Van Petten, 2006). By focusing on superior mnemonists, the current study sheds light on the neural dynamics during encoding in SMs who use a digit-image mnemonic. At the

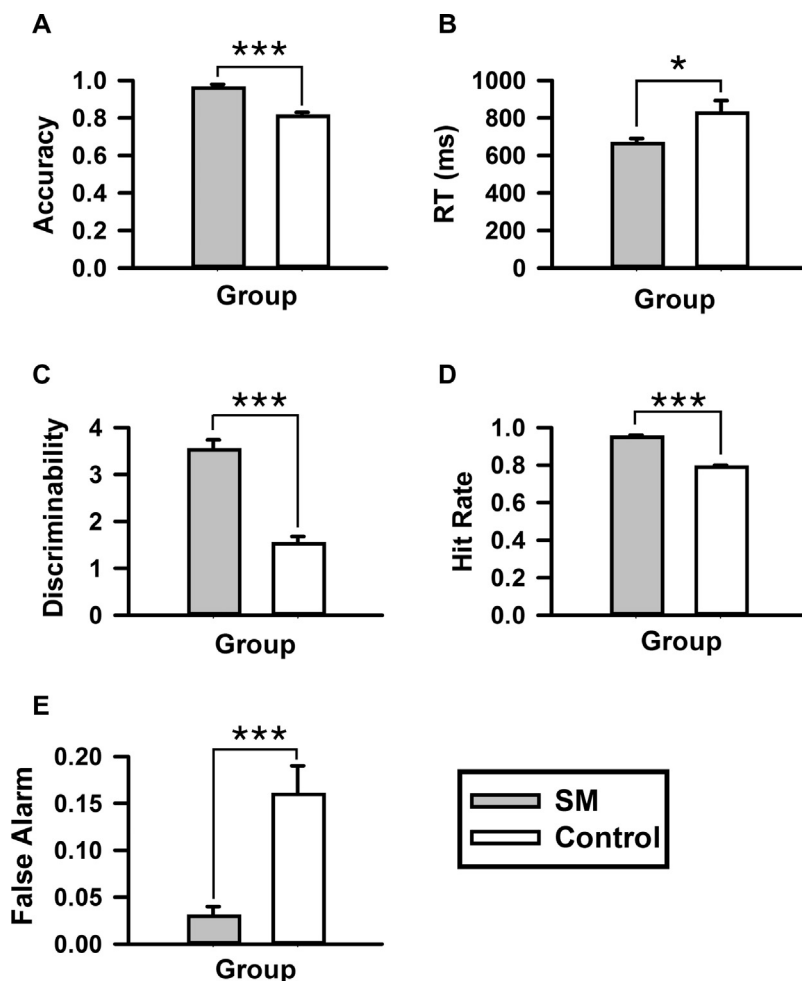


Fig. 2. Behavioral results. (A) Accuracy results. (B) RT results. (C) Discriminability results. (D) Hit rate results. (E) False alarm results. Error bars represent standard errors. Significant results are indicated by asterisks. * $p < 0.05$, *** $p < 0.001$.

behavioral level, SMs outperformed the control participants in memorization of digit sequences. The EEG results showed that the early processing of digits in the study phase was accompanied by enhanced P2 (150–250 ms) responses for encoding even-position digits, relative to odd-position digits, in the right central scalp regions. But this effect appeared only for SMs, not for the control participants. Moreover, mnemonists' encoding of even- and odd-position digits differed in the right posterior alpha-band oscillatory powers (500–1720 ms). Furthermore, memory performance in the recall phase in SMs correlated with the amplitude of P2 and the alpha-band power for processing even-position digits in the study phase. To our knowledge, these findings provide the first EEG evidence for the superior digit memory.

The P2 effect for the encoding of even- vs. odd-position digits occurred as early as 150 ms post-onset of the critical stimuli, consistent with other ERP findings on expert performance. For example, expert chess players showed enhanced N2 (about 200 ms post onset) responses to “check” targets on chessboards, reflecting rapid matching of current perceptual inputs with chunks stored in memory (Wright, Gobet, Chassy, & Ramchandani, 2013). Experts on specific categories of objects (e.g., birds or dogs) have also shown enhanced N170 responses to visual stimuli of these categories (Tanaka & Curran, 2001). These findings suggest that the expertise-related processing of information can start very early.

As for the functional meaning of P2, previous studies indicate that increased P2 could reflect the difference in early attentional processing (Peters, Suchan, Zhang, & Daum, 2005; Talsma, Slagter, Nieuwenhuis, Hage, & Kok, 2005), which might contribute to memory formation (Gazzaley & Nobre, 2012). The P2 in terms of attention allocation can depend on participants' state (e.g., Bernal et al., 2000), stimulus

salience (e.g., Huang & Luo, 2006), or task information (e.g., Luck & Hillyard, 1994). In the present study, the control participants only needed to attend to the digits themselves, whereas SMs additionally converted digits at the even-position into images. This imagery process may demand more top-down allocation of attentional resources, leading to enhanced P2 (Wu et al., 2006). This argument is further bolstered by the right-lateralization of the P2 effect. Strong evidence has been collected implicating the right-hemisphere activation for image processing (Blanke, Ionta, Fornari, Mohr, & Maeder, 2010; Ehrlichman & Barrett, 1983), spatial processing (Nagel, Herting, Maxwell, Bruno, & Fair, 2013; Shinohara et al., 2012), and visual mental imagery (Kosslyn, 1988). It is very likely that the P2 effect observed for the even-position digits in SMs reflects the early attentional process associated with the imagery mnemonic. Importantly, this P2 effect can predict subsequent memory performance in the recall phase, consistent with other studies showing similar patterns, e.g., the P2 predicting subsequent recall at the primacy- vs. plateau-portions of the serial-position curve (Rushby, Barry, & Johnstone, 2002). This indicates that the subsequent memory performance is to a large extent determined by the early attention allocation to stimuli in the study phase.

The high-alpha oscillatory power differentiating brain activations for even- vs. odd-position digits lasted from 500 ms to 1720 ms post-stimuli onset. A line of studies have demonstrated that ongoing alpha oscillations are enhanced with successful encoding of visual item information (Klimesch, Fellinger, & Freunberger, 2011; Nenert, Viswanathan, Dubuc, & Visscher, 2012). Alpha power is suppressed by eye-opening and visual processing, but increases during internal mental manipulation and working memory encoding (Johnson, Sutterer, Acheson, Lewis

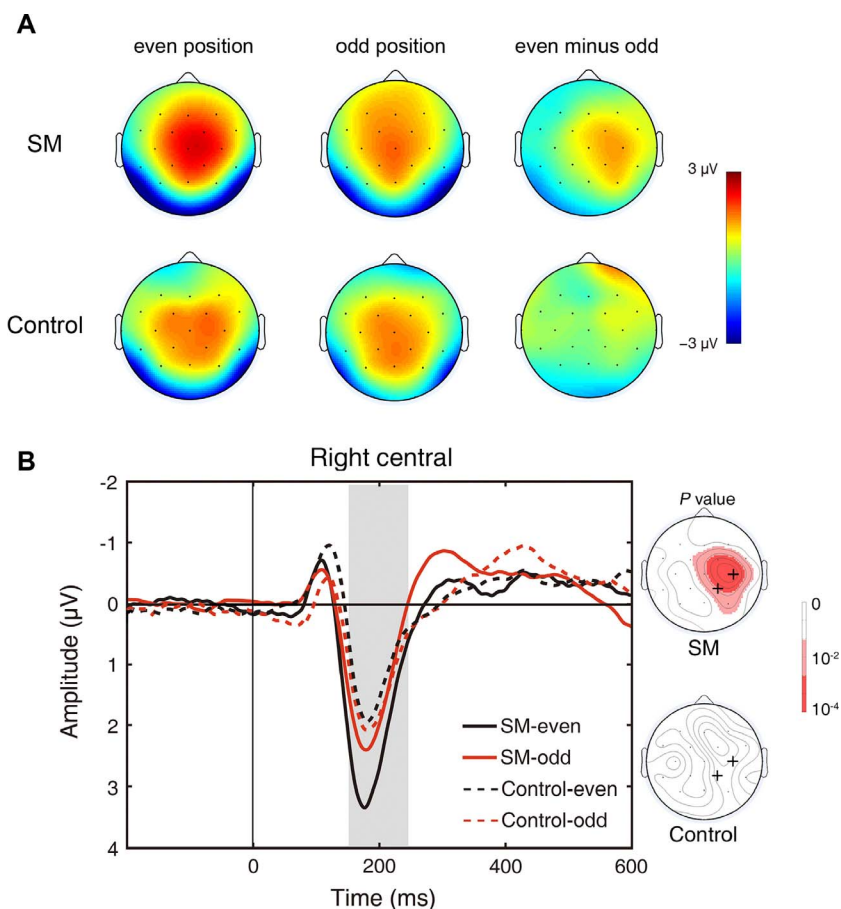


Fig. 3. ERP results. (A) Scalp topographic distribution of P2 for the even-position condition, the odd-position condition, and P2 position effect (even-position minus odd-position) in the SM and control groups in the time window of 150–250 ms post onset. (B) ERP amplitudes across time for each condition in the right central region are displayed for SMs and the controls (left graph). Electrodes where even-position minus odd-position difference was significant at $p \leq 0.01$ (t-test for the mean amplitudes in the 150–250 ms time window) are illustrated on the “p value” map (right graph).

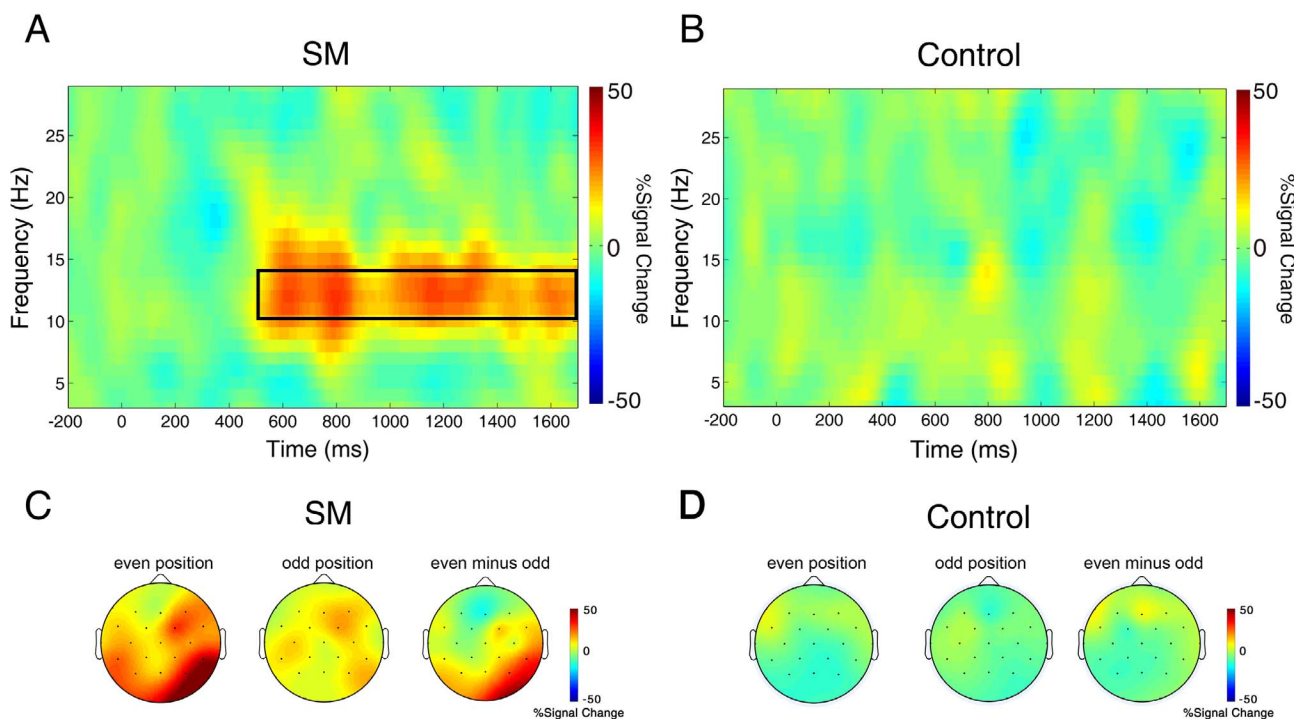


Fig. 4. Oscillatory results. Time-frequency plots of oscillatory powers averaged across all electrodes in (A) SMs and (B) the controls. Red/blue indicates more/less power for even- than odd-position condition, respectively. The time-frequency window, in which the significant difference between even- and odd-position conditions was found, is highlighted in a box. (C) For SMs, the high-alpha power on the even-position was larger than that on the odd-position at the right posterior area in the 500–1720 ms time window. (D) However, in the controls, no significant results were found. The color bar depicts -50% to +50% of signal change. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

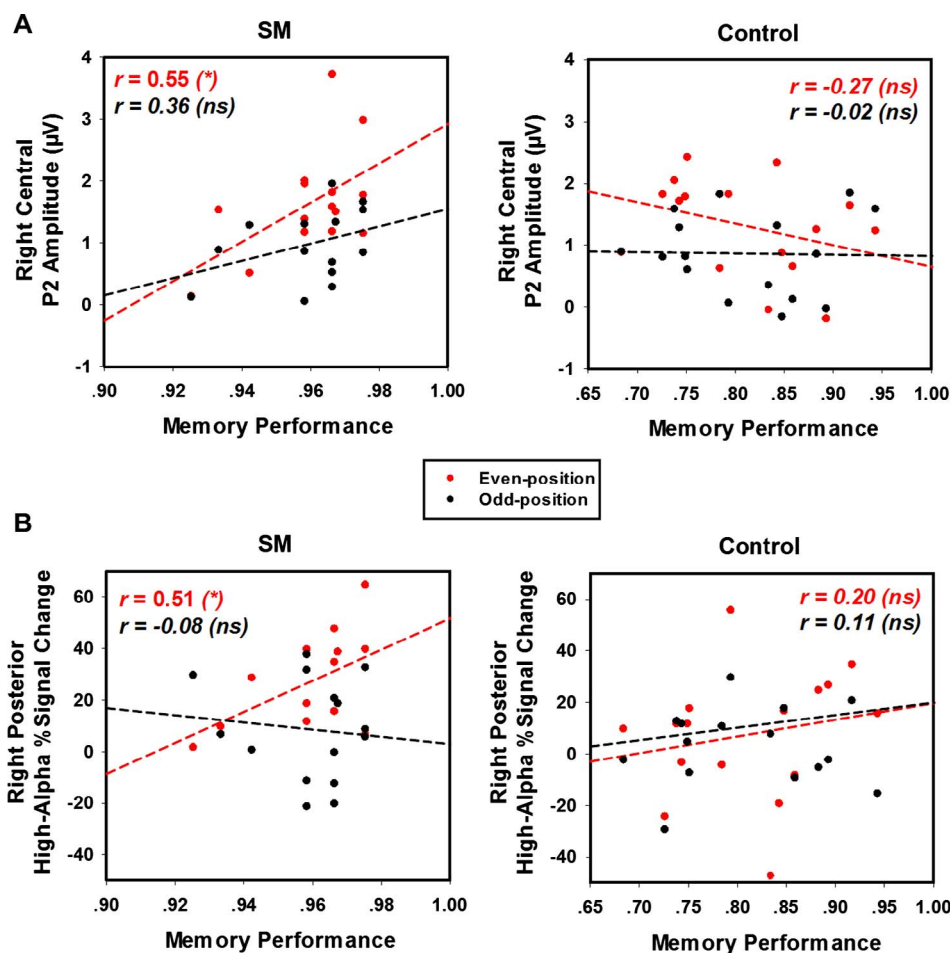


Fig. 5. Neural-behavioral correlations. Data for SMs and the controls are presented in the left and right columns, respectively. Correlation (A) between performance and the right central P2 amplitude, (B) between performance and the right posterior high-alpha power for the even- and odd-position conditions. Each dot represents a participant (SM: $n = 15$; control: $n = 16$). Pearson's correlation coefficients (r) were computed for even- and odd-position conditions separately and are displayed on scatter plots along with their statistical significance level (ns: $p > 0.05$; * $p < 0.05$). Red and dashed lines show the linear fit estimated for the even- and odd-position conditions, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Peacock, & Postle, 2011; Palva & Palva, 2007). Increased posterior alpha power might reflect the suppression of task-irrelevant information (Spitzer & Blankenburg, 2011) or the inhibition of sensory (bottom-up) processing via top-down controlled mechanisms (Klimesch, Freunberger, Sauseng, & Gruber, 2008; Klimesch, Sauseng, & Hanslmayr, 2007). Alpha oscillation enables access to stored information by inhibiting task-irrelevant neuronal structures and by timing cortical activity in task-relevant neuronal structures (Klimesch et al., 2011). This view is in accordance with the finding of increased alpha-band oscillations for processing internal mental stimuli vs. external stimuli (Cooper, Croft, Dominey, Burgess, & Gruzeliar, 2003) and for remembered vs. forgotten materials (Khader, Jost, Ranganath, & Rosler, 2010; Meeuwissen, Takashima, Fernandez, & Jensen, 2011). In our study, the use of the digit-image mnemonic is an internally oriented brain state, which depends considerably on endogenous signaling. Visual imagery processing, which may require active suppression of external visual inputs in order to protect effortful processing from interference, is reflected by heightened alpha oscillations over posterior areas (Bartsch et al., 2015). Taken as such, the high-alpha oscillatory power found in this study may represent a neural process that preserves information concerning digit-image representations in working memory, and these ongoing neural dynamics are strongly linked to the subsequent memory performance.

Based on the above analyses and our previous tests on SMs' detailed encoding processes (Hu & Ericsson, 2012; Hu et al., 2009), we propose that at least two processes are involved in using the digit-image mnemonic to encode stimuli in this study: the *early-stage attention allocation* for the critical stimuli, identified by the P2 component (150–250 ms), and the *sustained information preservation* process for memory formation, reflected by high-alpha oscillation (500–1720 ms). These two processes support the role of dynamic and efficient encoding in mnemonic expertise. As a note, the P2 effect (even- vs. odd-position) in SMs

could also be attributed to long-term extensive memory training and/or rich experience of memorizing digit materials (experience effect). In the present study, we cannot dissociate the experience effect from the use of digit-image mnemonic in SMs, since the skilled use of this strategy requires continuous memory training and deliberate practice. Previous studies found that experience effects were associated with FN400 (300–500 ms) in memory experts (e.g., Herzmann and Curran, 2010). However, in our study, we did not find any difference in this component, making the experience hypothesis a less likely account for our data. Indeed, when we computed the Pearson correlation between the training time (in months) of SMs and neural dynamics (even-odd position effect), we obtained no significant result (for the right central P2: $r = 0.12, p = 0.66$; for the right posterior alpha: $r = -0.15, p = 0.71$). But we do acknowledge that the experience hypothesis cannot be excluded completely, and the exact meaning of the neural dynamics in SMs remains to be explored.

Several limitations should be noted. First, we could not confirm whether the two groups of participants were matched in terms of general cognitive abilities (e.g., IQ, matrix reasoning). It is not clear whether these factors have contributed to the observed P2 effect and alpha oscillation effect. Second, this study could not really isolate purely encoding-related activity (remembered vs. forgotten) from task-related activity (task vs. baseline), as it was not possible for us to contrast successfully encoded trials with forgotten trials (the subsequent memory effect, cf. Paller & Wagner, 2002) in SMs. Third, the control group was not instructed to use the same strategy as SMs, as these participants had no training in using the digit-image mnemonic. To make the two groups more comparable, participants in the control group in future studies should complete a short-term digit-image mnemonic training procedure. Finally, it is conceivable that

participants carried out rehearsal of digits during the retention period, which would contribute to memory retrieval. Previous studies have shown that the EEG alpha power during rehearsal and memory maintenance is strongly linked to later performance (Bonnefond & Jensen, 2012; Khader et al., 2010; Xie, Feng, Xu, Bian, & Li, 2016); however, this effect was not observed in the current study (see Supplementary Materials, Fig. S2). Further studies are needed to verify whether this absence of effect is associated with the digit-image mnemonic strategy in particular.

In summary, this study explored the neural dynamics during encoding in superior memorists who used the digit-image mnemonic in remembering sequences of digits. We found that SMs had a larger P2 amplitude and a stronger alpha-band oscillation power for digits presented at the even-position than for digits at the odd-position. Moreover, the dynamic changes in brain activity could predict subsequent memory performance in SMs. However, no such effects were observed for the control participants. We propose that encoding digital stimuli by mnemonics in SMs recruits both the early-stage attention allocation and the sustained information preservation processes. Future studies may be conducted to investigate to what extent different mnemonic strategies share the same neural basis.

Conflict of interests

None declared.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.bandc.2017.06.012>.

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