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Normal aging selectively diminishes alpha lateralization in visual spatial attention

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ABSTRACT

EEG studies of cue-induced visual alpha power (8-13 Hz) lateralization have been conducted on young adults without examining differences that may develop as a consequence of normal aging. Here, we examined agerelated differences in spatial attention by comparing healthy older and younger adults. Our key finding is that cue-induced alpha power lateralization was observed in younger, but not older adults, even though both groups exhibited classic event-related potential signatures of spatial orienting. Specifically, both younger and older adults showed significant early directing-attention negativity (EDAN), anterior directing-attention negativity (ADAN), late directing-attention positivity (LDAP) and contingent negative variation (CNV). Furthermore, target-evoked sensory components were enhanced for attended relative to unattended targets in both younger and older groups. This pattern of results suggests that although older adults can successfully allocate spatial attention, they do so without the lateralization of alpha power that is commonly observed in younger adults. Taken together, our findings demonstrate that younger and older adults might engage different neural mechanisms for attentional orienting, and that alpha power lateralization during visual spatial attention is a phenomenon that diminishes during normal aging.

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Introduction

Observers can voluntarily deploy visual attention to a location in the visual field independently of the direction of their eye gaze (Posner, 1980). This covert orienting of visual spatial attention improves perception at the attended location compared to unattended locations (Carrasco et al., 2004; Luck et al., 1996; Posner, 1980). Such changes in perception are reflected in the enhanced neural responses to stimuli at an attended location compared with the responses to stimuli at an ignored location. This pattern has been observed in humans by analyzing stimulus-evoked event-related potentials (ERPs) (Grent-'t-Jong et al., 2011; Hillyard and Anllo-Vento, 1998; Mangun and Hillyard, 1991; Sauseng et al., 2005; Van Voorhis and Hillyard, 1977) and the hemodynamic response (Heinze et al., 1994; Mangun et al., 1998; Tootell et al., 1998), and has also been shown in monkeys with intracranial recordings (Briggs et al., 2013; Luck et al., 1997; McAdams and Maunsell, 2000; Moran and Desimone, 1985). Most models of attention posit that these changes in perceptual processing with attention are the results of top-down attentional control signals that bias the sensory systems, something referred to as preparatory attention (Corbetta and Shulman, 2002; Hopfinger et al., 2000; Kastner et al., 1999).

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One particularly robust electrophysiological marker for preparatory attention effects in the visual cortex is the modulation of the alpha (8-13 Hz) rhythm of the electroencephalogram (EEG). When subjects focus covert spatial attention to a left or right visual location, alpha power becomes lateralized, with stronger suppression over the hemisphere contralateral to the attended location, which is thought to reflect the modulation of cortical excitability in the visual cortex (Bengson et al., 2012; Capotosto et al., 2009; Grent-'t-Jong et al., 2011; Kelly et al., 2009; Liu et al., in press; Rajagovindan and Ding, 2011; Rihs et al., 2007, 2009; Sauseng et al., 2005, 2011; Thut et al., 2006; Worden et al., 2000). Furthermore, the degree of alpha lateralization during preparatory attention is correlated with behavioral performance. Specifically, subjects' reaction times are faster and discrimination accuracy is higher with greater alpha lateralization (Kelly et al., 2009; Thut et al., 2006), and they are less likely to make action errors (Bengson et al., 2012). Although cue-induced alpha lateralization has been commonly observed in young adults, to our knowledge, no study has examined alpha lateralization in older adults.

Although no prior work exists concerning the effect of normal aging on alpha lateralization, behavioral and ERP research has examined possible age-related changes in the orienting of spatial attention. In general, behavioral benefits and costs of cue-induced shifts of visual spatial attention are relatively resistant to normal aging (Greenwood et al., 1993; Hartley, 1993; Hartley et al., 1990; Madden, 1990; Nissen and Corkin, 1985), although some studies suggest that older adults might





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require more time to use the cue to guide spatial attention (Brodeur and Enns, 1997; Hoyer and Familant, 1987). Furthermore, age-related changes in attention have also been investigated using target-evoked sensory ERPs that are known to be sensitive to spatial attention (Curran et al., 2001; Lorenzo-Lopez et al., 2002; Nagamatsu et al., 2011). These studies have suggested that the ability to modulate incoming sensory signals is altered during aging, and that this might result, in part, from changes in the top-down control of attention. Consequently, cue-induced ERPs associated with top-down preparatory attention have also been used to investigate whether electrophysiological signs of preparatory attention would reveal age-related deficits in attentional control. These studies have demonstrated that cue-induced ERPs over anterior scalp regions related to attentional control are reduced during aging (Nagamatsu et al., 2011; Yamaguchi et al., 1995).

Given these findings, one would hypothesize that aging might influence another canonical electrophysiological marker of the orienting of attention: alpha power lateralization. Furthermore, given the similarities in behavioral consequences of attention in both younger and older adults described above, we may also expect to observe similarities in the classic event-related measures of attention, such as early directing-attention negativity (EDAN), anterior directing-attention negativity (ADAN), late directing-attention positivity (LDAP) (Harter et al., 1989; Hopf and Mangun, 2000; Jongen et al., 2007; Kelly et al., 2009; Nobre et al., 2000), contingent negative variation (CNV) (Brunia and Damen, 1988; Walter et al., 1964), and target-evoked responses (Mangun and Hillyard, 1991). Conversely, alpha lateralization may be consistent across older and younger groups and other event-related signatures of attention might be particularly sensitive to aging. In either case, older and younger adults may engage partially different methods of attentional orienting.

Materials and methods

Participants

Twenty-three healthy students from Shanghai Jiao Tong University (mean age: 21 years; range: 18–25 years; 7 females; all right-handed) and eighteen healthy older adults from a neighboring community (mean age: 61 years; range: 50–70 years; 11 females; all right-handed) participated in this study. Each participant was required to have a minimum of 9 years school education. All participants reported normal or corrected-to-normal vision, and no history of neurological or psychiatric disorders. All older participants were tested to have normal cognition using the Mini-Mental Status Examination (\geq 26/30; mean: 28), which was a typical score scale in prior aging studies (Curran et al., 2001; Nagamatsu et al., 2011). Each subject gave written informed consent prior to participating, and the experimental protocol that complied with the Declaration of Helsinki was approved by the ethical committee of Med-X Research Institute, Shanghai Jiao Tong University.

Stimuli and procedures

Stimuli were presented and responses were recorded using a commercially available software package (E-Prime 2.0, Psychology Software Tools, Inc., Sharpsburg, USA). All stimuli were presented on a 19 inch LCD monitor (Dell: P190SB) positioned 60 cm in front of the subject. A black central crosshair (1.38° by 1.38° visual angle) and two black location marks (2.39° by 2.39° visual angle, located 9.05° from the vertical meridian, and 7.2° below the horizontal meridian) were presented on a white background on the monitor during the experiment. Subjects were instructed to always maintain fixation on the central crosshair during each trial. Trial sequences and timing are shown in Fig. 1A. During each trial, one of two possible spatial arrow cues (black central arrow, 2.24° by 1.62° visual angle) was firstly presented for 200 ms, directing subjects to covertly attend either the lower-left or lower-right square with equal probability, while totally ignore the



Fig. 1. Experimental paradigm and EEG analyses. (*A*) An arrow cue instructed the subjects to shift attention to either the left or the right lower visual field randomly with equal probability in anticipation of a forthcoming lateralized target (the letter "x" or plus sign), and totally ignore the rest visual field. After a random cue–target interval of 1000–1200 ms, a target was presented in either the left or the right visual location randomly with equal probability. The target was either the left or the right visual location randomly across trials with equal probability. Subjects were required to make a button response as accurately and quickly as possible when the plus sign appeared at the attended location. (*B*) EEG analyses performed in this study.

other location. After a random cue–target interval (CTI, from cue offset to target onset) between 1000–1200 ms, a target (black letter "x" or plus sign stimulus, 1.67° by 1.67° visual angle) was presented for 200 ms inside either the attended or ignored square with equal probability. Whether the target was the letter "x" or the plus sign stimulus was randomized across trials with equal probability. Subjects were instructed to respond only to the plus sign targets presented at the attended location by pressing a button of the response box with the right index finger as quickly and accurately as possible. Responses to the plus sign within 1600 ms after target offset were considered as correct trials. A fixed delay of 2600 ms was presented between the target offset and the onset of next cue.

Each block consisted of 60 trials lasting for a total of about 5 min, with a 2 to 3 min break between successive blocks. Subjects were first given the experimental instructions, and then trained for at least 1 block to familiarize them with the task. There were 8 blocks obtained from the younger group, and 6 blocks from the older group, considering the fact that the older adults tended to be more likely to develop fatigue during the experiment. In total, 480 and 360 trials were recorded for each younger and older adult, respectively.

EEG recording and preprocessing

Throughout the experiment, EEG data were continuously recorded using the BrainAmp MR Plus amplifier and EasyCapTM (Brain Products GmbH, Gilching, Germany) from 30 scalp electrodes (Fp1, Fp2, F3, F4, F7, F8, Fz, FC1, FC2, FC5, FC6, C3, C4, Cz, T7, T8, CP1, CP2, CP5, CP6, P3, P4, P7, P8, Pz, O1, O2, Oz, TP9, TP10). Note that electrodes TP9 and TP10 refer to inferior temporal locations over the left and right mastoids, respectively. FCz (the 31st electrode) was used as recording reference and AFz (the 32nd electrode) was used as ground. The EEG signals were amplified and digitized at a sampling rate of 1000 Hz (0.016– 100 Hz band-pass). Electrode impedance at each electrode was maintained below 10 k Ω . In order to monitor eye movements and blinks, one electrode was placed on the outer left ocular canthus and another electrode was placed above the right eye to record horizontal and vertical electrooculograms (EOGs), respectively.

EEG preprocessing was performed in MATLAB-based EEGLAB Toolbox (Delorme and Makeig, 2004) (http://sccn.ucsd.edu/eeglab/) and ERPLAB Toolbox (http://www.erpinfo.org/erplab/). Raw EEG data were band-pass filtered into 0.1–40 Hz (a two-way, zero phase shift, Butterworth filter; roll-off slope: 12 dB/oct) with a Parks McClellan notch filter at 50 Hz. Artifacts in the EEG signals caused by eye blinks were corrected by independent component analysis that was based on Infomax algorithm (Jung et al., 2000). The continuous EEG data were re-referenced to the algebraic average of the two mastoid electrodes

(TP9 and TP10), and then segmented into two kinds of epochs: cuerelated epochs (-1000-1400 ms post-cue) and target-related epochs (-200-800 ms post-target). We excluded the last 200 ms of cuerelated epochs (1200-1400 ms post-cue) in the following analyses to avoid activity from target presentation. Artifacts were detected in each EEG epoch using ERPLAB functions in a semi-automatic way, according to the following steps: (i) a moving window (width: 200 ms; step: 50 ms) peak-to-peak function was used to examine the maximally allowed amplitude difference of all EEG channels, with voltage threshold of \pm 150 μ V; and (ii) a simple voltage threshold function was used to examine the absolute voltage value of all EEG channels, with voltage threshold of $\pm 100 \,\mu$ V. EEG epochs with overt eye movements during the entire epoch or eye blinks during stimulus presentation were marked as bad epochs and excluded in further analysis, according to the following steps: (i) a step function was used to detect eye movements on HEOG channel, with a moving window (width: 400 ms; step: 10 ms) and voltage threshold of \pm 40 μ V; and (ii) a step function was used to detect eye blinks on VEOG channel around the cue or target stimuli period (-200-200 ms), with voltage threshold of $\pm 50 \mu$ V. Finally, all EEG epochs were visually double checked to ensure the quality before subsequent analysis.

After artifact rejection, the average numbers [mean \pm SEM (stand error of the mean)] of cue-related epochs were 213.7 ± 3.1 (cue left) and 212.9 \pm 3.5 (cue right) for younger adults, and 147.5 \pm 5.0 (cue left) and 152.8 \pm 4.8 (cue right) for older adults. The average numbers (mean \pm SEM) of target-related epochs were 112.1 \pm 1.5 (left targets attended), 112.9 \pm 1.4 (left targets ignored), 111.9 \pm 1.6 (right targets attended) and 112.5 \pm 1.6 (right targets ignored) for younger adults, and 76.9 \pm 2.6 (left targets attended), 81.8 \pm 1.9 (left targets ignored), 79.7 \pm 2.1 (right targets attended) and 78.8 ± 2.4 (right targets ignored) for older adults. Further analysis would only consider the correctly performed trials that were also artifact-free in all channels. One older participant was excluded due to excessive eye movements during the experiment. As a result, twenty-three younger adults and seventeen older adults were included in the analyses. To assess the potential influences caused by different numbers of trials between the two groups, we also analyzed the data by selecting the EEG trials from the first six blocks in the younger group. Since we did not observe statistical influences caused by the trial numbers for any of our dependent measures, we only report the results based on eight blocks of EEG data from the younger group unless otherwise specified.

ERP analysis

Cue-related ERP analysis

Cue-related ERP waveforms have been shown to reflect the timing and sequence of attention-directing processes during spatial attention tasks. Specifically, three lateralized ERP components elicited by spatial cues have been consistently observed: (i) a negative component appearing during 200-300 ms post-cue over posterior areas contralateral to the cued location (EDAN) (Harter et al., 1989; Kelly et al., 2009; Nobre et al., 2000), (ii) a negative component appearing during 300– 500 ms post-cue over the contralateral frontal areas (ADAN) (Hopf and Mangun, 2000; Kelly et al., 2009) and (iii) a sustained positive component appearing after ~400 ms post-cue over the contralateral posterior areas (LDAP) (Harter et al., 1989; Hopf and Mangun, 2000; Kelly et al., 2009). In this study, cue-related EEG epochs were averaged across all trials with the same cue direction (left, right) with the -200-0 ms pre-cue as baseline, which yielded the cueevoked ERP for each electrode and participant. The ERP waveforms were averaged within four ROIs: left frontal (FL: F3, FC1, FC5), right frontal (FR: F4, FC2, FC6), left posterior (PL: P3, P7, O1) and right posterior (PR: P4, P8, O2). Time windows and ROIs were selected based on previous studies as well as our grand-averaged ERPs (see Fig. 2) to compute the amplitudes for EDAN (240-300 ms post-cue, PL and PR), ADAN (400–450 ms post-cue, FL and FR) and LDAP (400–550 ms post-cue, PL and PR) in both younger and older groups.

Another well documented ERP marker of cue-induced expectation of the forthcoming target is the contingent negative variation (CNV), which was typically observed over frontal-central areas preceding the target onset (Brunia and Damen, 1988; Walter et al., 1964). In this study, cue-related EEG epochs were averaged across all trials collapsed for two cue directions (left, right) with the - 200-0 ms pre-cue as baseline to get the non-lateralized ERPs for each electrode and participant. The amplitudes of CNV were then identified in the averaged ERPs within frontal-central electrodes (Fz, Cz, FC1, FC2) during the 800–1200 ms post-cue period (see Fig. 3C).

Target-related ERP analysis

The target-evoked N1 component (~170 ms after stimulus onset) of visual ERPs is one of the most extensively reported electrophysiological measures of visual spatial attention (Doesburg et al., 2008; Grent-'t-Jong et al., 2011; Hillyard and Anllo-Vento, 1998; Mangun and Hillyard, 1991; Sauseng et al., 2005). In this study, sensory facilitation due to visual spatial attention was indexed by examining the N1 time-locked to visual targets within two ROIs: PL and PR (see Fig. 4F). Here we only focused on the N1 component because we did not observe a significant attention effect on the shorter-latency occipital P1 component in either group. Target-related EEG epochs were averaged across all trials with the same target location (left, right) and attention (attended, ignored) with the -200-0 ms pre-target as baseline, which yielded the target-evoked ERP for each electrode and participant. Then, ERPs of a single electrode were averaged within two ROIs (PL, PR) for each participant. Finally, N1 amplitudes were averaged within a 40 ms time window centered at the component's peak latencies in the group's grand-averaged waveforms.

Alpha-band power analysis

Selection of electrodes and time windows

Based on previous electrophysiological studies that have documented the lateralization of alpha power over the visual cortex with spatial attention in healthy young adults (Grent-'t-Jong et al., 2011; Kelly et al., 2009; Rihs et al., 2009; Sauseng et al., 2005; Thut et al., 2006; Worden et al., 2000), we selected two symmetrical posterior ROIs (PL and PR, see Fig. 5F) for the alpha power analysis. It has been suggested that the earliest window between 0-400 ms post-cue would include the period when subjects were decoding the cue meaning and executing the cue instructions, and therefore may not have yet fully oriented attention; by 400 ms however, there is sufficient time for voluntary attentional orienting (Posner, 1980). Furthermore, the effect of alpha power lateralization was typically observed after ~400 ms post-cue, then became stronger, and reached the highest level before target presentation (Kelly et al., 2009; Worden et al., 2000). To characterize the time course of alpha power lateralization, we limited our analyses to the 400-1200 ms post-cue interval, and further, we divided this period into two sub-windows: the middle CTI (400-800 ms post-cue) and the late CTI (800-1200 ms post-cue).

Determination of alpha frequency

There have been studies (Doppelmayr et al., 1998; Klimesch, 1999) suggesting individual differences in the alpha frequency, although how to determine the precise alpha frequency is still under debate. In prior studies of visual spatial attention, both individual alpha frequency (IAF) (Capotosto et al., 2009; Thut et al., 2006) and constant alpha frequency (CAF) for all subjects (Bengson et al., 2012; Grent-'t-Jong et al., 2011; Rihs et al., 2009; Sauseng et al., 2005; Worden et al., 2000) have been used to analyze the alpha activity in younger adults. Moreover, recent EEG study of aging and non-spatial visual attention also used



Fig. 2. ERP waveforms elicited by spatial cues in the younger (*A*) and older (*B*) groups. The topographical maps of difference waves (cue left *minus* cue right) averaged within different time windows (EDAN: 240–300 ms post-cue; ADAN and LDAP: 400–450 ms post-cue) are shown in the right side.

CAF for both younger and older adults (Zanto et al., 2011), though IAF was suggested to decrease during aging (Klimesch, 1999).

Given the inconsistent definition of alpha frequency in previous studies, we used both IAF and CAF in order to assess its potential influence on the present results. In the IAF approach, we computed the power spectrum of the -1000-0 ms pre-cue period for each cuerelated EEG epoch and electrode using Fast Fourier transform, and averaged the spectrum across all posterior electrodes (P3, P4, Pz, P7, P8, O1, O2, Oz) and EEG epochs for each subject (Capotosto et al., 2009; Thut et al., 2006). The individual alpha band was then defined as IAF -2 Hz to IAF +2 Hz (Capotosto et al., 2009). The differences in IAF between the two groups approached statistical significance (mean \pm SEM; younger: 10.53 \pm 0.18 Hz vs. older: 9.77 \pm 0.38 Hz; $t_{(38)} = 1.949$, p = 0.059). In the CAF approach, we used 8–13 Hz as

the constant alpha band for both younger and older adults. Since our findings were not statistically different under either IAF or CAF approach, we only report the results hereafter based on the CAF approach (8–13 Hz) unless otherwise specified.

Temporal spectral evolution

Cue-related lateralization of posterior alpha power reflects the improved perception at attended locations and suppressed perception at ignored locations during anticipatory attention (Bengson et al., 2012; Kelly et al., 2009; Rihs et al., 2009; Sauseng et al., 2005; Thut et al., 2006; Worden et al., 2000). In this study, the alpha power of cuerelated EEG epochs was computed using a standard approach of temporal spectral evolution (TSE) (Rihs et al., 2009; Thut et al., 2006; Worden et al., 2000). Briefly, each cue-related EEG epoch was filtered into alpha



Fig. 3. Cue-related CNV component. Panel A presents the cue-related ERPs collapsed for the left and right cue trials in the two groups. Panel B presents the topographical maps of CNV component in the two groups.

band, rectified and then smoothed by averaging within a moving time window (width: 100 ms), and averaged across different epochs to get the alpha TSE for each cue direction (left, right), electrode and participant. After that, alpha TSE was averaged across the three electrodes within each ROI (PL, PR). Finally, to eliminate the influences of asymmetric baseline alpha power preceding the cue onset, we computed the event-related synchronization/desynchronization (ERD/ERS) using ERD% = $(E - R) / R \times 100\%$ (Pfurtscheller and Lopes da Silva, 1999), where E indicates the alpha power at each time point after the cue onset, and R indicates the mean value of alpha power during the baseline period (-600-0 ms pre-cue). The alpha ERD values were used in the following statistical analysis.

Statistical analysis

Both EEG data and behavioral data were analyzed using Repeated-Measures Analysis of Variance (ANOVA), within-group paired-samples *t*-test and between-group independent-samples *t*-test (two-tailed). All results were presented as the mean \pm SEM. Statistical analysis was performed in SPSS 16.0, and statistical significance was accepted for values of *p* < 0.05.

Results

Behavioral performance

Accuracy and reaction time (RT) were analyzed in this study, separately for the left and right cue trials. For each subject, accuracy was defined as the percentage of correctly performed trials, and RT was averaged across all correctly performed trials with responses to targets. A two-way ANOVA was conducted separately for accuracy and RT, with Cue Direction (left vs. right) as a within-group factor, and Age (younger vs. older) as a between-group factor. As shown in Table 1, younger adults had significantly better accuracy than older adults, but this reflected a very small difference (less than 1%). Younger adults responded significantly faster than older adults, which suggests the response slowing during aging. To analyze the Age \times Cue Direction interaction, paired-samples t-test was conducted by comparing accuracy and RT between the left and right cue trials in each group. Older adults had significantly longer RTs ($t_{(16)} = 3.066$, p = 0.007) and marginally lower accuracy ($t_{(16)} = -2.063$, p = 0.056) in the left cue trials than those in the right cue trials, while younger adults had similar accuracy ($t_{(22)} = 0.328$, p = 0.746) and RT ($t_{(22)} = -0.767$, p = 0.451) between the left and right cue trials. Such results suggest the poorer performance in the left visual field for older adults, which is consistent with recent findings (Nagamatsu et al., 2011).

Further, to test whether subjects focused attention on the cued location, we defined error rate as the percentage of false responses to the targets presented at the uncued location, separately for the left and right cue trials. The same ANOVA as used for accuracy and RT was conducted on error rate. As shown in Table 1, no main effect or interaction was observed. Overall, the average error rates were extremely low (<1% in both groups), which indicated that both younger and older adults were authentically following the task instructions. Otherwise, subjects were more likely to make false responses to the targets at the uncued location, because the targets were randomly presented at either the cued or uncued location with equal probability and subjects were not required to respond to the uncued targets.



Fig. 4. Target-related N1 component. Panels *A* and *C* present the grand-averaged ERPs within two ROIs evoked by attended targets versus ignored targets for younger and older adults, respectively. Panels *B* and *D* present the topographical maps of N1 for younger and older adults, respectively. Panel *E* illustrates the difference in attentional modulation of contralateral N1 (attended-target *minus* ignored-target) between the two groups. Vertical bars indicate mean ± SEM. ROIs are defined in panel *F*.

ERP results

Cue-related ERPs

The grand-averaged cue-related ERP waveforms elicited by the left and right cues within different ROIs (FL, FR, PL, PR) for younger and older adults are illustrated in Figs. 2A and B, respectively. The EDAN, ADAN and LDAP components could be clearly observed in the topographical maps of difference waves between the left and right cue trials in both younger and older groups. First, to examine whether these components were statistically significant in each group, the amplitudes from raw ERPs were tested by a two-way ANOVA with Cue Direction (left vs. right) and ROI Laterality (ipsilateral vs. contralateral to cue direction) as within-group factors for each component and group separately. As Table 2 illustrates, we observed main effects of ROI Laterality for all three components, suggesting that these three components were statistically significant in both groups. Second, we quantified the amplitudes of these components based on the difference waves (contralateral ROI minus ipsilateral ROI), then collapsed across the left and right cue trials. Between-group comparison showed that there was no significant difference in EDAN (younger: $-0.64 \pm 0.10 \mu V$ vs. older: $-0.47 \pm 0.13 \ \mu\text{V}$; $t_{(38)} = -1.035$, p > 0.3) or ADAN (younger: $-0.38 \pm 0.06 \ \mu\text{V}$ vs. older: $-0.23 \pm 0.10 \ \mu\text{V}$; $t_{(38)} = -1.427$, p > 0.1) between the two groups, while the older group showed stronger LDAP than the younger group (younger: $0.20 \pm 0.08 \ \mu\text{V}$ vs. older: $0.48 \pm 0.09 \ \mu\text{V}$; $t_{(38)} = -2.268$, p = 0.029). Taken together, these results suggest that EDAN, ADAN and LDAP components were well preserved during aging.

The grand-averaged cue-related ERP waveforms collapsed across the left and right cues within the frontal–central area for younger and older adults are illustrated in Fig. 3. The CNV component could be clearly observed in the topographical maps in both groups. Older adults showed larger amplitude of CNV than younger adults (younger: $-3.11 \pm 0.29 \,\mu$ V vs. older: $-5.16 \pm 0.81 \,\mu$ V; $t_{(20,111)} = 2.380$, p = 0.027). Such results provide further evidence that both younger and older adults could accomplish a biased attentional state in anticipation of the forthcoming targets.

Target-related ERPs

The grand-averaged target-related ERP waveforms within posterior ROIs (PL, PR) for younger and older adults are presented in Figs. 4A and



Fig. 5. Posterior alpha power. Panels *A* and *B* present the grand-averaged alpha power within two ROIs (PL, PR) for younger and old adults, respectively. Panels *C* and *D* are the topographical maps of alpha power differences (attend-left *minus* attend-right) averaged across 400–800 ms and 800–1200 ms post-cue periods for younger and old adults, respectively. Panel *E* illustrates the grand-averaged alpha-band ERD results averaged across 400–800 ms and 800–1200 ms post-cue periods in the two groups. Vertical bars indicate mean \pm SEM. ROIs are defined in panel *F*.

C, respectively. The scalp topographies of target-related N1 for younger and older adults are shown in Figs. 4B and D, respectively. The amplitudes of N1 were tested by a four-way ANOVA with Target Location (left vs. right), Attention (attend vs. ignore), and ROI (ipsilateral vs. contralateral to target location) as within-group factors, and Age (younger vs. older) as a between-group factor. We observed main effects of Attention ($F_{(1,38)} = 28.412, p < 0.001$) and ROI ($F_{(1,38)} = 101.941, p < 0.001$). There were two-way interactions of Attention × ROI ($F_{(1,38)} = 19.585, p < 0.001$) and Attention × Age ($F_{(1,38)} = 14.597, p < 0.001$). To investigate these interactions, we performed a two-way ANOVA with Target Location (left vs. right) and Attention (attend vs. ignore) as within-group factors for each ROI (ipsilateral vs. contralateral to target location) and each group (younger, older) separately, as shown in Table 3. These results show that spatial attention increased N1 amplitude within the contralateral ROI for both younger and older adults, suggesting enhanced sensory processing of attended targets versus ignored targets in both groups.

To better understand the nature of Attention \times Age interaction, we quantified attention effects by computing the attention-related difference waves (attended-target minus ignored-target) for N1

Table 1

Behavioral performance and results of two-way repeated measures ANOVA (Age: younger vs. older, Cue Direction: left vs. right). Behavioral results are presented in mean \pm SEM (ns: not significant).

		Group		Two-way repeated-measures ANOVA		
		Younger	Older	Age	Cue Direction	Age \times Cue Direction
Accuracy (%)	Cue Left Cue Right	99.54 ± 0.09 99.49 ± 0.13	98.66 ± 0.39 99.15 ± 0.27	$F_{(1,38)} = 4.658$ p = 0.037	$F_{(1,38)} = 2.665$ ns	$F_{(1,38)} = 4.007$ p = 0.052
RT (ms)	Cue Left Cue Right	$\begin{array}{r} 476.13 \pm 10.98 \\ 478.87 \pm 10.79 \end{array}$	567.78 ± 30.06 545.44 ± 27.25	$F_{(1,38)} = 8.344$ p = 0.006	$F_{(1,38)} = 6.842$ p = 0.013	$F_{(1,38)} = 11.194$ p = 0.002
Error rate (%)	Cue Left Cue Right	$\begin{array}{c} 0.25\pm0.08\\ 0.51\pm0.18\end{array}$	$\begin{array}{c} 0.91 \pm 0.33 \\ 0.78 \pm 0.24 \end{array}$	$F_{(1,38)} = 3.599$ ns	$F_{(1,38)} = 0.133$ ns	$F_{(1,38)} = 1.404$ ns

Table 2

Results of two-way repeated-measures ANOVA (Cue Direction: left vs. right, ROI Laterality: ipsilateral vs. contralateral to cue direction) of cue-related ERP component (EDAN, ADAN and LDAP) in each group (younger, older) separately (ns: not significant).

Group	Component	Two-way repeated-measure	Two-way repeated-measures ANOVA		
		Cue Direction	ROI Laterality	Cue Direction \times ROI Laterality	
Younger	EDAN	$F_{(1,22)} = 0.317$, ns	$F_{(1,22)} = 39.505, p < 0.001$	$F_{(1,22)} = 5.068, p = 0.035$	
	ADAN	$F_{(1,22)} = 0.461$, ns	$F_{(1,22)} = 46.868, p < 0.001$	$F_{(1,22)} = 0.506, \text{ ns}$	
	LDAP	$F_{(1,22)} = 0.003$, ns	$F_{(1,22)} = 6.220, p = 0.021$	$F_{(1,22)} = 5.097, p = 0.034$	
Older	EDAN	$F_{(1,16)} = 1.043$, ns	$F_{(1,16)} = 12.941, p = 0.002$	$F_{(1,16)} = 7.772, p = 0.013$	
	ADAN	$F_{(1,16)} = 1.199$, ns	$F_{(1,16)} = 5.467, p = 0.033$	$F_{(1,16)} = 0.662, \text{ ns}$	
	LDAP	$F_{(1,16)} = 0.599$, ns	$F_{(1,16)} = 27.709, p < 0.001$	$F_{(1,16)} = 0.105, \text{ ns}$	

amplitude within contralateral ROI in each group. A two-way ANOVA was performed with Target Location (left vs. right) as a within-group factor and Age (younger vs. older) as a between-group factor. As Fig. 4E illustrates, younger adults showed a stronger attention modulation on N1 amplitude than older adults, which was supported by a main effect of Age ($F_{(1,38)} = 8.508$, p = 0.006).

Alpha power lateralization

In order to test the critical hypothesis that attention-related alpha power lateralization might be specific to younger adults, we compared the cue-induced lateralization of alpha power between younger and older adults. Grand-averaged alpha-band TSE waveforms within two ROIs (PL, PR) are presented for younger (Fig. 5A) and older adults (Fig. 5B). The scalp topography of alpha power differences between the left and right cues was averaged within the middle (400-800 ms post-cue) and late (800–1200 ms post-cue) CTIs for younger (Fig. 5C) and older adults (Fig. 5D). To test the statistical significance of alpha power lateralization, alpha ERD values were averaged within the middle and late CTIs separately, and submitted to a four-way ANOVA with Time Window (middle vs. late), Cue Direction (left vs. right), and ROI Laterality (ipsilateral vs. contralateral to cue direction) as withingroup factors, and Age (younger vs. older) as a between-group factor (Fig. 5E). Main effect of ROI Laterality was observed ($F_{(1,38)} = 9.624$, p = 0.004), that is, alpha power was lower in the contralateral ROI versus the ipsilateral ROI. More importantly, we observed two-way interactions of ROI Laterality × Age ($F_{(1,38)} = 6.474$, p = 0.015) and Time Window × ROI Laterality ($F_{(1,38)} = 6.836, p = 0.013$).

To understand the interactions of ROI Laterality \times Age and Time Window \times ROI Laterality, a two-way ANOVA, with Cue Direction (left vs. right) and ROI Laterality (ipsilateral vs. contralateral to cue direction) as within-group factors was conducted for each time window (middle, late) and each group (younger, older) separately, as shown in Table 4. These results suggest that spatial attention lateralized posterior alpha power, that is, lower alpha power in the contralateral ROI compared to the ipsilateral ROI, only in younger adults during both the middle and late CTIs. In contrast, for older adults, no significant lateralization of posterior alpha power was observed during either the middle or late CTI. Taken together, our results illustrate an absence of attention-related alpha power lateralization in older adults even though classic measures of attentional orienting (EDAN, ADAN, LDAP and CNV) are present. This pattern of results suggests that cue-induced alpha power

lateralization is a marker of orienting attention that is specific to younger adults.

As shown in Fig. 5D, however, older adults seemed to develop some degree of alpha lateralization during the late CTI (800–1200 ms post-cue). To investigate the possible underestimation caused by the selection of ROIs, we performed the same analysis of alpha lateralization for older adults at every single channel within the ROIs (PL, PR). No main effect or interaction was observed for any pair of electrodes (P3 vs. P4; O1 vs. O2; P7 vs. P8) during either middle or late CTI.

Brain-behavior relationship

It was shown that older adults could successfully orient visual spatial attention without lateralizing alpha power. To investigate whether alpha power lateralization was related to behavioral performance in older adults, we further studied the brain-behavior relationship using both within- and between-subjects analyses. For the within-subjects analysis, the trials were divided into fast and slow RT trials for each older subject based on her or his own median reaction time. The fast trials had significantly shorter RTs than the slow trials (fast RT trials: 480.11 ± 21.55 ms; slow RT trials: 640.99 ± 37.01 ms; $t_{(16)} = -8.999$, p < 0.001). The same analysis of alpha power was performed for fast and slow RT trials. A fourway ANOVA was conducted on alpha ERD values with Response (fast vs. slow), Time Window (middle vs. late), Cue Direction (left vs. right) and ROI Laterality (ipsilateral vs. contralateral to cue direction) as withingroup factors. An interaction of Response \times Cue Direction \times ROI Laterality was observed ($F_{(1,16)} = 5.801$, p = 0.028). There were no other main effects or interactions. Furthermore, we performed a threeway ANOVA with Time Window (middle vs. late), Cue Direction (left vs. right) and ROI Laterality (ipsilateral vs. contralateral to cue direction) as within-group factors for fast and slow RT trials separately. However, no main effect or interaction of any factors was observed in either fast or slow RT trials (for ROI Laterality, Time Window \times ROI Laterality, Cue Direction \times ROI Laterality and Time Window \times Cue Direction \times ROI Laterality, all p > 0.1), suggesting that there was no significant alpha lateralization for either fast or slow RT trials in older adults. For the between-subjects analysis, we divided the older adults into fast and slow subgroups based on the group's median reaction time. The fast subgroup had significantly shorter RTs than the slow subgroup (fast: 9 subjects, 466.36 \pm 11.13 ms; slow: 8 subjects, 657.88 \pm 31.63 ms; $t_{(8.723)} = -5.711$, p < 0.001). A four-way ANOVA was conducted on alpha ERD values with Time Window (middle vs. late), Cue Direction (left vs. right), and ROI Laterality (ipsilateral vs. contralateral to cue

Table 3

Results of two-way repeated-measures ANOVA (Target Location: left vs. right, Attention: attend vs. ignore) of target-related N1 amplitude within different ROIs (ipsilateral, contralateral to target location) in each group (younger, older) separately (ns: not significant).

Group	ROI	Two-way repeated-measures ANOVA		
		Target Location	Attention	Target Location \times Attention
Younger	Ipsi	$F_{(1,22)} = 0.365$, ns	$F_{(1,22)} = 21.520, p < 0.001$	$F_{(1,22)} = 0.445$, ns
	Contra	$F_{(1,22)} = 0.782$, ns	$F_{(1,22)} = 63.143, p < 0.001$	$F_{(1,22)} = 0.129$, ns
Older	Ipsi	$F_{(1,16)} = 0.245$, ns	$F_{(1,16)} = 0.761$, ns	$F_{(1,16)} = 0.753$, ns
	Contra	$F_{(1,16)} = 0.842$, ns	$F_{(1,16)} = 5.988$, $p = 0.026$	$F_{(1,16)} = 0.431$, ns

Table 4

Results of two-way repeated-measures ANOVA (Cue Direction: left vs. right, ROI Laterality: ipsilateral vs. contralateral to cue direction) of cue-related posterior alpha power (ERD) during different time windows (middle CTI, late CTI) in each group (younger, older) separately (ns: not significant).

Group	Time Window	Two-way repeated-measures ANOVA		
		Cue Direction	ROI Laterality	Cue Direction \times ROI Laterality
Younger	Middle CTI	$F_{(1,22)} = 0.327$, ns	$F_{(1,22)} = 11.468, p = 0.003$	$F_{(1,22)} = 1.997$, ns
	Late CTI	$F_{(1,22)} = 0.090$, ns	$F_{(1,22)} = 13.831, p = 0.001$	$F_{(1,22)} = 1.365$, ns
Older	Middle CTI	$F_{(1,16)} = 0.217$, ns	$F_{(1,16)} = 0.093$, ns	$F_{(1,16)} = 0.019$, ns
	Late CTI	$F_{(1,16)} = 0.748$, ns	$F_{(1,16)} = 1.772$, ns	$F_{(1,16)} = 0.038$, ns

direction) as within-group factors, and Response (fast vs. slow) as a between-group factor. No main effect or interaction between or among any factors was observed, suggesting that there was no difference in alpha lateralization between fast and slow subgroups. Thus, in addition to the lack of alpha lateralization specifically for older adults, there was no evidence suggesting the relevance between alpha lateralization and reaction times in older adults.

Discussion

This study aimed to investigate how normal aging changes electrophysiological measures of visual spatial attention during trial-by-trial cueing of voluntary attention. Our findings can be summarized as follows. In behavioral performance, older adults responded more slowly than younger adults, while accuracy in both groups was high, a pattern often reported in the literature (Curran et al., 2001; Nagamatsu et al., 2011; Yamaguchi et al., 1995). The electrophysiology of spatial attention revealed different effects of age for different EEG measures. In ERP results, both younger and older adults showed significant electrophysiological signs of attentional orienting (EDAN, ADAN, LDAP and CNV) elicited by spatial cues, as well as significant attentional facilitation of the target-evoked N1 amplitude. The alpha-band activity in response to spatial cues, however, revealed important differences as a function of age. Specifically, younger adults showed the expected pattern of alpha power lateralization elicited by attention-directing cues, but older adults did not show this marker of lateralized attention. Taken together, these results suggest that younger and older adults recruit partially different neural mechanisms of top-down attentional control, and that alpha power lateralization is a marker of orienting attention that is specific to younger adults.

Age-related deficits in alpha power lateralization during preparatory spatial attention

Anticipation of a visual stimulus at a specific location leads to the lateralization of posterior alpha power with stronger suppression over the hemisphere contralateral versus ipsilateral to the attended location. It has been widely proposed that such lateralization of alpha power reflects the enhanced excitability of sensory areas coding the attended location and active suppression of sensory areas coding the ignored location (Grent-'t-Jong et al., 2011; Kelly et al., 2009; Liu et al., in press; Rihs et al., 2009; Sauseng et al., 2005; Thut et al., 2006; Worden et al., 2000). Our results of alpha power lateralization following an attention-directing cue in the younger group are in line with prior findings (Figs. 5A and C). In the older group, however, this attention-related lateralization of posterior alpha power following the cue was not observed (Figs. 5B and D), although they performed the task well, having high accuracy in target discrimination, and negligible errors at the uncued location (Table 1), and they also showed significant lateralized ERP components (EDAN, ADAN and LDAP) elicited by spatial cues (Fig. 2), the signs of spatial attention deployment (Harter et al., 1989; Hopf and Mangun, 2000; Kelly et al., 2009; Nagamatsu et al., 2011; Nobre et al., 2000), and they also showed prominent CNV component (Fig. 3), a sign of the anticipation of forthcoming targets (Brunia and Damen, 1988; Walter et al., 1964). Further, although displaying a smaller effect, the older adults, like the younger, showed significant amplitude modulations of the visually evoked posterior N1 component elicited by the targets, another sign of the selective allocation of visual attention in voluntary spatial cueing tasks (Fig. 4) (Hillyard and Anllo-Vento, 1998; Mangun and Hillyard, 1991). Therefore, our findings suggest that older adults have significant deficits in modulating visual cortical excitability during the post-cue, pre-target anticipatory state, although they could orient their visual attention and improve perception at the attended location. As can be observed in Fig. 5B, the absence of the lateralization of posterior alpha power for older adults mainly resulted from the quick increase (starting ~500 ms post-cue) in contralateral alpha power, which however, remained consistently suppressed throughout the CTI for younger adults, indicating an age-related deficit in cortical facilitation for sensory regions coding attended visual field locations (Rihs et al., 2009; Sauseng et al., 2005; Worden et al., 2000).

Another possibility is that alpha power lateralization might develop more slowly in older adults and thus not be fully captured by the CTI (1000-1200 ms) in this study. Inconsistent with this speculation, a previous study has shown that the facilitation of RTs by a valid cue in a spatial attention task was maximal around 500 ms SOA (stimulus onset asynchrony between the cue and target) compared with 200 ms and 800 ms SOAs, and such a RT facilitation associated with spatial cueing did not vary between younger and older adults (Yamaguchi et al., 1995). Therefore, 500 ms is likely to be enough for completing spatial attention orienting in either younger or older adults. Another study that compared different SOAs (100 ms, 300 ms and 500 ms) found that the behavioral spatial cueing effects even appeared earlier for older than younger adults (Hartley et al., 1990). Furthermore, in this study, we did observe the cue-related lateralized ERP components (EDAN, ADAN and LDAP) associated with spatial orienting within 500 ms post-cue. Concordantly, we did not observe a latency delay of these components in older adults (Fig. 2), suggesting that the neural activity associated with top-down attentional control was not delayed during normal aging.

In addition to the deficit in the lateralization of posterior alpha power, older adults also showed reduced attentional facilitation on target-evoked N1 amplitude compared with younger adults, which was consistent with previous finding of the age-related decline in task-related activity over visual cortex (Gazzaley et al., 2008; Grady, 2012; Grady et al., 1994; Spreng et al., 2010; Zanto et al., 2011). Further, prior study has reported a positive correlation between attentional modulation on the pre-target preparatory activity and subsequent target-evoked activity (Sylvester et al., 2009), so we might infer that the reduced attention effect on N1 amplitude in older adults was the result of the deficit in pre-target alpha power lateralization. However, previous ERP studies failed to report such differences in attentional modulation of N1 amplitude between different age groups (Curran et al., 2001; Nagamatsu et al., 2011). These apparent discrepancies might be due to the subtle differences in the paradigms used to investigate age-related changes in attention. Prior studies (Curran et al., 2001; Nagamatsu et al., 2011) used the classic Posner task, in which the cue predicted the target location in a high probability, but the subjects still needed to respond to the targets that appeared at the uncued locations (Posner, 1980). In these classic Posner paradigms, uncued locations are still relevant and may be attended to some extent, which is not ideal for

investigating attention modulation of alpha power or ERPs (Snyder and Foxe, 2010). Inspired by many related studies (Doesburg et al., 2008; Hopfinger et al., 2000; Kelly et al., 2009; Liu et al., in press; Snyder and Foxe, 2010; Worden et al., 2000), we used the instructional cueing method, in which the subjects were instructed to direct their full attention to the cued location and ignore the uncued locations. Furthermore, previous research has shown that the lateralized ERP components related to spatial orienting were stronger in the instructional cueing method than the probabilistic cueing method (Jongen et al., 2007). Therefore, the difference in the nature of focused attention may explain some of the differences between our findings and prior studies.

Age-related changes in the neural mechanisms of top-down attentional control

It should be noted that since the task discrimination is relatively simple in this study, older adults might simply react to the target stimuli when they appeared, which might lessen the requirement of attentional biasing of the visual cortex, and thus explain the slower RT in older adults. However, our EEG data clearly demonstrated that older adults could successfully orient their attention in this paradigm, exhibiting cue-induced lateralized ERP components associated with spatial orienting (EDAN, ADAN and LDAP), as well as attentional enhancement of the target-related sensory component (N1). Furthermore, the amplitudes of cue-related ERP components were not smaller (EDAN and ADAN), but even larger (LDAP) in the older than younger adults, suggesting that the neural activity associated with attentional control did not decline during normal aging. Finally, there have been many studies showing that in the classic Posner paradigm, although the absolute RT was much longer in older than younger adults, the magnitude of behavioral spatial cueing effect in older adults was as substantial as in younger adults (Curran et al., 2001; Greenwood et al., 1993; Hartley, 1993; Hartley et al., 1990; Nagamatsu et al., 2011; Nissen and Corkin, 1985; Yamaguchi et al., 1995). Taken together, our data suggest that although older adults responded more slowly than younger adults, they also went through the same top-down control process, and achieved a preparatory attentional state during the anticipatory period, even in the absence of alpha lateralization.

As discussed above, both behavioral and ERP results strongly indicate that older adults could successfully orient their covert visual attention and facilitate the perceptual processing at the cued location, which is consistent with the aging literature, that is, the ability of visual spatial attention is relatively resistant to normal aging (Greenwood et al., 1993; Hartley, 1993; Hartley et al., 1990; Madden, 1990; Nissen and Corkin, 1985; Plude et al., 1994). Although older adults did not show significant lateralization of posterior alpha power in response to spatial cues, they showed stronger LDAP and CNV components than younger adults. The LDAP is thought to reflect the modulation of excitability of the visual cortex in anticipation of the forthcoming visual stimulus (Dale et al., 2008; Hopf and Mangun, 2000; Kelly et al., 2009). Moreover, the CNV is usually observed following a warning cue that triggers the activation of cortical areas for the perceptual processing and motor preparation of the forthcoming stimulus (Brunia and Damen, 1988; Walter et al., 1964). Consistently, the CNV has been localized to anterior cingulate cortex and supplementary motor areas which are thought to mediate the preparation for perception and action (Gomez et al., 2003). Therefore, our findings suggest that older adults could recruit more activation in the above cortical regions instead of lateralizing alpha power in visual cortex during the anticipatory period. Such findings may represent an interesting case of cognitive compensation in visual spatial attention, which is comparable to what has been commonly observed in memory tasks (Cabeza et al., 1997, 2002; Grady, 2012).

Recent studies have shown that the magnitude of anticipatory alpha power modulation was smaller in older than younger adults (Deiber et al., 2013; Zanto et al., 2011). Compared to these studies, we explicitly examined the lateralized modulation of EEG activity elicited by spatial orienting, and our findings provide new implications for the relationship between alpha oscillations and attention. In this study, older adults performed the spatial attention task well with robust signs of spatial attention, including cue-related lateralized ERP components (EDAN, ADAN, LDAP) and attentional modulation of the target-related N1 component. This pattern of results suggests that the deployment of attention amongst older participants is not reliant upon alpha power lateralization. Thus, alpha power lateralization in spatial selective attention may be selectively impacted during normal aging.

Conflict of interest

The authors declare no conflicts of interest.

Acknowledgments

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