



Cue-related processing accounts for age differences in phasic alerting

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ABSTRACT

Alertness is fundamental for the efficiency of information processing. A person's level of alertness refers to the system's state of general responsiveness and can be temporarily increased by presenting a neutral warning cue shortly before an event occurs (Posner and Petersen, 1990). However, effects of alerts on subsequent stimulus processing are less consistent in older than in younger individuals. In this study, we investigated the neural underpinnings of age differences in processing of auditory alerting cues. We measured electroencephalographic power and phase locking in response to alerting cues in a visual letter report task, in which younger but not older adults showed a cue-related behavioral advantage. Alerting cues evoked a significant increase in power as well as in inter-trial phase locking, with a maximum effect in the alpha frequency (8–12 Hz) in both age groups. Importantly, these cue-related increases in phase locking and power were stronger in older than in younger adults and were negatively correlated with the behavioral alerting effect in the older sample. Our results are in accordance with the assumption that older adults' neural responses may be more strongly driven by external input and less variable than younger adults'. A stronger neural response of the system to the auditory cue may have hindered older adults' effective use of the warning signal to foster processing of the following visual stimulus.

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1. Introduction

Alertness is fundamental for the efficiency of information processing as its level determines response readiness (Posner and Petersen, 1990; Sturm et al., 1999), that is, a preparatory state to react efficiently to imminent stimuli (Sturm and Willmes, 2001). A short-lived, nonspecific change in the cognitive system's preparatory state (or increase in arousal) can be induced by presenting a neutral warning signal or uninformative cue (Coull et al., 2001; Posner and Petersen, 1990; Thiel and Fink, 2007), referred to as “phasic alerting effect.”

Although such effects are consistently reported in younger samples, examinations of older adults (OAs) are inconclusive: Some have reported preserved alerting effects (Fernandez-Duque and Black, 2006; Haupt et al., 2018; Rabbitt, 1984), whereas others have shown decreased or even absent alerting effects in older age

(e.g., Festa-Martino et al., 2004; Gamboz et al., 2010; Ishigami et al., 2016; Jennings et al., 2007; Wiegand et al., 2017b). The mechanisms underlying age-related decline in alerting may be elusive if age differences in processing of the alert itself are investigated in samples in which no benefit from the warning cue was observed (Wiegand et al., 2017b).

In younger adults (YAs), power modulations in the alpha band of the electroencephalogram (EEG) in response to various types of informative cues have been reported (Klimesch, 1999; Thut et al., 2006). These were suggested to reflect a preparatory state in expectation of the location or identity of the target stimulus (Hanslmayr et al., 2005, 2007; Jensen and Mazaheri, 2010) or the time of target stimulus onset (Rohenkohl and Nobre, 2011). Cue-related alpha power modulation was shown to be reduced in older compared to YAs (Deiber et al., 2013; Zanto et al., 2011). Similarly, event-related phase locking is assumed to reflect efficient temporal coordination of neural activation (Klimesch et al., 2007; Sauseng and Klimesch, 2008). Stronger phase locking indicates smaller intertrial variance and has been associated with better performance in YAs (Hanslmayr et al., 2005; Klimesch et al., 2004). With regard to age-related differences in phase locking, findings are inconsistent. Studies have reported reduced (Tran et al., 2016), comparable

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(Werkle-Bergner et al., 2012), and also increased phase locking for older relative to YAs (Müller et al., 2009; Sander et al., 2012). Possibly, the relationship between behavioral performance and phase locking may change with age (Werkle-Bergner et al., 2012), such that high levels of intertrial phase stability in OAs indicate a loss of complexity in the neurophysiological response and stronger entrainment by external stimulation (Garrett et al., 2013; Sander et al., 2012).

Recently, Tran et al (2016) investigated age differences in alpha power and phase locking in response to a visual, temporally predictive, alerting cue in a visual working memory task. Although they found no age differences in cue-related power, cue-related phase locking was reduced in older relative to YAs. Furthermore, lower phase locking was associated with worse performance. However, as every trial contained a cue, the relation between cue processing and the individual alerting effect (i.e., the cue-related facilitation of stimulus processing), and potential age differences in alerting effects, could not be tested.

In the present study, we examined age differences in the processing of an auditory alerting cue in a visual attention task (Wiegand et al., 2017a). Participants performed a “partial report task,” in which briefly presented letter stimuli had to be discriminated (Bundesen, 1990; Duncan et al., 1999). In half of the trials, the letter display was preceded by a cue, and in the other half, no alerting cue was presented. Note that we use the term “alerting cue” interchangeable with warning signal. We consider the auditory tone to be an uninformative warning signal that induces an increased level of alertness, facilitating the processing of the upcoming target. The signal is uninformative of the identity, location, or exact time point of stimulus occurrence. It only carried unspecific temporal information about the upcoming target but did not allow for temporal orienting (Nobre, 2001). We previously demonstrated an age-specific alerting effect on visual stimulus processing in this sample (Wiegand et al., 2017a,b [Note that the behavioral data from these publications are reused in the current analysis. Both publications analyzed also event-related lateralizations locked to stimulus onset. Cue-related activity was not analyzed before.]). Discrimination performance was significantly increased in the YAs after the warning cue, but not in the OAs. We hypothesized that the age-related decline in the alerting effect may be due to age differences in processing of the cue itself. In this study, we therefore measured power and phase locking in response to the alerting cue and examined the relations between the cue-related EEG modulations and the behavioral alerting effect in younger and OAs.

2. Methods

2.1. Participants

The participants in this study have been described earlier by Wiegand et al. (2017a). The sample consisted of 18 YAs (age: $M_{YA} = 24.3$ $SD_{YA} = 3.1$, sex: 12 female, 8 male) and 17 OAs (age: $M_{OA} = 62.9$ $SD_{OA} = 7.6$; sex: 9 female, 8 male). All participants had normal or corrected-to-normal vision, and none were color-blind. According to their self-report, participants were not suffering from any chronic somatic diseases or any psychiatric or neurological impairments. The older participants were further screened for cognitive and sensory impairments. All participants reached scores of 26 or higher in the Mini-Mental State Examination (Folstein et al., 1975). None of the OAs showed severe deficits in hearing [mean (SD) hearing thresholds (dB) were 22.7 (4.3) for 500 Hz and 23.4 (5.7) for 1000 Hz] or vision [mean (SD) of visual acuity 0.7 (0.2) as measured with the Snellen test]. Written informed consent according to the Declaration of Helsinki II was obtained before the experiment was carried out, and the participants received gift cards (600–700 DKK) for their participation.

2.2. Task

The PC-controlled experiment was conducted in a dimly lit, soundproof and electrically shielded cabin. Stimuli were presented on a CRT 17” monitor (1024×768 pixel screen resolution; 100 Hz refresh rate). Participants were seated in a comfortable chair at a viewing distance of approximately 90 cm from the screen. Each participant completed two experimental sessions on two separate days. In each of the two sessions, a total of 800 trials were run, divided into 20 blocks with 40 trials each, which lasted around 1.5 hours. Participants were given standardized written and oral instructions, and example displays were presented on the screen to illustrate the task before the experiment began.

On each trial (see Fig. 1), either a single target, two targets, or a target and a distractor were presented. Two letters were presented either vertically (unilateral display) or horizontally (bilateral display), but never diagonally, resulting in 16 different display conditions. A trial began with a circle presented in the center of the screen, which participants were instructed to fixate throughout the whole trial. Then the letter array was presented on a gray background. Participants’ task was to verbally report only the red (target) letters and ignore the blue (distractor) letters. The report could be given in any (arbitrary) order and without emphasis on response speed. Participants were instructed to report only those letters they had recognized “fairly certainly” and refrain from pure guessing. The experimenter entered the responses on the keyboard and pressed a button to initiate the next trial.

The exposure duration (ED) of the letter displays was determined individually in a calibration before the experiment (see Wiegand et al., 2017a, for details). This was done to minimize individual differences in task difficulty because of variations in perceptual threshold. EDs were chosen so that performance was 60%–90% correct in single-target displays and >50% correct for individual targets within dual-target displays. Mean (SD) EDs (in ms) were 108.112 (46.211) for OAs and 39.668 (13.755) for YAs.

In half of the trials, randomly selected, the letter array was preceded by a loud auditory warning cue played for 200 ms. The tone was 85 dB loud and varied randomly in pitch between 500 and 900 Hz to prevent habituation effects. Participants were told not to pay attention to the warning cue while performing the partial report task. The intertrial intervals (ITIs) were drawn from a geometrical distribution with a constant hazard rate of 1/3 and a range of 1600–4400 ms using time steps of 200 ms. This was done to keep the hazard rate constant and prevent response preparation, specifically to prevent a gradual increase in temporal expectancy over the time of the ITI (“foreperiod effect,” Niemi and Näätänen, 1981) that could potentially interact with the cue-related alerting effect. The cue-target intervals (CTIs) were uniformly distributed with a range of 240–330 ms using time steps of 10 ms. In trials without a cue, time intervals identical to the CTIs were added to the ITIs to keep timing constant over conditions (see Fig. 1). Note that, in principle, a gradual buildup of expectancy over the CTI duration may have been possible. However, given that the CTI duration randomly varied within a very short range, we consider this negligible, and the paradigm was not designed to analyze data as a function of CTI duration.

Cue and display conditions were balanced across blocks, and each subject was presented with the same displays in a different random order. Letter stimuli were presented in Arial 16-point font, with equal frequencies at each of four possible display locations forming an imaginary square, with a distance of approximately 8 cm from the fixation circle. The red target color and the blue distractor color were equiluminant (2.1 cd/cm², measured with ColorCAL MKII Colorimeter, Cambridge Research Systems). The letters of a given trial were randomly chosen, without replacement, from a prespecified set (ABDEFGHJKLMNPRSTVXZ).

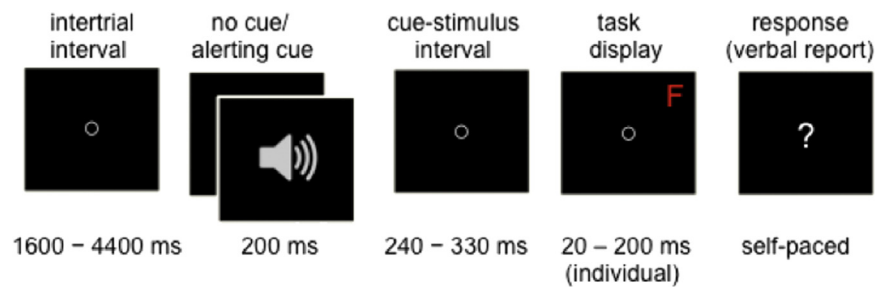


Fig. 1. Trial procedure in the letter report task.

2.3. Behavioral data analyses

Performance was measured as report accuracy (mean scores), that is, the rate of correctly reported individual targets in a display collapsed over upper/lower and left/right letter arrangements. As previous analyses did not find an effect of the alerting cue on distractor processing (Wiegand et al., 2017a,b), we compared accuracy between trials with and without the alerting cue across all display conditions between YAs and OAs via a mixed ANOVA with CUE (2) as the within-subject factor and AGE GROUP (2) as the between-subject factor.

2.4. EEG recording and preprocessing

The EEG was recorded using a Biosemi amplifier system (Amsterdam, BioSemi Active 2) from 64 active Ag-Cl electrodes mounted on an elastic cap, placed according to the International 10/10 system (American Electroencephalographic Society, 1994). Five additional electrodes were placed on the left and right mastoids, at the outer canthi of the eyes (horizontal electrooculogram), and beneath the left eye (vertical electrooculogram). The signal was recorded at a sampling rate of 512 Hz bandwidth DC–100 Hz and referenced online to a Common Mode Sense - Driven Right Leg ground, which drives the average potential (i.e., common mode voltage) as close to the AC reference voltage of the analog-to-digital box as possible (see <http://biosemi.com> for an explanation of the Biosemi system). The continuous signal was filtered offline with a 0.1 high-pass filter and re-referenced to the averaged mastoids and downsampled to 128 Hz. An Infomax Independent Component Analysis (Bell and Sejnowski, 1995) using the runica algorithm implemented in EEGLAB (Delorme and Makeig, 2004) was run to identify and backtransform ocular artifacts (Jung et al., 2000). The EEG was segmented into epochs of 2 seconds (from -1 second before and 1 second after cue onset). In no-cue trials, EEG triggers were set before stimulus onset using time intervals identical to the CTIs in cue trials (randomly drawn from a uniform distribution with a range of 240–330 ms, using time steps of 10 ms). Trials with signals exceeding $\pm 100 \mu\text{V}$ on any of the scalp electrodes were discarded as artifacts. The mean number of trials after artifact rejection did not differ between conditions or age groups [YAs: $M_{\text{cue}} = 599.89$ ($SD = 119.3$), $M_{\text{no cue}} = 601.47$ ($SD = 120.8$); OAs: $M_{\text{cue}} = 591.11$ ($SD = 125.56$), $M_{\text{no cue}} = 589.00$ ($SD = 128.94$)].

2.5. EEG data analysis

Data were analyzed with Fieldtrip (Oostenveld et al., 2011), a software package developed at the F. C. Donders Centre for Cognitive Neuroimaging, Nijmegen, The Netherlands (<http://fieldtrip.fcdonders.nl/>) supplemented by custom-made MATLAB code (MathWorks Inc., Natick, MA, USA). All codes would be shared on publication on reasonable request.

Only Independent Component Analysis—cleaned, artifact-free EEG trials were analyzed. Time frequency power was calculated using Hanning tapers with a fixed temporal window size of 250 ms from 4 Hz to 32 Hz in steps of 4 Hz. After frequency decomposition, we assessed the phase stability across trials with the phase-locking index (PLI, see Lachaux et al., 1999, Tallon-Baudry et al., 1996; following Delorme and Makeig, 2004). The Fourier spectrum was divided by its amplitude, and the normalized, absolute value of the sum of angles was taken. Given that the resulting phase-locking vector varies between 0 and 1 and is potentially not normally distributed, we applied Fisher's z-transformation. Power was log-transformed to take into account age-related changes in the 1/f ratio (Voytek et al., 2015). Power and phase locking across trials were computed for each subject, electrode, and time-frequency point, separately for cue and no-cue conditions across all trials time-locked to cue onset. In a first step, we compared power and phase locking between the cue and no-cue conditions using dependent sample t-tests. Multiple comparison correction was achieved by a cluster-based permutation statistics approach (Maris and Oostenveld, 2007). Clusters were formed based on electrodes when a minimum of three adjacent electrodes reached $p_{\text{uncorrected}} < 0.05$. The cluster-level permutation null distribution was determined by repeating the paired t-test 1000 times, swapping the assignment for cue/no-cue conditions randomly. The summed t-values within a cluster formed the relevant test statistic. Topographical clusters were considered significant at $p < 0.025$ (two-sided test). These analyses revealed reliable cue effects in both age groups in both neural measures. In a second step, we therefore tested directly for age differences in the amount of power increases and phase locking after the cue by comparing within-subject power and PLI differences in the cue and no-cue condition between YAs and OAs. To do so, we applied independent sample t-tests corrected for multiple testing again via a cluster-based permutation statistics approach. Clusters were formed based on electrodes when a minimum of three adjacent electrodes reached $p_{\text{uncorrected}} < 0.01$. Cluster-level permutation null distribution was determined by repeating the independent samples t-test 1000 times, swapping the assignment for groups randomly. The summed t-values within a cluster formed the relevant test statistic. Topographical clusters were considered significant at $p < 0.025$ (two-sided test). Finally, using Pearson correlations, we investigated whether age differences in these neural measures were related to age differences in the behavioral cue effect.

3. Results

3.1. Effects of the alerting cue on report accuracy

The mixed ANOVA with cue (2) as within-subject factor and age group (2) as between-subject factor revealed a reliable effect of the alerting cue on accuracy [$F(1,33) = 19.1849$, $p < 0.001$] with higher

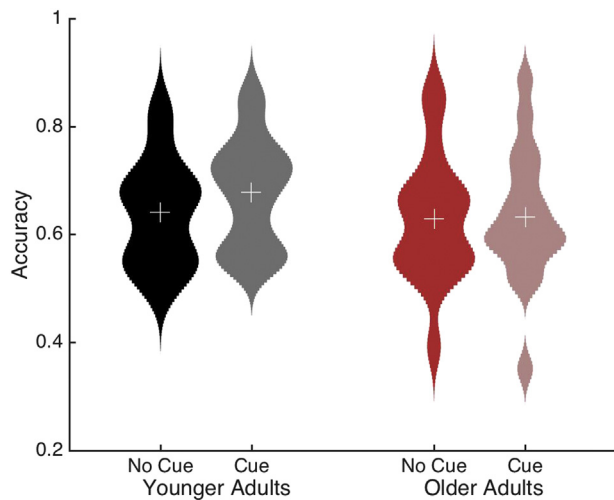


Fig. 2. Accuracy in the letter report task for younger and older adults with and without a preceding alerting cue. Means are represented by a white cross. Whereas younger adults (YAs) show better performance in the cue condition, the group of older adults (OAs) does not benefit from the presentation of a cue.

accuracy in trials with the alerting cue compared with trials without cue ($M_{cue} = 0.656$, $SD_{cue} = 0.145$; $M_{no\ cue} = 0.635$, $SD_{no\ cue} = 0.111$). Importantly, while there were no overall differences between age groups, $F(1,33) = 0.60139$, $p = 0.44357$, there was a significant interaction between cue and age group, $F(1,33) = 13.891$, $p < 0.001$, indicating that the alerting effect had a significant effect on report accuracy in the group of YAs (cue: $M_{YA} = 0.679$, $SD_{YA} = 0.10$; no cue: $M_{YA} = 0.641$, $SD_{YA} = 0.10$; $t(17) = -7.46$; $p < 0.001$), but not in the group of OAs (cue: $M_{OA} = 0.632$, $SD_{OA} = 0.13$; no cue: $M_{OA} = 0.629$, $SD_{OA} = 0.12$; $t(16) = -0.3825$; $p = 0.71$; see Fig. 2).

3.2. Effects of the alerting cue on ongoing power

Cluster-based permutation statistics yielded one significant cluster of reliable power differences between cue and no-cue trials both for the younger and the OAs ($p_{corr} = 0.001$ in both samples). The power effects spanned frequencies in the theta, alpha, and beta range (4–20 Hz) and encompassed all electrodes. In both age groups, maximum differences between the two conditions showed a frontocentral distribution and were found in the alpha band approximately 50–200 ms after the cue onset (Fig. 3). Within the respective cluster, (log) power was higher in trials in which a cue was presented than in trials without a cue, both in YAs (no cue: $M_{YA} = 0.7261$, $SD_{YA} = 0.2347$; cue: $M_{YA} = 0.8379$, $SD_{YA} = 0.2314$) and OAs (no cue: $M_{OA} = 0.7284$, $SD_{OA} = 0.2000$; cue: $M_{OA} = 0.8396$, $SD_{OA} = 0.1789$). Thus, both age groups demonstrated a reliable increase in power after the presentation of an alerting cue.

3.3. Effects of the alerting cue on ongoing phase locking

Cluster-based permutation statistics also yielded one significant cluster of reliable PLI differences between cue and no-cue trials for both age groups ($p_{corr} = 0.001$ in both samples). The PLI effects were broadly distributed across all frequencies and electrodes in the postcue time window (0–500 ms), with a maximal difference over frontocentral electrodes in the alpha band around 0–300 ms after the cue onset (Fig. 4). Phase locking was stronger in trials with a cue than in those without in both younger (no cue: $M_{YA} = 0.0504$, $SD_{YA} = 0.0075$; cue: $M_{YA} = 0.1694$, $SD_{YA} = 0.0385$) and OAs (no cue: $M_{OA} = 0.0652$, $SD_{OA} = 0.0171$; cue: $M_{OA} = 0.2089$, $SD_{OA} = 0.0409$) in the respective cluster. Thus, both age groups demonstrated reliable modulations of the neural signal after an alerting cue.

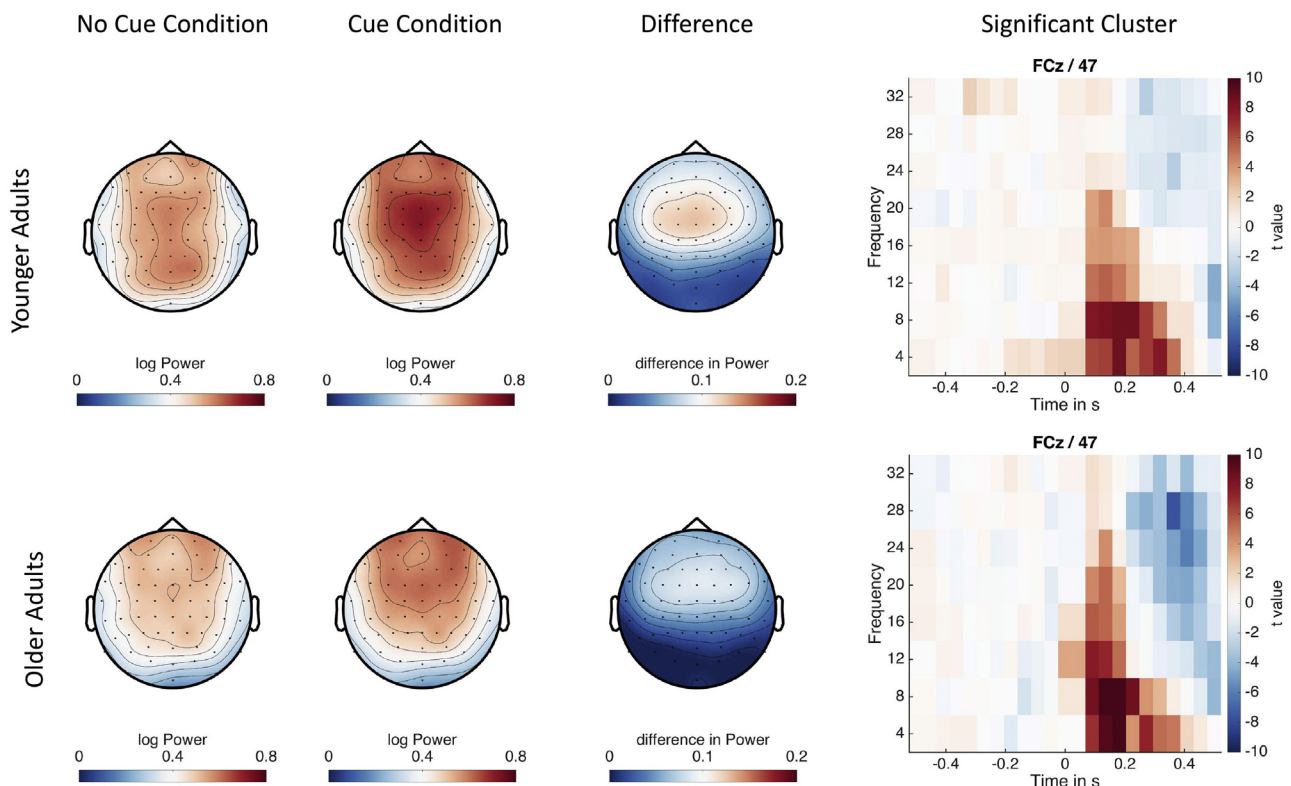


Fig. 3. Cue-related (log-transformed) power modulation in younger (upper panel) and older adults (lower panel). Both age groups show a reliable increase in power over centrofrontal electrodes shortly after the presentation of the cue. For illustration, significant clusters at FCz are highlighted.

3.4. Age differences in the effects of the alerting cue

Given that we observed reliable increases in both power and phase locking in both age groups after the presentation of a cue while only YAs seemed to benefit on the behavioral level, we set out to test directly for age differences in these seemingly similar effects. We therefore subtracted power/PLI in no-cue trials from power/PLI in cue trials for each participant and searched for age differences in the cue effect via cluster permutation statistics. With regard to power, this direct age comparison yielded one significant cluster ($p_{corr} = 0.023$) at around 50–100 ms in the alpha band (8–12 Hz). OAs showed a larger difference in power (i.e., a stronger effect of the cue) than YAs ($M_{YA} = 0.0978$, $SD_{YA} = 0.0554$; $M_{OA} = 0.2117$, $SD_{OA} = 0.0965$).

With regard to the cue effect on the PLI, the direct age comparison revealed a clear difference ($p_{corr} = 0.001$) in the alpha/beta range (8–16 Hz) in a short time window after cue onset (0–100 ms) with a frontocentral distribution (Fig. 5). Importantly, this difference was again driven by OAs showing a larger difference in phase locking (i.e., a stronger effect of the cue) than YAs ($M_{YA} = 0.2471$, $SD_{YA} = 0.0893$; $M_{OA} = 0.4134$, $SD_{OA} = 0.1167$).

Next, we investigated whether the higher power and phase locking to the cue in older age was related to age differences in the behavioral cue effect. The cue effect (i.e., the cue–no-cue difference) on PLI and the cue effect on accuracy were indeed negatively related in the OA sample ($r = -0.611$, $p < 0.01$), and the relation between the cue effect on power and the cue effect on accuracy showed a trend in the same direction ($r = -0.4769$, $p = 0.05$). By contrast, there was no relation between the cue effects on accuracy and power or PLI in the YA sample (power: $r = -0.2553$, $p = 0.3065$, PLI: $r = 0.0097$, $p = 0.97$). Testing post hoc whether the correlation between PLI and accuracy was reliably stronger in the

older than the YAs revealed a significant difference for the PLI accuracy correlation (one-sided test, $z = -1.936$, $p = 0.026$) but not for the power-accuracy correlation (one-sided test, $z = -0.694$, $p = 0.244$). However, given our relatively small sample sizes, age group differences of the correlations should be interpreted with caution. Importantly, as can be seen in Fig. 5, the correlations between accuracy and both power and PLI in the OAs also indicate that despite overall age differences, those OAs who showed a cue-related performance benefit also showed PLI and power effects within the range of young adults.

4. Discussion

The present study investigated age differences in power and intertrial phase stability in response to an auditory warning cue in a phasic alerting paradigm. In both younger and OAs, the cue elicited similar levels of power increase over frontocentral areas in the alpha range. Differences between age groups were nevertheless found both in power and in phase locking. Strikingly, OAs showed stronger phase locking than YAs and higher phase locking was associated with a smaller behavioral alerting effect in the older age group. In fact, OAs with relatively high phase locking to the alerting cue even experienced a detrimental effect in accuracy. These age differences in phase locking with simultaneous increases in power may be indicative of a stronger phase reset in older than in YAs.

Higher phase locking in OAs than YAs, similar to our results, has been reported previously in a visual working memory task (Sander et al., 2012) and an auditory oddball task (Müller et al., 2009). These age effects were suggested to indicate that sensory processing in older age is more automatic, stimulus-driven, and less easily modulated in a top-down, task-driven manner. As a consequence, older individuals' system is less flexible and more responsive to

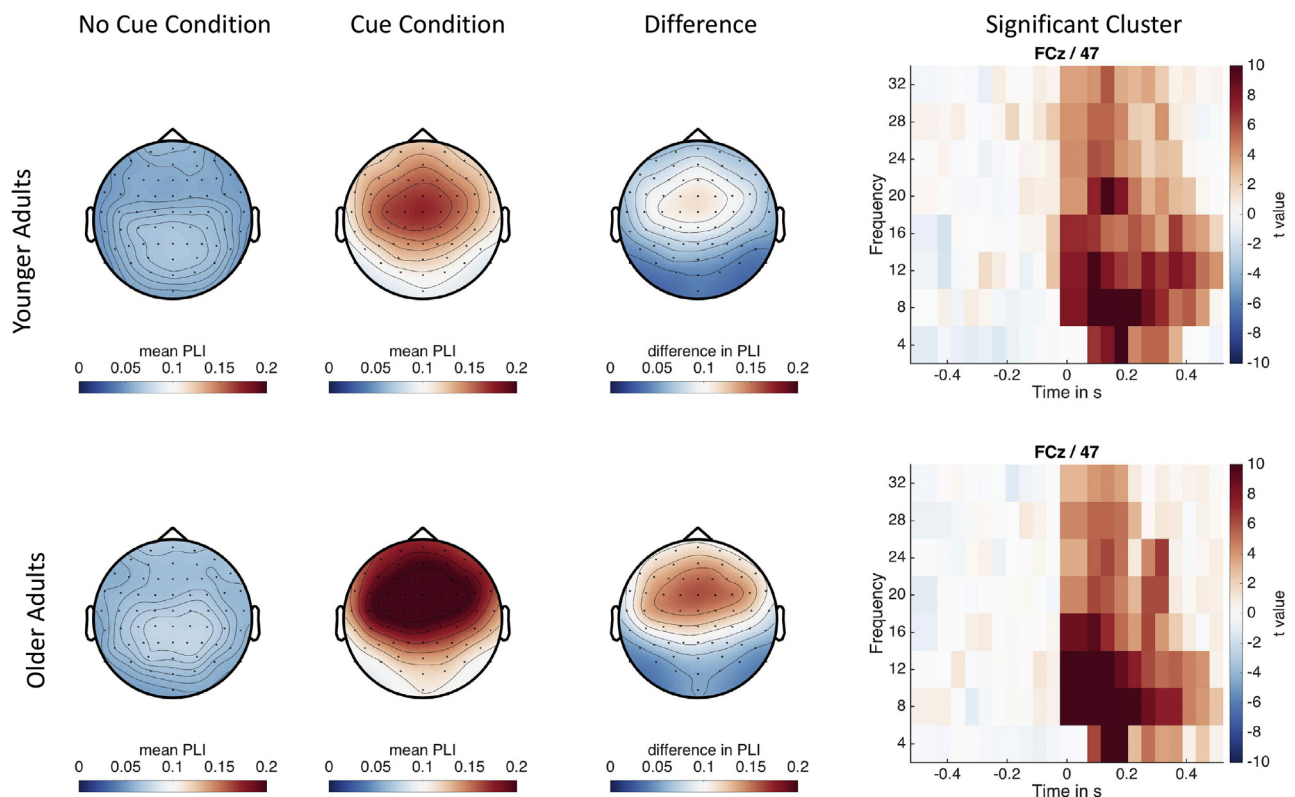


Fig. 4. Cue-related phase-locking index (PLI) modulations in younger (upper panel) and older adults (lower panel). Both age groups display a reliable increase in phase locking over frontocentral electrodes shortly after the cue presentation. For illustration, significant clusters at FCz are highlighted.

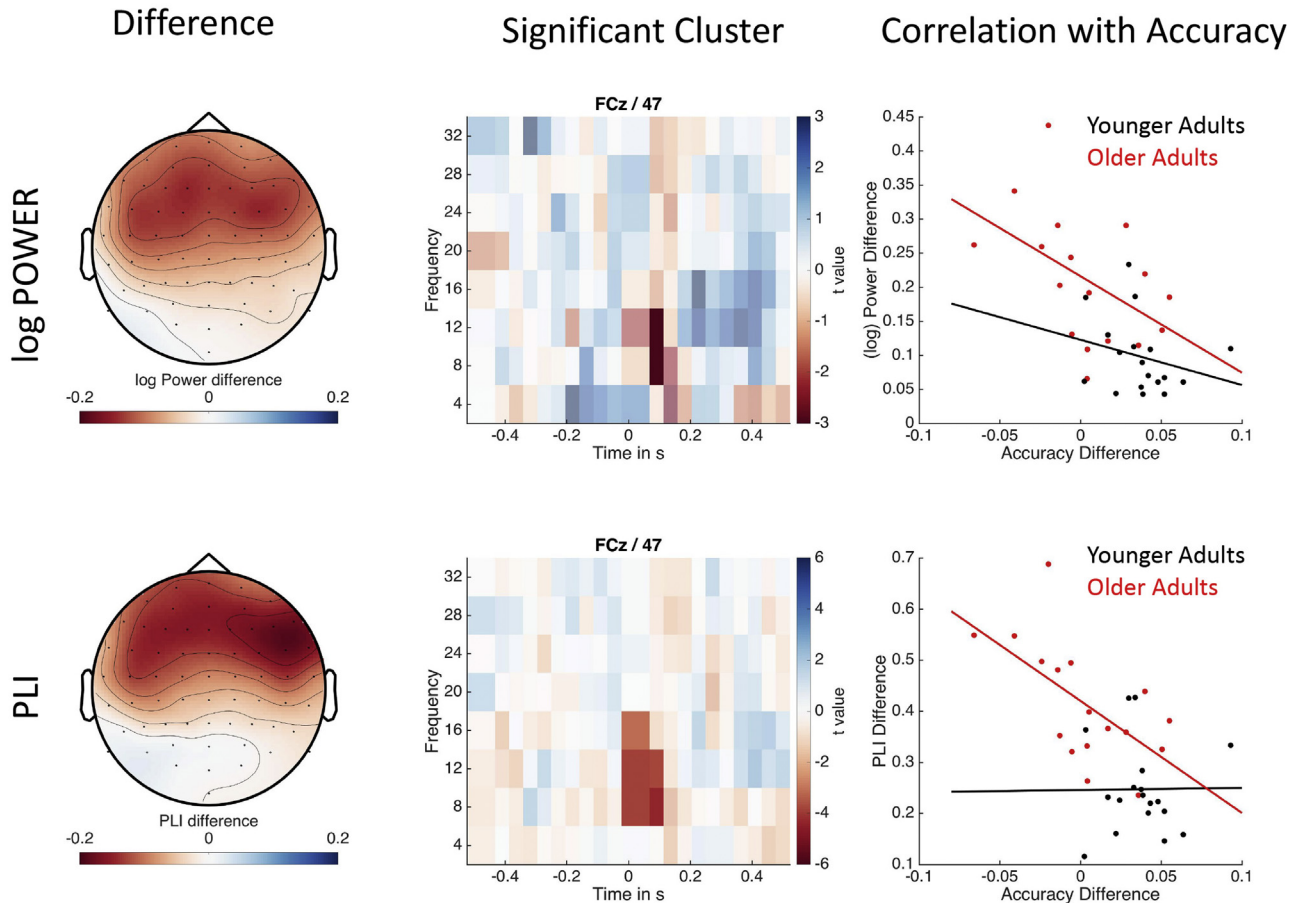


Fig. 5. Age group differences in the cue effect as reflected in (log) power (upper panel) and phase-locking index (PLI) (lower panel) and their relation to the behavioral cue effect. Figure displays topography (left), significant cluster (highlighted) at FCz (middle), and the correlation with accuracy (right). Older adults show a stronger modulation of power and phase locking by the alerting cue that is related to a detrimental effect on accuracy.

external stimulation (Lindenberger and Mayr, 2014). The results of the present study are in line with this interpretation. Furthermore, the inverse relation between age and alerting effects on performance and phase locking implies that those OAs who showed a stronger stimulus-driven response to the cue benefitted less from it or were even impaired by it. Presumably, if the cue induced a strong automatic neural response, it hindered OAs from effectively using the warning signal to facilitate subsequent stimulus processing, as they could not disengage from processing the cue (or did so too slowly). In fact, the alerting cue may have served as distracter for a subsample of the OAs. The present findings lend indirect support to the notion that the duration and predictability of the time interval between the cue and subsequent stimulus is key to observing age differences (or not) (Zhou et al., 2011). Specifically, if disengagement from the cue is impaired in OAs, OAs are more likely to benefit from an alerting cue if time intervals between the cue and the stimulus are either consistent or otherwise long enough to reset the system to process the task stimulus (e.g., Haupt et al., 2018).

Notably, our results are in sharp contrast with a recent study that examined cue-related power and phase-locking effects in a visual working memory task in YAs and OAs (Tran et al., 2016). This earlier study reported less consistent phase locking in OAs than in YAs, which in turn predicted later visual memory performance. A number of important differences between this study and ours could explain the different results. First, Tran et al. (2016) presented alerting cues on each trial, whereas we presented them in only 50% of the trials. This design allowed us to quantify and compare both

behavioral and neuronal alerting effects, that is, the difference in responses between cue and no-cue trials. In addition, while the CTI varied randomly from trial to trial in our task, it was constant in the study by Tran et al. Notably, effects of alerting are often additive and even confounded with temporal cueing effects (Weinbach and Henik, 2012, 2013). Alerting effects have been attributed to a short and nonspecific increase in arousal after a warning signal (Posner and Boies, 1971). Temporal cues that predict the exact timing of stimulus occurrence also reduce response times and increase accuracy, however, through voluntary attentional orienting to a specific point in time (Coull and Nobre, 1998). Thus, as the time of stimulus occurrence was predictable, voluntary temporal orienting (Weinbach and Henik, 2012), and potentially age differences therein (Chauvin et al., 2016; Zanto et al., 2011), may have contributed to the effects reported by Tran et al. (2016), besides bottom-up, reflexive alerting effects. If the target onset is temporally predictable, individuals are able to shift the phase of their alpha-band oscillations before target onset to optimize stimulus discrimination (Samaha et al., 2015). Accordingly, in the study by Tran et al. (2016), young participants may have reset their phase to optimize stimulus processing in response to the cue. Arguably, although the CTI was not predictable in our study, the cue also contained some temporal information about the imminent occurrence of the upcoming stimulus. However, as the cue was not informative of the exact time of stimulus occurrence, we assume that temporal preparation in our design was rather minimal (Weinbach and Henik, 2013) and that phase resetting to the

stimulus itself rather than to the cue onset would have been beneficial. In our study, strong phase locking to the cue may have hindered the OAs from imminently resetting their alpha oscillations to a phase that would be optimal for target stimulus processing shortly after the cue. Most importantly, the alerting cues used by the two studies differed. Whereas Tran et al. (2016) used transient (50 ms) color changes of the fixation cross, we used a loud tone as a cue. The latter is presumably more alerting and can hardly be missed because of eye blinks or attentional lapses, both of which are more frequent in OAs than in YAs (e.g., see Carriere et al., 2010; McDowd and Shaw, 2000). Furthermore, the cross-modal experimental design with an auditory alerting cue in the visual task allowed us to separate alerting effects from modality-specific sensory processing components that may overlap in time when both the cue and task stimulus are presented visually (as in Tran et al., 2016).

Finally, our results provide further evidence for the notion that the maintenance of a youth-like brain is key for healthy cognitive aging (Nyberg et al., 2012). Thus, despite an overall stronger phase locking in the OAs than in the YAs, some of the OAs' cue-related power and phase-locking effects were within the upper range of YAs. Interestingly, such OAs with a more youth-like pattern also showed reliable performance benefits after the presentation of an alerting cue. Our finding is thus in line with the idea that high individual variability in OAs as reflected in the temporal dynamics of neural oscillations may be a valid marker for the functionality of attentional mechanisms (Mok et al., 2016). The functionality of attentional mechanisms, and more specifically, phasic alerting may in turn critically depend on brainstem structures (e.g., the noradrenergic and cholinergic system) that undergo strong changes over the lifespan (Robertson, 2013, 2014). Only recently, Dahl et al. (2018) provided evidence that OAs' memory performance was positively related to a more youth-like integrity of the locus coeruleus. It is an intriguing possibility that individual differences in arousal may also be driven by the integrity of the locus coeruleus. Thus, a promising road for future research is to understand how structural integrity of brainstem structures relates to individual differences in neural oscillations and alerting performance.

Disclosure

None.

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