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Phasic alerting increases visual attention capacity in younger but not in older individuals

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ABSTRACT

In the present study, we investigated effects of phasic alerting on visual attention in younger and older adults. We modelled parameters of visual attention based on the computational Theory of Visual Attention (TVA) and measured event-related lateralizations (ERLs) in a partial report task, in which half of the displays were preceded by an auditory warning cue. Younger adults showed an alertness-related visual processing facilitation: TVA parameter *sensory effectiveness a*, a measure of visual processing capacity, was significantly increased, and latencies of visual ERLs were significantly reduced following the warning cue. By contrast, older adults did not benefit from the alerting cue: TVA parameter *sensory effectiveness a* and ERL latencies did not differ between conditions with and without cues. The findings indicate age-related changes in the brain network underlying alertness and attention, which governs the responsiveness to external cues and is critical for general cognitive functioning in aging.

Visual attention is the cognitive function that enables the observer to select and process information, and guides behaviour in our visual environment (Wolfe, 2014). Thus, age-related changes in visual attention functions are considered to contribute to difficulties older individuals experience in many everyday tasks (Hoffman, McDowd, Atchley, & Dubinsky, 2005; Owsley & McGwin, 2004). Attention is not a unitary function, rather, it is understood as a family of processes supported by a neural network spanning sensory, thalamic, and fronto-parietal areas (Corbetta & Shulman, 2002, 2011; Desimone & Duncan, 1995; Fan, McCandliss, Fossella, Flombaum, & Posner, 2005; Petersen & Posner, 2012; Posner & Boies, 1971). Aging affects aspects of visual attention differently (McDowd & Shaw, 2000), presumably reflecting alterations in specific parts of these brain structures (Madden et al., 2007).

A fundamental process closely linked to the efficiency of visual attention is alertness. Alertness refers to the system's state of general readiness to react to sensory stimuli, with increased levels of alertness facilitating stimulus processing and response initiation

(Posner & Petersen, 1990; Sturm et al., 1999). The level of alertness can be temporarily increased by presenting a neutral warning cue shortly before a task stimulus occurs, sometimes also referred to as an "accessory stimulus" (Nickerson, 1973), which typically speeds the response to the task stimulus (Coull, Nobre, & Frith, 2001; Fernandez-Duque & Posner, 1997; Thiel & Fink, 2007). This phasic alerting effect on reaction times (RT) had originally been suggested to originate at stages of motor preparation and/or execution (Hackley & Valle-Inclán, 2003; Posner, 1980; Sturm & Willmes, 2001), however, it has recently been shown that alerting already affects early stages of sensory and attentional stimulus processing (Brown et al., 2015; Kusnir, Chica, Mitsumasu, & Bartolomeo, 2011; Matthias et al., 2010).

A brain network linked to alertness and attention has been identified, including areas in the right frontal and right parietal cortex, the thalamus, and the locus coeruleus (LC), which is the principal brainstem nucleus for the synthesis of norepinephrine (NE) (Aston-Jones & Cohen, 2005; Berger & Posner, 2000; Fan et al., 2005; Sturm & Willmes, 2001). Age

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differences in phasic alerting effects on attentional functions might indicate age-related changes in this network. Importantly, the integrity of a right hemisphere network linked to noradrenergic functions has recently been proposed to be a critical determinant of the cognitive status in older age, as it mediates the effects of environmental enrichment for brain protection and plasticity (Robertson, 2013, 2014). Thus, interactions of alertness and attention seem to be relevant for understanding age-related changes in processing environmental cues and to identify conditions that support high functioning in older age (Lindenberger & Mayr, 2014).

Previous behavioural investigations on phasic alerting in aging have yielded inconsistent results. Some studies have reported preserved or even increased phasic alerting in older compared with younger adults (Fernandez-Duque & Black, 2006; Nebes & Brady, 1993; Rabbitt, 1984), while other studies have shown decreased or absent alerting effects in older age (e.g., Festa-Martino, Ott, & Heindel, 2004; Gamboz, Zamarian, & Cavallero, 2010; Ishigami et al., 2016; Jennings, Dagenbach, Engle, & Funke, 2007; Zhou, Fan, Lee, Wang, & Wang, 2011). The diversity of findings has been suggested to result from variations in the sensory, cognitive, and motor components involved in a given task. Importantly, phasic alerting in aging has typically been investigated using tasks that require speeded motor responses (e.g., Rabbitt, 1984). However, as highlighted by recent work from Humphreys and colleagues, RT measures can be problematic when assessing populations with non-specific motor slowing, such as aging participants (Shalev, Humphreys, & Demeyere, 2016). Accordingly, isolating alerting effects on sensory-attentional processing stages may provide more reliable measures of age-related changes in the network of alertness and visual attention. While alerting effects on visual processing have been demonstrated in younger adults (Brown et al., 2015; Kusnir et al., 2011), it currently remains unexplored whether they also occur in older individuals.

We recently introduced an approach that permits measuring phasic alerting effects on cognitive and neuronal visual attention components unconfounded by motor processes (Wiegand et al., 2017). Specifically, we combined parametric assessment based on the Theory of Visual Attention (TVA; Bundesen, 1990) with visual event-related lateralizations (ERLs; Eimer,

1996; Heinze, Luck, Mangun, & Hillyard, 1990; Luck, Heinze, Mangun, & Hillyard, 1990; Mangun & Hillyard, 1990; Töllner, Rangelov, & Müller, 2012; Woodman & Luck, 1999). TVA is a computational model closely related to the "biased competition" account (Desimone & Duncan, 1995). TVA partitions attention into distinct parameters, which can be measured based on performance in simple psychophysical tasks (Duncan et al., 1999; Habekost, Vangkilde, & Petersen, 2014). The method has been used to explain attentional phenomena in normal individuals (e.g., Ásgeirsson, Kristjánsson, & Bundesen, 2015; Matthias et al., 2010; Petersen, Kyllingsbæk, & Bundesen, 2012; Vangkilde, Coull, & Bundesen, 2012), and to quantify attentional deficits in special populations (e.g., Bublak et al., 2011; Finke et al., 2011, 2012; Redel et al., 2012; Stenneken et al., 2011; Wiegand et al., 2016) including older individuals (Habekost et al., 2013; McAvinue et al., 2012). Complemented by neuroscientific techniques, Humphreys and others have successfully linked the TVA parameters to distinct neural activity patterns in the visual attention network (Chechlacz, Mantini, Gillebert, & Humphreys, 2015; Gillebert et al., 2012; Wiegand, Töllner, Habekost, et al., 2014) and to changes in this network relevant to attentional functions specifically in older age (Espeseth, Vangkilde, Petersen, Dyrholm, & Westlye, 2014; Wiegand, Töllner, Dyrholm, et al., 2014).

Here, we used a partial report task (Duncan et al., 1999), in which subjects had to identify briefly presented letters of a pre-specified feature category: The participants were instructed to select letters by colour by identifying red and ignoring blue ones. Targets and distractors were presented either in the same (ipsilateral) or in opposite (contralateral) hemifields. In half of the trials in the experiment, displays were preceded by an auditory warning cue. Accuracy-based performance measures made it possible to investigate phasic alerting effects on visual perceptual processes independent of effects on motor-related processes. Specifically, we tested in groups of younger and older adults whether the presence of a warning cue would modulate three parameters of spatial and non-spatial aspects of visual attention: (1) parameter *sensory effectiveness a*, a measure of processing capacity that is independent of how attentional weights are distributed among the different objects in the visual field; (2) parameter *spatial bias* w_{index}, which reflects the distribution of attentional weights

to the left vs. right hemifield (independent of the total visual processing capacity); and (3) parameter *top-down control α*, which reflects the distribution of attentional weights between targets and distractors (independent of the location of the object and independent of the total visual processing capacity).

In a group of younger adults, we recently showed that phasic alerting selectively increased *sensory effectiveness a* (Wiegand et al., 2017). By contrast, the distribution of the attentional resources as reflected in parameters *spatial bias* w_{index} and *top-down control α* were unaffected by the alerting manipulation. The enhanced processing capacity following a warning cue co-occurred with a latency reduction in visual ERLs elicited by the letter displays. Visual ERLs are computed by subtracting activity over the hemisphere ipsilateral to a laterally presented visual stimulus from activity contralateral to the stimulus. The latencies of ERLs are considered to mark the timing of the allocation of processing resources to retinotopically organized, extrastriate areas, in which the visual features of the to-be-encoded stimulus are represented (Eimer, 1996; Luck & Hillyard, 1994; Luck, Woodman, & Vogel, 2000; Töllner et al., 2012; Woodman & Luck, 1999). We interpreted the alerting-related ERL latency reduction in younger adults to reflect that higher levels of alertness led to faster visual categorizations. This view is in accordance with the Neural Theory of Visual Attention (Bundesen, Habekost, & Kyllingsbæk, 2005) and a recent extension of the model (Bundesen, Vangkilde, & Habekost, 2015). The latter incorporates a mathematical description of how phasic alertness increases the system's overall level of activation by multiplying all neural activations representing visual categorizations with a common factor, thereby leading to generally faster visual categorizations.

In the present study, we used the same approach described above to examine alerting effects on visual attention in aging. We compared the previously tested younger sample (Wiegand et al., 2017) with an older sample to investigate whether the increase in visual processing capacity and reduction in ERL latencies by phasic alerting would be preserved or changed in older age. We further explored whether the selective distribution of attentional weights would be unaffected by phasic alerting also in older age or would differ between the two age groups.

Methods

Participants

Twenty-three younger [mean (*SD*) and range in years: 24.9 (3.1) 20–30] and 27 older healthy volunteers [mean (*SD*) and range in years: 62.9 (7.6) 57–71] participated in the experiment. Five younger and 10 older participants had to be excluded; two because of technical problems during the EEG recording, and the rest because of bad data quality and/or excessive eye-movements, leading to a rejection of more than 30% of the trials due to artefacts. In the remaining sample (18 younger and 17 older participants), all participants had normal or corrected-to-normal vision and none were colour blind. Participants reported to not suffer from any chronic somatic disease, or any psychiatric or neurological impairment. The data of the younger sample have been analysed and reported in a parallel article (Wiegand et al., 2017). The gender distribution was comparable in the two age groups (younger f/m: 12/6, older f/m: 9/8). The younger group consisted of university students or recent graduates from university; nine were bachelor students, six were master students, and three had obtained their master's degree. The educational level was more diverse in the older compared to the younger sample, which is representative for the general increase in educational level in Denmark in the last 30 years (Statistics Denmark, Statistical Yearbook, 2016). In the older sample, eight had no secondary education, six had a medium-long theoretical education, and three had a longer academic education. Similarly, the Danish Adult Reading Test (Danish adaptation of the National Adult Reading

Table 1. Descriptive summary of older participant screening.

MMSE		28.9 (0.9)
DART		37.3 (7.7)
MFI	general	7.1 (2.4)
	physical	7.3 (3.0)
	mental	8.0 (3.1)
	motivation	5.4 (1.5)
	activity	6.8 (2.9)
Visual Acuity		0.7 (0.2)
Audiometry	500 Hz	22.7 (4.3)
	1000 Hz	23.4 (5.7)

Note: Older participants were screened for signs of cognitive impairments. Mini-Mental State Examination, MMSE (Folstein et al., 1975); verbal IQ (Danish Adult Reading Test, DART, a Danish version adapted from the National Adult Reading Test, NART, Nelson & Willison, 1991); general and sub-components of fatigue (Multidimensional Fatigue Inventory, MFI, Smets et al., 1995); sensory deficits in vision (Snellen test) and hearing (audiometer Oscilla® USB-310, hearing thresholds in dB). Reported are means and standard deviations (in parentheses).

Test; Nelson & Willison, 1991) indicated a broad, relatively high level of verbal intelligence in the older sample (see Table 1). We asked all participants to rate their level of alertness before the beginning of the experiment using a visual-analogue scale from 0 ("drowsy") to 100 ("alert") on a tablet PC (CANTAB, Cambridge Cognition, Cambridge, UK) to examine whether the subjective feeling of intrinsic (or tonic) alertness would differ between age groups. Alertness ratings were significantly lower in the older [mean (*SD*) ratings: 14.0 (11.4)] compared to the younger adults [mean (*SD*) ratings: 36.9 (21.2); $t(33) = 4.5$, $p < .001$], which is in accordance with the typical linear increase of fatigue with aging (Schwarz, Krauss, & Hinz, 2003). The Multidimensional Fatigue Inventory (MFI-20; Smets, Garssen, Bonke, & De Haes, 1995) demonstrated that older participants did not show any signs of fatigue symptoms indicative of abnormal tonic alertness levels (see Table 1); in fact, our sample scored slightly higher than would be expected from age-matched normative data (Schwarz et al., 2003). Older participants were screened for symptoms of beginning dementia by the Mini-Mental State Examination (MMSE; Folstein, Folstein, & McHugh, 1975), on which all participants scored above the cut-off of 26 (see Table 1). We further tested older participants' vision and hearing in order to exclude that severe sensory impairments would affect processing of the visual letter stimuli and auditory warning tones used in the experiment. None of the participants showed sensory impairments on these tests (see Table 1). The study was approved by the Committees on Health Research Ethics for the Capital Region of Denmark (De Videnskabsetiske Komiteer for Region Hovedstaden; Project No H-2-2013-009). This study was carried out in accordance with the recommendations of The Regional Committee on Health Research Ethics with written informed consent from all subjects according to the Declaration of Helsinki II, which was obtained before the experiment was carried out. The participants received gift cards (600–700 DKK) for their participation.

Procedure

The PC-controlled experiment was conducted in a dimly lit, soundproof and electrically shielded cabin. Stimuli were presented on a CRT 17-inch 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, conducted at the same time of day to avoid daytime influences which may affect individual levels of tonic alertness (Dijk, Duffy, & Czeisler, 1992). Daytime of testing (morning, noon, afternoon) did not differ between the two age groups [$\chi^2(2) = 3.16$; $p = .37$]. Each session lasted about 1.5 h. 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 Figure 1A), either a single target, two targets, or a target and a distractor were presented. Two letters were presented either vertically (ipsilateral display) or horizontally (contralateral display), but never diagonally, resulting in 16 different display conditions (Figure 1B). A trial began with a circle presented in the centre of the screen, which participants were instructed to fixate throughout the
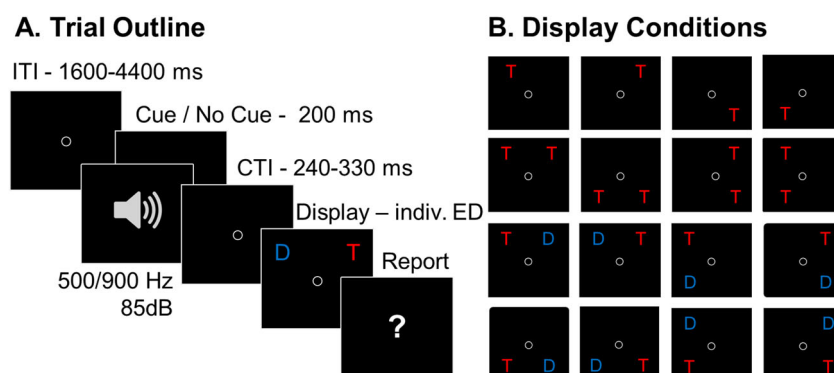

Figure 1. Task procedure and stimuli. (A) Trial sequence in the partial-report task. Half of the trials included an auditory warning cue that was played shortly before the onset of the stimulus display. (B) 16 conditions with varying target and distractor configurations. Targets ("T") were presented in red and distractors ("D") were presented in blue.

whole trial. Then the letter array was presented on a grey background for an individually adapted exposure duration (ED), which was determined in a calibration prior to the experiment (see below). In a randomly selected half of the trials, the letter array was preceded by an auditory warning cue played for 200 ms. We played an 85 dB tone, which, in order to reduce habituation effects, was presented with a pitch of 500 or 900 Hz, randomly varying but equally often over trials within a block. Participants were told not to pay attention to the warning cue while performing the partial report task. Their 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 inter-trial 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 (see Figure 1A). Similar to previous research on alerting effects (Matthias et al., 2010; Niemi & Näätänen, 1981; Posner, 1980), we chose a brief cue-target interval (CTIs), uniformly distributed with a range of 240–330 ms using time-steps of 10 ms (Rolke & Hofmann, 2007). In trials without cue, time intervals identical to the CTIs were added to the ITIs to keep timing constant over conditions.

In each of the two sessions, a total of 800 trials were run divided into 20 blocks of 40 trials. Conditions were balanced across blocks and all subjects were presented with the same displays in different random orders. Letter stimuli were presented in Arial font 16, with equal frequency at each of four possible letter locations forming an imaginary square, with a distance of approximately 8 cm between the possible letter locations and the fixation circle. The luminance of the red target colour and the blue distractor colour were the same (2.1 cd/cm^3). The letters of a given trial were randomly chosen, without replacement, from a pre-specified set (ABDEFGHJKLMNOPRSTVXZ).

At the beginning of the first experimental session, a pre-test was conducted to practice the partial-report task and determine the ED for the test individually for each participant. First, 32 trials (two of each display condition) were run with an ED of 40 ms to familiarize the participant with the trial procedure. Then a calibration procedure containing 48 trials followed, in which the ED was adapted stepwise based on performance in 24 dual-target trials. When the participant reported both targets correctly in a given trial, ED was decreased by 10 ms in the following trial; when the participant reported one letter correctly, the ED was kept at the current value; and when the participants reported no letter correctly, the ED was increased by 10 ms. Another 48 trials were then run with the ED identified by the calibration and performance was monitored. The ED was kept when performance was 60–90% in single-target displays and > 50% in dual-target displays. The calibration procedure was repeated until the criterion was reached. Similar to the experimental task, the auditory warning cue preceded the letter display in 50% of the trials; the ED was identical for cued and non-cued trials.

EDs were individually determined to control for individual differences, and particularly age group differences, in baseline performance. EDs ranged between 20–70 ms in younger participants and between 50–200 ms in older participants. Note that in all cases EDs were short enough to prevent participants from performing microsaccades during the stimulus displays, which otherwise could contaminate the ERLs (Luck, 2005).

Parameter estimation

TVA parameters were derived by modelling individual report accuracy across the different partial report conditions (see Figure 1B) by a TVA-based algorithm using a maximum likelihood method (see Dyrholm, Kyllingsbæk, Espeseth, & Bundesen, 2011; Kyllingsbæk, 2006, for detailed descriptions of the algorithms). We fitted TVA parameters separately based on performance in trials with and without a warning cue. Parameter *sensory effectiveness a* reflects the total visual processing capacity at a given ED and is independent of how attentional resources are divided across different objects in the visual field. In more detail, *a* is the total visual processing capacity integrated over the time of the stimulus' effective ED (see Duncan et al., 1999). Individual differences in encoding time were corrected for by adjusting the ED individually in the calibration procedure. The *spatial bias* parameter w_{index} reflects the distribution of attentional weights across the left (w_{left}) and the right (w_{right}) visual hemifield

and is defined as the ratio $w_{left}/(w_{left} + w_{right})$. w_{index} is independent of the overall processing capacity and reflects weightings between objects in the left and right hemifield. A value of $w_{index} = 0.5$ indicates balanced weighting, a value of $w_{index} > 0.5$ indicates a leftward bias, and a value of $w_{index} < 0.5$ indicates a rightward spatial bias. Finally, the *top-down control* parameter alpha reflects the task-related differences in weights for targets (w_T) and distractors (w_D), and is defined as the ratio w_D/w_T. Theoretically, perfect selection would imply that all attentional weight was on targets and none on distractors, resulting in $\alpha = 0$. By contrast, unselective processing would imply equally weighted target and distractor processing, resulting in $\alpha = 1$. Accordingly, lower α values indicate more efficient top-down control.

EEG recording

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 electro-oculogram, HEOG), and beneath the left eye (vertical electro-oculogram, VEOG). The signal was recorded at a sampling rate of 512 Hz bandwith DC-100 Hz) and referenced online to a CMS-DRL ground, which drives the average potential (i.e., common mode voltage) as close as possible to the AC reference voltage of the analogue-to-digital box (see http://biosemi.com for an explanation of the Biosemi system). Offline data processing and analyses was done using EEGLAB (Delorme & Makeig, 2004) and ERPLAB (Lopez-Calderon & Luck, 2014) software. The continuous signal was filtered offline with a 0.1 high-pass filter and re-referenced to the averaged mastoids. An Infomax Independent Component Analysis (Bell & Sejnowski, 1995) using the runica algorithm implemented in EEGLAB (Delorme & Makeig, 2004) was run to identify and backtransform ocular artefacts (Jung et al., 2000). The EEG was segmented into epochs of 2 s (from −1 s prior to and 1 s following stimulus display onset) for ERL analyses. Trials with signals exceeding ± 100 μV in the time window −200–800 ms on any of the scalp electrodes were discarded as artefacts. As eye-movements have critical

impact on lateralized visual activity, we chose a more conservative threshold of ± 50 μV on the HEOG channels for rejecting trials.

Analyses of event-related lateralizations

Only trials in which letters were reported correctly were included in the analyses. Epochs were averaged separately for trials in which the target was on the left side and trials in which the target was on the right side in the different conditions (see Figure 1B). We computed ERLs in four types of conditions: one single target was presented (1T); two targets were presented in the same hemifield (2T); one target accompanied by a distractor in the same hemifield was presented (TD ipsi); or one target accompanied by a distractor in the opposite hemifield was presented (TD contra). ERLs were calculated by subtracting event-related potentials (ERPs) at electrodes ipsilateral from those at electrodes contralateral to the target(s), averaged over presentations in the upper and lower visual field. In bilateral displays with two targets in opposite hemifields, no ERL could be determined as both sensory input and attention to the targets is bilaterally distributed and thus no distinct contra-minus-ipsilateral activity can be measured; these trials however were important for the TVA-based fitting of the behavioural data.

We examined peak latencies of negative ERLs on pooled posterior-occipital electrodes over the left (PO7/O1) and right (PO8/O2) hemisphere using the measurement tool implemented in the ERPLAB software (Lopez-Calderon & Luck, 2014). In unilateral displays, in which either a single target, or a target and a distractor, or two targets were in the same hemifield, we determined peak latencies in the time window 120–210 ms for younger adults and 150–240 ms for older adults. In bilateral displays (with target and distractor in opposite hemifields), peak latencies were determined in the time window 180–290 ms for younger adults and 240–350 ms for older adults.

Statistical analyses

Individual parameter estimates of *sensory effectiveness a*, *spatial bias* w_{index}, and *top-down control a*, were entered into mixed ANOVAs with the between-subject factor Age (younger, older) and within-subject factor Alerting (No Cue, Cue). Sensory effectiveness was estimated separately for the left and right

hemifield. ERL latencies were entered into a mixed ANOVA with the between-subject factor Age (younger, older) and the within subject factors Alerting (No Cue, Cue), and Display Condition (1T, 2T, TD ipsi, TD contra). Significant main effects or interactions were followed-up by separate ANOVAs for each age group. In an initial analysis, we had entered the factor Hemifield (left, right). However, as there were no significant main effects or interactions involving Hemifield, and for the sake of simplicity, we removed the factor from the analyses presented here. This included the analysis of sensory effectiveness, and the reported sensory effectiveness is thus the mean of the left and right hemifield-specific estimates. Finally, we repeated all analyses with Self-rated Alertness included as a covariate in order to examine whether the relevant effects and interactions including the factors Age and Alerting would remain significant and not be explained by the group differences in Self-rated Alertness.

Results

Behaviour

Parameter estimates

See Table 2A for an overview of the TVA parameter estimates in the two groups. The ANOVA on parameter estimates of *sensory effectiveness a* revealed a significant effect of the factor Alerting [$F(1,33) = 12.17$, $p = .001$, $\eta_p^2 = .27$], and a significant interaction of Alerting and Age [$F(1,33) = 4.35$, $p = .045$, $\eta_p^2 = .12$]. The alerting effect on *a* was significant in the younger group [$F(1,17) = 28.54$, $p < .001$, $\eta^2 = .63$], but not in the older group [$F(1,16) = 0.65$, $p = .43$, $\eta^2 = .04$] (Table 2A). There was no significant main effect of Age [$F(1,33) = 0.18$, $p = .68$, $\eta_p^2 = .01$]. The ANOVAs on parameter estimates of *top-down control α* and *spatial bias* w_{index} did not reveal any significant main effects or interactions of the factors Alerting and Age [all Fs < 1.00, all ps > .30]. In summary, phasic alerting increased the total visual processing capacity only in younger adults (see Figure 2A). In both age groups, the distribution of attentional weights with respect to objects' spatial location (see Figure 2B) and task-relevance (see Figure 2C) was not affected by phasic alerting.[1]

In the ANCOVA including Self-rated Alertness as covariate, the Age × Alerting interaction on parameter *sensory effectiveness a* was confirmed [$F(1,32) = 6.00$, $p = .02$, $\eta_p^2 = .16$]. The main effect of Alerting, however, was not significant [$F < 2.4$, $p > .10$]. The ANCOVAs on parameters *top-down control α* and *spatial bias* w_{index} did not reveal any significant main effects or interactions [all Fs < 2.00, all ps > .15].

Exposure duration and raw performance

As expected, the ED identified during the calibration procedure was significantly shorter for younger participants than older participants [mean (SD) young: 39.66 ms (13.76); mean (SD) older: 108.11 ms (11.21); $F(1,33) = 36.15$, $p < .001$, $\eta^2 = .34$]. The individual calibration ED successfully controlled for group differences in baseline performance: the report accuracy in the younger group and in the older group did not differ [mean (SD) young: 0.66 (0.10); mean (SD) older: 0.64 (0.12); $F(1,33) = 0.66$, $p = .42$, $\eta^2 = .02$].

Electrophysiology

See Table 2B and Figure 3 for an overview of the ERP results. The ANOVA on ERL latencies revealed a significant main effect of Alerting [$F(1,33) = 14.75$, $p = .001$, $\eta_p^2 = .31$], reflecting that ERLs peaked earlier when target displays were preceded by a warning cue compared to when no cue was played (Table 2B). In addition, we found a main effect of Age [$F(1,33) =

Table 2. Descriptives for (A) TVA parameter estimates and (B) ERL latencies measured in four display conditions of the partial report task (1T: single target letter, 2T ipsi: target plus second target in the ipsilateral hemifield, TD ipsi: target plus distractor the ipsilateral hemifield, TD contra: target plus distracter in the contralateral hemifield), separately for trials with (cue) and without an alerting tone (no cue) in the groups of younger adults and older adults. Reported are means and standard deviations (in parentheses).

		Younger Adults	Older Adults
A			
Parameter estimates			
Sensory effectiveness	No Cue	1.60 (0.52)	1.59 (0.58)
	Cue	1.78 (0.56)	1.63 (0.72)
Top-down control	No Cue	0.38 (0.14)	0.42 (0.20)
	Cue	0.38 (0.16)	0.45 (0.23)
Spatial bias	No Cue	0.50 (0.05)	0.51 (0.08)
	Cue	0.49 (0.06)	0.51 (0.07)
B			
ERL latencies (ms)			
1T	No Cue	185.55 (19.10)	202.67 (14.01)
	Cue	181.64 (16.85)	193.93 (15.06)
2T ipsi	No Cue	178.17 (16.63)	197.38 (17.48)
	Cue	173.83 (11.47)	190.95 (11.63)
TD ipsi	No Cue	172.09 (10.07)	190.03 (13.67)
	Cue	154.51 (18.72)	183.82 (17.00)
TD contra	No Cue	252.17 (25.04)	289.75 (15.39)
	Cue	230.47 (25.46)	292.74 (27.81)

A. Sensory Effectiveness
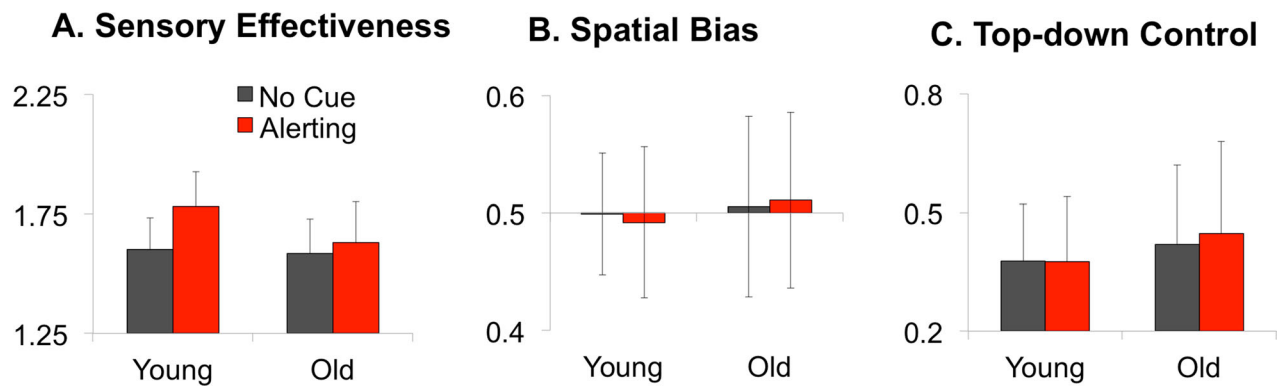

B. Spatial Bias

C. Top-down Control

Figure 2. Parameter estimates. Parameter estimates of (A) sensory effectiveness a, (B) spatial bias w_{index}, and (C) top-down control a for younger adults (grey bars) and older adults (red bars). Error bars indicate standard errors of the means.

91.35, $p < .001$, $\eta_p^2 = .74$], resulting from longer ERL latencies in the older compared with the younger group. We also found a significant main effect of Condition [$F(3,99) = 343.36$, $p < .001$, $\eta_p^2 = .91$]. There was a trend for an interaction between Age and Alerting [$F(1,33) = 2.88$, $p = .10$, $\eta_p^2 = .08$] and significant interactions between Age and Condition [$F(1,33) = 12.54$, $p < .001$, $\eta_p^2 = .28$], and Age, Alerting and Condition [$F(3,99) = 3.77$, $p = .01$, $\eta_p^2 = .10$]. Follow-up ANOVAs conducted separately for the two age groups revealed a main effect of Alerting, that is, reduced ERL latencies for cued relative to uncued

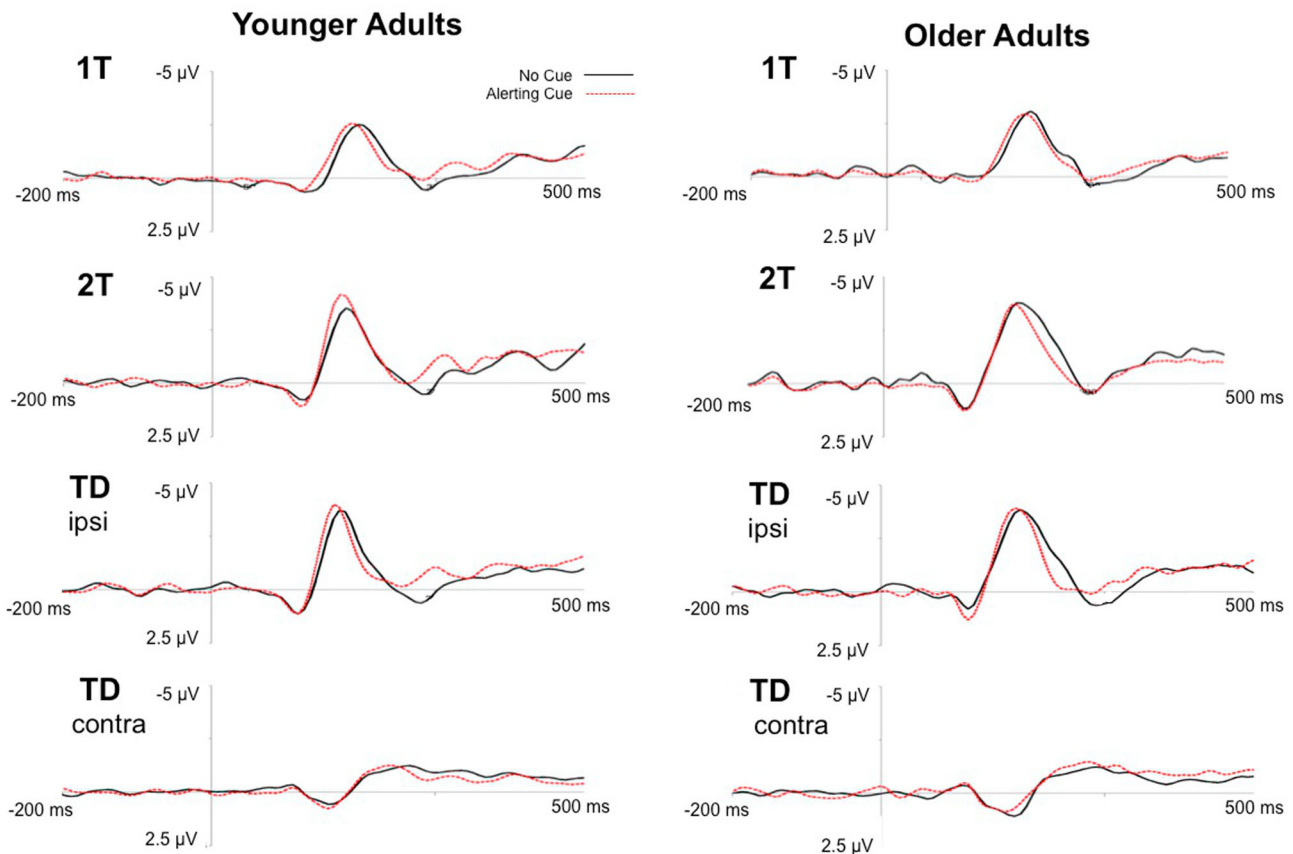**Figure 3. Event-related lateralizations.** Grand-averaged ERLs for (A) younger adults and (B) older adults comparing trials with alerting cue (red dashed line) and no cue (black solid line) in the partial report conditions with a single target (1T), two targets in the same hemifield (2T), target and distractor in the same hemifield (TD ipsi), and target and distractor in opposite hemifields (TD contra).

displays, in the younger sample [$F(1,17) = 15.70$, $p = .001$, $\eta_p^2 = .48$] (see Figure 3A), while there was no significant effect of Alerting found for the older sample [$F(1,16) = 2.24$, $p = .15$, $\eta_p^2 = .12$] (see Figure 3B). Both groups showed a main effect of condition [both $Fs > 120$, both $ps < .001$]. In younger and older adults, ERL latencies in the bilateral target-distractor conditions were longer than in all unilateral display conditions [all $ts > 9.00$, all $ps < .001$], reflecting the later lateralization due to attentional processes only when sensory differences in hemifields were balanced. Latencies in the condition with a target and distractor in the same hemifield were further shorter than latencies in the single target and dual target conditions [all $ts < 4.00$, $ps < .01$], and latencies in the dual target condition were shorter than in the single target condition [both $ts > 2.00$, $ps < .02$] (Table 2B).

In the ANCOVA, the main effects of Age and Condition, and the Age × Condition, Alerting × Age × Condition interactions were also significant when including Self-rated Alertness as a covariate [all $Fs > 2.5$, $ps < .05$]. The main effect of Alerting, however, was not significant in this analysis [$F(1,32) < 1.60$, $p > .20$].

Discussion

The present study investigated age differences in phasic alerting effects on visual attention by combining computational modelling based on the TVA model (Bundesen, 1990) and visual ERLs. In younger adults, phasic alerting increased *sensory effectiveness a*, a measure of visual processing capacity, and reduced latencies of ERLs, indicating a processing facilitation in the visual stream following a warning signal. Older adults, by contrast, did not show the behavioural nor the electrophysiological phasic alerting effect.

Age-related changes in the network of alertness and attention

Alertness and attention functions have been linked to a network of right fronto-parietal areas and the LC-NE system (e.g., Aston-Jones & Cohen, 2005). The visual processing facilitation induced by the temporal increase in alertness in younger adults presumably reflects a speeded subcortico-cortical signal transmission through phasic NE release elicited by the cue (Fernandez-Duque & Posner, 1997; Hackley & Valle-Inclán, 2003; Périn, Godefroy, Fall, & De Marco, 2010;

Sturm & Willmes, 2001). The absence of alerting effects on visual attention capacity in the older group lends support to the notion that the LC-NE system is affected by aging (e.g., Lohr & Jeste, 1988; Manaye, McIntire, Mann, & German, 1995; Mather & Harley, 2016; Vijayashankar & Brody, 1979). Presumably, deficient NE signalling mitigated the responsiveness to the warning cues (Coull et al., 2001; Oberlin, Alford, & Marrocco, 2005; Witte & Marrocco, 1997), and attenuated or even abolished the phasic alerting effect in the older group (see Ishigami et al., 2016). More specifically, our results suggest that this deficit has already affected early visual processing stages: albeit numerically, the alerting effect on ERLs in the older group was not entirely absent, but clearly reduced compared to the younger group. Whether the signatures of age and alerting effects on visual processing stages identified by our methodology could serve as neuro-cognitive indices of the efficiency of the LC-NE system in aging could now be tested further by incorporating measures more directly linked to LC-NE activation, such as the pupillary response (e.g., Gilzenrat, Nieuwenhuis, Jepma, & Cohen, 2010; Gabay, Pertzov, & Henik, 2011; Jepma & Nieuwenhuis, 2011; Murphy, O'Connell, O'Sullivan, Robertson, & Balsters, 2014).

While reduced or absent behavioural alerting-effects in aging have been shown previously (e.g., Festa-Martino et al., 2004; Gamboz et al., 2010; Jennings et al., 2007), some studies have reported preserved, or even increased, responsiveness to warning cues in older age (Fernandez-Duque & Black, 2006; Nebes & Brady, 1993; Rabbitt, 1984; Williams et al., 2016).[2] The divergent findings likely result from varying demands and temporal contingencies in the given task. In particular, the duration of the CTI has been suggested to interact with alerting effects and age (Zhou et al., 2011). Possibly, with increasing age, the transition of the brain stem signals to cortical areas slows down, rather than being fully disrupted. As a consequence, although the cue itself is processed, older adults may not be able to effectively use it when presented very shortly before a task display. Related to this, in addition to phasic alerting, temporal orienting in response to the cue (Coull & Nobre, 1998), and potential age differences in temporal orienting (Zanto et al., 2011), may have influenced stimulus processing. Although the exact time point when the target display would occur could not be anticipated from the jittered CTIs, the warning cue still carried

temporal information about the immediate occurrence of the target display (Weinbach & Henik, 2012). Therefore, response preparation due to temporal expectations learned over trials (Los & Van der Burg, 2013; Los, Kruijne, & Meeter, 2017; Taatgen & Van Rijn, 2011) may have contributed to the increased processing capacity following the cue in younger adults (Vangkilde et al., 2012). The role of temporal contingencies for phasic alerting effects in aging should therefore be tested systematically in future studies with varying, including longer, CTIs.

In contrast to deteriorated alerting effects in the healthy elderly, several studies have shown that patients with visuo-spatial neglect after damage to the right side of the brain benefit from phasic cues. Specifically, phasic alerting mitigates their pathological right-ward spatial bias (Finke et al., 2012; Robertson, Mattingley, Rorden, & Driver, 1998). Spatial processing, by contrast, was completely unaffected by phasic alerting in the present healthy older (and also younger) group. We assume that aging affects the NE pathways in a different manner than right-parietal lesions typically associated with visuo-spatial neglect. Presumably, the lesion disrupts NE brain stem projections to cortical areas, which also contributes to the general hypoarousal experienced by these patients.

Age-related changes in tonic alertness and strategy

It is possible that alerting effects on visual processing were diminished in the older group because they adopted a different strategy to use the external cue (Lindenberger & Mayr, 2014). According to the adaptive-gain theory (Aston-Jones & Cohen, 2005), phasic alerting effects vary with the level of baseline alertness (or tonic arousal level) over a sustained period of time (Parasuraman, Warm, & See, 1998). Assuming an inverted U-shaped arousal curve (Yerkes & Dodson, 1908), performance and phasic responses were suggested to be optimal at an intermediate level of arousal, while shifts toward either end of the tonic activity continuum would be associated with reduced performance and attenuated or unspecific phasic responses. If older participants adopted a highly focused, relatively more alert, state compared to the younger participants in the demanding attention task, baseline activation and/or the apex of the alertness curve may have shifted, making the phasic response smaller or ineffective for performance. Contradictory to this explanation, however, subjective alertness ratings were lower in the older compared to the younger group; we interpret the self-rating with caution, because age differences in response-bias are likely (Gibson, 1997). A systematic investigation of baseline and temporal changes in alertness within and between age groups (Paus et al., 1997; Robertson, Manly, Andrade, Baddeley, & Yiend, 1997) would be interesting to better understand the interactions of tonic and phasic activation states in aging.

General age-related slowing on visual and motor processing stages

As recently pointed out by Humphreys and colleagues (Shalev et al., 2016), when testing older individuals, or any other population suffering from non-specific changes in the motor system, incorporating cognitive measures unconfounded by motor processes is key. One critical advantage of the present approach is that it enabled us to derive behavioural and electrophysiological measures of alerting effects on perceptual and attentional processing stages independently of motor processes. RT tasks, by contrast, rely on sensory-motor integration, response preparation, and execution processes, which are strongly affected by general age-related slowing and, thus, potentially blur alerting effects on cognitive processing stages.

Our results further provide a measure of general age-related slowing on visual processing stages. Previous TVA-based studies have demonstrated slower visual processing rates and elevated perceptual thresholds in older compared to younger adults (Habekost et al., 2013; McAvinue et al., 2012; Wiegand, Töllner, Dyrholm, et al., 2014). In the present task, the differences in processing rates and perceptual thresholds between age groups are reflected in the longer EDs in the older compared to the younger sample. This was accompanied by a general increase in ERL latencies in older as compared to younger adults, which is in accordance with previous ERL studies on visual search, and can be interpreted to reflect slower allocation of attention to target stimuli in older age (Lorenzo-López, Amenedo, & Cadaveira, 2008; Wiegand, Finke, Müller, & Töllner, 2013; Wiegand et al., 2015).

Summary and conclusions

The present study demonstrated a decline in phasic alerting effects on visual processing in older age. This result is indicative of age-related changes in the right fronto-parietal and LC-NE system regulating alertness and attention (Aston-Jones & Cohen, 2005). The brain network is assumed to play a major role in mediating experience-dependent plastic changes in the aging brain and, therefore, to be a critical determinant of cognitive reserve (Mather & Harley, 2016; Robertson, 2013, 2014). Future work following up on our finding may now investigate whether the age-specific changes in response to warning signals are indeed linked to alterations in the LC-NE system, whether effects are generalizable across different task conditions, and whether they are potentially malleable within individuals, which would be an indicator of preserved plasticity in the underlying brain network (Brosnan et al., 2017).

Notes

1. The analyses on the TVA parameter estimates revealed the same results when participants with bad EEG data quality were included (five younger and 10 older participants): For parameter *sensory effectiveness a*, there was a main effect of Alerting [$F(1,48) = 11.65, p < .01, \eta_p^2 = .20$], and a significant interaction of Alerting and Age [$F(1,48) = 5.01, p = .03, \eta_p^2 = .10$], resulting from a significant alerting effect in the younger group [$F(1,22) = 17.29, p < .001$], but not in the older group [$F(1,26) = 0.67, p = .42$]. For parameters *top-down control a* and *spatial bias w*$_{index}$, there were no significant main effects of alerting, or age, or interaction of the factors [all $Fs < 1.30$; all $ps > .25$].
2. Note that mere sensory deficits are not a likely explanation for the absent alerting effect in the present study, since auditory perception thresholds were normal on an audiometric screening test, and individual hearing thresholds did not correlate significantly with the alerting effect on *sensory effectiveness* in the older group [$r = -.26, p = .31$].

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No potential conflict of interest was reported by the authors.

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