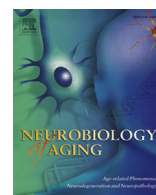




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Neural correlates of age-related decline and compensation in visual attention capacity

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ABSTRACT

We identified neural correlates of declined and preserved basic visual attention functions in aging individuals based on Bundesen “Theory of Visual Attention”. In an interindividual difference approach, we contrasted electrophysiology of higher- and lower-performing younger and older participants. In both age groups, the same distinct components indexed performance levels of parameters visual processing speed *C* and visual short-term memory storage capacity *K*. The posterior N1 marked interindividual differences in *C* and the contralateral delay activity marked interindividual differences in *K*. Moreover, both parameters were selectively related to 2 further event-related potential waves in older age. The anterior N1 was reduced for older participants with lower processing speed, indicating that age-related loss of attentional resources slows encoding. An enhanced right-central positivity was found only for older participants with high storage capacity, suggesting compensatory recruitment for retaining visual short-term memory performance. Together, our results demonstrate that attentional capacity in older age depends on both preservation and successful reorganization of the underlying brain circuits.

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1. Introduction

Visual attention abilities are known to decline with aging, affecting performance in a variety of daily tasks (Park and Hutchess, 2000). These impairments are likely to result from substantial structural and functional changes in the fronto-parietal parts of the visual attention brain network during aging (Madden et al., 2007). Functional neuroimaging techniques permit brain-behavior relationships underlying cerebral and cognitive decline to be investigated by analyzing age differences in task-related brain activity. However, age effects on brain activity are nonuniform, with some studies reporting enhanced and others reduced brain activity for older compared with younger adults (for recent reviews, see Fabiani, 2012; Grady, 2012). These findings suggest that age differences in neural activation have multiple sources. They may partly

imply neural loss but also comprise compensatory activity to counteract the deterioration processes. The functional implications of age effects, that is, whether they index cognitive decrements or preserved abilities, can only be resolved by taking interindividual differences in older adults’ task performance into account (Cabeza et al., 2002).

The efficiency of neural networks mediating fundamental processing functions, such as the speed of information processing (Deary, 2000) and short-term storage capacity (Conway et al., 2003) are considered critical determinants of cognitive abilities in older age (Salthouse, 1994). In the visual domain, these 2 functions are formally integrated within the “Theory of Visual Attention” (TVA, Bundesen, 1990): (1) visual processing speed *C*, the amount of visual information that can be processed per second; and (2) visual short-term memory (vSTM) storage capacity *K*, the maximum number of objects that can be perceived at one point in time. The TVA model permits these 2 parameters to be quantified for a particular individual based on performance in a psychophysical “whole report” task. In close relation to the “biased competition model” (Desimone and Duncan, 1995), TVA assumes that all elements in the visual field compete in a “race”, with those elements

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processed fastest becoming encoded into the capacity-limited vSTM. The theory's neural interpretation (NTVA, [Bundesen et al., 2005, 2011](#)) states further that distinct brain processes support the 2 components. In a recent study on young, healthy participants, this assumption was validated by linking distinct event-related potentials (ERPs) to individual differences in the 2 parameters ([Wiegand et al., 2014](#)). First, when participants were split according to their level of processing speed C , faster- relative to slower-encoding participants exhibited a significantly smaller posterior N1. The visual N1 has been associated with stimulus discrimination processes ([Vogel and Luck, 2000](#)). Accordingly, [Wiegand et al. \(2014\)](#) took the relation between its amplitude and the processing speed parameter C to reflect that faster individuals need to recruit a relatively smaller amount of their available attentional resources when categorizing objects. Second, when the same individuals were split according to their level of storage capacity K , those with higher, as compared with lower, storage capacity exhibited a significantly larger contralateral delay activity (CDA). The CDA is quantified by calculating the difference between activity contralateral and activity ipsilateral to the attended hemifield when attention during encoding is oriented to only one side of a bilateral stimulus array ([Klaver et al., 1999](#); [Töllner et al., 2013](#)). Its amplitude has been suggested to reflect the number of representations currently held in vSTM ([Vogel and Machizawa, 2004](#)) and may thus be considered to index the individual vSTM capacity limits expressed in TVA parameter storage capacity K .

Combining the methodological advantages of the TVA-based assessment with ERP, correlates of these distinct visual attention capacity functions offers a promising approach to identify the neural underpinnings of age decrements in these abilities. First, age-related decline in processing speed and storage capacity are quantified in a highly principled way ([Duncan et al., 1999](#)). Second, the assessment is based on accuracy in an unspeeded verbal report task, unaffected by age-related motor slowing or potential speed-accuracy trade-off effects. Finally, the task simplicity and the use of short, individually adapted, exposure durations render systematic age variations in task strategy and difficulty (owing to differences in perceptual thresholds) very unlikely. Behavioral TVA-based parameter modeling has recently demonstrated age-related decline in visual processing speed and storage capacity ([Habekost et al., 2013](#); [McAvinue et al., 2012](#)). However, it remains unclear whether the same neural mechanisms underlying interindividual performance differences in younger individuals also contribute to age-related decline of the 2 functions, or whether different mechanisms account for performance variations in older age.

The methodology of the present study was identical to the prior study ([Wiegand et al., 2014](#)), with the aim of establishing age-related changes in distinct neural markers of visual processing speed C and short-term storage capacity K , respectively. We hypothesized that the previously identified ERP markers of performance differences in younger individuals may also reflect the age-related decline in processing speed (indicated by increased N1 responses) and vSTM storage capacity (indicated by decreased CDA responses). In fact, findings available to date are largely in agreement with these hypotheses. An age-related CDA reduction has been associated with lower vSTM capacity in older age ([Jost et al., 2010](#); [Sander et al., 2011](#); [Wiegand et al., 2013](#)). No previous study has systematically analyzed the relationship between visual processing speed and age differences in the posterior N1. A number of studies reported an increase of N1 amplitudes with age in visual tasks ([Kutas et al., 1994](#); [Yordanova et al., 2004](#)), whereas others revealed either no difference ([Falkenstein et al., 2006](#)) or even a decrease with age ([Czigler and Balázs, 2005](#)). Additionally, age-related changes in the visual N1 scalp distribution have been observed ([DeSanctis et al., 2008](#)).

Besides ERPs that distinguish high- and low-performing younger individuals, it is likely that additional components specifically differentiate between high- and low-performing older individuals. In particular, ERP studies have demonstrated age-related changes indicative of alterations in frontally-mediated control processes ([Fabiani, 2012](#)), which are known to increasingly influence cognitive functioning with aging ([West, 1996](#)). We therefore assumed that components related to attentional or executive control processes might exclusively vary with older participants' performance level.

By coupling electrophysiological brain responses to attentional performance measures in different age groups, we aimed at dissociating activity patterns related to reduced and preserved abilities in older age ([Daffner et al., 2011](#); [Riis et al., 2008](#)). Specifically, we compared ERPs of younger and older participants who were both divided into subgroups of high- and low-performers based on their TVA parameter estimates of processing speed C and storage capacity K , respectively. The disclosure of components that differentiate between performance subgroups in both age groups (main effect performance level) would indicate that the underlying neural circuits determine interindividual differences in visual attention abilities in any age. If the same components mark age-related decline (main effect age), one would infer that these circuits are affected by normal aging. In contrast, revealing components that differentiate between performance levels only in the older but not the younger, sample (interaction between performance level and age) would imply that attentional abilities rely on different neural processes in older age. Conceivably, compensatory processes recruited to retain fast processing speed or high storage capacity in older age might become manifest in neural activity changes exhibited exclusively by the subgroup of high-performing older participants (old high \neq old low = young). Alternatively, some neural processes supporting attentional function may be intact in high-performing older participants, as well as generally in young adults, while being selectively impaired in low-performing older participants; this would become manifest in activity changes exclusive to the latter subgroup (old low \neq old high = young).

2. Methods

2.1. Participants

Twenty younger participants and 20 older participants were included in the sample. Note that the data of the younger participants has already been reported in our prior study ([Wiegand et al., 2014](#)), whereas the older participants' data were obtained for the present study. Four older and 3 younger participants, who made systematic horizontal eye-movements or produced artifacts on more than 25% of all trials during the electroencephalography (EEG)-experiment, were excluded. None of the participants reported any history of neurologic, psychiatric, chronic somatic, or eye diseases. All participants had normal or corrected-to-normal vision, with visual acuity being 0.63 or better ([Snellen, 1868](#)) and were not color-blind. The Mini Mental State Examination ([Folstein et al., 1975](#)) ruled out any symptoms prognostic of dementia (all scores ≥ 27) (for information on demographics and differences between performance subgroups, see [Table 1](#) and section 3.1). All participants were fluent in German and 35 of them native speakers. The 5 nonnative German speakers were either temporally studying (3 younger participants) or permanently resident in Germany (2 older participants). The participants were naïve as to the procedure of the TVA-based experiments. All participants received payment and gave written informed consent according to the Declaration of Helsinki II. The study was approved by the Ethics Committee of the Department of Psychology, LMU Munich.

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