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Components of aging:
Neurophysiological markers of age-related changes in visual attention

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Summary

Age-related cognitive decline has been linked to a reduction in attentional resources that are assumed to result from alterations in the aging brain. A core ability that is subject to age-related decline is visual attention, which enables individuals to select the most important information for conscious processing and action. However, visual attention is considered a conglomerate of various functions and the specific components underlying age differences in performance remain little understood. The present PhD project aimed at dissociating age effects on several (sub-) components that concur in visual attention tasks within a neurocognitive approach. Established and theoretically grounded psychological paradigms that allow separating various attentional components were combined with event-related potentials (ERPs), which provide a temporally fine-graded dissociation of cognitive processes involved in a task.

1st Project

The first project was designed to determine the origin(s) of age-related decline in visual search, a key paradigm of attention research. To pursue this goal on a micro-level, response time measures in a compound-search task, in which the target-defining feature of a pop-out target (color/shape) was dissociated from the response-defining feature (orientation), were coupled with lateralized ERPs. Several ERP components tracked the timing of processing stages involved in this task, these being (1) allocation of attention to the target, marked by the posterior-contralateral negativity (PCN), (2) target analyses in vSTM, marked by the sustained posterior-contralateral negativity (SPCN), (3) response selection, marked by the stimulus-locked lateralized readiness potential (LRP) and (4) response execution, marked by the response-locked LRP. Slowed response times (RT) in older participants were associated with age differences in all analyzed ERPs, indicating that behavioural slowing accrues across multiple stages within the information processing stream. Furthermore,

behavioral data and ERPs were analyzed with respect to age and carry-over effects from one trial to the next. The intertrial analyses revealed relatively automatic processes – such as dimension weighting facilitating the early stage of visual selection, and response weighting facilitating the late stage of response execution – to be preserved in older age. By contrast, more controlled processes – such as the flexible stimulus-response (S-R) (re-) mapping across trials on the intermediate stages of response selection - were particularly affected by aging. This indicates that besides general slowing, specific age decrements in executively controlled processes contribute to age-related decline in visual search.

2nd Project

The second project explored neural markers of individual and age differences in attention parameters formally integrated in Bundesen's computational Theory of Visual Attention (TVA). According to the model, two parameters of general visual attention capacity, perceptual *processing speed C* and visual short-term memory (vSTM) *storage capacity K* are defined and can be modeled mathematically independently for a particular individual. More recently, the neural interpretation of the model (NTVA) suggested that the two functions (at least partly) rely on distinct brain mechanisms. To test this assumption in an empirical approach, individual TVA-based estimates were derived in a standard TVA whole report task, and ERPs of the same participants were recorded in an adapted EEG-compatible version of the task. In the first study of the second project, we explored neurophysiological markers of interindividual differences in the two functions in younger participants. The results revealed distinct ERP correlates to be related to the parameters: Individuals with higher compared to lower processing speed *C* had significantly smaller posterior N1 amplitudes, suggesting that the rate of object categorization is associated with the efficiency of early visual processing. Individuals with higher compared to lower storage capacity showed stronger contralateral delay activity (CDA) over visual areas, indicating that the limit of

vSTM relies on topographically-organized sustained activation within the visual system. These results can be regarded as direct neuroscientific evidence for central assumptions of the theoretical framework.

In the second study of the second project, the same approach was pursued to investigate whether and how TVA attentional capacity parameters and their neural markers change with aging. First, the same ERP correlates of processing speed and storage capacity indexing individual differences in younger participants (i.e., the posterior N1 marked differences in processing speed *C* and the CDA marked differences in storage capacity *K*, respectively) were found to be valid also in the older group. In addition to this, two further components marked performance differences in the parameters exclusively within the older group: Older participants with lower processing speed showed smaller anterior N1 amplitudes relative to faster older and all younger participants, suggesting a selective loss of resources supporting early control of attentional guidance. Older participants with higher storage capacity exhibited a stronger right-central positivity than older participants with lower storage capacity and all younger participants. This pattern is indicative of compensatory recruitment of additional neural resources in high-functioning older individuals, presumably related to enhanced executive control fostering sustained activation of vSTM representations. Again, these findings strongly support the NTVA framework, proposing distinct neural mechanisms underlying processing speed and storage capacity. Furthermore, they show that distinct mechanisms of attentional control determine the two functions in older age.

List of abbreviations

CDA	contralateral delay activity
DWA	dimension weighting account
dDdR	different dimension/different response
dDsR	different dimension/same response
EEG	electroencephalography
ERP	event-related potentials
fMRI	functional magnetic resonance imaging
LRP	lateralized readiness potential
MMSE	mini-mental state examination
MWT-B	Mehrfachwahl-Wortschatz-Intelligenz-Test B
NTVA	neural theory of visual attention
PCN	posterior contralateral negativity
PET	positron emission tomography
PRC	partial repetition costs
rLRP	response-locked lateralized readiness potential
RT	response times
sDdR	same dimension/different response
sDsR	same dimension/same response
sLRP	stimulus-locked lateralized readiness potential
SPCN	sustained posterior contralateral negativity
S-R	stimulus-response
TVA	theory of visual attention
vSTM	visual short-term memory

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I. General Introduction

1.1. Aging research in cognitive neuroscience

The cognitive status of aging individuals determines their independence, quality of life, and further physical and psychological development (e.g., Fillit et al., 2002; Harada, 2010). Therefore, it is of paramount importance to understand the mechanisms involved in cognitive aging. From the perspective of cognitive neuroscience, aging processes are investigated in the context of their neurobiological underpinnings. A main goal in this research field is to link behavioral phenomena to underlying, latent psychological and neurophysiological factors.

One cognitive domain with a major influence on every-day life functioning in older age is visual attention (Madden, 1990; Suto & Kumada, 2010). Essentially, visual attention is the ability to cope with the visual information overload we are constantly exposed to. It enables the observer to select the relevant information and determines the processing of this information according to the observer's states and goals (Allport, 1989; Duncan, 1984; Posner & Petersen, 1990). Thus, visual attention is a crucial basis for intelligent interaction with our environment, and its integrity ensures confidence and safety when navigating through the overwhelming visual surrounding (Das et al., 2007; Hartley, 1992). Accordingly, attentional functions have been suggested to act as a mediator of age-related decline in various complex cognitive abilities (e.g., Craik, 2006). However, attention is considered as a set of various processes, and there is still no consensus on the exact nature and origins of the attentional resource limitations. A higher degree of specificity could be achieved by identifying neural correlates of distinct attentional components or resources, which might be differentially affected by aging. The aim of the present PhD thesis was to specify the nature of diverse attentional resource limitation(s) by dissociating several attentional components on the behavioral and neuronal level. In particular, psychological paradigms that allow disentangling processes involved in visual attention tasks were combined with ERPs in order to isolate brain activity related to the diverse processes.

In the following, I will give an overview of theories that influenced aging research in the last decades with a special focus on the role of (visual) attention functions in these models. First, earlier theories based on behavioral observations will be outlined. Second, these will be integrated with more recent developments ensuing from the availability of neuro-cognitive methods. Following this, the method of event-related potentials (ERPs) will be introduced with particular emphasis on its application in the study of cognitive aging and visual attention. The last section of the introduction deals with theoretical frameworks of visual attention that, in combination with ERPs, were utilized to target the present work's research questions.

1.2 Neuro-cognitive theories of aging

Age-related changes in cognition are not uniform: most, but not all functions are subject to decline, and different abilities are affected to varying degrees. Nevertheless, regularities are observable across tasks, sensory modalities, and cognitive domains (Figure 1.1).

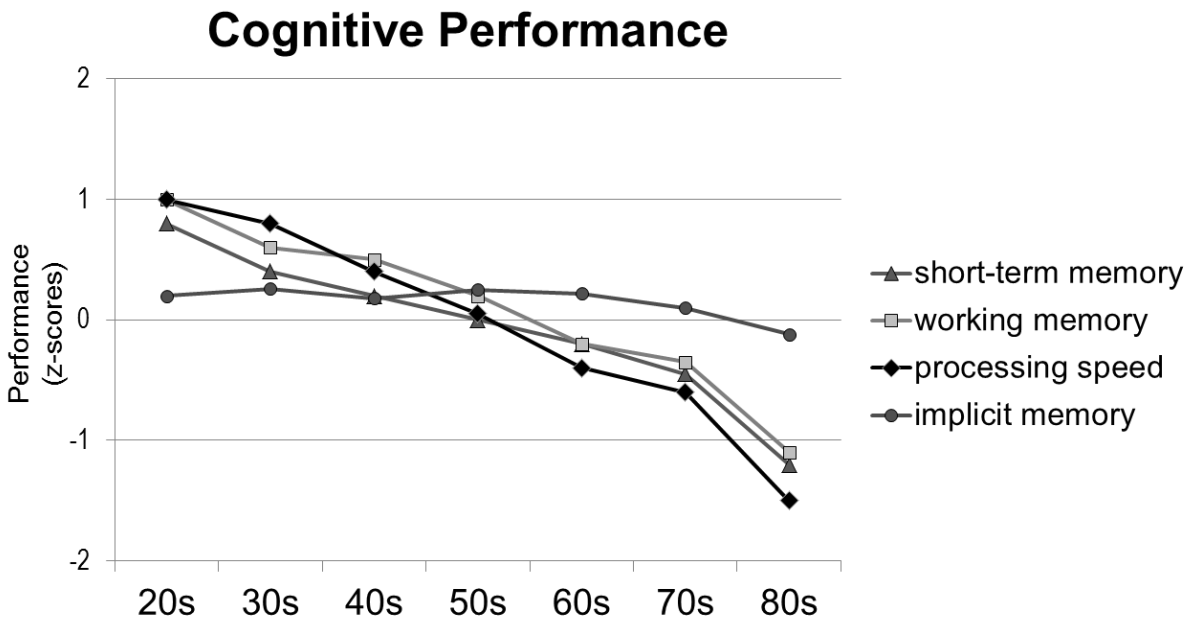

Figure 1.1: Schematic illustration of age-related decline in different cognitive abilities during adulthood (adapted from Park et al., 2002).

Age decrements are generally more marked in tasks that require flexible on-line processing and rely heavily on attentional control (e.g., Grady, 2008). Furthermore, impairments become more severe with increasing difficulty or complexity of the task (Craik & Salthouse, 2000). In contrast, when operations are based on relatively easy implicit or automatic processes, performance is often preserved in older age (Jennings & Jacoby, 1993).

1.2.1 One-factor models of cognitive aging

In the 1980s and 1990s, several unitary frameworks have been developed that attributed age-related cognitive impairments to one central capacity limitation in the processing system (Cabeza et al., 2005). A prominent example is the 'resource deficit theory', which claims that a general reduction in the amount of available (attentional) resources with age accounts for the observable performance decline in various tasks (Craik, 1982). Consequently, deficits are assumed to become more marked when a larger amount of resources is required, such as under difficult, or complex, task conditions. In contrast, age effects would be absent, or relatively small, in easy tasks requiring fewer resources (e.g., McDowd & Craik, 1988).

Subsequent approaches specified the mechanisms that might underlie reduced attentional capacity or resources in older age more precisely. For instance, the 'inhibition deficit theory' (Hasher & Zacks, 1988), states that age-related cognitive decline results from a central deficit in suppressing irrelevant representations or response tendencies, which leads to interference in further processing operations. The original framework mainly focused on the role of inhibition in controlling the contents of working memory, but more recent developments have proposed that the inhibition deficit already affects stages earlier in the processing stream, such as (pre-)attentional selection (Johnson et al., 2004).

According to the 'processing speed deficit theory', cognitive decline is attributable to a general age-related reduction in mental speed. In fact, behavioral slowing is one of the most

ubiquitous findings in aging research, and explains a large amount of variance in age effects across multiple cognitive tasks (Cerella, 1985; Salthouse, 1996). A contentious point in aging research, however, is whether age-related slowing is specific to particular processes (sensory, cognitive, or motor processes) or reflects widespread, unspecific influences (e.g., Salthouse, 2000; Wei et al., 2011). Related to this, general slowing has also been suggested to be a confounding factor in aging studies that potentially superimposes specific age-effects (e.g., Faust et al., 1999).

Finally, the pattern of cognitive impairments in older age has been linked to a specific deficit in executive functions or 'supervisory attentional functions', such as mental flexibility, inhibition and control (e.g., Andrès & Van der Linden, 2000; Norman & Shallice, 1986; West, 1996). In particular, age effects are more marked under complex experimental task conditions, which require participants to switch between task sets, or which induce response conflicts (e.g., Eriksen flanker task, Simon task, and Go-NoGo task; Verhaegen & Cerella, 2002; Verhaegen, 2011). For example, the flexible handling of stimulus-response (S-R) mappings in the tasks mentioned is assumed to be executively controlled and therefore prone to age-related decline (e.g., Castel et al., 2007; Hommel et al., 2011). However, it is difficult to decide whether age deficits indeed arise from this (or another) processing component, since a number of cognitive operations are involved in these or comparably complex tasks. Furthermore, it has been argued that simply this higher degree of task complexity but not executive processes per se cause larger age decrements, and deficits resulting from age-related decline in core cognitive abilities, such as processing speed or working memory span, would accumulate across mental operations involved in a task (e.g., Verhaegen, 2011).

1.2.2 Cognitive neuroscience of aging

The aging brain undergoes substantial anatomical and structural changes (e.g., Kemper, 1994). It is generally assumed that age decrements in cognitive functioning are

intimately linked to these alterations, and especially to a predominant decomposition of brain networks involving frontal areas (Moscovitch & Winocur, 1992; West, 1996). Accordingly, the attentional resource reduction in older age is suggested to stem from less efficient frontally-mediated attentional control functions (Craik & Byrd, 1982; Raz et al., 1999). Structural neuroimaging studies have confirmed that the pre-frontal cortex, and areas highly connected to it, are more susceptible to age-related reduction in brain volume and white matter deterioration compared with primary (e.g., visual) areas (Raz, 2000; Raz et al., 2005; Resnick et al., 2003). Furthermore, the dopaminergic system, which is known to regulate the efficiency of pre-frontal functions (Mattay et al., 2002), is particularly prone to age-related decline (e.g., Volkow et al., 2000).

Functional neuroimaging provides a fruitful means to examine the relationship between cognitive and cerebral aging more directly by measuring brain activity while participants are engaged in a cognitive task (e.g., Grady, 2008, 2012). Task-related age differences in brain activity were has been shown to be most pronounced in frontally-mediated circuits supporting executively controlled processes (e.g., Cabeza et al., 2002), whereas brain activity underlying automatic processes (e.g., implicit memory, priming) is comparable in younger and older age (e.g., Soldan et al., 2008). Importantly, findings from functional imaging studies have further shifted the view on aging from a one-sided focus on decline to a multifaceted picture of reorganization (e.g., Fabiani, 2012; Grady, 2012). In particular, aging can have opposing effects on brain activity, with activity being sometimes reduced and sometimes enhanced in older as compared to younger individuals. A decrease in activity with age is typically interpreted to reflect deficient processing due to neural loss in older adults (e.g., Grady et al., 1995), whereas an increase in brain activity can have multiple implications. It may indicate dedifferentiation, that is, less selective recruitment of resources that is unrelated to performance or potentially hampers cognitive functioning (e.g., Li & Lindenberger, 1999). On the contrary, higher activity in older compared to younger

participants may reflect compensatory recruitment in order to counteract degeneration effects (e.g. Cabeza et al., 2002).

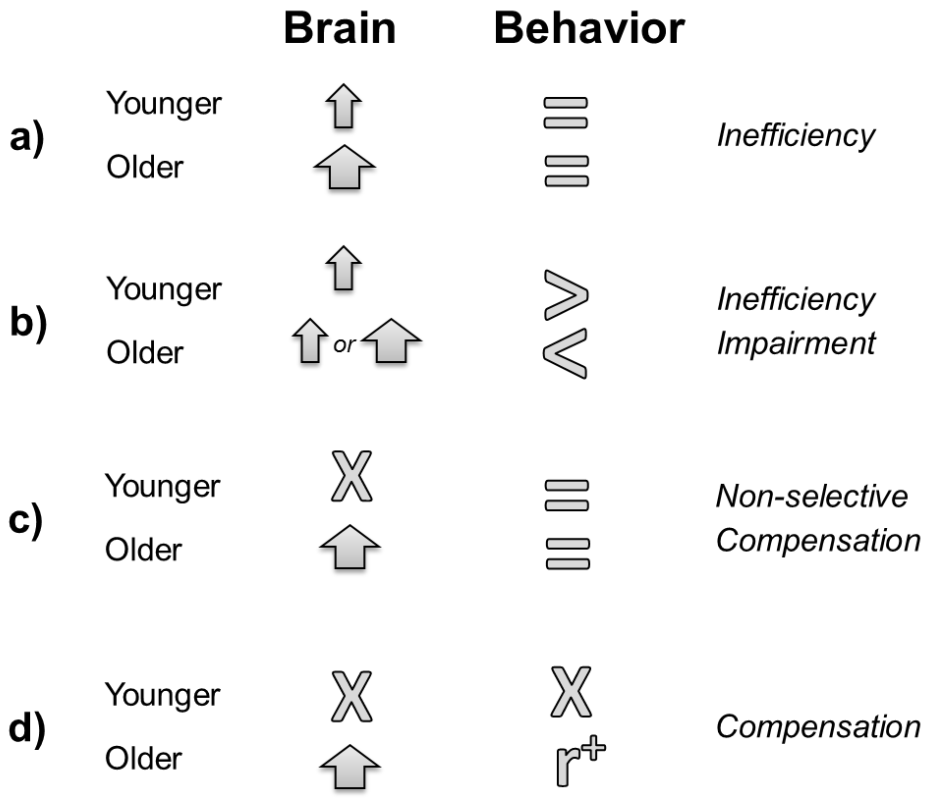

Figure 1.2: Possible explanations for age differences in brain activity.
a) Higher activity and equal performance in older relative to younger participants. b) Similar or higher activity but worse performance in older relative to younger participants; a) and b) have been interpreted as evidence of less efficient neural processing. c) Additional activity and equal performance in older relative to younger participants could be either related to compensatory or non-selective recruitment. d) Additional activity correlated with performance only in older participants is evidence of compensatory activity (adapted from Grady, 2008).

This ambiguity can only be solved by evaluating individuals' brain activity according to their achievements in cognitive tasks. This way, it is possible to dissociate brain activity patterns related to retained performance levels in older age from those associated with significant cognitive decline (Grady, 2012; Reuter-Lorenz & Park, 2010; Figure 1.2). This line of research revealed fronto-parietal areas in the attention network to critically determine brain-behavior relationships during aging (e.g., Cabeza, 2002; Valessi et al., 2011). In general, increase in activity in frontal areas associated with better performance in the elderly is taken as evidence for compensatory recruitment (e.g., Davis et al., 2008; McIntosh et al.,

1999). Specifically in visual attention tasks, effective attentional control in elderly has been demonstrated to correlate with increased activity in fronto-parietal areas (Madden et al., 2007).

To sum up, attentional capacity or resources supported by fronto-cortical structures appear to mediate cognitive performance especially in older age (e.g., Craik, 2006). However, there is as yet no clarification about the characteristics and origins of the attentional resource limitations and whether and how they contribute to age-related changes in performance. A higher degree of specificity could be achieved by unveiling neural correlates of distinct attentional components or resources being differentially affected by aging.

1.3 Event-related potentials in the study of cognitive aging

Brain-behavior relationships in cognitive aging have mainly been inferred from functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) data, which provided valuable insights into the anatomical locus of age-related changes in brain processes (e.g., Grady, 2008, 2012). However, owing to their reliance on inherently slow hemodynamic responses, these methods are inappropriate to map contemporaneous processes within a short period of time (e.g., Fabiani et al., 2012). Critically, the fate of visual input is assumed to be jointly determined by multiple attentional components within the first second after information is encountered (Posner & Boies, 1971). Thus, in order to dissociate age effects on different sub-components of attention, a method with high temporal precision is favorable.

1.3.1 Separating processing components of visual attention with ERPs

ERPs have an excellent temporal resolution that permits to neurophysiologically separate cognitive processes on a millisecond scale (Luck, 2005). They are extracted from the

ongoing signal of the electroencephalogram (EEG) by averaging signals that are linked in time to a repeated physical or mental event (Figure 1.3). By this means, characteristic mean voltage deflections (ERP components) marking sensory as well as higher-level cognitive processes have been identified. In general, ERP latencies track the timing of a sequence of consecutive processes and their amplitudes index the amount of neural resources engaged in the respective processes (e.g., Luck et al., 2000; Polich, 2007). Latencies, amplitudes and topography of ERP components vary across different task conditions or states of the observer, and also between different subject groups, such as younger and older participants. In either case, changes in the appearance of the ERP indicate alterations in the underlying generator networks. Although it is technically impossible to reconstruct the exact intracranial source of a scalp-recorded EEG signal, EEG source localization methods and fMRI/PET data have been successfully used to delineate generators of ERP components in many cases (e.g., Pascual-Marqui et al., 2002).

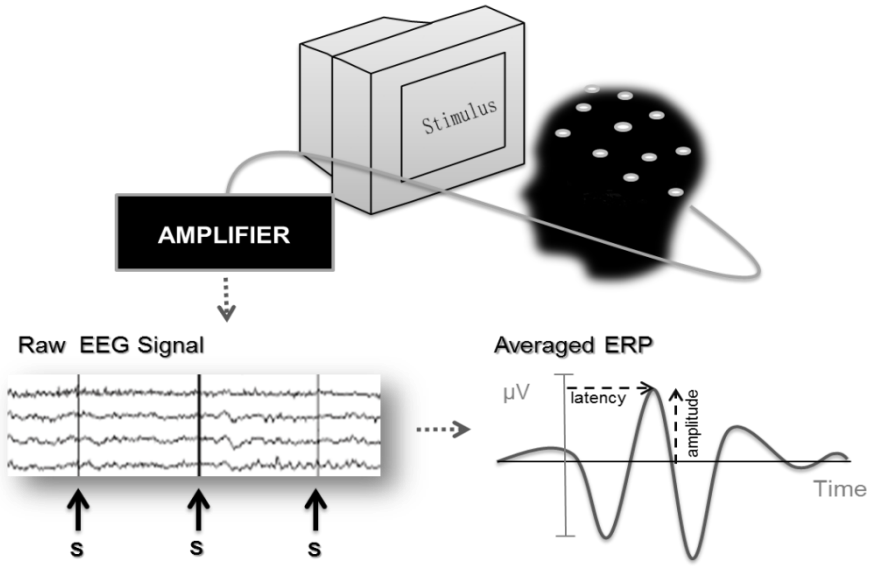

Figure 1.3: Schematic illustration of ERP acquisition.
EEG is recorded while the participant performs a cognitive task. The ongoing signal is amplified and later segmented according to the event of interest. ERP waves are the average of all trial segments time-locked to the event (e.g., presentation of the visual stimulus).

ERPs have substantially contributed to a better understanding of the neural mechanisms underlying visual attentional functions. Distinct components have been shown to be sensitive to attentional effects on various stimulus-related stages, as well as on response-related stages (e.g., Töllner et al., 2008). Thus, ERPs can be used to isolate and track the timing of several operations involved in visual attention (Luck et al., 2000; Table 1.1).

Table 1.1: Overview of ERP components marking different processes involved in attention tasks.
For a detailed description, quantification, analyses and interpretation of the components see sections below (and see Eimer, 1996; Eimer & Coles, 2003; Hillyard et al., 1998; Luck et al., 2000; Polich, 2007; Vogel & Luck, 2000)

ERP Component	Process
P1	Perceptual stimulus processing
Posterior N1	Discrimination of visual stimuli
Anterior N1	Voluntary attentional guidance
Central Positivity (P3)	Attentional processing of stimuli
PCN (N2pc)	Spatial allocation of attention to visual stimulus
SPCN (CDA)	Analyses and storage of visual information in visual short-term memory
sLRP	Selection of motor response
sLRP	Execution of motor response

1.3.2 Mapping age-related changes with ERPs

The latencies of several ERP components are typically prolonged for older relative to younger participants (e.g., Curran et al., 2001; Falkenstein et al., 2006). These latency delays are interpreted to index the slowing of sensory, cognitive, and motor processes due to aging (e.g., Fabiani et al., 2007). Amplitudes can be enhanced, or reduced, or unaffected by age, depending on the task and the component of interest (e.g., Friedman, 2003). Furthermore, the topographical distribution of some components systematically differs between age groups, indicative of changes in sources that generate the scalp potential (e.g., Fabiani, 2012).

Generally, age differences in ERPs indicate that the neural resources allocated to different processing components engaged in a task vary with age. The cognitive mechanisms underlying these age-related changes apparent in ERPs can be approached by combining EEG recordings with behavioral measures. Thus, together with appropriate experimental paradigms, ERPs are a promising tool to separate and identify distinct components of visual attention functions in older age (Braver et al., 2009).

1.4 Theoretical frameworks and rationale of the studies

The present PhD project aimed at providing a characterization of the complex neural mechanisms underlying age-related changes in visual attention. To achieve this goal, we combined the ERP technique with psychophysical tasks that allow the disentangling of attentional processing components in a highly specific manner. The studies were based on influential theoretical concepts and established paradigms in visual attention research, which will be briefly outlined in the following section. First, the 'Dimension Weighting Account' (DWA; Found & Müller, 1996) will be introduced, and how attentional processes involved in visual search can be interpreted according to the framework. Second, the 'Theory of Visual Attention' (TVA; Bundesen, 1990) will be outlined, and how distinct parameters of general attentional can be quantified according to the framework.

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4.1 Separating attentional processes in visual search based on the 'Dimension Weighting Account'

The first project was based on the DWA (Found & Müller, 1996; Müller et al., 1995), which interprets visual selection mechanisms in terms of allocation of capacity-limited attentional resources, or 'weights' (cf. Duncan & Humphreys, 1989). More precisely, attentional weights are assumed to be allocated to various basic visual dimensions (such as, color, shape, or size), with the total attentional weight being limited (e.g., Found & Müller,

1996). The efficiency of attentional selection can be measured by performance in visual search, a task that requires an individual to scan the visual environment for a particular object (the target) among other objects (non-targets). Target-selection in search tasks is assumed to be limited by the nature of required discriminations between different features or dimensions of stimulus attributes (Allport, 1971). Thereby, search performance on a given trial *n* is modulated by attributes of the preceding trial *n-1*, which has been explained by implicit memory traces that influence processing from one trial episode to the next (e.g., Found & Müller, 1996; Maljkovic & Nakayama, 1994). For instance, in a simple visual pop-out search task, in which the target automatically 'pops out' from the visual scene by differing from the non-targets by a unique feature, response times (RT) are faster if the target is defined in the same feature dimension as on the previous trial (i.e., color – color) compared to when the target-defining dimension changes across trials (i.e., color – shape; left panel of Figure 1.4). According to DWA, detection of a target requires that attentional weight is allocated to its defining dimension, amplifying its signal on an integrating overall saliency map of the visual display, which guides attentional selection (see also Wolfe, 1994). If a target in a given trial is defined by the same dimension as in the previous trial, stimulus selection is assumed to be faster due to enhanced coding of feature contrast of the already weighted dimension onto the saliency map, which speeds up the allocation of focal selective attention. In contrast, if the dimension of the target-defining feature changes across trials, a time-consuming re-weighting from the old to the new dimension is required, and target selection is therefore slowed (Found & Müller, 1996; Müller et al., 1995).

Processing components in visual compound search

Search performance can be considered a superposition of a sequence of processes, with the specific operations involved depending on the specific requirements of a given task (e.g., Töllner et al., 2012). In a compound search paradigm (Duncan, 1985), the observer has

to find a pop-out target among non-targets (e.g., defined by a unique color or shape), and has to respond to another (not target-defining) feature of the target (e.g., its orientation; right panel of Figure 1.4). In this case, one processing cycle consists of the following stages: target selection based on the target-defining feature, discrimination of the response-relevant target-feature, response selection based on this discrimination, and finally, the execution of the selected response (e.g., Töllner, et al., 2008).

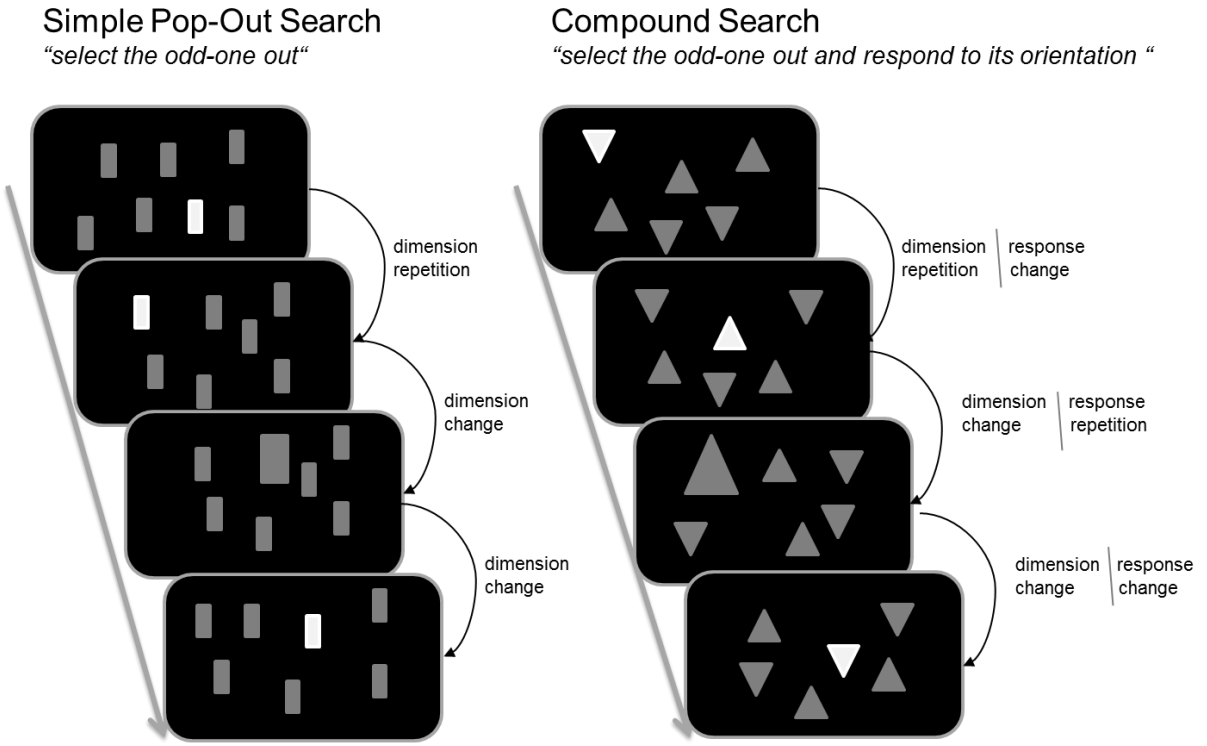

Figure 1.4: Intertrial effects in visual search.
Sequence of trials in a pop-out search task (left panel) and a compound search task (right panel). In both tasks, the pop-out target is defined either by a unique color or size, with the target-defining dimension varying randomly across trials. In the compound search task, the required motor response depends on the orientation of the target (triangle points up- or downwards), with the orientation also varying randomly across trial episodes and being statistically independent from changes/repetitions in the target-defining dimension.

Furthermore, different types of intertrial effects are inherent in this task, which are suggested to operate at different stages of the processing cycle (e.g., Töllner et al., 2012; Zehetleitner et al., 2012). First − according to DWA − repetition of the target-defining dimension is assumed to facilitate the guidance of focal attention by enhanced saliency coding

of a target at pre-attentive processing stages. In contrast, in case of a change, attentional weight would have to be shifted from the old to the new target-defining dimension. Second − analogously to the process postulated for dimension changes in DWA − repetition of the motor response is suggested to facilitate response execution on motor production stages by carrying over activation from the previous trial reducing the threshold at which the response is executed. In contrast, a change of the response is assumed to require a time-consuming shift from the old to the new response needing a stronger motor signal to reach the execution threshold (see Töllner et al., 2010, for 'Response Weighting Account'). Finally, the association of the target-defining dimension and executed response can be either changed or repeated across trials, referred to as S-R mapping. The adaptation of S-R mappings across trial episodes is assumed to be an attentionally controlled mechanism (e.g., Hommel et al., 2004) governed by stages supporting S-R transmission processes, which are intermediate to stimulus selection and response execution stages (Töllner et al., 2008; Pollmann et al., 2006; Figure 1.5).

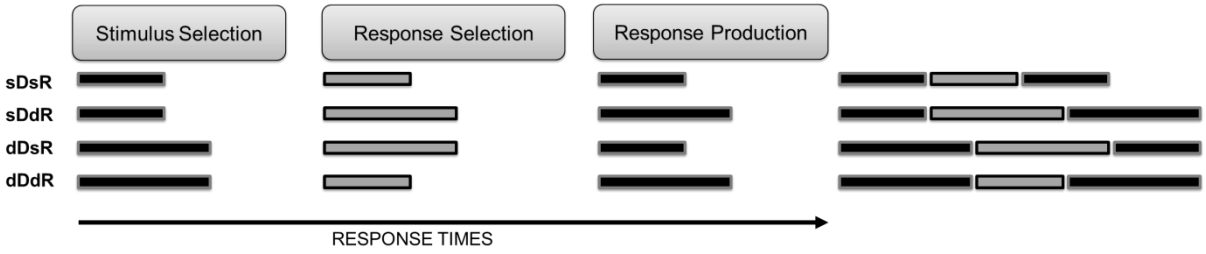

Figure 1.5: Schematic illustration of processing times across stages in a compound search task.
The inferred processing times (black and gray lines) required by successive stages are depicted for each combination of intertrial effects in the task. The summed processing times of the three stages yield the overall reaction time for a given condition. sDsR = same dimension/same response; sDdR = same dimension/different response; dDsR = different dimension/same response; dDdR = different dimension/different response (adapted from Töllner et al., 2008).

Rationale of the 1st project

The first study was designed to examine the origins of age-related slowing in visual search. In addition, we aimed to dissociate general slowing from potential task-specific age

effects. The approach was built on the DWA, which has been proven to provide a theoretical framework for interpreting brain correlates of several capacity-limited attentional components (e.g., Pollmann et al., 2000; Weidner et al., 2002). To dissociate age effects on distinct processing components involved in visual search we used a compound search paradigm, which is an extremely simple task that allows separating processes with potentially differing sensitivity to aging. Combined with neuro-cognitive methods, the paradigm permits to isolate the brain mechanisms underlying these diverse processes[1] (e.g., Pollmann et al., 2006; Töllner et al., 2008; 2012). Specifically, response times (RT) were coupled with ERP latency measures that index the speed of various stimulus- and response-related stages and, thus, can mark age-related slowing on the respective stages. First, we wanted to measure whether one or several stages are specifically slowed in older age, or whether all stages within one processing cycle contribute to the overall slowing, as it was proposed by one-factor models (Brinley, 1965; Salthouse, 1996). Furthermore, besides the general slowing factor, we aimed at dissociating between brain processes underlying relatively automatic from those underlying more attentionally controlled processes. In particular, analyses of intertrial effects were assumed to reveal whether aging would affect flexible re-mapping of S-R associations more than rather automatic weighting of a previously selected dimension or executed response, as it was proposed by models of aging that assume specific age decrements in executively controlled processes (e.g., West, 1996).

1.4.2 Separating attentional parameters based on the 'Theory of Visual Attention'

The second project was based on the TVA, which is a computational framework that allows partitioning attentional components into distinct mathematically defined parameters

[1] Note that the processes cannot be disentagled based on behavioral measures. RTs in compound tasks typically show an interactive pattern of trial-to-trial changes in the target defining dimension and response (Figure 1.5). The fastest RTs occur with full repetitions, whereas RTs are slowest when one feature repeats and the other changes, termed partial-repetition costs (PRCs; e.g., Müller & Krummenacher, 2006; Töllner et al., 2008).

(Bundesen, 1990). Similar to the biased competition model (Desimone & Duncan, 1995), TVA assumes that elements in the visual field race in parallel and compete to become encoded (Figure 1.6). In TVA, selection or categorization of an object equals encoding into visual short-term memory (vSTM) and is described in the form of 'element *x* belongs to category *i*', where *x* is an object in the visual field, and *i* is a perceptual category.

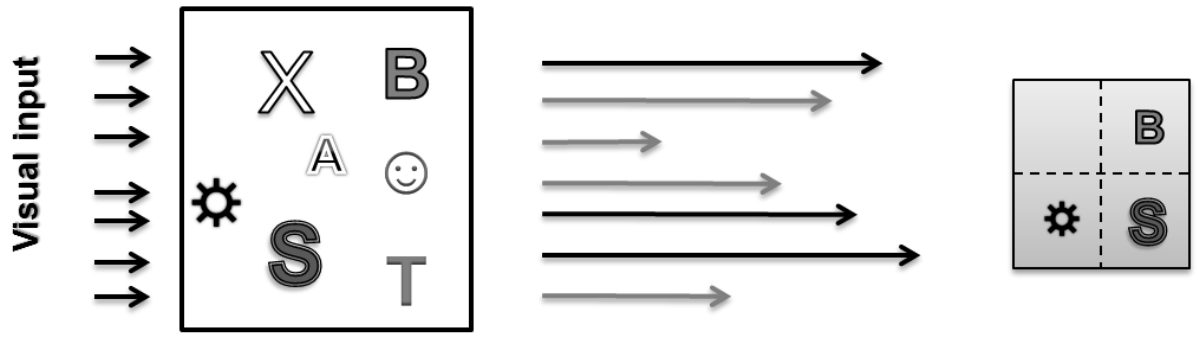

Figure 1.6: Encoding process in TVA.
At a first stage, each object in a visual field is weighted according to its importance of being attended. Based on the weights, processing capacity is distributed, which determines each object's speed/propability of becoming encoded into vSTM, before it has been filled up with other items and/or the effective exposure duration has expired (adapted from Shibuya & Bundesen, 1988).

The storage capacity of vSTM is limited to a number of *K* elements, and categorization requires that space in the limited vSTM is available. Thus, only those objects that complete processing fastest will enter vSTM. An element's processing rate (v) is determined by the amount of processing capacity allocated to it. The way processing capacity is distributed among the elements is determined by a combination of the objects' sensory strength (η), the observers' perceptual decision bias (β_i) associated with a certain category and the relative attentional weight (w_x) of object *x* relative to attentional weights across all objects in the visual field (S). Attentional weights of objects are derived from pertinence values (π_j), a measure of the importance of attending to objects that belong to category *j*. These processes are expressed in the two central equations of TVA:

1. **Weight equation**: computation of attentional weights 'w'

$$w_x = \sum_{j \in R} \eta(x,j)\pi_i$$

R: set of perceptual categories; η (x, j): strength of the sensory evidence that element x belongs to category j; πj*:* pertinence value (importance of attending to elements that belong to category j).

2. **Rate equation**: probability 'v' of an object to be encoded into vSTM

$$v(x,i) = \eta(x,i)\beta_i \frac{w_x}{\sum_{z \in S} w_z}$$

S: elements in the visual field; η (x, i): strength of the sensory evidence that element x belongs to category i; β_i*:* perceptual decision bias associated with category i ($0<\beta_i<1$); w_x and w_z : attentional weights of elements x and z (expresses the *relative* attentional weight of element x)

The Neural Theory of Visual Attention

More recently, correspondences between central equations of TVA and neuronal activity in the visual system have been proposed within the 'Neural Theory of Visual Attention' (NTVA, Bundesen et al., 2005, 2011). NTVA assumes that the total activation representing an object is proportional to both the number of neurons representing this categorization (pertinence π_i) and the firing rates of the neurons coding this objects' features (bias β_i). Sensory information in the striate cortex is used for computing pertinence values within higher areas of the visual system. Based on these signals, a 'priority map' of attentional weights is configured, which determines the processing resources allocated to objects in the visual field. The pulvinar nucleus of the thalamus has been proposed as its most probable anatomical locus, but other areas linked to processing of visual relevance were also considered, such as the inferior parietal lobe and the lateral intraparietal area (Bundesen & Habekost, 2008). On the following selective stage, attentional capacity is distributed towards cortical visual areas based on the dispatched weight signals, which are multiplied by bias values. The product is used to instantiate a vSTM map of location. The vSTM map is

suggested to be located within the thalamic reticular nucleus, a topographically organized, highly interconnected area. The race of objects in the visual field starts when the vSTM map is initialized. Representations that 'won' the race and, thus, become encoded into vSTM, are maintained via reverberating circuits between the thalamus and cortical areas (Figure 1.7). Notably, NTVA is a fairly general neurophysiological interpretation of the theoretical model, and proposed anatomical implementation should be considered tentatively (Bundesen & Habekost, 2008).

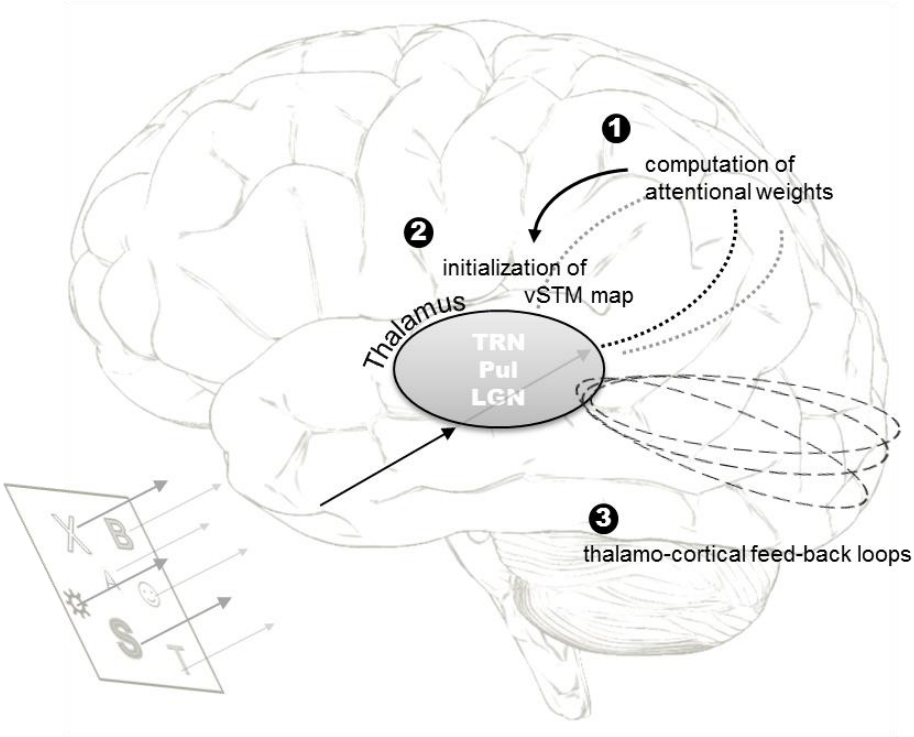

Figure 1.7: Simplified illustration of the brain mechanisms underlying visual categorization proposed by NTVA. For more detailed illustrations of the mechanisms see Bundesen et al. (2005, 2011). TRN: thalamic reticular nucleus; Pul: pulvinar nucleus; LGN: lateral genicular nucleus.

Parameter modeling based on TVA

The equations of the TVA model can be used to analyze behavioral data derived from simple experimental tasks. Specifically, in the TVA whole report, a number of letters are briefly presented and the participant is required to name as many letters as possible. The probability of encoding letter stimuli (measured by number of correct reports) develops

systematically as a function of exposure duration (see Duncan et al., 1999). The exposure duration of the display is varied, typically covering a range from the individual's perception threshold to presentation time that allows filling up vSTM to its limit. The analysis of performance in this task yields individual estimates of central parameters of visual capacity. First, parameter visual processing speed *C* refers to the limited amount of information that can be processed within a given time and is expressed as the number of objects encoded as a function of time. In displays with multiple elements, *C* equals the sum of processing rates of all objects ($C = \sum v$). Second, parameter vSTM storage capacity *K* refers to the maximum number of objects that can be perceived at one point in time. The upper limit of the visual apprehension span is a well replicated finding that has also been found by using other paradigms (e.g., change detection; Luck & Vogel, 1997), and is about four items for young, healthy subjects. The reliability of TVA-based modeled parameters can be evaluated in terms of measurement errors ('goodness-of-fit'), which can be considered minimal given testing conditions are appropriate (Finke et al., 2005). TVA-based assessment is further an exceptionally valid measurement, being grounded on an established theoretical framework. Most importantly, TVA provides unique specificity by defining and analyzing *C* and *K* mathematically independent of each other, which is a critical advantage over conventional neuropsychological test procedures in which the influence of both components is not dissociable. The general capacity parameters processing speed *C* and storage capacity *K* are considered fundamental attentional resources that jointly determine performance across a broad range of cognitive tasks (e.g., Cowan, 2001; Deary, 2010). Furthermore, they have been suggested to reflect attentional limitations that account for age-related changes in various cognitive abilities (e.g., Salthouse, 2000). The fact that NTVA has also proposed distinct brain mechanisms underlying the two parameters bears the potential to link the independent estimates to separate neurophysiological variables.

Rationale of the 2nd project

TVA-based assessment permits to quantify age-related changes in a uniquely specific manner (e.g., Habekost et al., 2012; McAvinue et al., 2012). Furthermore, NTVA provides a basis for interpreting the neural mechanisms underlying age-related changes in visual perceptual processing speed *C* and vSTM storage capacity *K*, respectively. However, an empirical neuro-cognitive approach that allows measuring brain processes underlying the two central limitations of visual attention directly has not yet been established. Particularly in the context of aging, it would be promising to dissociate brain activity patterns related to attentional decline from those related to reserved abilities in older age.

Therefore, with the second project we pursued two goals: In the first study of the second project, we aimed to develop an experimental setup that permits to directly test the neuronal separability of processing speed and storage capacity by dissociating neural markers of individual performance differences in the two functions. In the second study of the second project, we aimed to apply the approach evolved in the pioneering work to define the neural underpinnings of age-related alterations in attentional capacity parameters. Specifically, we combined TVA-based assessment with ERPs in an 'interindividual differences' design. Participants were grouped according to their behavioral performance, separately for *C* and *K*. In the initial study, ERP responses of subgroups of younger participants according to their performance level were compared twice: First, brain activity that marks individual levels of processing speed *C* was isolated by comparing ERPs of participants with relatively fast and slow processing speed. Second, brain activity that marks individual levels of storage capacity *K* was isolated by comparing ERPs of participants with relatively high and low storage capacity. In the following aging study, ERPs of younger and older participants, with each group being again separated according to performance level in processing speed and storage capacity, respectively, were compared. This way, we examined whether the same neural correlates of individual differences in processing speed and storage capacity would be

replicated in an older sample and mark age-related decline in the respective parameter estimates. Furthermore, the design permitted to pinpoint additional neural markers of specific age-related decline– or reserve– in the two parameters, which may differentiate between higher- and lower performing elderly.

1.5 References

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II. Components of aging in visual search

Wiegand, I., Finke, K., Müller, H. J., & Töllner, T. (2013). Event-related potentials dissociate perceptual from response-related age effects in visual search. *Neurobiology of Aging*, *34*(3), 973-985.

2.1 Event-related potentials dissociate perceptual from response-related age effects in visual search

2.1.1 Abstract

Attentional decline plays a major role in cognitive changes with aging. However, which specific aspects of attention contribute to this decline is as yet little understood. To identify the contributions of various potential sources of age decrements in visual search, we combined response time measures with lateralized event-related potentials of younger and older adults performing a compound-search task, in which the target-defining dimension of a pop-out target (color/shape) and the response-critical target feature (vertical/horizontal stripes) varied independently across trials. Slower responses in older participants were associated with age differences in all analyzed event-related potentials from perception to response, indicating that behavioral slowing originates from multiple stages within the information-processing stream. Furthermore, analyses of carry-over effects from one trial to the next revealed repetition facilitation of the target-defining dimension and of the motor response – originating from preattentive perceptual and motor execution stages, respectively – to be independent of age. Critically, we demonstrated specific age deficits on intermediate processing stages when intertrial changes required more executively controlled processes, such as flexible stimulus-response (re-)mapping across trials.

2.1.2 Introduction

One essential daily task that becomes slower with age is visual search: our ability to discern and react upon a visually more or less distinctive item in a cluttered scene (Madden et al., 2004). Age-related slowing in the performance of visual search tasks might be attributable to a selective stage in the information-processing cycle, or it might originate from several stages and accrue across the sequential processes making up the cycle. Candidate stages are the selection of task-relevant sensory information, the identification of response-critical information, and/or the selection and execution of the required motor response (e.g., Kok, 2000; Salthouse, 2000). The present study was designed to examine this question at the micro-level of separable processing stages.

Performance in visual search tasks is known to be influenced by recently encountered stimuli and actions performed in response to them, within a sequence of trial episodes (e.g., Maljkovic & Nakayama, 1994; Müller et al., 2010). A special instance that might pose particular problems for older adults is the re-mapping of previously encoded stimulus-response (S-R) associations across such episodes (Hommel et al., 2011). Presumably, the fast adaptation processes involving flexible S-R re-mapping from one trial episode to the next require a higher degree of executive control processes, which are particularly age-sensitive (e.g., Park, 2000).

Using a cognitive neuroscience approach (e.g., Grady, 2008; Reuter-Lorenz & Park, 2010), we examined behavioral performance together with lateralized event-related potentials (ERPs) of younger and older adults in order to determine the relative contributions of separable sources to age-related decrements in the performance of a visual pop-out search task. A pop-out target differs from distractors in a simple feature, providing a strong bottom-up signal for focal-attentional selection (Treisman & Gormican, 1988; Wolfe, 1994). Thus, this task is highly suitable for assessing the effects of aging, because the underlying cognitive architecture and the processing stages involved – perceptual selection, perceptual

identification, response selection, response execution – are clearly defined (e.g., Müller & Krummenacher, 2006; Töllner et al., 2012b). Performance of a simple pop-out search task can be assumed to be relatively unaffected by strategies. This is a critical advantage compared to more complex search tasks, which are prone to search strategies that might systematically differ between younger and older adults (e.g., more careful search in older adults; see Hommel et al., 2004). Accordingly, age differences in pop-out search can be relatively unequivocally attributed to the well-defined processing stages involved.

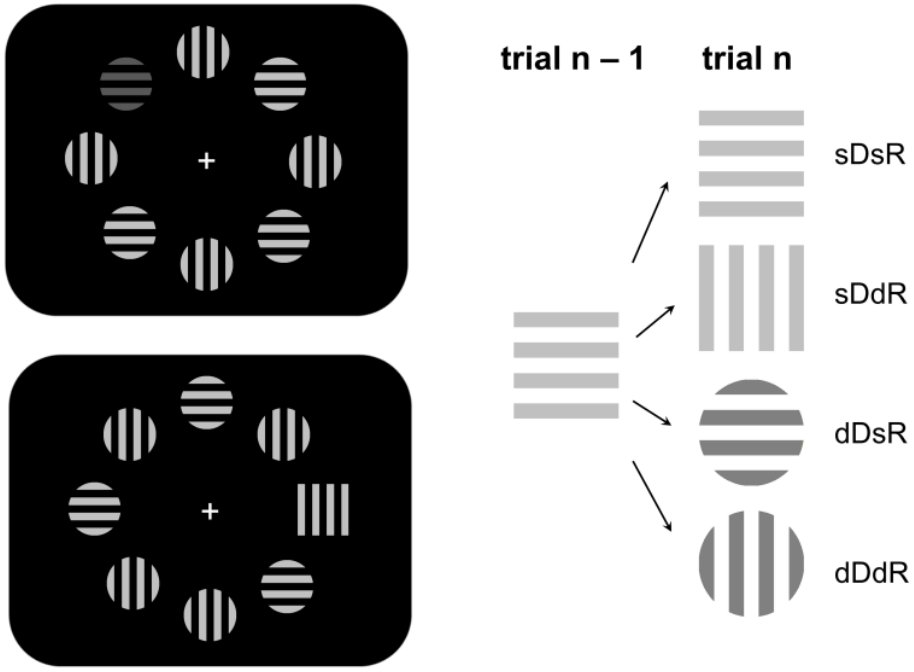

Figure 2.1: Stimuli and intertrial effects in the compound search task.
Left: Illustration of search arrays in the present compound-search task. The target was equally likely defined by a unique color (upper panel) or a unique shape (lower panel). The task was to discriminate the orientation of the singleton target's surface stripes (horizontal vs. vertical), which was independent of its defining dimension. *Right:* Illustration of the four resulting intertrial effect conditions. sDsR = same dimension/same response; sDdR = same dimension/different response; dDsR = different dimension/same response; dDdR = different dimension/different response.

Here, we used a variation of the classic pop-out paradigm, the so-called compound-search task (e.g., Bravo & Nakayama, 1992; Duncan, 1985), in which the selection- and the response-defining target features vary independently of each other across consecutive trials. The pop-out target was defined, variably across trials, by a unique feature in either the color

dimension: a single red (striped) circle within a display of yellow (striped) circles, or in the shape dimension: a yellow (striped) square among yellow (striped) circles. Thus, target selection depended on detecting a salient color or, respectively, shape difference in the search array. Independently of this, the response was defined by the orientation of the pop-out target's stripes: 'vertical' or 'horizontal' orientation was responded to by a left or, respectively, right mouse button press (Figure 2.1).

By analyzing carry-over effects from one trial to the next in this task (repetition vs. change of the target-defining dimension, repetition vs. change of the response-defining feature), we were able to compare the influence of recently encountered selection- and response-specific information between age groups. If a target on a given trial *n* is defined by the same feature or in the same dimension as the target on the preceding trial *n-1*, attentional guidance is facilitated, due to featural/dimensional 'priming' or 'weighting' (e.g., Found & Müller, 1996; Maljkovic & Nakayama, 1994, 2000; see also Töllner et al., 2009, for 'modality-weighting'): responses are faster compared to when the search-critical feature or dimension changes across trials (e.g., a color target preceded by a color target vs. a color target preceded by a motion target). Note that featural/dimensional weighting operates largely implicitly and automatically. For instance, with regard to dimension weighting, this is evidenced by the fact that prioritization of the target-defining dimension on the preceding trial cannot be completely overcome by top-down control processes (Müller et al., 2003; Töllner et al., 2010) and is not dependent on explicit memory of the trial history (Müller et al., 2004). Critically, repetition facilitation has been shown to be largely spared from age-related decline (Kumada & Hibi; 2004; Madden et al., 2004; McCarley et al., 2004). However, in compound-search tasks, response times (RT) also vary with changes in the to-be-performed motor response across trials, more critically, with changes (vs. repetitions) of the S-R mapping (e.g., Lamy et al., 2010; Töllner et al., 2008). Although changes in the target-defining dimension and the response-defining feature are statistically independent of each other, an interactive RT

pattern (e.g., Müller & Krummenacher, 2006) indicative of partial repetition costs (PRCs; e.g., Hommel, 2004) is typically observed: Responses are faster when both the dimension- and response-defining attributes are repeated or when both change, and slower when only one of the two attributes changes while the other one is repeated (e.g., Pollmann et al., 2006; Töllner et al., 2008). The magnitude of such PRCs has been suggested to depend on an individual's ability to flexibly break up the S-R association established on the previous trial and configure a new linkage – that is, essentially, the efficiency of executive control processes (Colzato et al., 2006; Hommel et al., 2011). It has previously been suggested that age-related changes in executive control processes, which are known to be particularly affected by aging, critically contribute to over-proportional RT costs in elderly when stimulus-response re-mappings over trial sequences are required, as, for example, in the Simon Task (e.g., Castel et al., 2007) or in task-switching paradigms (e.g., Mayr, 2001). In particular, it has been proposed that control over response selection might be a crucial determinant of age effects (Hartley, 2001) and could be localized best by using tasks involving the control of more general or primitive sets of S-R-mapping (Castel et al., 2007). On this basis, we tested whether PRCs in a simple compound-search task would also be particularly marked in older, in comparison with younger, adults.

By examining lateralized ERP responses in combination with RT measures (Posner, 2005), it becomes possible to disentangle the effects of aging, including their interactions with intertrial effects, on distinct stages of processing in visual search, in particular: those of (1) preattentive perceptual, (2) post-selective perceptual, (3) response selection, and (4) response production processing (Mazza et al., 2009; Perron et al., 2009; Töllner et al., 2011b). Pursuing this approach (Figure 2.2), we analyzed the following lateralized ERP components: the Posterior Contralateral Negativity (PCN; this component is traditionally referred to as N2-Posterior-Contralateral (N2pc); however, we prefer the term PCN to emphasize its independence from the non-lateralized N2; see e.g., Shedden & Nordgaard, 2001; Töllner et

al., 2011a); the Sustained Posterior Contralateral Negativity (SPCN; also referred to as Contralateral Delay Activity, CDA; see Vogel and Machizawa, 2004); the stimulus-locked Lateralized Readiness Potential (sLRP); and the response-locked LRP (rLRP).

The first parameter of interest, the PCN component, is a negative-going deflection elicited over lateral parieto-occipital sites contralateral to the location of an attended stimulus in the time window approximately 175-300 ms post-stimulus (e.g., Luck & Hillyard, 1994; Woodman & Luck, 1999). The PCN is generally thought to reflect focal-attentional selection of task-relevant target objects amongst distracter items in visual space (e.g., Eimer, 1996; Woodman & Luck, 1999). It has been demonstrated that its latency varies markedly depending on a variety of top-down (e.g., featural task set: Eimer & Kiss, 2008; dimensional set: Töllner et al., 2010, 2012a), bottom-up (e.g., stimulus intensity: Brisson et al., 2007; stimulus saliency: Töllner et al., 2011a), and intertrial factors (e.g., dimensional target identity of the previous trial: Töllner et al., 2008). Thus, given that the deployment of focal-attention is guided by the outcome of early sensory feature-contrast computations, the timing of the PCN can be used as a temporal marker of the transition from the preattentive perceptual coding of the whole search array to the focal attentional processing of the selected (target) stimulus (e.g., Luck et al., 2006). Recently, a delayed PCN has been found to index age-related slowing in visual attentional selection (Lorenzo-Lopez et al., 2008).

Another lateralized posterior component manifesting at somewhat longer, 300–700 ms, post-stimulus latencies (e.g., Jolicoeur et al., 2006; Perron et al., 2009), the SPCN, is assumed to reflect active visual short-term memory (vSTM) maintenance (e.g., Jolicoeur et al., 2006). This component is generated in visual attention tasks, including pop-out search (Mazza et. al., 2007), which require detailed analysis of the selected target in vSTM (e.g., Dell'Acqua et al., 2006; Mazza et al., 2009). Thus far, the SPCN has not been examined for age-related changes in visual search tasks. However, in change detection tasks, especially in older age, the SPCN amplitude is modulated by the timing and efficiency of prior,

attentionally controlled selection processes (Jost et al., 2010; Sander et al., 2011).

Finally, the LRP is a negative-going deflection over the motor areas contralateral to the side of a unimanual response and has been linked to the activation and execution of effector-specific motor responses (e.g., Coles, 1989; Kutas & Donchin, 1980). The LRP onset calculated relative to stimulus onset (sLRP) indicates the point in time at which one of several possible responses is preferred – thus, reflects the time required to initiate an effector-specific motor activation (i.e., response selection) after the completion of stimulus-response translation processes (e.g., Töllner et al., 2012b). By contrast, the LRP computed relative to response onset (rLRP) reflects the time demands required to produce and execute this response (e.g., Miller et al., 1998). Recently, age-related slowing in speeded RT tasks has been found to be related to prolonged and enhanced amplitudes of the rLRP – indicating that older adults require higher activation levels for motor execution, which are time-consuming to build up (Falkenstein et al., 2006; Yordanova et al., 2004).

In a pioneering study on young adults, Töllner et al. (2008) were able to attribute presumably automatic intertrial repetition facilitation and more controlled S-R (re-)mapping effects in a compound-search task to distinct sub-stages of processing, based on combined PCN, sLRP, and rLRP analyses. The authors found, irrespective of motor response changes, repetitions (relative to changes) of the target-defining dimension to produce shorter latencies of the PCN, indicating that (at least part of) the dimension-specific intertrial facilitation originates at the preattentive stage of saliency coding. In turn, irrespective of dimension changes, repetitions (relative to changes) of the generated motor response reduced amplitudes of the rLRP, indicating that response-specific intertrial facilitation originates at the stage of motor-response production. Importantly, the sLRP was found to be modulated interactively by dimension and response changes versus repetitions: its onset latencies were delayed for partial repetitions, that is, when either only the dimension or only the response changed, compared with complete repetitions or changes. Thus, the sLRP latencies showed a PRC-type

pattern, indicative of time-consuming S-R (re-)mapping processes at stages of response selection as the main source of the PRC effect found in the RT. Accordingly, assuming that S-R re-mapping across trials is particularly affected in older age, this should show up in alterations of this stage concerned with response selection (Figure 2.2).

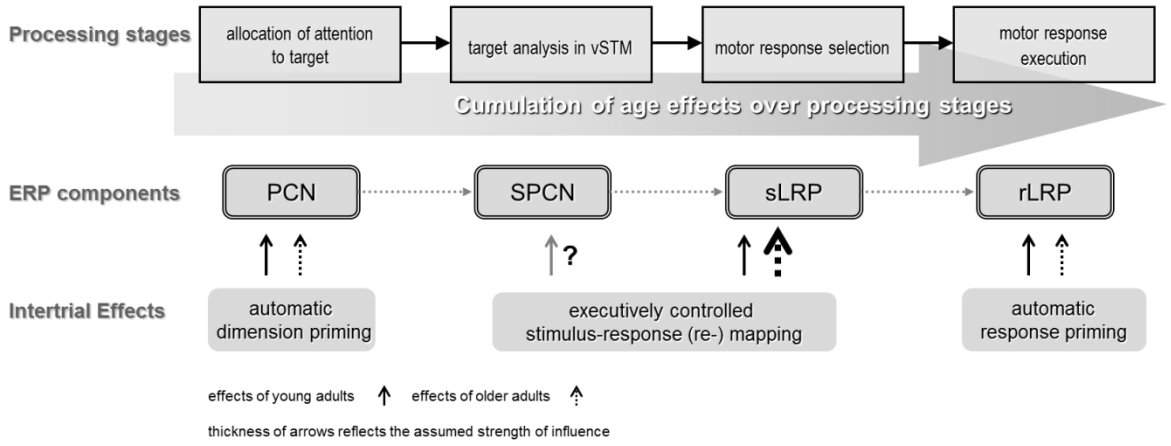

Figure 2.2: Schematic illustration of the inferred intertrial and age effects.
Upper row: processing stages involved in performing a compound-search task; the shaded arrow represents the assumed slowing with age that accumulates over successive stages. *Middle row:* ERP components from which potential effects on each of the processing stages may be derived (PCN = posterior contralateral negativity; SPCN = sustained posterior contralateral negativity; sLRP = stimulus-locked lateralized readiness potential; rLRP = response-locked lateralized readiness potential). *Lower row:* processes underlying intertrial effects on each processing stage; arrows indicate, for younger (solid arrows) and older adults (dotted arrows), the hypothesized influence of intertrial effects on each processing stage and the explored intertrial effects on post-selective processing stages (grey arrow).

Taken together, the present study was designed to provide a complete and comprehensive picture of age-related changes in visual (pop-out) search by combining measures of (behavioral) response speed with those of event-related lateralizations. First, we examined separable stages of processing in task performance that might, selectively or additively, contribute to age-related slowing: (1) slower allocation of focal-attention in older compared with younger adults should be reflected in prolonged PCN latencies; (2) less effective target analysis in vSTM should be reflected in attenuated SPCN amplitudes; (3) retarded response selection should be reflected in delayed sLRPs (over and above any PCN latency difference); and (4) slowed motor response execution should be reflected in prolonged

rLRPs. Second, we examined whether older adults would show particular decrements in S-R (re-)mapping across trials: Based on previous reports with young adults (Töllner et al., 2008), we assumed increased behavioral PRCs in older adults to originate at processing stages concerned with S-R transmission. In particular, finding more prolonged sLRP latencies for partial repetitions vs. complete repetitions/changes in older, compared with younger, adults would argue that the age deficit is attributable to stages of response selection. Further, we examined whether SPCN amplitudes would be modulated by PRCs and age. A critical involvement of this component would support the functional interpretation relating the SPCN to the identification of response-critical target attributes during post-selective maintenance of visual object information (e.g., Eimer & Kiss, 2010), indicative of post-selective perceptual processing contributing to age-related decline in S-R (re-)mapping.

2.1.3 Methods

Participants

Eighteen 'young' and eighteen 'old' adults were included in the sample (Table 2.1). Two further older participants and one further younger participant were excluded from analyses due to excessive amounts of eye movement activity. Further exclusion criteria were any history of neurological (e.g., traumatic brain injury, stroke), psychiatric (e.g., depression, anxiety disorders), chronic somatic (e.g., hypertension, diabetes), and chronic eye diseases (e.g., glaucoma, cataract). 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 (MMSE; Folstein et al., 1975) ruled out any symptoms prognostic of dementia: all participants achieved a score of 27 points or higher (cut-off: <24). The educational level was overall lower in the older compared with the younger participants, which is representative for the German post-world-war-II generation. However, the older participants achieved significantly higher IQ scores in a test of crystallized intelligence

(Mehrfach-Wortwahl-Test, MWT-B; Lehrl, 1977; Table 2.1). This is a common result, since crystallized intelligence measures reflect knowledge based on learning and past experiences, which accumulates during aging (e.g., Deary et al., 2010). Given this, the levels of intelligence can be considered comparable between the two groups. All participants gave informed consent and received payment for participating.

Table 2.1: Group demographics.
Gender distribution; Mean, SD (in parentheses) and range of age, education, and crystalline IQ; Shi^2 or T-values of group comparisons. F: female; M: male; School: Duration of education (attended school years); MWT-B: German Multiple-Choice Vocabulary Test (Lehrl et al., 1977).

	Younger Adults	Older Adults	Chi^2 or T
Sex (F/M)	10/8	7/11	Chi^2 = 1,00; *p* = *.32*
Age (years)	26.18 (3.20) 19-30	67.39 (3.80) 61-75	t(34) = 35.57; *p* < *.001*
Education (years)	13.00 (0.00) 13-13	11.78 (1.59) 9-13	t(34) = 3.26; *p* < *.005*
IQ (MWT-B)	114.80 (10.42) 101- 130	134.94 (6.31) 118-143	t(34) = 7.87; *p* <*.001*

Task and stimuli

The visual search displays were similar to those used by Töllner et al. (2008): they consisted of eight stimuli – seven yellow circles plus one singleton 'pop-out' target (see below) – equidistantly arranged on the circumference of an imaginary circle (3.3° of visual angle in radius) around a central fixation cross (Figure 2.1). On each trial, a singleton, either a red circle (color-defined target) or a yellow square (shape-defined target), was presented at one of the six lateral positions among the seven yellow circle distracters. Each stimulus outline shape contained vertical or horizontal stripes composed of four colored bars separated by three black gaps. The orientation of the stripes within the stimuli was balanced on any given trial (4 vertical and 4 horizontal). All stimuli were isoluminant (17 cd/m2). Target

position, target-defining dimension (color, shape), and orientation of the stripes inside the target stimulus (horizontal, vertical) were randomized across trials.

Procedure

Participants were seated in a dimly lit, sound-attenuated, and electrically shielded cabin (IAC). They viewed the stimuli from a distance of approximately 65 cm on a 17" CRT monitor (1280 x 1024 pixels resolution; 100-Hz refresh rate). To control for task proficiency, all participants took part in a practice session some 5–10 days before the EEG session. They performed two to four practice blocks of trials until they achieved a minimum of 90% correct responses and a mean reaction time below 1000 ms. Participants who were unable to reach these criteria were not admitted to the EEG experiment (1 of 40 participants). The EEG experiment consisted of 12 experimental blocks of 72 trials each. A trial started with a white fixation cross presented centrally for 500 ms, followed by the search display presented for 200 ms. The following blank display was terminated by the participant's response or after a maximum (time-out) duration of 2000 ms. The subsequent intertrial interval, during which a central white fixation cross was presented, lasted randomly 950, 1000, or 1050 ms. Participants were instructed to maintain central eye fixation throughout the experiment. They were asked to produce a speeded 2-alternative-forced-choice response indicating the orientation, horizontal vs. vertical, of the singleton target's stripes. In case of an incorrect response or a response latency longer than 2000 ms, the word 'FALSCH' (German word for 'INCORRECT') appeared centrally for 1000 ms. Participants responded ('vertical' or 'horizontal') by mouse button press, using their left or their right thumb, respectively. Initial orientation to mouse button assignments were counterbalanced across participants and reversed for each participant after the first experimental half (6 blocks, 72 trials each). To ensure correct S-R mapping, participants performed at least one practice block prior to the start of each experimental half. Participants were instructed to maintain a reasonably low error

rate, of 5% to 10% errors. This was done to ensure similar error rates across the two age groups, that is, to rule out differential response criteria and speed-accuracy trade-offs, which could have had an influence on RT and ERP patterns especially in the older adults (Rinkenauer et al., 2004; Wild-Wall et al., 2008). After each block, participants received feedback about their mean response accuracy and mean RTs.

EEG data acquisition

The EEG was continuously digitized from 64 active Ag/AgCl electrodes (actiCap System, Brain Products, Munich) at 1 KHz. Electrodes were mounted on an elastic cap (Easy Cap, FMS, Munich, Germany), placed according to the International 10/10 system (American Electroencephalographic Society, 1994). All electrophysiological signals were referenced to FCz and re-referenced off-line to averaged mastoids. Horizontal eye movements were recorded by means of electrodes F9 and F10 and vertical eye movements were recorded from Fp1 and an electrode placed beneath the left eye. EEG and electrooculogram were amplified by BrainAmp amplifiers (BrainProducts) using a 0.1–250-Hz bandpass, and filtered off-line using a 0.5-Hz high-pass filter (Butterworth zero phase, 24 dB/Octave). Next, the EEG data was visually inspected in order to detect and manually remove epochs of non-stereotypical artifacts. This was followed by an Infomax Independent Component Analysis, as implemented in the Brain Vision Analyzer software (BrainProducts, Munich), run to identify and back-transform ocular artifacts (blinks and horizontal eye movements) before the EEG was segmented into stimulus-locked (see PCN, SPCN, and sLRP analyses below) and response-locked epochs (see rLRP analysis below). Trials involving incorrect behavioral responses or artifacts – defined as any signals exceeding ± 60 µV on any electrode, ± 30 µV on electrodes F9 and F10, bursts of electromyographic (permitted maximal voltage steps/sampling point of 50 µV) – were excluded from the averages.

For the PCN and SPCN analyses, EEG was averaged starting 200 ms prior to the onset

of the target display until 600 ms post display onset, baseline corrected based on the 200-ms pre-stimulus period. The components were quantified by subtracting ERPs at electrodes PO7/PO8 ipsilateral to the side of the target in the search array from the contralateral ERPs. The PCN latencies were determined as the maximum negative deflection within the 170–320-ms time window post-stimulus. Analyses of the SPCN were conducted on mean amplitudes for the 350–600 ms post-stimulus interval.

For the LRP analysis, stimulus- and response-locked waveforms were extracted from the EEG data by subtracting ERPs at electrodes C3/C4 ipsilateral to the side of uni-manual hand responses from contralateral ERPs. Stimulus-locked waveforms were epoched into 800-ms segments following the onset of the search display, relative to a 200-ms prestimulus baseline. Response-locked LRPs were extracted by segmenting waveforms from 800 ms before to 200 ms after response onset. Onset latencies of sLRP and rLRP were determined according to Ulrich and Miller's (2001; see also Miller et al., 1998) jackknife-based scoring method, defining LRP onset as the point in time at which the amplitude reaches a specific criterion relative to the baseline period. As suggested by Miller et al. (1998), we used 50% for sLRPs and 90% for rLRPs as optimal criteria to determine the onset latencies. Amplitudes of rLRPs were defined as averaging five sample points before and after the maximum deflection obtained in the time window 100–20 ms before response onset.

Statistical analyses

Behavioral data and ERP components were examined using the same statistical analyses. For ERP and RT analyses, we excluded trials on which observers made an incorrect response and trials on which the RT was excessively low (< 200 ms) or high (> 1200 ms). We excluded trials with RTs more than ±2.0 standard deviations from each participant's condition mean. To control for overall age-related slowing effects, we examined individually z-transformed RTs (Faust et al., 1999). In this analysis, for each individual, the overall mean

was subtracted of each condition's mean, and divided by the standard deviation of the condition means; these z-scores then entered the ANOVAs. This z-transformation rescales the differences between conditions relative to each individual's performance and eliminates mean differences in RT between individuals, including age-related differences.

Analyses of variance (ANOVAs) were used for all statistical tests and all probability values were adjusted applying the Greenhouse-Geisser epsilon correction for nonsphericity (Jennings & Wood, 1976) whenever appropriate. Behavioral data and ERP waveforms were subjected to three-way ANOVAs with the between-subject factor Age (younger, older) and the within-subject factors Dimension Change (same, different) and Response Change (same, different). The magnitudes of potential PRCs were examined by calculating the difference between the mean for partial repetitions [same dimension and different response (sDdR), or vice versa, different dimension and same response (dDsR)] and the mean for complete repetitions (sDsR) and complete changes (dDdR). Note that PRCs are immune to possible main effects of dimension or response changes (see Hommel et al., 2011). Age differences in PRCs were examined by planned dependent *t* tests comparing the magnitude of PRCs of younger and older adults.

2.1.4 Results

Behavior

Raw response times. The ANOVA on RTs showed that, in general, older participants responded more slowly than younger participants (703 vs. 566 ms) [main effect Age: $F(1,34) = 38.01$; $p<.001$]. Further, intertrial effects followed an interactive pattern, which varied with age [main effect Dimension Change: $F(1,34) = 15.96$; $p<.001$; Dimension Change * Response Change interaction: $F(1,34) = 72.05$; $p<.001$; Dimension Change * Response Change * Age interaction: $F(1,34) = 8.81$; $p<.01$]. In particular, the PRC pattern – characterized by lower RTs on trials on which both the dimension and response were repeated (sDsR) or both

attributes changed (dDdR), and higher RTs on trials on which only one attribute changed (sDdR, dDsR) – was more pronounced for older participants [t(34) = -2.10; p<.05)] (Figure 2.3).

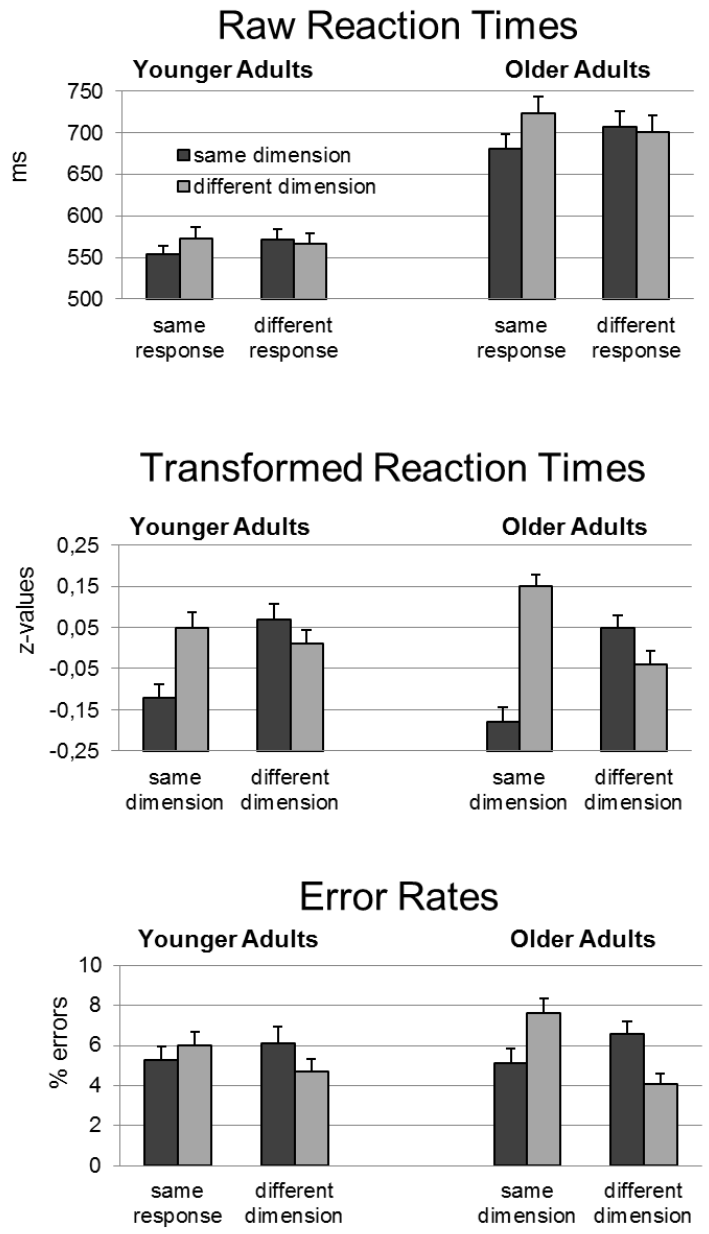

Figure 2.3: Behavioral data.
Raw response times (upper panel), z-transformed response times (central panel), and error rates (lower panel) as a function of the target-defining dimension and the motor response on the previous trial, for younger and for older adults. Error bars indicate standard error of the means.

Standardized response times. The ANOVA on transformed RT data revealed similar effects as the analysis of the raw RTs [main effect Dimension Change: F(1,34) = 17.19;

p<.005; interaction Dimension Change * Response Change: F(1,34) = 69.89; p<.001; Dimension Change * Response Change * Age interaction: F(1,34) = 4.55; p<.05], but no main effect of age [F(1,34) = 0.89]. Importantly, however, the PRCs were revealed to be larger in older than in younger adults in the transformed data, too [t(34) = -2.13; p<.05)] – demonstrating that the increase in PRCs with age was not simply a concomitant effect of the general age-related slowing.

Error rates. Similar to the RTs, error rates varied as function of the attributes of the target on the previous trial and of age [Dimension Change * Response Change interaction: F(1,34) = 31.51; p<.001; Dimension Change * Response Change * Age interaction: F(1,34) = 5.37; p<.05]. Again, PRCs in terms of error rates – that is, the increase in error rates for partial- vs. complete-repetition trials – were more marked for older participants [t(34) = -2.32; p<.05] (Figure 2.3). Given that the overall error rates did not differ between younger and older participants (p=.67) and that the error rates and RTs showed a similar pattern overall, the reported effects are not attributable to speed-accuracy trade-offs.

Electrophysiology

PCN. For both age groups, a solid PCN was triggered in all conditions (sDsR, sDdR, dDsR, dDdR) – as can be seen from more negative- (i.e., less positive-) going deflections over contra- compared with ipsilateral parieto-occipital sites (PO7/PO8) relative to the side of the target. Comparison of the waveforms shows that, while the PCN was equally pronounced in both age groups, it was markedly delayed in older compared with younger adults (262 vs. 233 ms) [main effect Age: F(1,34) = 26.17; p<.001]. Furthermore, independent of the observers' age, the PCN latencies were shorter when the target-defining dimension was repeated across trials (sDsR, sDdR: 240 ms) compared with when it changed (dDsR, dDdR: 254 ms) [main effect Dimension Change: F(1,34) = 81.48; p<.001]. Accordingly, PRCs did not affect PCN latencies [t(35) = - .62; p=.54] and did not differ between age groups [t(34) = -.21; p=.83]

(Figure 2.4).

SPCN. A sustained lateralized activity followed the PCN component in both age groups, though it appeared to rise later and to be less pronounced in older adults (Figure 2.4). Given the clearly visible age differences in time course, we included the factor Time Window (350–400 ms, 400–450 ms, 450–500 ms, 500–550 ms, 550–600 ms) in the ANOVA of the SPCN amplitudes, besides the standard factors Age, Dimension Change, and Response Change. This analysis revealed the SPCN to differ between age groups in terms of both time course and intertrial effects [main effect Age: $F(1,34) = 8.12$; $p<.01$; Time Window * Age interaction: $F(4, 136) = 5.29$; $p<.001$; Dimension Change * Response Change * Age interaction: $F(1,34) = 4.23$; $p<.05$; Time Window * Dimension Change * Response Change * Age interaction: $F(4,136) = 3.57$; $p<.01$]. The SPCN amplitudes were significantly reduced for older adults in all conditions for early time windows (350-400 ms, 400–450 ms, 450–500 ms; all $t(34) > 1.69$; $p<.05$), but not the later windows (500–550 ms, 550–600; all $t(34) < 1.69$; $p>.05$). Given these age differences in time course, we conducted follow-up ANOVAs on adjusted time windows (each 150 ms in length) within which the SPCN deflection was maximal: 350–500 ms for younger and 450–600 ms for older adults. An ANOVA with the standard factors Age, Dimension Change, and Response Change revealed the three-way interaction to be significant. The SPCN was overall more pronounced for younger than for older adults and differentially modulated by intertrial effects between the two age groups [main effect Age: $F(1,34) = 6.46$; $p<.05$; Dimension Change * Response Change * Age interaction: $F(1,34) = 5.00$; $p<.05$]. With respect to PRCs, we found the SPCN to be enhanced for partial repetition trials (sDdR, dDsR), compared with complete repetition/change trials (sDsR, dDdR), only in younger adults [$t(17) = -2.26$; $p<.05$] (Figure 2.4). In older adults, by contrast, no such difference between complete- and partial-repetition trials was evident [$t(17) = 0.32$; $p=.75$]. This differential pattern manifested in significant differences in the PRC magnitudes between the two age groups [$t(34) = -2.24$; $p<.05$], in this case, characterized by

larger PRCs in the younger, compared with the older, group.

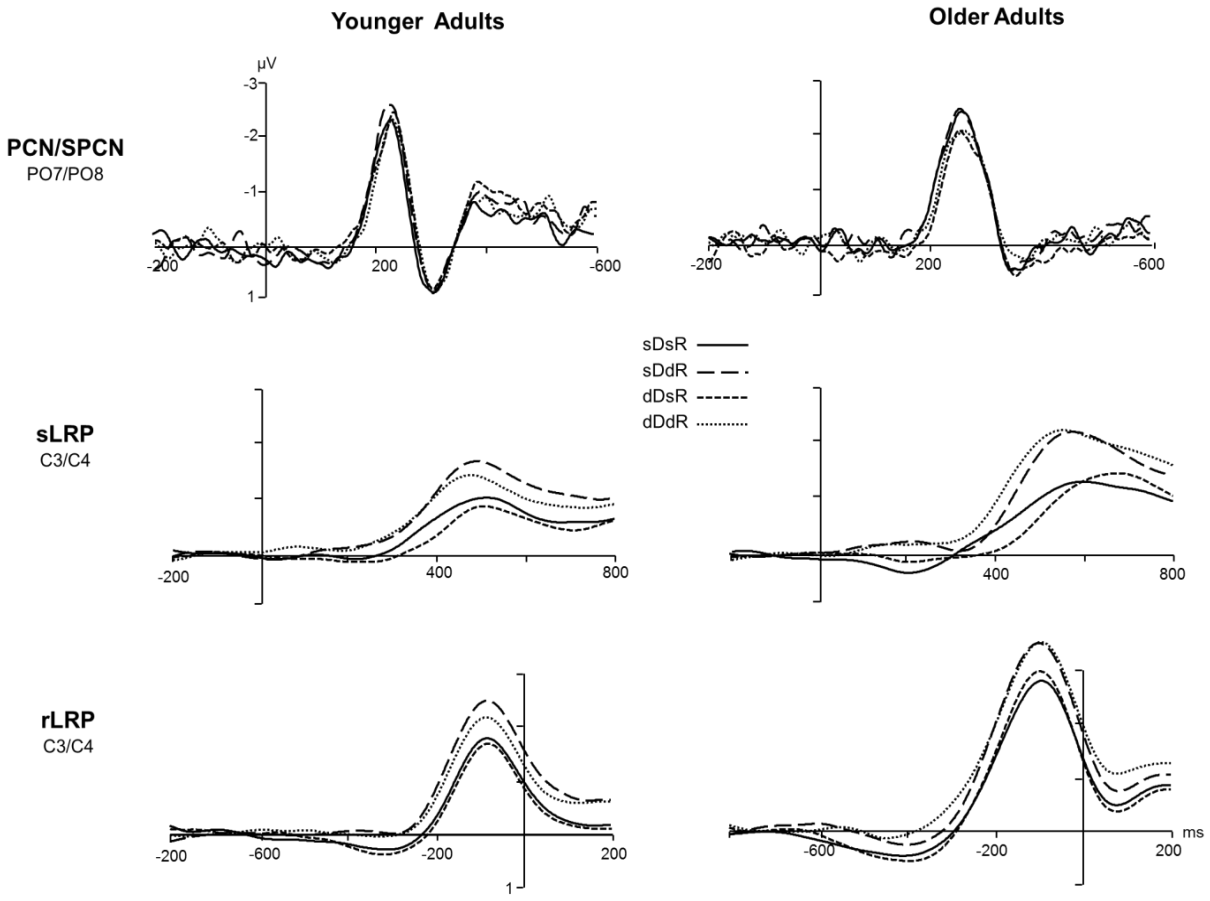

Figure 2.4: Electrophysiological data.
Grand averaged ERP difference waveforms as a function of the target-defining dimension and the motor response on the previous trial, for younger (left panels) and for older participants (right panels). *Upper row*: PCN/SPCN difference waves elicited in the 600-ms interval following stimulus onset at electrode positions PO7/PO8. *Central row*: sLRP difference waves elicited in the 800-ms interval following stimulus onset at electrode positions C3/C4. *Lower row*: rLRP difference waves elicited in the 800-ms interval prior to response onset at electrode positions C3/C4.

Stimulus-locked LRP. Motor-related lateralization (C3/C4), with stronger negativity over areas contralateral versus ipsilateral to the side of the required uni-manual response, was clearly evident in both age groups. For the sLRP, the difference waves were overall prolonged (375 vs. 449 ms) for older compared with younger adults [main effects Age: $F(1,34) = 12.66$; $p<.001$]. Note that this latency difference was substantially larger than that observed for the PCN (29 ms; see above). Furthermore, for both age groups, the sLRP onset latencies were modulated by an interaction of the previous target's dimensional and response attributes (Fig.

4) [main effect Dimension Change: $F(1,34) = 3.88$; $p<.05$; main effect Response Change: $F(1,34) = 8.40$; $p<.001$; interaction Dimension Change * Response Change: $F(1,34) = 26.31$; $p<.001$], reflecting that sLRP onsets were delayed in partial repetition trials (sDdR, dDsR), compared with complete repetition/change trials (sDsR, dDdR), in both younger adults [$t(17) = -2.61$; $p<.01$] and older adults [$t(17) = -4.67$; $p<.001$]. Based on our hypothesis, we further examined age differences in PRCs (in terms of prolonged sLRP onset latencies), even though the Age x PRC interaction did not reach statistical significance. Post-Hoc analyses revealed only a trend [$t(34) = -1.52$; $p=.07$], suggestive of PRCs being more pronounced in older than in younger adults (50 vs. 29 ms).

Response-locked LRP. The rLRP was more pronounced (-3,2 vs. -2,2 µV) and prolonged (relative to response onset) for older than younger participants (-137 vs. -116 ms) [main effects of Age on latencies: $F(1,34) = 4.35$; $p<.05$, and on amplitudes: $F(1,34) = 8.96$; $p=.005$]. Moreover, in both age groups, a change in the motor response across trials caused a prolonged and more negative-going deflection compared with a response repetition [main effect Response Change on latencies: $F(1,34) = 4.8$; $p<.05$, and amplitudes: $F(1,34) = 39.54$; $p<.001$]. In contrast to the SPCN and sLRP components, no interactions of the factors Age, Dimension Change, and Response Change were obtained for the rLRP. Accordingly, PRCs did not differ between age groups [latencies: $t(34) = 1.11$; $p=.14$; amplitudes $t(34) = -.04$; $p=.97$] and did not modulate rLRP onset latencies [$t(35) = -.18$; $p=.42$] and amplitudes [$t(35) = -.99$; $p=.33$] at all (Figure 2.4).

2.1.5 Discussion

The present study was designed to examine age-related changes in visual search by a combined analysis of behavioral RTs and lateralized ERP components recorded while younger and older participants performed a compound-search task. There was a marked general effect of age on behavioral response speed, in line with previous visual search studies

(e.g., Hommel et al., 2004; Madden et al., 2004). Our results show that this RT cost is associated with age differences at all dissociable sub-stages of processing, in particular: preattentive perception, post-selective perception, response selection, and response production. This is indicative of a general, non-specific factor of aging being responsible for the slowing of multiple processes within task performance, as expected on 'one-dimensional' accounts of cognitive aging (e.g., Brinley, 1965; Cerella, 1994). However, our analyses of intertrial effects revealed a specific age deficit in the re-mapping of S-R associations across consecutive trials. This finding indicates that a comprehensive picture of cognitive aging includes predominant age decrements in more executively controlled processes, in addition to a generalized slowing of cognitive processing (e.g., Reuter-Lorenz & Park, 2010) (Figure 2.2).

Preserved dimension and response weighting in older age

Older participants showed considerably longer PCN latencies (on average 29 ms) compared with younger participants, adding further evidence that older adults require generally more time to focally select task-relevant target objects in visual space (Lorenzo-Lopez et al., 2008). However, similar to the younger adults in the present and previous studies (Töllner et al., 2008, 2010), repetitions (vs. changes) of the target-defining dimension (for feature-repetition effects, see Mazza et al., 2009) across trials were associated with shorter PCN latencies and faster RTs also in older adults. Thus, our results show that implicit attentional guidance based on primed or weighted target attributes (Fecteau & Munoz, 2003; Found & Müller, 1996; Gramann et al., 2007, 2010; Maljkovic & Nakayama, 1994, 2000) – resulting in faster allocation of attention – operates independently of age. Given this, our results complement previous behavioral findings (Kumada & Hibi; 2004; McCarley et al., 2004; Rybash, 1996) by providing electrophysiological evidence of preserved implicit memory guidance in older age.

Similarly, a global effect of age-related slowing but spared intertrial response repetition facilitation was found in the rLRP. Older compared with younger participants displayed enhanced and prolonged rLRPs in all conditions, showing that older adults need more time to execute the response after completion of response selection. Similar changes have been observed in a variety of tasks and are indicative of a general dysregulation of motor-response production in older adults, requiring stronger and temporally extended activations of the contralateral motor cortex for executing a selected response (Falkenstein et al., 2006; Wild-Wall et al., 2008; Yordanova et al., 2004). However, response changes (vs. repetitions) across trials enhanced and prolonged rLRPs in a similar manner for both age groups (replicating the Töllner et al.'s, 2008, results for younger adults in older adults). Crucially, this indicates that for older as well as for younger adults, response changes required additional motor activation and time-consuming (cross-hemisphere) shifting processes in order to reach the threshold for activating and executing the response. Accordingly, response repetition facilitation at the stage of motor-response execution is not subject to age-related decline.

Together, the PCN and rLRP results clearly demonstrate that facilitation of performance by repetition of a previously critical (target-defining) dimension or, respectively, a previously executed action, which are likely to operate via relatively direct, automatic pathways, remains largely unimpaired during aging. This corroborates findings from brain imaging studies showing that reductions in neural activity associated with repetition facilitation are preserved in older age (Lustig & Buckner, 2004; Soldan et al., 2008).

Age-related decline in stimulus-response re-mapping

Despite the statistical independence of dimension and response changes across trials in our compound-search task, the behavioral results indicate that the cognitive processes associated with dimension and response changes do not operate independently. Rather, they

are interdependent, and this dependency becomes more marked with age. Replicating findings on younger adults (e.g., Pollmann et al., 2006; Töllner et al., 2008), we observed behavioral RTs to follow an interactive pattern: there was repetition facilitation only if both target- and response-defining attributes remained the same across trials. By contrast, PRCs were evident when only one attribute was repeated from the previous trial while the other one changed, compared with complete repetitions or changes (e.g., Lamy et al., 2010; Müller & Krummenacher, 2006). As we expected, the behavioral PRCs were more pronounced in older compared with younger adults. This new result confirms our idea that older adults' performance is characterized by an increased 'stickiness' to previously established S-R mappings, that is: their performance is more reliant on (implicit) expectations of a constancy of the S-R mapping, and/or they show a reduced flexibility in breaking up an established S-R association and re-link a changed response to a repeated dimension or a changed dimension to a repeated response across consecutive trials.

As hypothesized, this age-dependent decrement in S-R re-mapping was associated with changes in lateralized ERPs related to processing stages intermediate between preattentive perceptual target processing and motor response execution. First of all, the SPCN component – which is likely to reflect in-depth analysis of the response-critical target information following target selection (i.e., in the present experiment, the orientation of the stripes) in vSTM (e.g, Eimer and Kiss, 2010; Hilimire et al., 2011; Mazza et al., 2007, 2009) – was flattened and ascended later in older compared with younger adults. This result corroborates findings of SPCN amplitudes being reduced with age in change detection paradigms, especially in earlier time windows (Jost et al., 2010; Sander et al., 2011), and might reflect the well-established reduction of vSTM capacity in older age (e.g., Cowan et al., 2006). Furthermore, the slower rise of SPCN activity displayed by older adults in the present experiment suggests that perceptual analysis of the selected stimulus in vSTM is impeded by delayed, and/or less efficient, attentional selection of the target in the first instance (Gazzaley

et al., 2008; Jost et al., 2010; Sander et al., 2011), as also indicated by the age effects on PCN latencies that we established. However, as amplitudes are not directly related to speed of processing, caution is advised in inferring a contribution from hampered post-selective processes of target analysis to age-related slowing. Nevertheless, the observed SPCN amplitude modulation may at least in part account for the age-related increase in PRCs evident in the RTs as well as in the error rates. For younger adults, the SPCN amplitude was enhanced on partial-repetition, compared with complete-repetition, trials. Although, admittedly, there is as yet no definite functional interpretation of the SPCN in visual search (Hilimire et al., 2011; Mazza et al., 2007), we cautiously interpret this pattern as suggesting that more vSTM resources are required for in-depth analysis of the selected stimulus if previously linked target- and response-defining attributes change across trials (see discussion below). Critically, we further observed that this SPCN modulation by changes of associated stimulus- and response-defining target features does change with age: for the older participants, intertrial effects had virtually no effect at all on SPCN amplitudes, which is in contrast to the pattern displayed by the younger adults. Combined with the finding that older adults show enhanced PRCs, this suggests that, in younger adults, the re-mapping of S-R associations benefits from an increased availability of processing resources on post-selective perceptual stages.

Furthermore, we found overall age-related changes in the sLRPs: older adults showed a substantial delay in the sLRP onset latencies, which was much more marked than the delay they exhibited in the preceding PCN. This pattern indicates that, over and above a slowing in perceptual processing, older adults also needed more time for deciding upon the appropriate response to the selected (target) stimulus. The present results concur with the idea that this slowing of response selection results from impaired visuo-motor transmission due to age-related loss in brain connectivity (Van der Lubbe & Verleger, 2002), especially under conditions in which response selection is based on detailed analysis of stimulus features. In

addition to this general age-related slowing, there was a trend for partial (vs. complete) repetitions/changes to prolong sLRP latencies more for older than for younger adults. This suggests that, besides deficient processing on post-selective perceptual stages, part of the increased PRCs in older age appear to arise on stages involved in response selection. In older, compared with younger, adults, the initiation of a repeated motor response might have been particularly difficult under conditions that required the re-setting of dimensional weights from the previous to the current selection-relevant dimension. Additionally, the initiation of a changed motor response seems to be especially difficult following the selection of a target that was defined within the same dimension as that on the previous trial, thus reinforcing the dimensional weight setting. This interpretation is more general in line with previous aging studies that adopted paradigms traditionally used to study executive control. For instance, in task-switching paradigms, the disproportional increase of switch costs in older age was assumed to arise from the predominant age-related decline in executive functions governing constant updating of internal control settings, and, specifically, deficient reconfiguration of S-R assignments across trial episodes (Mayr, 2001; Wasylyshyn et al., 2011). Correspondingly, ERP studies that employed tasks assumed to influence S-R re-mappings across trials (see Hommel, 2004), such as the Eriksen Flanker and Simon tasks, also reported prolonged sLRPs in older compared with younger participants (Van der Lubbe & Verleger, 2002; Wild-Wall et al., 2008). It is likely that the inherent PRCs in this task provoked the differential age-related decline in response selection processes (e.g., Castel et al., 2007). By contrast, no age differences in the sLRP onset were found in simple visual selection tasks (Falkenstein et al., 2006; Yordanova et al., 2004).

Finally, several accounts have been proposed to explain PRCs in younger adults, which all share the assumption that the human system implicitly assumes, or builds up, a linkage between two or more attributes on a given trial, even if this contravenes the actual event statistics (e.g., Müller & Krummenacher, 2006; Töllner et al., 2008). Such associations

(between target-defining dimension and response-defining feature), possibly stored as 'linked expectancies' or higher-level memory representations, may be automatically retrieved when participants are subsequently encountering one or more of the previously bound attributes (Hillstrom, 2000; Hommel, 2004; Huang et al., 2004; Kingstone, 1992). In contrast, when one of the previous trial's attributes changes while the other one is repeated, the previously established binding is found to be contravened and a new one has to be actively (re-) configured, which results in PRCs. The present findings indicate that, in older adults, the cognitive system is especially hampered by such inconsistencies, as it is set to 'prefer' a change of both attributes to a change of just one across trials. Accordingly, dealing with partial repetitions would require increased involvement of higher-order functions, such as inhibition and cognitive flexibility. These are core functions of the executive system that are known to be particularly vulnerable to age-related decline (e.g., Park, 2000). Thus, in the present experiment, reduced flexibility in the older participants may have impeded processes involved in the un-binding of previously established S-R associations and the (re-)formation of a new association. Presumably, this is related to predominant age-dependent changes in frontal and parietal brain structures (e.g., Grady, 2008) affecting parts of the fronto-parietal attentional network that underlies S-R (re-)mapping across trials (Pollmann et al., 2006). Similar to our interpretation, it has been suggested that poorer executive control in individuals with lower, compared with higher, fluid intelligence (Colzato et al., 2006) and of older, compared with younger, age compromises the ability to flexibly handle episodic events that involve the binding of perceptual and response features, resulting in increased PRCs in such individuals (Hommel et al., 2011).

2.1.6 Conclusions

In conclusion, the present findings show that age-related slowing originates from several processing stages in visual search, which accrue to result in the final behavioral output

slowing. However, our findings also demonstrate that one-dimensional accounts – on which slowing is attributable to a general, non-specific factor of aging (e.g., Brinley, 1965; Cerella, 1994) – are insufficient. As revealed by our intertrial analyses, older adults' performance was particularly affected when the S-R mapping did change across trials. This is probably due to predominant age-related decline in executive functions, such as inhibition of the automatic reactivation of the previously encountered S-R association and controlled re-mapping of the current S-R association. Given this, our results lend support to recent models of neuro-cognitive aging proposing that general as well as specific factors jointly contribute to cognitive changes in aging (e.g., Reuter-Lorenz & Park, 2010).

Author contributions

I.W., K.F., and T.T. designed the study, based on experimental procedures formerly designed by T.T.. I.W. programmed and conducted the experiment, analyzed the data, and wrote the paper. K.F., H. J.M., and T.T. commented and revised the manuscript.

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III. Neural markers of individual and age differences in attentional capacity parameters

Wiegand, I., Töllner, T., Habekost, T., Dyrholm, M., Müller, H. J., & Finke, K. (under review). Distinct neural markers of TVA-based visual processing speed and short-term storage capacity parameters.

Manuscript under review.

Wiegand, I., Töllner, T., Dyrholm, M., Müller, H. J., & Finke, K. (in preparation). Neural markers of age-related decline and reserve in visual processing speed and visual short-term memory storage capacity.

Manuscript in preparation.

3.1 Distinct neural markers of TVA-based visual processing speed and short-term storage capacity parameters

3.1.1 Abstract

According to the Neural Theory of Visual Attention (NTVA; Bundesen et al., 2005, 2011), an individual's attentional capacity is characterized by two parameters that reflect distinct brain mechanisms: visual perceptual processing speed *C* (rate of object categorization) and visual short-term memory (vSTM) storage capacity *K* (maximum number of objects). Estimates of these parameters can be obtained from mathematical modeling of performance in a whole report task. Using an interindividual difference approach, the present study was designed to establish the respective ERP correlates of these two parameters. Participants with higher as compared to lower processing speed were found to show significantly smaller visual N1 responses, indicative of higher efficiency in early visual processing. By contrast, for participants with higher as compared to lower vSTM storage capacity, contralateral delay activity over visual areas was enhanced while overall non-lateralized delay activity was reduced, indicating that holding (the maximum number of) items in vSTM relies on topographically specific sustained activation within the visual system. Taken together, our findings show that the two main aspects of visual attentional capacity are reflected in separable neurophysiological markers, validating a central assumption of NTVA.

3.1.2 Introduction

Interindividual differences across a broad range of different tasks have been suggested to reflect variations in a set of fundamental abilities or processing resources (e.g., Spearman, 1904; Vernon, 1983). In the visual system, two such key functions jointly determine an individual's capacity for processing information: First, visual processing speed, the amount of visual information that can be processed within a certain time (Deary et al., 2010; Duncan et al., 1999). Second, the capacity limit of visual short-term memory (vSTM), the maximum number of objects that can be perceived at one point in time (Cowan, 2001; Sperling, 1960).

The Theory of Visual Attention (TVA, Bundesen, 1990) provides a mathematical framework for disentangling these general capacity parameters. A unique feature of TVA is the explicit modeling of the parameters visual processing speed *C* and visual short-term memory (vSTM) storage capacity *K*. The theory's neural interpretation (NTVA; Bundesen et al., 2005, 2011) further suggests distinct brain mechanisms underlying the two components. In close relation to the biased competition model of Desimone and Duncan (1995), (N)TVA assumes a race among objects in the visual field that are processed in parallel and compete for selection. An individual encountering multiple visual elements will encode up to *K* objects into vSTM in the order of which they complete processing. The speed of visual categorizations[2] is determined by both the sensory strength of competing objects and attentional biases of the observer. At the single-cell level, encoding speed is assumed to be proportional to both the number and firing rates of neurons that code for specific features of the objects in the visual field. In contrast, the number of objects stored in vSTM depends on activity in neurons coding the *K* 'winner' elements that are sustained via recurrent thalamo-cortical feedback loops (Bundesen et al., 2005).

TVA-based assessment permits the quantification of these parameters for a particular individual using the simple psychophysical 'whole report' task. The procedure yields

[2] In TVA, the categorization of an object is synonymous to its encoding into vSTM

mathematically independent estimates of the two functional components by modeling the amount of information that can be consciously perceived and reported from a briefly presented visual display as a function of exposure duration[3]. Empirically, however, *C* and *K* typically correlate moderately across individuals (e.g., Finke et al., 2005; Habekost & Starrfelt, 2009). This indicates that both parameters might be influenced by a shared general cognitive efficiency factor (perhaps related to intelligence), but it also implies that they reflect distinct processing components to a certain extent. Psychophysical, pharmacological, and patient studies support this functional separability. First, enhancement of phasic alertness by the use of warning cues has been shown to influence processing speed *C*, but not storage capacity *K* (Matthias et al., 2010). Second, the psychostimulant methylphenidate enhances processing speed (Finke et al., 2010), the cholinergic neurotransmitter nicotine slows processing speed (Vangkilde et al., 2011), whereas storage capacity is not affected by either drug. Finally, behavioral TVA-based assessment of different patient groups has revealed a double dissociation: While adult dyslexics exhibited a significantly reduced processing speed but a preserved storage capacity compared to normal matched individuals (Stenneken et al., 2011), the reverse pattern was found in adult attention deficit hyperactivity disorder patients, who displayed a deficit in storage capacity with preserved processing speed (Finke et al., 2011). However, in patients with circumscribed acquired brain lesions, reductions of processing speed and storage capacity typically co-occur (Bublak et al., 2005; Duncan et al., 2003). This covariance indicates that the two functions depend on partly overlapping neural structures that probably include areas in the extrastriate, parietal, and frontal cortices as well as the basal ganglia (Habekost & Starrfelt, 2009). Lesion size might be a critical confounding factor here, with larger lesions increasing the probability of impairments in both components (Peers et al., 2005).

[3] A detailed formal description of the equations can be found in Bundesen (1990).

A more appropriate way to disentangle distinct brain processes underlying the two components might be the examination of healthy individuals' brain activity measured while they are performing a visual attention task. In particular, it has been argued that assumptions about basic parameters of attention and working memory may be validated by an individual-difference approach establishing associations and dissociations between cognitive measures and neurophysiological measures (Vogel & Awh, 2008; Rypma & Prabhakarank, 2009). Such neurophysiological indices could be identified by means of event-related potentials (ERPs). ERPs have been proven to provide online markers of multiple independent but overlapping subcomponents of cognition engaged in one task (Luck, 2005). Recently, based on their reliability across repeated measurements and tasks, ERPs have even been designated as neuronal trait markers of individual cognitive abilities (Cassidy et al., 2012).

To identify potential correlates of the attention capacity parameters postulated by NTVA, we focus on ERP components that are already established as neural markers of cognitive operations involved in visual attention and vSTM processing. The early visual P1 and N1 are candidate components for depicting individual differences in the visual processing speed parameter. Their amplitudes are enhanced when selective attention is directed to a visual stimulus (e.g., Heinze et al., 1990; Hillyard et al., 1998; Luck et al., 1990). The P1 attention effect is associated with enhanced sensory stimulus coding (Gramann et al., 2010; Johannes et al., 1995). In addition to this, N1 amplitudes have been suggested to index attention-related facilitation of object identification (Vogel & Luck, 2000). In within-subject designs, the N1 increases with increasing difficulty of visual discriminations (Kiefer, 2001; Tanaka et al., 1999). Given this, we hypothesize that under task conditions with controlled (constant) levels of difficulty, amplitudes of early visual components reflect the relative amount of an individual's limited attentional resources required for object discrimination. In accordance with TVA, this efficiency of resource allocation determines the rate of

information uptake expressed in parameter *C* (Bundesen & Habekost, 2008)[4]. In attempting to identify electrophysiological correlates of the individual storage capacity *K*, we focused on 'delay activity' (McCollough et al., 2007) subsequent to stimulus presentation. The overall delay activity is assumed to reflect vSTM maintenance as well as more general, non-mnemonic processes, such as arousal or response preparation; that is, its amplitude has been related to the general amount of resources required to retain visual information (LaBerge, 1997; Mecklinger & Pfeiffer, 1996; Rushkin et al., 1995). Processes more directly related to vSTM storage can be isolated in tasks with lateralized presentation of to-be-attended (and stored) information in bilateral stimulus arrays (Klaver et al., 1999). Calculating the difference between activity contra- and ipsilateral to the attended hemifield cancels out the task-general activity (Gratton, 1998). The amplitude of the resulting difference wave, the Contralateral Delay Activity (CDA: Vogel & Machizawa, 2004; also referred to as Sustained Posterior Contralateral Negativity, SPCN: Jolicoeur et al., 2006), systematically increases with the number of objects that have to be maintained and level off when the individual vSTM capacity limit is reached. This sensitivity to interindividual differences qualifies the CDA as a potential correlate of TVA parameter storage capacity *K*. Furthermore, recent studies have revealed a CDA in other visual attention tasks requiring vSTM, such as attentional blink (Jolicoeur et al., 2006) and visual search (Perron et al., 2009; Wiegand et al., 2013), suggesting that the component might mark the latent storage capacity limit underlying visual operations in various tasks.

[4] It should be noted that this definition of processing speed is at variance with previous ERP approaches which rather focused either on the point in time at which the waveforms of two conditions start to differ in an component-independent manner (e.g., Thorpe et al., 1996), or on component timing differences (e.g., Töllner et al., 2011, 2012)

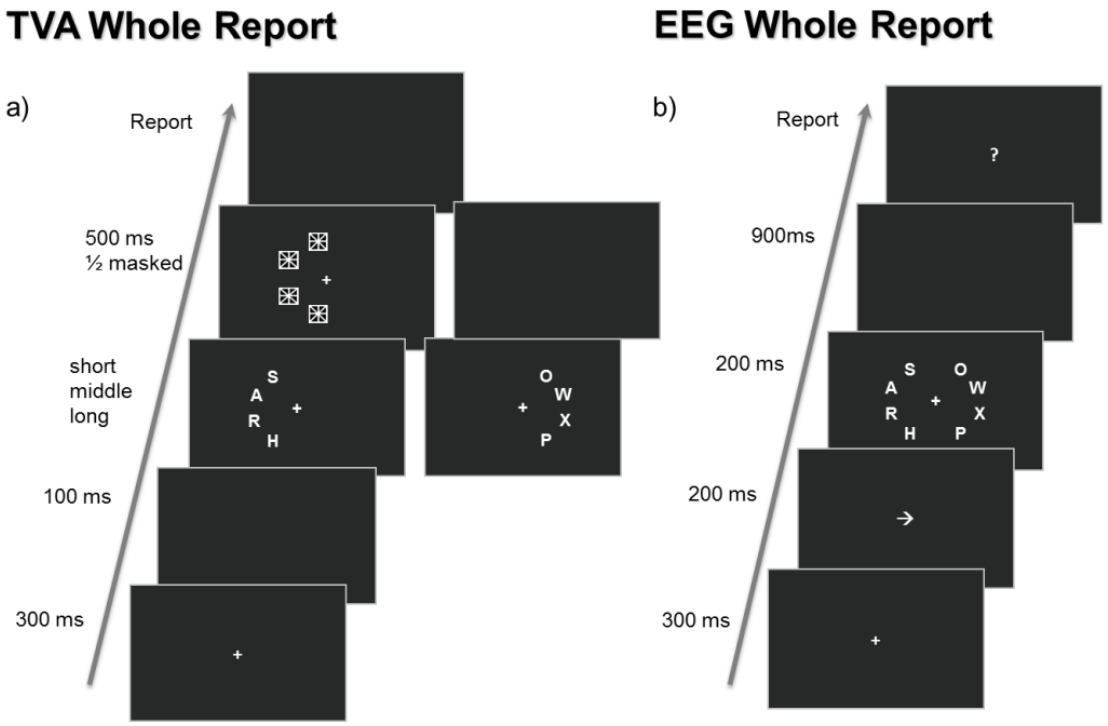

Figure 3.1: Experimental procedures.
a) Procedure used for TVA parameter assessment. Four equidistant letters arranged in a half circle were presented (randomly changing) either in green or red, and either on the left or right side of the display, for three different individually adjusted exposure durations. Letter arrays were masked in half of the trials. b) Procedure used for the EEG acquisition. On each trial, letters were presented for 200 ms on the left and the right of the fixation cross. The to-be-attended side was indicated by a central arrow pre-cue. Letters in one hemifield were green and those in the other hemifield red (randomly changing).

In the present study, we aim to test and validate the assumption of neurally distinct attentional capacity mechanisms by identifying electrophysiological correlates of visual processing speed *C* and storage capacity *K*. Using a standard behavioral whole report task (see Duncan et al., 1999; Finke et al., 2005), we assessed estimates of each participant's parameters. Letters were used as objects and the task was to report as many letters as possible per stimulus array. Additionally, we recorded the EEG of the same participant sample during a cued 'EEG whole report' task that allowed for analyses of lateralized and non-lateralized ERP components (Figure 3.1). In the EEG whole report, the task was to report as many letters as possible from the cued hemifield while ignoring the letters presented in the un-cued hemifield. Participants were assigned to groups based on a median split of their attentional parameter estimates derived from the standard behavioral procedure (Table 3.1).

Table 3.1: Descriptive statistics of parameter estimates**.**
Descriptive statistics of the TVA parameters *K* and *C*, for all participants and separately for high and low performers (based on a median split for parameters *K* and *C*, respectively), along with statistical tests of the high vs. low performer group differences.

	All Participants	High Performers	Low Performers	F-values*
K	Median (Range) 3.44 (2.31 – 3.84)	Mean 3.61	Mean 2.99	F(20,1) = 26.11 p < .001
C	Median (Range) 30.80 (17.53 – 90.04)	Mean 64.6	Mean 24.5	F(20,1) = 28.27 p < .001

* Group differences were examined by ANOVAs with the between-subject factor *C*-level (high vs. low processing speed) and *K*-level (high vs. low storage capacity).

We hypothesized that the ERP correlates of visual attention capacity parameters *C* and *K* would be specific in the sense that processing speed relates to amplitudes of early visual ERP components whereas storage capacity relates to CDA during maintenance after the perceptual stimulation had expired. The specificity of the ERP correlates of each parameter was tested by comparing amplitudes of the P1, N1, and delay activity of high and low performers with regard to visual processing speed *C* and storage capacity *K*, respectively. Furthermore, we tested the continuity of an identified relationship via correlation analyses of individual parameter values and ERP amplitudes across all participants.

3.1.3 Methods

Participants

Twenty-five right-handed healthy young volunteers, 13 of them female and 12 male, with a mean age of 25.9 years (SD: 3.01; range: 19-30) took part in the study. All participants had normal or corrected-to-normal vision, and none of them suffered from color blindness. The participants were naïve to the procedure of the TVA based experiments. Three participants were excluded from analyses due to systematic eye movements to the cue in the EEG-experiment. Written informed consent according to the Declaration of Helsinki II was

obtained from all participants. All participants received payment. The study was approved by the Ethics Committee of the Faculty of Psychology, LMU Munich.

Experimental Design

Setup and task. Participants completed two test sessions: first the standard TVA whole report and 5–10 days later the EEG whole report task (Figure 3.1). Daytime of testing, testing chamber, equipment, viewing distance, background and stimulus type, size, positions, and luminance were the same in both sessions. The PC-controlled tests were conducted in a dimly lit room with stimuli presented on a 17-inch monitor (1024 x 768 pixel screen resolution; 70 Hz refresh rate) and viewed at a distance of 65 cm. Participants were instructed to report as many letters as possible from a briefly presented array with four target letters. They were told to report only those target letters that they were fairly certain to have recognized. The verbal report was performed without stress on response speed. The experimenter entered the responses on the keyboard and started the next trial. Letters were chosen from a pre-specified set {ACEHJOPRSTWX}. Participants fixated on a central white cross (0.7° of visual angle in size) on a black background. Four letters (1.1° in size) appeared at positions on an imaginary circle with a radius of 2.5° of visual angle around central fixation.

Standard whole report procedure. Prior to the parameter assessment procedure, we identified the most appropriate individual exposure durations in a pre-test consisting of 24 masked trials. The presentation time at which a participant could report, on average, one letter per trial correctly (i.e., 25% report accuracy) was chosen as intermediate exposure duration, together with a shorter (half as long) and a longer (twice as long) exposure duration (mean intermediate exposure duration: 54.9 ms; range: 24–90 ms). In this way, we ensured maximum reliability of parameter estimation by obtaining a broad range of performance scores (dependent on exposure duration) for each individual, from around perceptual threshold to asymptotic vSTM storage performance. Note that the (variation in) exposure

durations provide(s) a means for optimal TVA based modeling of an individual's performance score, rather than being a determinant of the TVA parameters themselves.

In each trial, the fixation cross was presented for 300 ms, then a blank screen of 100 ms, then the letter array. The letter array consisted of four isoluminant letters, randomly chosen to be either red or green. All four letters were presented either on the left or the right side of central fixation. A given letter appeared only once in each trial display. In half of the trials, the letter array was followed by a mask with a duration of 500 ms at each stimulus location, which consisted of a square box outline filled with a '+' and an 'x' overlaid (1.2° in size) (Figure 3.1). Exposure durations were effectively prolonged in unmasked compared to masked conditions, owing to visual afterimage persistence (Sperling, 1960): The combination of the presence/absence of masks with three exposure durations (short, intermediate, long) resulted in six different 'effective' exposure durations. Exposure duration (short, intermediate, long), masking (masked, non-masked), and letter array hemifield (left, right) varied randomly, resulting in 12 conditions equally frequent across 6 blocks of 40 trials each. The first block consisted of 40 practice trials, and data were modeled based on the 200 remaining trials, including at least 16 trials of each condition.

Whole report procedure in the EEG experiment. In the EEG experiment, the classical whole report paradigm was adapted to be suitable for analyzing lateralized and non-lateralized ERP components. To ensure a balanced physical stimulation in both hemifields on each trial, we presented two letter arrays bilaterally, with the to-be-attended hemifield indicated by a 100% valid arrow pre-cue, with the cued side varying randomly from trial to trial (based on the classical lateralized vSTM paradigm, e.g., Vogel & Machizawa, 2004). The same letter was presented only once in a given trial display, either as to-be-reported target letters (cued hemifield), or as task-irrelevant filler letters (un-cued hemifield). To aid target letter selection (in face of the presentation of additional stimuli), target and filler letters were different in color, that is: either all target letters were green and all filler letters red, or vice versa, in a

randomly changing fashion. Each trial started with the central fixation cross presented for 100 ms, followed by the arrow cue for 200 ms. Then the letter array was presented for 200 ms (not masked). After a delay of 900 ms with a blank screen, a question mark appeared in the center, prompting the verbal report (Figure 3.1). After a practice block of 16 trials, EEG recording was started and a total of 240 trials were run.

Parameter Estimation

The accuracy of letter report as a function of effective exposure duration derived in the standard procedure was modeled according to TVA using a maximum likelihood fitting procedure (Kyllingsbæk, 2006; Dyrholm et al., 2011). The modeling was based on estimating four parameters defining the psychometric function depicted in Figure 3.2 (see also Bundesen, 1990): (1) parameter t_0, the minimal effective exposure duration (in ms) below which information uptake from the display is assumed to be zero; (2) parameter μ, the persistence of the visual afterimage on unmasked trials (i.e., effective exposure prolongation in ms, estimated from performance differences between unmasked and masked trials); (3) parameter *C*, the visual processing speed, the 'fixed capacity' sum of speed values across stimulus positions (estimated as number of elements processed per second); and (4) parameter *K*, the storage capacity (estimated as the expected value of the maximum number of elements that can possibly be represented simultaneously in vSTM). *C* reflects the slope of the exponential psychometric (growth) function at its origin t_0, and *K* reflects the asymptote of the function. In the current study, parameters t_0 and μ were mainly estimated in order to obtain valid estimates of the two parameters of focal interest, *C* and *K*. Estimates of t_0 and μ did not significantly differ between participants with higher and lower processing speed *C* and between participants with higher and lower storage capacity *K* [all $F<1.40$, $p>.25$].

An additional measure of top-down control, parameter α, defined as the fraction of processing capacity allocated to the fillers, was estimated by a further parameter fitting

procedure in which trials from the EEG session, in addition to trials from the standard experiment, were included in the model. A low α-value (close to zero) indicates a good ability to prioritize task-relevant objects in the processing. An α-value of zero would imply that the participant was able to use the spatial cue to completely 'filter out' the fillers. An α-value significantly higher than zero would indicate imperfect top-down control, with filler letters potentially interfering with the report of the cued target letters. We systematically examined, on the individual participant level, whether attentional resources were allocated to filler items by testing the significance of α (i.e., whether letters presented as fillers on the un-cued side in the EEG paradigm received a significant amount of attentional weighting) by means of Likelihood Ratio tests[5].

EEG data acquisition

The EEG was recorded from 64 active Ag/AgCl electrodes (actiCap System, Brain Products, Munich), placed according to the International 10/10 system (American Electroencephalographic Society, 1994). EEG and electrooculogram were amplified by BrainAmp amplifiers (BrainProducts, Munich) using a 0.1 – 250-Hz bandpass filter. The data was sampled at 1 kHz, and filtered offline with a 0.5 Hz high-pass filter (Butterworth zero phase, 24 dB/Octave). An Infomax Independent Component Analysis (Bell & Sejnowski, 1995), as implemented in the Brain Vision Analyzer software (BrainProducts, Munich), was run to identify and backtransform ocular artifacts (blinks and horizontal eye movements; see also Jung et al., 2000). All electrodes were recorded with reference to FCz, and re-referenced offline to averaged mastoids. Horizontal eye movements were recorded by electrodes F9 and F10 and vertical eye movements were recorded from Fp1 and an electrode placed beneath the left eye. Before the EEG was segmented into epochs for ERP analyses, the signal was filtered

[5] The fits of two models were compared. One model treated fillers as 'distractors' that competed for vSTM storage but were not to be reported, the second model assumed fillers as absent. Note that all analyses involving parameters *C* and *K* were based on the fitting including only trials of the standard procedure. The distractor model used one extra degree of freedom per fit, and the test was to see if this resulted in a significantly better fit.

with a 40 Hz low-pass filter (Butterworth zero phase, 24 dB/Octave). Trials with artifacts — defined as any signal exceeding ± 60 µV on any of the electrodes, ± 30 µV on electrodes F9 and F10, and bursts of electromyographic activity (permitted maximal voltage steps/sampling point of 50 µV) — were excluded from the averages.

For the ERP analysis, EEG epochs of 1400 ms (from 400 ms before onset of the letter array to 1000 ms after), were averaged separately for attend-left and attend-right conditions. Baseline correction was based on the 400-200 ms pre-display period (i.e., the 200 ms that preceded the cue). To examine potential relationships between TVA parameters and ERP components, we focused on early visual components (P1, N1) and delay activity over posterior areas. Time windows for analyses on mean amplitudes were derived from visual inspection of the grand-average potentials of these components (Table 3.2).

Table 3.2: Time windows and electrodes used for determining mean amplitudes of ERP components. Difference waves were calculated by subtracting ipsilateral from contralateral activity (relative to the attended hemifield) at lateral electrodes.

Component	Time Window (ms)	Electrodes
P1	80 – 110	P7, Pz, P8 PO7, POz, PO8 O1, Oz, O2
N1	120 – 150	
Contralateral Delay Activity	450 – 600	
Overall Delay Activity	600 – 800	

Statistical Analyses

Participants were classified according to their parameter estimates derived in the standard procedure. Based on median splits of the *C* and *K* values, they were assigned to groups of (1) participants having either a relatively high or a low processing speed *C*, and (2) participants having either a relatively high or a low storage capacity *K*. The relationships between the estimated TVA parameters and the ERP components were examined by separate

ANOVAs contrasting participants with regard to their *C*-level (high processing speed / low processing speed) and their *K*-level (high storage capacity / low storage capacity). To examine topography and lateralization, we further included the within-subjects factors Attended Hemifield (left/right), Electrode Position (left/central/right), and Electrode Site (P/PO/O) in the ANOVAs. In case of a significant interaction of Attended Hemifield and Electrode Position, we examined lateralized ERPs by calculating difference waves, quantified by subtracting ERPs at electrodes ipsilateral from those at electrodes contralateral to the attended array. For the sake of brevity, we only report significant main effects and interactions including the factors *C*-level and *K*-level. Significant main effects and interactions were examined using pairwise post-hoc contrasts. Potential relationships between TVA parameters and ERPs revealed by ANOVAs were re-examined by calculating Spearman correlation coefficients between individual parameter values and the mean amplitudes at electrodes where the effect was maximal.

3.1.4 Results

Parameter Estimation

For each subject, the accuracy of letter report as a function of effective exposure duration was modeled by a TVA-based function representing the best fit of the data according to the maximum likelihood method (Dyrholm et al., 2011; Kyllingsbæk, 2006) (Figure 3.2). The efficiency of selection guided by the cue was assessed by estimating an attentional weight index α to the un-cued hemifield using trials of the EEG experiment in addition to the trials of the standard experiment. On the group level, the hypothesis of perfect cue-guided selection (i.e., that α is zero) was rejected ($\chi^2(22)=308.9$; $p<0.01$). Individual Likelihood Ratio tests revealed that for 12 of the participants, objects on the un-cued side received a significant amount of attentional weight ($p<.05$). On average, however, α-values were very low (indicative of highly efficient selection) with a mean of 0.04 (range: 0.00–0.27), that is, on

average only 2% of the participants' processing capacity was allocated to the not-to-be-attended side (an α-value of 1.00 would indicate a 50/50 split of processing capacity between cued and un-cued objects).

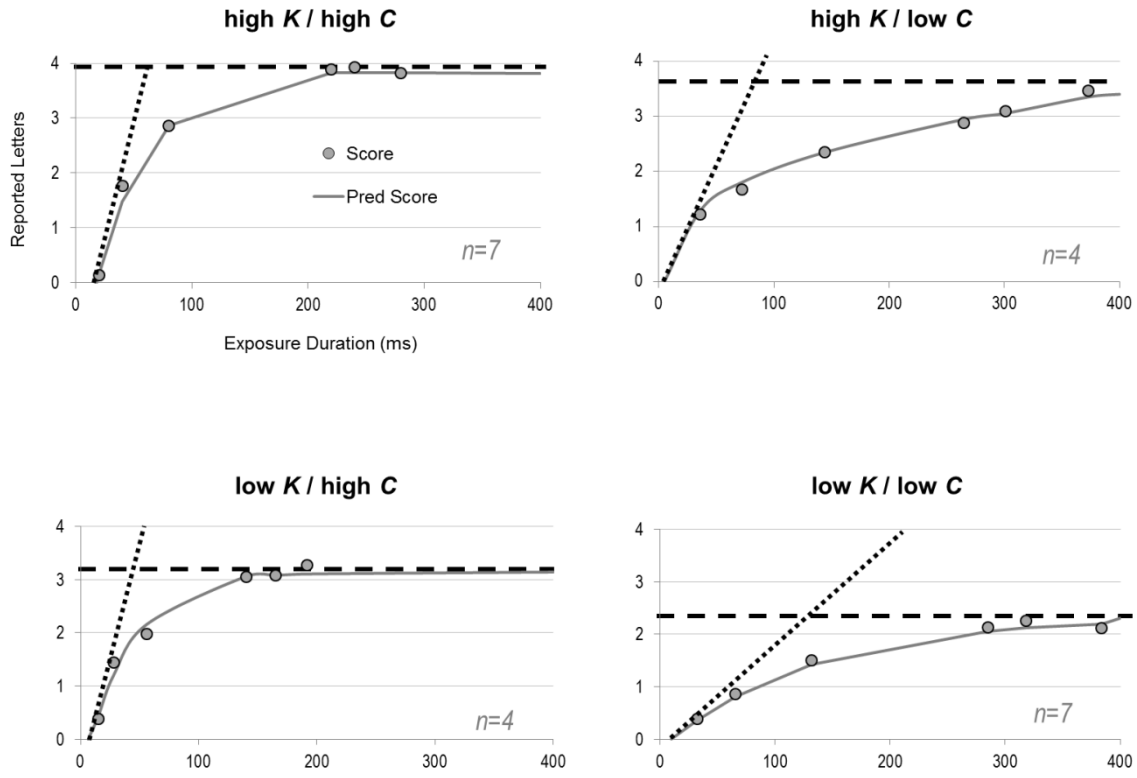

Figure 3.2: Performance of representative subjects.
Mean number of reported letters as a function of the effective exposure duration. Observed performance (dots) and performance predicted by the TVA-based fitting procedure (solid grey line) is shown for four representative participants. The slope of the functions at their origins (dotted line) provide estimates of the TVA parameter perceptual processing speed *C*, and the asymptote (dashed line) of the parameter storage capacity *K*. Panel headings indicate the respective participant's assignment to a group of high vs. low performers (based on a median split) for the parameters *C* and *K*, respectively. The number of participants assigned to each group is given in the lower right of each panel.

Overall, there was a close correspondence between the theoretically and the empirically obtained mean scores. Goodness-of-fit measures averaged across all participants showed that 95% of variance in the observed scores was accounted for by the maximum likelihood fits (R^2 (n = 22) mean: 0.95; range: 0.82-0.99). Estimates of the TVA parameters processing speed *C* and storage capacity *K* were significantly correlated across participants ($r=.56$, $p<.01$).

Event-related potentials

The onset of the stimulus array elicited visual P1 and N1 components, with the latter showing substantially higher amplitudes in the individuals with lower processing speed *C* compared to those with higher processing speed *C* (Figure 3.3). Delay activity started around 300 ms after the stimulus onset and persisted until the end of the retention period, and was more negative over recording sites contralateral than ipsilateral to the attended hemifield. This lateralization, particularly within an earlier time range, was more pronounced for the individuals with higher storage capacity *K* compared to those with lower storage capacity *K* (Figure 3.4). In contrast, overall delay activity, strongest over occipital sites later in the retention period, was larger in individuals with lower storage capacity *K* compared to those with higher storage capacity *K* (Figure 3.3).

P1. The ANOVAs (see above for details) of the P1 amplitudes contrasting participants with higher and lower processing speed did not yield a significant main effect of *C*-level [$F(1,20)=0.05$; $p=.82$], and no significant interactions involving this factor [$F(2,40)<1.44$; $F(4,80)<0.85$; all $p>.25$]. Thus, there was no evidence of a P1 modulation by individuals' level of processing speed.

The analogous ANOVA including the factor *K*-level also did not reveal a significant main effect [$F(21,1)=0.02$; $p=.88$] or interactions involving this factor [$F(2,40) <1.99$; $F(2,80)<1.71$; all $p>.15$].

N1. The ANOVA of the N1 amplitudes comparing participants with higher and lower processing speed revealed a main effect of *C*-level to be significant [$F(1,20)=5.50$; $p<.05$], as well as the interaction of *C*-level and Electrode Site [$F(2,40)=5.04$; $p<.05$]. These effects were due to the N1 being more pronounced for participants with lower compared to higher processing speed and that these individual differences were more marked at occipital [$F(1,20)=6.85$; $p<.05$] compared to posterior-occipital [$F(1,20)=4.82$; $p<.05$] and parietal electrode sites [$F(1,20)=3.31$; $p=.08$] (Figure 3.3). This relationship was confirmed by a

significant correlation between individual *C*-values and N1 amplitudes [r=.44; p<.05] (Figure 3.5).

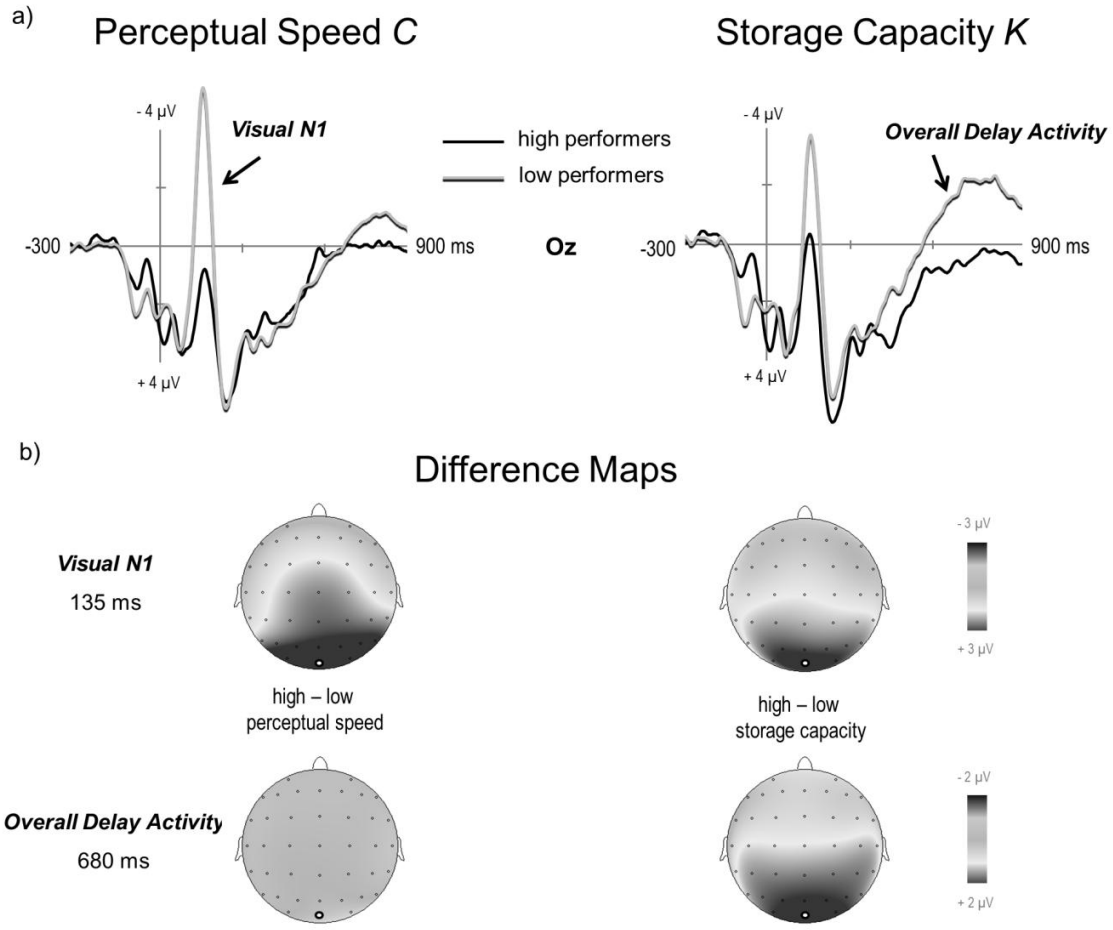

Figure 3.3: Event-related potentials (non-lateralized).
a) Grand-averaged ERPs at occipital-central electrodes comparing high performers (black line) and low performers (grey line). *Left:* Participants assigned to groups with high vs. low processing speed *C*. *Right:* Participants assigned to groups with high vs. low storage capacity *K*. b) Topographic maps of the difference in activity between participants with high and low processing speed *C* (left) and, respectively, participants with high and low storage capacity *K* (right), in the time range of the visual N1 (upper maps) and that of Delay Activity (lower maps).

In contrast, the analogous ANOVA involving the factor *K*-level did not yield a main effect [F(1,20)=2.16; p=.16] or any interactions [all F<1.64; all p>.30] with this factor. Individual *K*-values did not correlate significantly with N1 amplitudes [r=.31; p>.15].

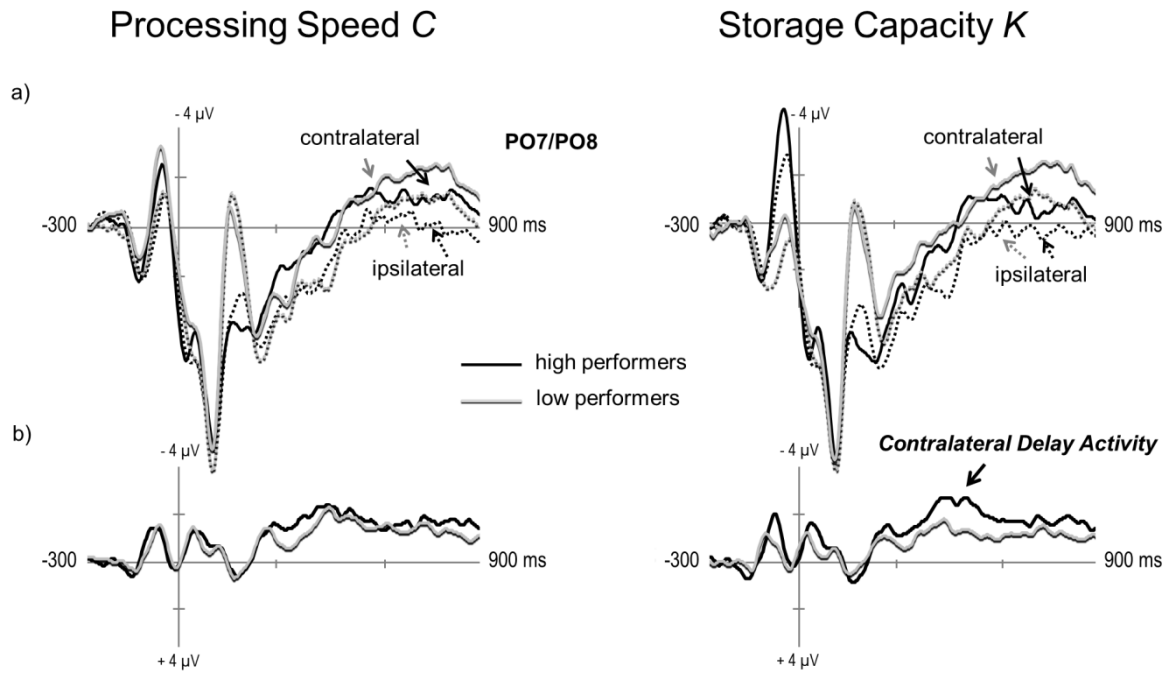

Figure 3.4: Lateralized event-related potentials.
a) Grand-averaged ERPs ipsi- and contralateral to the attended hemifield, comparing high performers (black line) and low performers (grey line). *Left:* Participants assigned to groups with high vs. low processing speed *C*. *Right:* Participants assigned to groups with high vs. low storage capacity *K*. b) Difference waves comparing participants with high and low processing speed *C* and, respectively, participants with high and low storage capacity *K*.

Contralateral (Early) Delay Activity. The ANOVA comparing delay activity of participants with higher and lower storage capacity in the 450-600 ms time window revealed a significant interaction of Electrode Side and Attended Hemifield [$F(2,40)=28.46$; $p<.001$]: activity was higher contralateral to the attended hemifield for all participants. Furthermore, there was a significant interaction between Electrode Site, Attended Hemifield, and *K*–level, [$F(2,40)=4.07$; $p<.05$], indicating that this lateralization varied with individual storage capacity. A follow-up ANOVA on CDA amplitudes revealed the difference between contra- and ipsilateral activity to be larger in participants with higher compared to lower storage capacity [$F(1,20)=4.60$; $p<.05$]. Individual *K*-values were significantly negatively correlated with CDA amplitudes [$r=-47$; $p<.05$], confirming that the degree of lateralization systematically increased with storage capacity (Figure 3.5).

In contrast, the analogous ANOVA comparing participants with higher and lower perceptual processing speed did neither yield a main effect of *C*-level on overall delay activity

[F(1,20)=0.26, p=.26], nor a main effect of *C*-level on CDA amplitudes [F(1,20)=0.01; p=.93], nor any interactions involving the factor *C*-level [all F<1.74; all p>.05]. Individual *C*-values were not significantly correlated with CDA amplitudes [r=-17; p>.25].

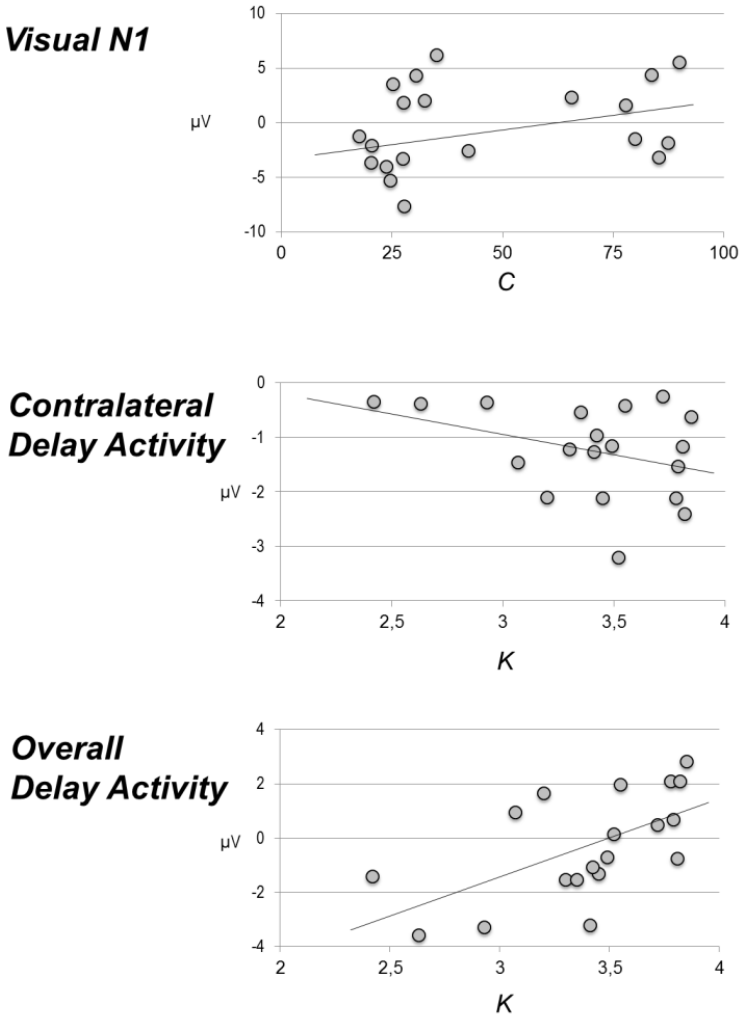

Figure 3.5: Correlations between TVA parameters and ERPs.
Spearman correlations between individual estimates of perceptual processing speed *C* and mean amplitudes of the visual N1 at electrode Oz in the time window of 120–150 ms (upper panel). Spearman correlations between individual estimates of storage capacity *K* and mean amplitudes of the CDA at electrodes PO7/PO8 in the time window of 450–600 ms (central panel). Spearman correlations between individual estimates of storage capacity *K* and mean amplitudes of the overall delay activity at electrode Oz in the time window of 600–800 ms (lower panel).

(Late) Delay Activity. The ANOVA comparing delay activity of participants with higher and lower storage capacity in the 600-800 ms time window revealed a significant main effect of *K*-level [F(1,20) = 6.83; p<.05]: overall (non-lateralized) negativity was higher for individuals with lower compared to higher storage capacity. Again, a significant interaction of

Electrode Site and Attended Hemifield [$F(2,40)=49.10$; $p<.001$] demonstrated that attention-related lateralization across all participants persisted into this late time period. In contrast to the earlier time window, *K*-level did not interact with Electrode Side and Attended Hemifield [$F(2,40)<1.44$; $p=.25$]. *K*-values were significantly positively correlated with delay activity in this late time window [$r=.55$; $p<.05$], corroborating that overall activity increased with lower individual storage capacity (Figure 3.5).

The analogous ANOVA comparing participants with higher and lower perceptual processing speed did neither yield to a main effect of *C*-level [$F(1,20)=0.35$, $p=.56$] nor any interactions involving this factor [all $F<1.37$; all $p>.25$]. Again, individual *C*-values were not correlated with overall delay activity [$r=.29$; $p>.15$].

Effects of top-down control in the EEG Experiment

To control for the influence of attentional weight potentially (mis-)allocated to filler letters on the un-cued side in the EEG experiment, we additionally contrasted ERP components of participants with perfect and imperfect top-down control ($\alpha>0$ (n=12) vs. $\alpha=0$ (n=10)). We found no significant main effects of α-level or interactions with α-level for any of the analyzed ERP components, [all $F<1.74$; all $p>.15$]. Individual α-values were also not correlated with amplitudes of any of the analyzed ERP components [all $p>.25$].

3.1.5 Discussion

We identified distinct ERP correlates of the two visual attention capacity parameters implemented in the formal TVA framework (Bundesen, 1990): visual processing speed *C* and vSTM storage capacity *K*. Interindividual differences in visual processing speed were reflected in smaller posterior N1 amplitudes for participants with higher relative to lower encoding rates. In contrast, interindividual differences in storage capacity were related to posterior delay activity after the perceptual stimulation had expired. More specifically,

participants with higher storage capacity exhibited stronger CDA in the early phase of the retention interval, whereas they showed a weaker longer-lasting overall negativity as compared to participants with lower storage capacity.

ERP correlates of visual perceptual processing speed C

The association between the TVA parameter visual processing speed *C* and N1 amplitudes complements previous ERP research on visual object processing and is compatible with basic assumptions of NTVA. According to NTVA, faster visual information processing is associated with increased activity in specific populations of neurons that represent the properties of the attended objects. Initially, this may seem to be at variance with our finding of larger ERP amplitudes in slower individuals. However, ERPs reflect summated activity of large numbers of cortical nerve cells, thus, amplitudes do not depict highly specific neuronal activity in single neurons (Bundesen & Habekost, 2008). Rather, they reflect the general amount of neural resources activated during a cognitive process (Luck, 2005), with (potentially less specific) activation of many neurons manifesting in higher ERP amplitudes. Cognitive efficiency theories (e.g., Vernon, 1983), in fact, predict a reversed relationship between amplitude and performance level, as we found it in the present study. Less activation in higher compared to lower performing individuals is interpreted to indicate more efficient brain functioning associated with high cognitive abilities (e.g., Haier et al., 1988; Rypma et al., 2002). Processing speed is assumed to be one of several basic determinants of general processing efficiency, that is, if cognitive operations can be performed quickly, resource allocation may be minimized and performance maximized (e.g., Deary et al., 2010; Neubauer, 1997). The present ERP variations characterize interindividual differences in this key function: Reduced N1 amplitudes for participants with higher as compared to lower perceptual processing speed, under the same task demands, indicate that faster individuals

recruit a relatively smaller amount of their available neural resources during early object processing.

Several mechanisms may contribute to this ratio between the available and actually engaged resources. In general, the N1 component has been related to visual discrimination processes within the attentional focus (Hillyard et al., 1998; Vogel & Luck, 2000). Slower participants' signal-to-noise ratio may be decreased in these processes by additional neuronal activity involved in unspecific processing of visual input; or it may result from increased attentional weight being expended on 'ghost objects' (Bundesen & Habekost, 2008). By comparison, categorization might be speeded up in faster processing participants by effective application of stored internal templates, which match the currently perceived stimuli to a high degree (Bundesen et al., 2011). In previous within-subject studies with varying task requirements, N1 amplitudes were observed to be less negative when the similarity between objects that had to be classified was reduced (Tanaka et al., 1999; Tokudome & Wang, 2011; Töllner et al., 2009). This suggests that reduced competition between object templates accessed during visual discrimination is accompanied by a weaker electrophysiological response. Furthermore, in a study requiring the discrimination of novel stimuli, N1 amplitudes were found to decrease with increasing numbers of repetitions of the stimuli (Groh-Bordin et al., 2007). Given this, N1 amplitudes may signify the quality of activated internal representations of to-be-discriminated objects (Curran et al., 2002). Taken together, consistent with NTVA, these findings suggest that the ability to deploy stored templates might have contributed to the individual differences in perceptual processing speed and N1 amplitudes observed in the present study.

Finally, our results compare with ERP differences between groups of individuals known to differ in visual processing speed, that is: young and elderly adults (McAvinue et al., 2012). Age-related slowing is associated with larger N1 amplitudes for older relative to younger participants in various visual tasks (e.g., Kutas et al., 1994; Yordanova et al., 2004).

Presumably, the N1 enhancement in older age is an electrophysiological marker of slowing in visual discrimination processes, manifesting in more global age-related performance changes (e.g., Cerella, 1991; Salthouse, 1996).

In contrast to the N1, the earlier visual P1 component did not vary with individual differences in visual processing speed. P1 amplitudes are known to vary with physical stimulus properties, such as luminance and contrast (Johannes et al., 1995) and might indicate changes in the processing rate due to varying sensory strength. The present study, however, addressed interindividual differences by keeping objective physical stimulation constant.

ERP correlates of visual short-term memory storage capacity K

The relationship established between TVA parameter storage capacity *K* and ERP delay activity substantiates previous EEG findings and supports the neural mechanisms proposed by NTVA. In particular, NTVA assumes that vSTM storage relies on spatio-topically organized sustained activity, implemented via recurrent feedback loops between the thalamus and sensory neurons in visual cortical areas (Bundesen et al., 2005). The posterior-contralateral distribution (relative to the hemifield of encoded information) of the delay activity associated with storage capacity *K* supports the visuo-topic organization of this recurrent activation. As suggested previously, delay activity during retention periods arises from thalamo-cortical activation (Birbaumer et al., 1990; LaBerge, 1997). The present findings demonstrate that the overall delay activity and the lateralized proportion of this activity are dissociable with respect to their relationship to individual differences in vSTM limits: Overall non-lateralized activity was higher in participants with lower storage capacity; conversely, CDA amplitudes were larger in participants with higher storage capacity. This dissociation suggests that individuals with comparatively high storage capacity are characterized by efficient neural recruitment, that is, instantaneous contralateral activity specifically associated with the storage of attended information, while minimizing later

additional unspecific activity. The latter may involve unprofitable remote activity, processing of extraneous noise, or strategic compensational mechanisms during a time period in which the vSTM representation would already have started to decay. In contrast to the current study, relationships between CDA and individual differences in storage capacity have previously been revealed only by varying load conditions (e.g., McCollough et al., 2007; Vogel et al., 2005). The individual vSTM limit was associated with the relative point at which the CDA reached an asymptote; for example, participants with relatively low storage capacity reached the CDA asymptote already at low vSTM loads, whereas the CDA amplitude increased further with increasing loads for participants exhibiting higher storage capacity. Thus, typically, correlations were found between individual behavioral vSTM capacity measures and the relative increase of the CDA amplitude from lower loads (e.g., two items) to higher loads (e.g., four items) (e.g., McCollough et al., 2007; Vogel et al., 2005). By contrast, we were able to establish a systematic relationship between the CDA and storage capacity under constant load conditions, likely owing to the highly reliable estimation of the individual TVA parameter *K*. Note that this straightforward correlation was found despite the relatively long temporal gap (of 5–10 days) between parameter assessment and EEG recordings. Furthermore, we controlled for a critical confound by estimating storage capacity independently of visual processing speed outside of the EEG experiment (i.e., in the TVA whole report experiment). Usually, vSTM performance and ERPs are assessed under conditions of a single, constant presentation time of to-be-encoded stimulus array (e.g., Vogel & Machizawa, 2004; but see Sander et al., 2011). Thus, interindividual differences in perceptual processing speed potentially influence both storage capacity measures and CDA amplitudes. For slower participants especially, the brief presentation times necessary for ERP examination in vSTM tasks may have been too short to fill up vSTM to its capacity limit, leading to systematic underestimations of the maximum storage capacity for such participants. The design of the present study enabled us to control for this factor by parameter estimates of

the two attentional capacity limiting components based on the standard procedure with varying exposure durations. This way, we can rule out that differences in processing speed during the encoding of information into vSTM account for individual differences in CDA amplitudes.

Integrating our results with findings from functional magnetic resonance imaging (fMRI) studies permits cautious inferences to be drawn about neural generators underlying the identified ERP correlates of storage capacity *K*. Recently, TVA parameter *K* has been shown to correlate with activity in the middle intraparietal sulcus (IPS), the dorsomedial-prefrontal cortex, and the frontal eye fields (Gillebert et al., 2012). Activity in the IPS has previously been assumed to be one (of several) generators of the CDA (Todd & Marois, 2004, 2005). Thus, individual difference in IPS activity may have also contributed to the present CDA modulations. In contrast, task-general fMRI delay activity in the prefrontal cortex has been shown to follow a similar pattern as to what we demonstrated for the overall delay activity, with greater activity displayed by participants with lower, as compared to higher, storage capacity (Rypma et al., 2002). This suggests that the later, un-specific activity may be partly driven by frontal brain regions.

Processing of non-attended letters

The combination of TVA-based parameter assessment with ERPs further contributes to an ongoing discussion about the impact of filler items inherent in the lateralized vSTM paradigm (e.g., Arend & Zimmer, 2011). Previous studies measuring the CDA have usually not systematically assessed whether objects in the not-to-be-attended hemifield receive attentional weight that could potentially influence behavioral vSTM measures and EEG responses. However, the ability to filter out irrelevant information is a critical determinant of interindividual differences in vSTM limits and CDA amplitudes (e.g., Vogel et al., 2005). The present approach enabled us to control for this potential influence of letters in the un-cued

hemifield. Storage capacity *K* was estimated based on performance in the standard procedure using unilateral arrays when the total attentional weight could be allocated to the target letters. Including trials from the EEG session in an extended fit permitted us to estimate the relative weights of cued and un-cued letters for each participant, expressed in the TVA top-down control parameter α (Kyllingsbæk, 2006). The results indicate that participants allocated the largest part of their available attentional weight (98%, on average) to the cued (target) letters. ERP activity did not differ between individuals with perfect and imperfect top-down control. This makes it unlikely that the processing of letters on the non-attended side accounted for individual differences in CDA amplitudes. Thus, in the present study, attentional resources allocated to the filler letters appeared to be of negligible impact. However, the general (usually implicit) assumption that items on the un-cued side in a lateralized vSTM paradigm simply serve as fillers becomes questionable in the face of a measurable amount of attentional weight that is (mis-) allocated to letters on the un-cued side, at least for some of the participants. In particular, in aging or clinical populations of individuals who suffer from a deficit in top-down attentional control, fillers may have a significant distracting impact and this should thus be taken into account when interpreting behavioral as well as electrophysiological responses.

3.1.6 Conclusions

In the present study, we used an inter-individual differences approach to provide electrophysiological evidence for the neural independence of two distinct latent visual attention capacity parameters formally implemented in the NTVA framework (Bundesen et al., 2005, 2011): First, faster perceptual processing speed was associated with lower brain activity during early object discrimination. Second, higher storage capacity was associated with a larger amount of delay activity specifically related to vSTM processing, while overall unspecific activity was less negative.

The identified ERP correlates of the two TVA parameters may be regarded as general neural efficiency measures of separate fundamental abilities and, thus, as a promising tool in the study of brain mechanisms underlying individual differences in more complex behavior (Cassidy et al., 2012; Neubauer, 1997; Vernon, 1983). Furthermore, if comparable reliability of the ERP correlates could be proven in different age groups and patient populations, they may have the potential to serve as neural markers disclosing age- and disease-related changes in attentional functions. These might then be used to quantify brain-behavior relationships in recovery, pharmacological treatment, and rehabilitation training in a highly sensitive manner.

Author contributions

I.W., K.F., and T.T. designed the study. I.W. programmed and conducted the experiment, analyzed the data, and wrote the paper. M.D. programmed the TVA-fitting procedures and performed the analyses of the parameter alpha. K.F., H.J.M., T.T., T.H., and M.D. commented and revised the manuscript.

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3.2 Neural markers of cognitive decline and reserve in visual processing speed and visual short-term storage capacity

3.2.1 Abstract

Attentional decrements are assumed to be a major determinant of general cognitive decline in older age. The present study aimed at identifying neural markers of declined and preserved basic visual attention functions based on Bundesen's formal 'Theory of Visual Attention' in aging individuals. We investigated the relationship between neurophysiology, individual performance and age by (1) contrasting ERPs of higher- and lower-performing younger and older participants and (2) conducting correlation analyses of behavioral measures and ERPs, separately for TVA parameters *visual perceptual processing speed C* and *vSTM storage capacity K*. First, in both age groups, the same distinct components marked interindividual differences in *C* and *K*, respectively: The posterior N1 was augmented for participants with higher as compared to lower processing speed and its amplitude correlated with individual *C*-values. For participants with higher relative to lower storage capacity, the contralateral delay activity was enhanced, and correlated with individual *K*-values. Second, in older age, both parameters were related to two further distinct ERP correlates: The anterior N1 was reduced only for older participants with lower processing and its amplitude correlated with individual *C*-values only in the older sample, indicative of selective loss of attentional resources associated with slowed encoding rates in older age. Conversely, only elderly with high levels of storage capacity exhibited a right-central positivity, which correlated with individual *K*-values only in the older sample, indicative of compensatory resource recruitment fostering reserved storage capacity in older age.

3.2.2 Introduction

Visual attention abilities are known to decline in senescence, affecting performance in a variety of daily tasks (Park & Hall Gutchess, 2000). These impairments likely result from substantial structural and functional changes in the brain during aging, which affect large parts of the visual attention network (e.g., Madden et al., 2007). Aging studies using functional neuroimaging techniques provide the opportunity to investigate brain-behavior relationships underlying cerebral and cognitive decline by analyzing age differences in task-related brain activity. In some cases, brain activity is found to be reduced for older compared to younger adults, whereas in other cases, it is found to be enhanced (for recent reviews, see Fabiani, 2012; Grady, 2012). However, the interpretation of age effects on brain activity is not trivial. Age-related variations in neural activation may partly reflect neural loss and cognitive decline, but may also comprise neural compensation fostering 'cognitive reserve', that is, preserved abilities in older age (Stern, 2002, 2009). Furthermore, age differences may result from reduced specificity in brain activation. In order to be able to differentiate between age-related loss, compensation, and dedifferentiation, interindividual differences in older adults' cognitive performance must be taken into account (e.g., Cabeza et al., 2005).

Interindividual variability in cognitive tasks is assumed to result from variations in fundamental cognitive abilities or processing resources that are suggested to account for performance in a broad range of cognitive tasks (e.g., Spearman, 1904; Vernon, 1983). Similarly, the widespread age-related cognitive decrements have been attributed to a decline in basic fluid processing components, in particular, a general slowing of information processing (e.g., Cerella, 1994; Deary et al., 2010; Salthouse, 1996) and reduction of short-term storage capacity (e.g., Baddeley, 2002; Salthouse, 1994). In the visual domain, these key 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. Based on performance in a psychophysical whole report task, the mathematical model permits to quantify these parameters for a particular individual (e.g., Duncan et al., 1999). In close relation to the 'biased competition model' (Desimone & Duncan, 1995), TVA assumes a race of multiple elements in the visual field that are processed in parallel and compete for selection. Those objects that complete processing fastest will be encoded into vSTM[6]. The theory's neural interpretation (NTVA, Bundesen et al., 2005, 2011) further claims that distinct brain processes underlie the two components. Recently, in a pioneering study on young, healthy participants, this assumption was validated by linking distinct event-related potentials (ERPs) to individual differences in the two parameters (Wiegand et al., under review). First, when participants were split according to their processing speed level, faster relative to slower participants exhibited a significantly smaller posterior N1, with amplitudes being inversely correlated with processing speed across all participants. The visual N1 amplitudes are assumed to index the amount of neural resource allocated for object discrimination processes (Vogel & Luck, 2000). Accordingly, the relation of visual N1 amplitudes to parameter processing speed *C* was interpreted to reflect that faster individuals need to recruit a relatively smaller proportion of their available neural resources when categorizing objects. Second, when the same individuals were split according to their storage capacity level, those with higher relative to lower storage capacity exhibited a significantly larger contralateral delay activity (CDA). The CDA amplitude was further correlated with individual storage capacity across all participants. The component is quantified by calculating the difference between delay activity contra- and ipsilateral to the attended hemifield when attention during encoding is directed to only one hemifield of a bilateral stimulus array (Klaver et al., 1999). The amplitude of the difference wave has been proven to be a direct measure of the number of representations currently held in vSTM (McCollough et al., 2007; Vogel & Machizawa,

[6] In TVA, the categorization of an object is synonymous to its encoding into vSTM

2004). Thus, the amount of topographically specific activity was interpreted to mark the individual vSTM capacity limits expressed in TVA parameter storage capacity *K*.

Combining TVA-based assessment with ERP markers of the distinct visual attention capacity parameters is also a promising approach to identify the neural underpinnings of age decrements in these functions. As a critical advantage over conventional neuropsychological attention tests, the TVA procedure allows estimating age-related decline in processing speed and storage capacity in an unconfounded manner on the basis of mathematically independent parameter fitting (Duncan et al., 1999; Finke et al., 2005). The assessment is based on response accuracy of unspeeded verbal report, and thus, rather unaffected by age-related motor slowing or potential speed-accuracy trade-off effects. Furthermore, the simplicity of task instructions and the use of short exposure durations render systematic age variations in strategy very unlikely. The individually adapted exposure durations further control for potential confounding differences in individual perceptual thresholds (Habekost et al., 2012). Recently, behavioral TVA-based parameter modeling has been used to quantify age-related decline in visual processing speed and storage capacity (McAvinue et al., 2012; Habekost et al., 2012). However, a systematic investigation of the neural mechanisms underlying these changes has not been carried out yet. Thus, it remains unclear, whether the same neural mechanisms underlying interindividual performance differences in younger individuals also contribute to age-related decline of the two functions or whether different mechanisms account for performance variations in older age.

In the present study, we used the same methodology as employed by Wiegand et al. (under review) to establish age-related changes in distinct electro-cortical markers of visual processing speed *C* and short-term storage capacity *K*, respectively. In particular, we assume that neural markers of processing speed and storage capacity differentiating between young individuals with higher and lower parameter levels may also reflect the age-related decline in processing speed (by increased N1 amplitudes) and vSTM storage capacity (by decreased

CDA amplitudes). In fact, previous EEG findings are largely in agreement with these hypotheses. A number of studies showed age-related increases of the posterior N1 in visual tasks (e.g., Kutas et al., 1994; Yordanova et al., 2004). Conversely, some studies also reported no differences (Falkenstein et al., 2006; Riis et al., 2008) or even a decrease in older relative to younger participants (Czigler & Balàsz, 2005). Notably, all these age-effects have been obtained ancillary to the main focus of these studies. Thus, they have not been related to performance in the employed tasks and were suggested to simply reflect genuine age differences in sensory processing (see DeSanctis et al., 2008, for review). The CDA was previously found to be reduced in older, as compared to younger, adults. Therefore, it has been declared a marker of the age-related reduction in vSTM storage capacity (Jost et al., 2010; Sander et al., 2011; Wiegand et al., 2013).

Besides components that distinguished high- and low-performing younger participants, it is possible that additional neural correlates specifically differentiate between high- and low-performing *elderly*. In particular, frontally-mediated control processes are known to have a rising influence on cognitive abilities with advancing age (e.g., Grady, 2012; West, 1996). Accordingly, former ERP studies have demonstrated alterations in activity attributable to age-related changes in the attentional control network (e.g., Fabiani et al., 2012). For example, the anterior visual N1, which has been linked to voluntary shifts of spatial- and feature-specific attentional weights (Golomb et al., 2010; He et al., 2004, 2008; Töllner et al., 2009), is commonly reduced in older individuals (Curran et al., 2001; Kutas et al., 1994; Snyder and Hillyard, 1979). Similarly, a broad centro-parietally distributed positivity occurring about 200-400 ms following the presentation of visual stimuli, was found to be augmented in older age (e.g., Finnigan et al., 2011; see Kok, 2000 for a review). This activity is assumed to mark allocation of attentional resources fostering information encoding (e.g., Kok, 2001; Lefèbre et al., 2005). Thus, its reduction in older participants is presumably related to the age-related decline in executive control. Based on these previous findings, we

assumed that components related to attentional control processes might differ between higher- and lower-performing elderly, without necessarily differentiating among younger participants with different performance levels.

By coupling event-related brain responses to individual performance levels in different age groups, we aimed at differentiating between activity patterns related to cognitive decline and those related to preserved performance levels in aging participants (Daffner et al., 2011; Riis et al., 2008; Stern, 2002). Specifically, we compared ERPs of younger and older participants, who were divided into subgroups of relatively high and low performers based on behavioral TVA parameter estimates of processing speed and storage capacity, respectively. The finding of ERP components that differentiate between participants with higher and lower performance in both age groups (main effect Performance Level) and between younger and older participants (main effect Age) would suggest that the same underlying neural circuits determine visual attention abilities in both older and younger participants and that these circuits are affected by normal aging. In contrast, ERP variations that differentiate between performance levels only in the older sample, but do not differ between higher and lower performing younger individuals (interaction of Performance Level and Age), would imply that attentional abilities in older age rely on different neural processes than in younger individuals. On the one hand, these might be compensatory processes, in support of successful task accomplishment. Such compensatory recruitment of resources should become manifest in activity changes especially within the high-performing older participants (Old high ≠ Old low = Young). On the other hand, neural processes that are generally optimized in younger age may exclusively decline in older participants with low performance levels. Such neural deterioration processes should become manifest in activity changes only in low-performing older participants (Old low ≠ Old high = Young). Finally, age-related activity changes unrelated to task performance (Old low = Old high ≠ Young) would rather imply

dedifferentiation that does not promote cognitive functioning (e.g., Cabeza et al., 2005; Stern, 2009).

3.2.3 Methods

Participants

Twenty younger participants and twenty older participants were included in the sample (Table 3.3). The younger participants were also included in the prior study (Wiegand et al., under review). Participants who made systematic eye-movements in the EEG-experiment or for whom more than 25% of all trials were rejected because of artifacts were excluded (four older and three younger participants). None of the participants reported any history of neurological (e.g., traumatic brain injury, stroke), psychiatric (e.g., depression, anxiety disorders), chronic somatic (e.g., hypertension, diabetes), and chronic eye diseases (e.g., glaucoma, cataract). 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 (MMSE; Folstein et al., 1975) ruled out any symptoms prognostic of dementia: all participants achieved a score of 27 points or higher. The educational level was significantly lower in the older group (see Table 3.3), which is representative for the German post World War II generation. Notably, IQ scores derived from a test of German vocabulary test (Mehrfach-Wortwahl-Test; Lehrl, 1977) indicated comparable levels of crystallized intelligence for the two groups. The participants were naïve 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 Faculty of Psychology, LMU Munich.

Table 3.3: Demographic variables of the groups.
Gender distribution; mean and standard deviation (in parentheses) and range of age, education, and crystalline IQ; Chi^2- and **T-**values and significance of group comparisons. F: female; M: male; Age: years; Education: attended school years; MWT-B: German Multiple-Choice Vocabulary Test (Lehrl et al., 1977).

	Young	Old	Significance Test
Sex (F/M)	11/9	10/10	Chi^2=.20; *p>.50*
Age	26.30 (3.01) 19-30	67.30 (3.89) 61-75	t(38) = 36.09; *p<.001*
Education	13.00 (0.00) 13-13	11.25 (1.51) 9-13	t(38) = 3.28; *p<.01*
IQ* (MWT-B)	113.44 (8.94) 101- 130	133.76 (7.98) 107-143	t(33) = 1.74; *p=.09*

*MWT-B scores of 5 non-native German-speaking participants (3 younger and 2 older) were excluded

Procedure

Experimental setup and task. Participants completed two test sessions, first the standard TVA whole report, and 5–10 days later the EEG whole report task (Figure 3.1). Daytime of testing, ambient, equipment, viewing distance, background and stimuli type, size, positions and luminance were the same during both sessions. The PC-controlled tests were conducted in a dimly lit room with stimuli presented on a 17-inch monitor (1024- by 768-pixel screen resolution; 85-Hz refresh rate) from a viewing distance of 65 cm. Participants were instructed to report as many letters as possible from a briefly presented letter array without speed stressing. They were requested to report only those letters they recognized 'fairly certain'. The experimenter entered the responses on the keyboard and started the next trial. Four letters were chosen from a pre-specified set of well-distinguishable letters [ACEHJOPRSTWX] and presented with a size of 1.1° visual angle at lateral positions on an imaginary circle around a central white fixation cross of 0.7° visual angle on a black background.

Standard whole report procedure. Prior to the parameter assessment procedure, we identified the most appropriate individual exposure durations in a pre-test consisting of 24

masked trials. The presentation time at which a participant could report, on average, one letter per trial correctly (i.e., 25% report accuracy) was chosen as intermediate exposure duration in the assessment procedure, together with a shorter (half as long) and longer (twice as long) exposure duration. This provides a means for optimal modeling of parameters by delivering a broad range of performances from each individual (from around perceptual threshold to maximum storage capacity). The exposure duration by itself, however, is not a determinant of the parameters obtained. The mean medium exposure duration was 53.45 ms (range: 24-90) for younger and 85.00 ms (range: 60-100) for older participants.

In the standard TVA whole report experiment, the fixation cross was presented for 300 ms. After a blank screen of 100 ms, the letter array was presented. Isoluminant letters were presented on the left or right side of the central fixation, randomly chosen to be either red or green. The same letter appeared only once in each trial. In half of the trials, the array was followed by a mask presented for 500 ms at each stimulus location, which consisted of a square filled with a '+' and an 'x' (1.2° visual angle). Owing to visual persistence, exposure durations are effectively prolonged in unmasked compared to masked conditions (Sperling, 1960). Together with the three varying exposure durations, this resulted in six different effective exposure durations. Exposure duration (short, medium, long), masking (masked, non-masked), and hemifield (left, right) varied randomly, resulting in 12 equally frequent conditions presented in 6 blocks of 40 trials each. The first block consisted of 40 practice trials, and data were modeled based on the 200 remaining trials.

Whole report procedure in the EEG experiment. In the EEG experiment, the classical whole report paradigm was adapted to be suitable for analyzing lateralized as well as non-lateralized ERP responses. Participants were instructed to remain central eye fixation throughout the whole experimental blocks. To ensure balanced physical stimulation across hemifields, we presented letters bilaterally and the to-be-attended hemifield was indicated by a 100%-valid spatial arrow pre-cue with the cued side varying randomly from trial to trial

(based on the classical lateralized vSTM paradigm, e.g., Vogel & Machizawa, 2004). Letters were presented only once in a given trial, either as target letter (cued hemifield), or as filler letter (un-cued hemifield). Target selection in face of additional visual stimulus presentation was further facilitated by separating targets and placeholders by color, i.e. either all target letters were green and all distractor letters were red, or vice versa, in a randomly changing fashion. Each trial started with the central fixation cross, presented for 100 ms followed by the cue for 200 ms. Then the letter array was presented for 200 ms. After a delay of 900 ms with a blank screen, a question mark appeared in the center, prompting the verbal report (Figure 3.1). After a practice block of 16 trials, EEG recording was started and a whole of 240 trials were run.

Parameter Estimation

The accuracy of letter report as a function of effective exposure duration derived in the standard procedure was modeled according to TVA by the method of maximum likelihood (Kyllingsbæk, 2006; Dyrholm et al., 2011). The modeling was based on estimating four parameters defining the psychometric function (Bundesen, 1990; see also Figure 3.2): (1) parameter t_0, the minimal effective exposure (in ms) duration, below which information uptake from the display is assumed to be zero; (2) parameter μ, the persistence of the iconic memory trace (estimated in ms from performance differences between unmasked and masked trials); (3) parameter *C*, the visual processing speed, the sum of estimated speed values across stimulus positions (estimated as number of elements processed per second); and (4) parameter *K*, the storage capacity (estimated as the maximum number of elements represented simultaneously in vSTM). *C* reflects the slope of the exponential at its origin t_0, *K* reflects the asymptote of the exponential psychometric function. In the current study, parameters t_0 and μ were estimated in order to receive valid estimates of the two parameters of main interest, *C*

and *K*. In accordance with previous reports (McAvinue et al., 2012), t_0 was marginally significantly longer in older than younger participants [t(38)=1.98; p=.06].

We estimated parameter top-down control α for each participant by a further fitting procedure in which trials from the EEG session, in addition to trials form the standard experiment, were included in the model. An α-value of zero would imply that the participant was able to use the spatial cue to completely 'filter out' the fillers, whereas an α-value significantly higher than zero would indicate that attentional weights were allocated to filler letters. For each participant, we tested the significance of α (i.e., whether letters presented as fillers on the un-cued side in the EEG paradigm received a significant amount of attentional weighting) by means of Likelihood Ratio tests[7].

EEG data acquisition

The EEG was recorded from 64 active Ag/AgCl electrodes (actiCap System, Brain Products, Munich), placed according to the International 10/10 system (American Electroencephalographic Society, 1994). EEG and electrooculogram were amplified by BrainAmp amplifiers (BrainProducts, Munich) using a 0.1 – 250-Hz bandpass filter. The data was sampled at 1 kHz, and filtered offline with a 0.5 Hz high-pass filter (Butterworth zero phase, 24 dB/Octave). An Infomax Independent Component Analysis (Bell & Sejnowski, 1995), as implemented in the Brain Vision Analyzer software (BrainProducts, Munich), was run to identify components of the EEG that represent ocular artifacts (i.e., blinks and/or horizontal eye movements; see also Jung et al., 2000) and to remove those before back-projection of the residual components. All electrodes were referenced to FCz, and re-referenced offline to averaged mastoids. Horizontal eye movements were recorded by

[7] The fits of two models were compared. One model treated fillers as 'distractors' that competed for vSTM storage but were not to be reported, the second model assumed fillers as absent. Note that all analyses involving parameters *C* and *K* were based on the fitting including only trials of the standard procedure. The distractor model used one extra degree of freedom per fit, and the test was to see if this resulted in a significantly better fit.

electrodes F9 and F10 and vertical eye movements were recorded from Fp1 and an electrode placed beneath the left eye. Before the EEG was segmented into epochs for ERP analyses, the signal was filtered with a 40 Hz low-pass filter (Butterworth zero phase, 24 dB/Octave). Trials with artifacts — defined as any signal exceeding ± 60 µV on any of the electrodes, ± 30 µV on electrodes F9 and F10, and bursts of electromyographic activity (permitted maximal voltage steps/sampling point of 50 µV) — were excluded from the averages.

Table 3.4: Time windows and electrodes used for determining mean amplitudes of the ERP components.

Component	Time Window (ms)	Electrodes
Anterior N1	90-120	F3, Fz, F4 FC3, FCz, FC4
Posterior N1	130-170	PO7, POz, PO8 O1, Oz, O2
Central Positivity	200-350	C3, Cz, C4 CP3, CPz, CP4
Contralateral Delay Activity	450-650	PO7/PO8 O1/O2

For the ERP analysis, EEG epochs of 1400 ms (from 400 ms before onset of the letter display to 1000 ms after), were averaged separately for attend-left and attend-right conditions. Baseline correction was based on the 400-200 ms pre-display period (i.e., the 200 ms pre-cue period). The CDA difference waves were quantified by subtracting ERPs at electrodes ipsilateral from electrodes contralateral to the attended array. To examine age-related changes in ERP correlates of TVA parameters, we focused on the correlates that were previously identified as neural indices of differences in processing speed and capacity in younger participants, the posterior N1 and CDA, and additional components that showed associations with the parameters in older participants, the anterior N1 and central positivity. Mean amplitudes and recording sites for analyses were derived from visual inspection of the grand-average potentials of these components (Table 3.4).

Statistical Analyses

Each age group was divided twice into groups of high and low performers by conducting median splits based on their behavioral parameter estimates, first according to those of *C* and second according to those of *K*. Behavioral differences between age groups and between high and low performers were examined by two separate univariate ANOVAs, one using parameter *C* and one on parameter *K* as dependent variable. Both included the between-subject factor Age (younger, older). An additional between-subject factor Performance Level contrasted participants with higher and lower processing speed *C* (*C*-level) in the former ANOVA and participants with higher and lower storage capacity *K* (*K*-level) in the latter. The modulation of ERP responses by age and interindividual performance differences in older and younger participants were examined as follows: For each component of interest, two separate mixed ANOVAs were calculated. Both employed the within-subjects factors Electrode Site (anterior, posterior) and Electrode Position (left, central, right) and the between-subject factor Age (younger, older). Again, the between-subject factor *C*-level was included in one ANOVA and *K*-level in the other. Note that the factor Electrode Position was not included in CDA analyses, which were performed on (contralateral-minus-ipsilateral) difference waves (see above). Following our hypotheses, we were most interested in interactions involving Age and Performance Level, which would indicate age-dependent differences in neural correlates of TVA parameters. For the sake of brevity, only main effects or interactions including the factors Age and/or Performance Level are reported. To further explore interactions, subsidiary ANOVAs and pairwise contrast were employed. We calculated Spearman correlation coefficients to examine the continuous relationships between individual parameter estimates and ERP measures at electrodes where the effect was most pronounced (as revealed by topographical analyses). Correlations were performed across the whole sample (N=40). In case the ANOVA revealed a significant interaction of Age and Performance Level, indicating that the relationship between ERPs and performance differed

between younger and older participants, correlation coefficients were further calculated separately for the two age groups

3.2.4 Results

Parameter Estimation

Attention parameters of visual processing capacity. For each participant, the accuracy of letter report as a function of effective exposure duration was modeled by a TVA-based function representing the best fit of the data according to the maximum likelihood method (Dyrholm et al., 2011; Kyllingsbæk, 2006). Overall, there was a close correspondence between the theoretically and the empirically obtained mean scores. Goodness-of-fit measures showed that more than 94 % of variance in the observed scores was accounted for by the maximum likelihood fits (Young: mean R^2=.95; Old: mean R^2=.93). Across all participants, estimates of the TVA parameters processing speed *C* and storage capacity *K* were significantly correlated (r=.55, p<.01), however, separate correlation analyses for both age groups revealed the correlation only to be significant within the younger (r=.54, p<.05), but not the older sample (r=.26; p>.25). The ANOVAs revealed that both parameters were overall significantly higher in younger than older participants [main effect Age: both F(1,36)>14.00; p<.001], and significantly higher for high than low performing individuals [main effect Performance Level: both F(1,36)>8.00; p<.001]. There was further a significant interaction of Age and *C*-level [F(1,36)>16.12, p<.001], reflecting that the difference between younger and older participants with relatively high processing speed was larger than the difference between younger and older participants with relatively low processing speed (Figure 3.6).

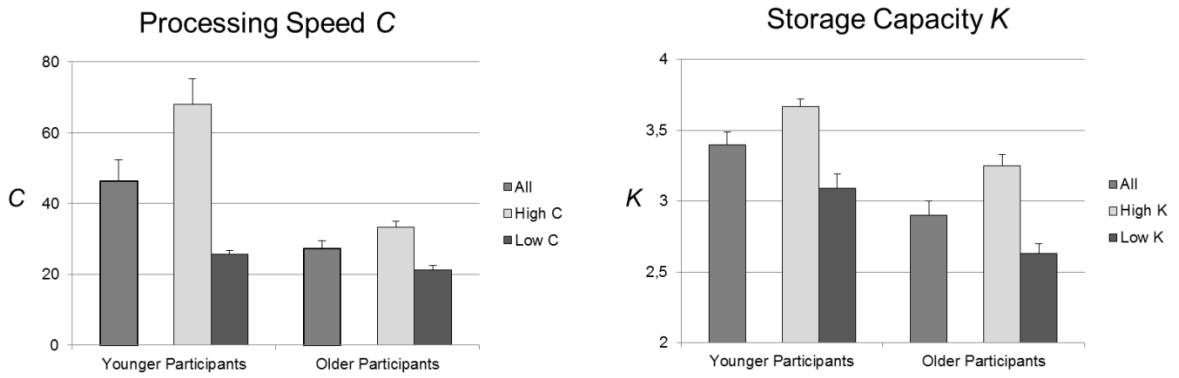

Figure 3.6: Behavioral parameter estimates of younger and older participants.
Mean and standard error of parameter estimates, for groups of all younger and older participants and subgroups of higher and lower performing individuals based on the median split of processing speed (left panel) and storage capacity (right panel).

Top-down control parameter α. For each participant, we estimated the efficiency of selection guided by the cue in the EEG experiment. We calculated the attentional weight index α (attentional weight of filler letters dividing by attentional weight of target letters) by including trials of the EEG experiment in addition to the trials of the standard experiment in a further fitting procedure. Individual Likelihood Ratio tests revealed that for 11 younger and for 15 older participants objects on the un-cued side received a significant amount of attentional weight ($p<.05$). Across the whole sample, α-values were rather low with a mean of 0.07 (SD: 0.10), that is, on average only 3.5% of the participants' processing capacity was allocated to the not-to-be-attended side (an α-value of 1.00 would indicate a 50/50 split of processing capacity between cued and un-cued objects). Younger participants (mean: 0.04; SD: 0.06) showed a marginally significantly more efficient top-down control α compared with older participants (mean: 0.10; SD: 0.12) [$t(38)=2.02$; $p=.05$]. Three participants (one younger and two older participants) showed individual α-values which exceeded 2.5 standard deviations of the whole sample's mean α, i.e. their top-down control was not representative for the participants tested in this study. The remaining participants had almost perfect top-down control values, indicative of highly efficient selection (Younger participants: mean: 0.02; SD: 0.03; Older participants: mean: 0.06; SD: 0.05). In order to control for the influence

of attentional weight potentially (mis-)allocated to filler letters on the ERP correlates of the general capacity parameters *C* and *K*, ERP results were verified by repeating the analyses on ERP amplitudes without the three outlier participants.

Event-related potentials

The ERP waveforms averaged time-locked to the onset of the stimulus array showed clear visual P1 and N1 components followed by a broadly distributed central positivity. The waveforms then devolved into a posteriorly pronounced sustained negativity, which was higher over electrodes contra- than ipsilateral to the attended hemifield. In both age groups, the posterior N1 response was smaller for participants with higher relative to lower processing speed (Figure 3.7). Furthermore, the N1 at frontal sites was larger in older participants with faster relative to slower processing speed (Figure 3.8). The lateralized ERPs showed an enhanced CDA for participants with higher as compared to those with lower storage capacity *K* in both age groups (Figure 3.9). Additionally, an increased right-central positivity was found in older participants with higher as compared to those with lower storage capacity (Figure 3.10).

Posterior N1. *C*-level: The ANOVA on N1 amplitudes at posterior electrode sites revealed a significant main effect of *C*-level [$F(1,36)=10.66$; $p<.01$] and an interaction of Electrode Site and *C*-level [$F(1,36)=10.21$; $p<.01$]. These results confirm reduced activation levels in faster compared to slower participants across age groups, with the difference being more pronounced at occipital [$t(38)=3.67$; $p=.001$] than parieto-occipital [$t(38)=2.85$; $p<.01$] electrode sites. Accordingly, individual *C*-values were significantly correlated with posterior N1 amplitudes at occipital electrodes across the whole sample ($r=.41$; $p<.05$; Figure 3.7). The main effect of Age [$F(1,36)=.002$; $p=.97$] and the interaction of Age and *C*-level [$F(1,36)=.95$; $p=.35$] were not significant.

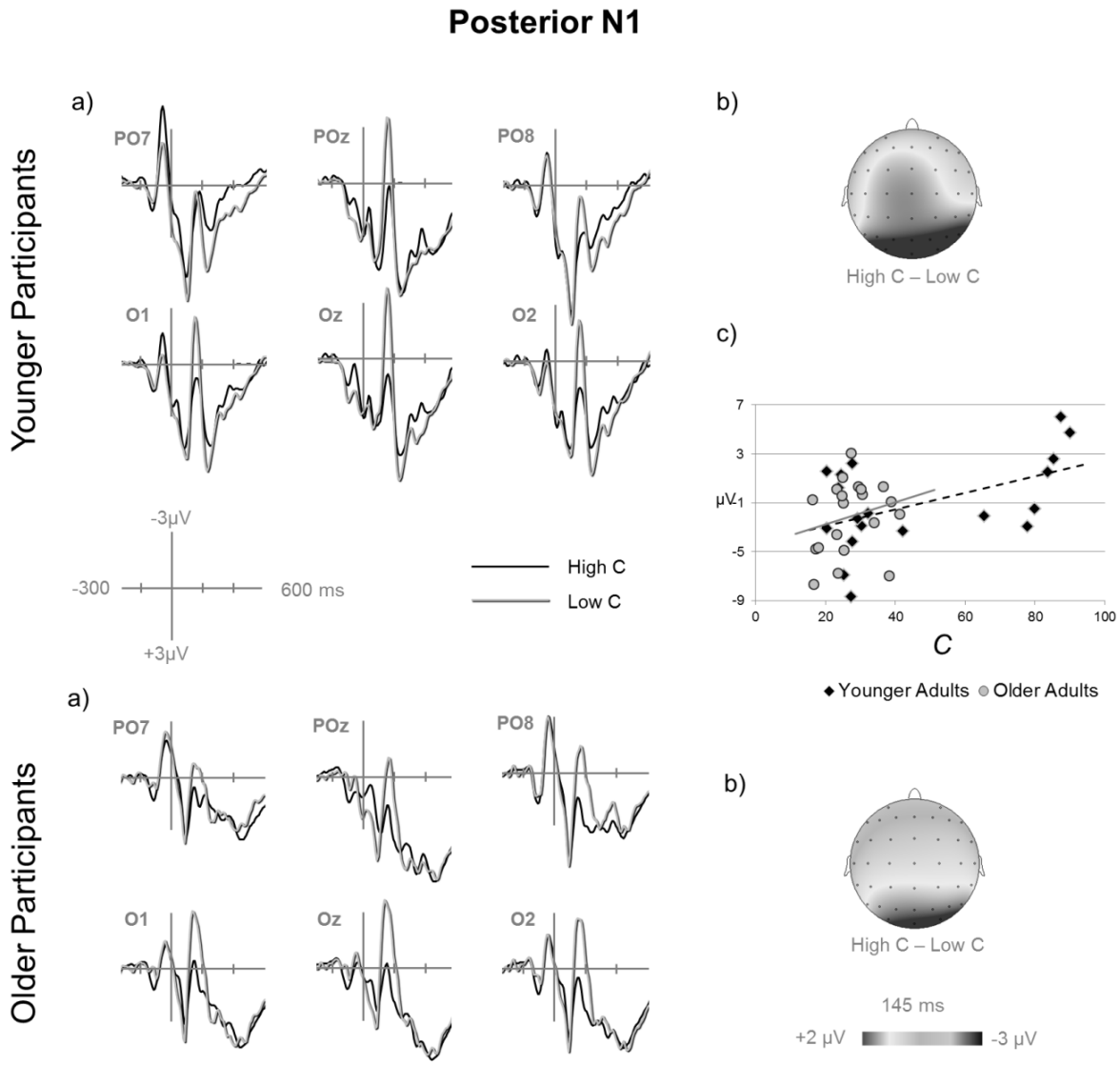

Figure 3.7: Posterior N1 as a neural marker of individual differences in processing speed *C*.
a) Grand-averaged ERPs for younger participants (upper panel) and older participants (lower panel), for participants with higher (black line) and lower processing speed *C* (grey line) at posterior electrode sites. b) Difference maps showing the activity of participants with lower processing speed subtracted from activity of participants with higher processing speed in the posterior N1 time range. c) Spearman correlations between posterior N1 amplitudes and individual *C*-values.

Additionally, there was a significant interaction of Electrode Site, Electrode Position and Age [$F(2,72)=9.88$; $p<.01$], indicating a different topography in older and younger participants. Separate follow-up analyses for the two groups revealed a significant main effect of Electrode Site for older participants [$F(1,19)=40.21$; $p<.001$] which reflected stronger deflections at occipital than parieto-occipital sites. In younger participants, this effect was also observable [$F(1,19)=28.26$; $p<.001$]. Moreover, a significant main effect of Electrode Position

[F(2,38)=7.69; p<.01] was found in this group only. A significant interaction between Electrode Site and Electrode Position [F(2,38)=8.54; p<.01] reflected that the posterior N1 was significantly more negative at occipital than parieto-occipital sites only at lateral [both t(19)>2.81; p<.01] but not at central electrodes [t(19)=.68; p>.50].

K-level: The ANOVA revealed the main effect of *K*-level [F(1,36)=5.43; p<.05] to be significant. However, individual *K*-values were not significantly correlated with posterior N1 amplitudes (r=.23, p>.15)[8] and the effect of *K*-level was smaller than the effect of *C*-level (2.75 vs. 3.70 µV).

Anterior N1. *C*-level: The ANOVA on anterior N1 amplitudes revealed a significant main effect of Age [F(1,36)=9.61; p<.01], reflecting overall less negative-going deflections in older than younger participants [F(1,36)=11.29; p<.01], and a significant interaction of Age and *C*-level [F(4,148)=2.04; p<.05]. The main effect of *C*-level was not significant [F(1,36)=1.10; p=.30]. The anterior N1 was significantly larger in older participants with higher than lower processing speed [t(18)=3.68; p<.01]. In contrast, *C*-level did not significantly modulate the anterior N1 in the younger group [t(18)=1.44; p>.15]. There was no difference between older and younger participants with relatively high processing speed [t(18).=.20; p>.50], but there was a significant reduction for older as opposed to younger participants with relatively low processing speed [t(18)=4.26; p<.001] (Figure 3.8). Individual *C*-values were not significantly correlated with anterior N1 amplitudes across the whole sample [r=-.23; p=.14] or within the younger group [r=.25; p=.28]. However, a significant correlation was obtained in the older group [r=-.58; p<.01] (Figure 3.8).

K-level: Apart from the main effect of Age [F(1,36)=4.08; p<.05] already documented in the previous analysis, the ANOVA did not reveal any further significant main effects or interactions involving *K*-level.

[8] We assume the main effect of *K*-level to be a side effect of the covariance between both parameters (Finke et al., 2005; Habekost & Starrfelt, 2009), which resulted in a large overlap of participants' group assignments for comparisons of high- and low-performers regarding *C* and *K*.

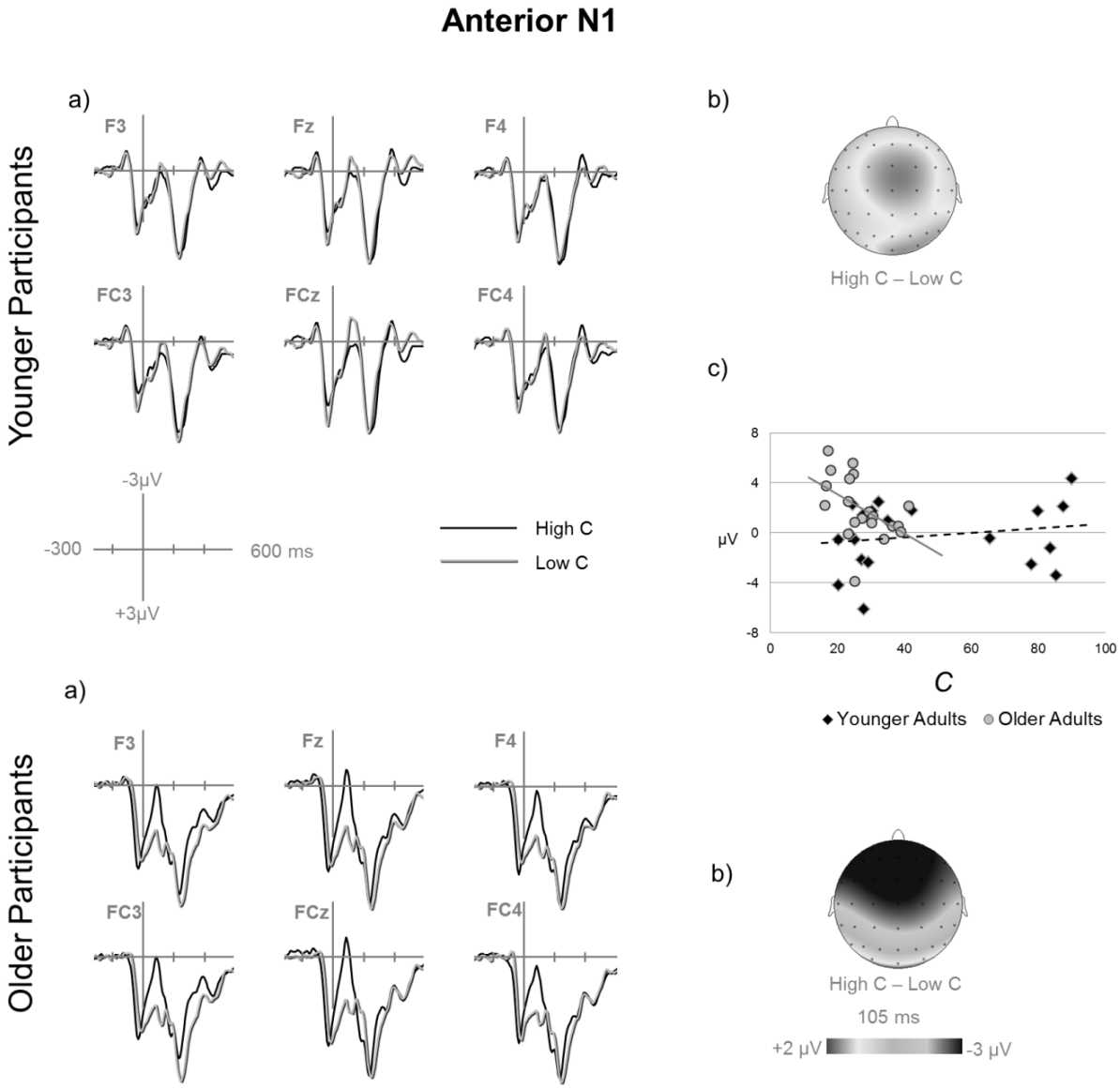

Figure 3.8: Anterior N1 as a neural marker of age-related decline in processing speed *C*. a) Grand-averaged ERPs of younger participants (upper panel) and older participants (lower panel), for participants with higher (black line) and lower processing speed *C* (grey line) at anterior electrode sites. b) Difference maps showing the activity of participants with lower processing speed subtracted from activity of participants with higher processing speed in the anterior N1 time range. c) Spearman correlations between anterior N1 amplitudes and individual *C*-values.

Contralateral delay activity. <u>*K*-level:</u> The ANOVA on CDA amplitudes gave rise to a significant main effect of Age [$F(1,36)=4.94$; $p<.05$], reflecting overall higher amplitudes in younger compared to older individuals, and a significant main effect of *K*-level [$F(1,36)=7.82$; $p<.01$], reflecting enhanced activations for participants with higher relative to lower storage capacity across age groups (Figure 3.9). There was no interaction of Age and *K*-

level [F(36,1)=.09; p=.76]. Accordingly, across all participants, individual *K*-values were significantly correlated with CDA amplitudes (r=-.55; p<.001; Figure 3.9).

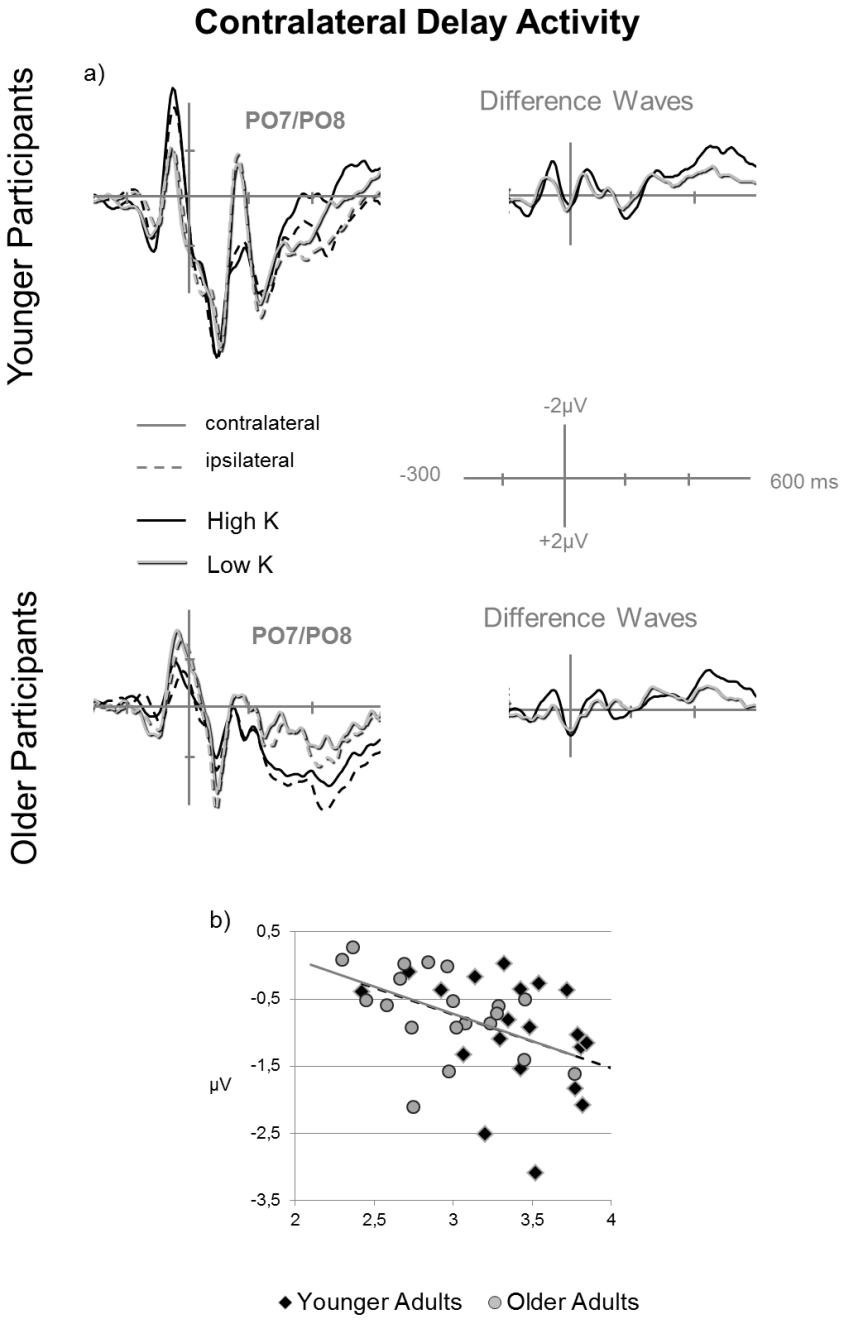

Figure 3.9: Contralateral delay activity as a neural marker of individual differences in storage capacity *K*.
The CDA in younger participants (upper panel) and older participants (lower panel). a) Grand-averaged ERPs (left) ipsilateral (dashed line) and contralateral (solid line) to the attended hemifield and (ipsi-minus-contra) difference waves of participants with higher (black line) and lower storage capacity *K* (grey line) at posterior-occipital electrodes. b) Spearman correlations between CDA amplitudes and individual *K*-values

C-level: Apart from the main effect of Age [$F(1,36)=4.15$; $p<.05$] already documented in the previous analysis, the ANOVA did not reveal any further significant main effects or interactions including *C*-level [all $F<.50$; all $p>.50$].

Central positivity. K-level: The ANOVA on central positivity 200-350 ms following array onset yielded a significant interaction of Electrode Position, Age, and *K*-level [$F(2,72)=4.60$; $p<.05$]. Separate follow-up analyses for the two age groups revealed a significant interaction of Electrode Position and *K*-level in the older group [$F(2,36)=4.45$; $p<.01$]. The interaction reflected a significantly higher activation for participants with higher as compared to lower storage capacity at right-hemispheric electrodes [$t(18)=2.61$, $p<.05$] but not at central and left electrodes [both $t(18)<1.50$, $p>.15$]. In contrast, *K*-level did not significantly modulate the activation level in the younger group [all $F<1.15$; all $p>.25$)]. When participants with relatively high storage capacity were compared across age levels, the central positivity was also significantly more pronounced at right electrodes [$t(18)=2.64$; $p<.05$], but not at central and left electrodes [both $t(18)<1.50$; $p>.15$]. When participants with relatively low storage capacity were compared, positivity did not significantly differ between older and younger participants, at any electrode position [all $t(18)<1.73$; all $p>.10$] (Figure 3.10). Across the whole sample, positivity at right electrodes was not significantly correlated with individual *K*-values ($r=11$; $p>.15$). Separate analyses for both age groups, however, revealed the correlation to be significant for older participants ($r=.51$; $p<.05$), but not for younger participants ($r=.27$; $p>.15$; Figure 3.10). Furthermore, a significant interaction of Site and Age [$F(1,36)=7.18$; $p<.05$] indicated comparable positivity at both sites in older participants [$t(19)<1.19$; $p<.25$] while in younger participants, positivity was significantly higher at central compared to centro-parietal sites [$t(19)=3.10$; $p<.01$].

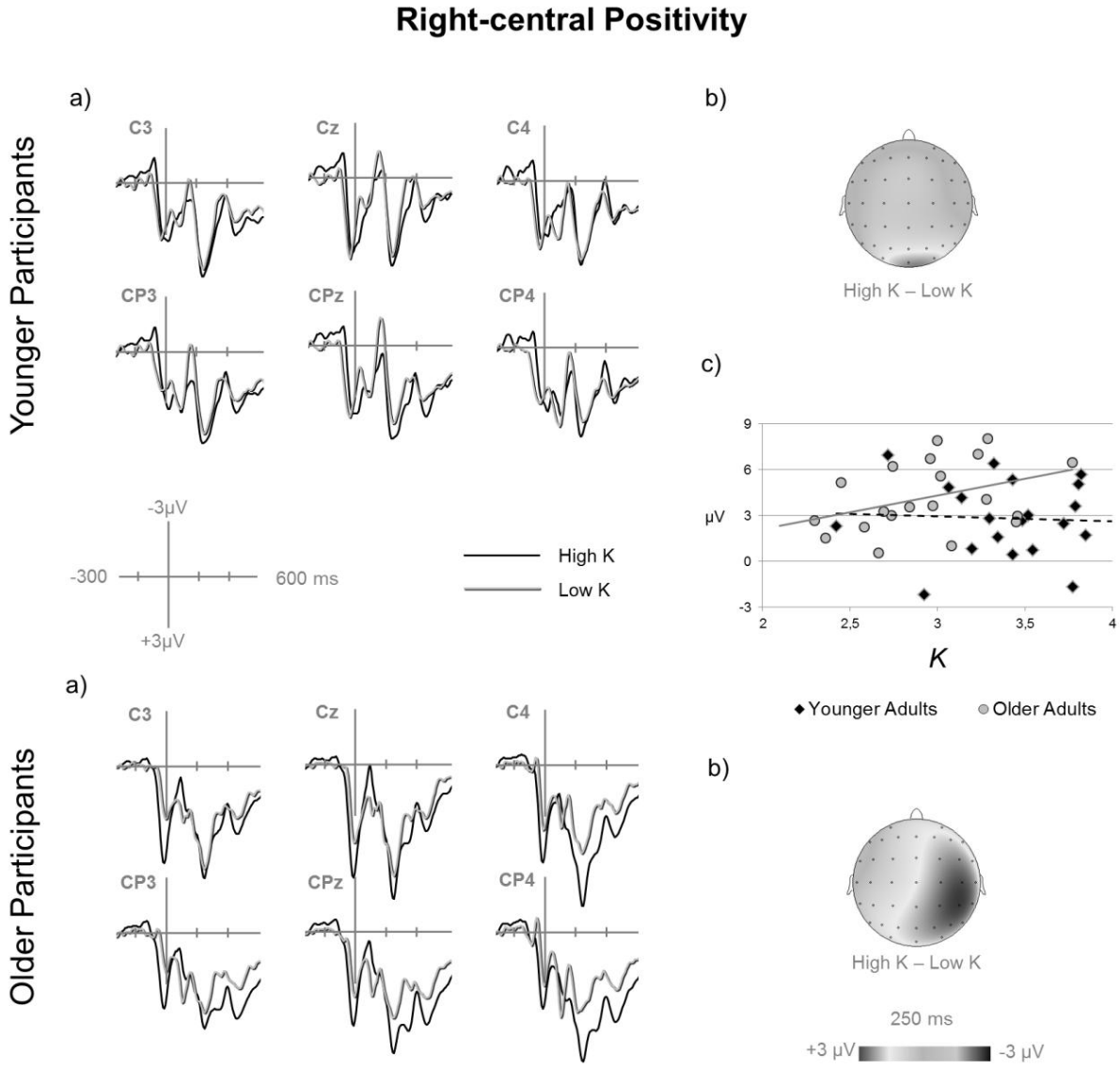

Figure 3.10: Right-central positivity as a neural marker of age-related reserve in storage capacity *K*.
The right-central positivity in younger participants (upper panel) and older participants (lower panel). a) Grand-averaged ERPs of participants with higher (black line) and lower processing speed *C* (grey line) at central electrode sites. b) Difference maps showing activity of participants with lower storage capacity subtracted from activity of participants with higher storage capacity in the time range of the right-central positivity. c) Spearman correlations between amplitudes of the right-central positivity and individual *K*-values.

C-level: The ANOVA revealed no significant main effect or interactions involving *C*-level [all F<.3.6; all p>.05], but gave rise to a significant interaction of Electrode Site, Electrode Position, and Age [F(2,72)=9.16; p<.01]. For older participants, a significant main effect of Electrode Position [F(2,72)=4.46; p<.01] was found, which indicated that positivity was amplified at right and central compared with left electrodes [both (t(19)>2.10; p <.05],

but did not differ between right and central electrodes [t(19)<.16; p=.87]. In younger participants, the main effect of Electrode Site [F(1,36)=9.62; p<.01] and the interaction of Electrode Site and Electrode Position [F(2,72)=9.16; p<.01] were significant, reflecting stronger positive deflections at centro-parietal than central sites, and that this difference was more pronounced at right and midline [both t(19)>2.10; p<.05] than left electrodes [t(19)=2.00; p=.06].

Influence of un-cued letters in the EEG experiment on ERP markers of processing speed and storage capacity

We controlled for the influence of attentional weight potentially (mis-)allocated to filler letters on the un-cued side in the EEG experiment by repeating all analyses (see above) without three outliers with enhanced α-values. In the remaining sample, the ERP correlates found for parameters processing speed *C* and storage capacity *K* could not be explained by individual differences in the efficiency of top-down control (because these are non-existent or negligibly small). For all ERP measures (posterior N1, anterior N1, CDA, right-central positivity), the same critical main effects and interactions involving the factors Performance Level and Age were revealed to be significant.

3.2.5 Discussion

In the present study, we compared ERPs of younger and older participants, who were divided into subgroups of relatively high and low performers according to individual TVA parameter estimates of visual processing speed *C* and vSTM storage capacity *K*, respectively. We found distinct ERP responses related to interindividual performance differences in the two functions across age groups, and furthermore, we dissociated neural correlates of decline and reserve specifically in aging participants.

ERP marker of individual differences in processing speed: The posterior N1. Visual processing speed *C* was reduced for older relative to younger participants, which is in accordance with age-related slowing that is commonly demonstrated in visual attention and many other cognitive tasks (e.g., Birren & Fisher, 1995; Bucur et al., 2008; Salthouse, 1994). The ERP marker of interindividual differences in processing speed identified for younger participants in the initial study (Wiegand et al., under review) was verified also in the older sample: Similar to the younger group, posterior N1 amplitudes were significantly lower in faster compared to slower elderly participants. N1 amplitudes have been previously shown to index the amount of neural resources required for the discrimination of visual object features (Vogel & Luck, 2000). Under conditions with constant task demands as in the present design, the component is considered to mark individual differences in the efficiency of visual discrimination processes. In particular, we assumed that the posterior N1 amplitude reflects the relative amount of available neural resources an individual must engage to discriminate the same visual stimuli at a given exposure duration (see also Wiegand et al., under review). The present results indicate that this relation is age-invariant. For younger as well as older participants, individuals with higher relative to lower encoding rates need to spend less attentional capacities for categorizing the letter stimuli successfully.

In contrast, the general age-related reduction in processing speed was not reflected in the posterior N1, i.e., amplitudes were not significantly higher in older than younger participants. Previous results are mixed, showing enhanced (e.g., Kutas et al., 1994; Yordanova et al. 2004), but also unvarying (Falkenstein et al., 2006; Kolev et al., 2006), or even reduced N1 amplitudes in older age (Czigler & Balazs, 2005). Critically, prior studies did not test whether age effects on N1 amplitudes are related to age differences in stimulus categorization processes, since the quality of visual discrimination (and potential age differences in the quality) has not been directly controlled for (DeSanctis et al., 2008). By

contrast, in the present whole report task, the effectiveness of conscious encoding and processing was directly assessed. In this case, N1 amplitudes marked performance differences only between relatively fast and relatively slow participants within, but not across, age groups. This result suggests that other mechanisms than the efficiency of resource allocation during object categorization, i.e., mechanisms that do not modulate the posterior N1 amplitudes, contributed to age decrements in processing speed.

Furthermore, the topography of the posterior N1 differed between age groups. A focal maximum at central-occipital sites was found for younger participants, whereas the component was more broadly distributed in older participants. These results are in line with earlier reports of age variations in the N1 scalp distribution (e.g., Polich, 1997). Specifically, a shift of the visual N1 distribution in older age has been previously suggested to indicate decline in basic sensory processing (DeSanctis et al., 2008; Plomp et al., 2012). However, the present age-related changes in N1 scalp distribution were found in all, faster as well as slower, older participants (Old low = Old high ≠ Young). This does not indicate that especially participants with a broader distribution of the N1 obtained a loss of distinctiveness of object representations; rather, it affected all older participants to a comparable degree. Presumably, the topography change is related to general age-related dedifferentiation in the visual cortex that might be compensated by only a subgroup of elderly individuals by additional mechanisms (see discussion below). Alternatively, it might result from anatomical and physical changes unrelated to performance (e.g., Frodl et al., 2001; Raz & Rodriguez, 2006; Sullivan & Pfefferbaum, 2006).

ERP marker of age-related decline in processing speed: The anterior N1. Interestingly, the anterior N1 was exclusively reduced in slower older participants relative to younger participants and older participants with faster processing speed. In addition, its amplitude was positively correlated with visual processing speed only in the older participant group (Old low ≠ Old high = Young). This pattern suggests that the anterior N1 reduction

indexes a selective loss of a speed-critical component of visual attentional functions in the elderly. In former studies on younger individuals, the anterior N1 was associated with early attentional control mechanisms that optimize stimulus processing, more precisely, voluntary attentional weight settings of task-relevant object features (Golomb et al., 2010; He et al., 2004, 2008; Töllner et al., 2009). Accordingly, sources of the anterior N1 have been localized within fronto-parietal areas (Clark et al., 1995; Di Russo et al., 2003) related to attentional control functions (Corbetta et al., 1998; Nobre et al., 1997). In former aging studies, a decrease of the anterior N1 co-occurred with visual encoding deficits in older participants (e.g., Curran et al., 2001; Czigler & Balász, 2005; Kutas et al., 1994; Snyder & Hillyard, 1979), indicating that the component marks age-related decline of fronto-parietal control processes required for visual stimulus encoding. The present results indicate that reduced anterior N1 responses are specifically associated with age-related slowing in visual processing speed, which results from impaired control of attentional guidance. Such early attentional control functions might be generally optimized in (higher and lower-performing) younger participants and their availability seems to be preserved in faster processing elderly. This interpretation can also be integrated with NTVA: The model assumes that within the N1 time range around 100-200 ms, attentional weights for a to-be-encoded stimulus array are computed at higher areas in the visual stream in order to prepare the processing system for the following information uptake. The lower N1 amplitude in slower older participants might reflect deficient setting of weight signals, which results in reduced encoding rates (Bundesen & Habekost, 2008).

Neural markers of visual short-term storage capacity K

ERP markers of individual and age differences in storage capacity level: The contralateral delay activity. In line with numerous previous aging studies, storage capacity *K* also significantly declined with age (e.g., Verhaegen et al., 1993). On the electrophysiological

level, the storage capacity decrement was associated with lower CDA amplitudes in older relative to younger participants. Furthermore, the CDA marked interindividual differences in storage capacity irrespective of age, being larger in participants with higher as compared to lower storage capacity in both samples. Correspondingly, CDA amplitudes were correlated with individual estimates of storage capacity across age groups. According to NTVA, storage in vSTM is neurally implemented as visuo-topically organized activation, which is sustained via recurrent feedback loops between the thalamus and visual cortical areas (Bundesen et al., 2005). The timing and topographical distribution of the CDA corresponds well to this proposed mechanism (see Wiegand et al., under review, for a detailed discussion).

The association between CDA magnitude and storage capacity was previously found to be weaker in older than in younger participants (Sander et al., 2011; but see Jost et al., 2010). Notably, in vSTM experiments with a single exposure duration (e.g., Luck & Vogel, 1997), an individuals' performance is presumably determined by both functions, storage capacity and also processing speed. However, the respective influence of the two components cannot be disentangled (e.g., Salthouse, 1994). In contrast, TVA-based assessment allows quantifying both parameters independently of each other by systematically varying the exposure duration (Duncan et al., 1999; Habekost & Starrfelt, 2009). Accordingly, we suggest that in order to obtain a reliable relationship with CDA amplitudes, it is essential to measure storage capacity appropriately, that is, unconfounded by processing speed. This is of particular relevance in aging studies, when systematic group differences in speed can be expected.

ERP marker of age-related reserve in storage capacity: The right-central positivity. Specifically in older individuals, storage capacity was associated with a right-lateralized centro-parietal positivity in addition to the (age-independent) CDA. Critically, the positivity was significantly larger in older participants with higher storage capacity compared to younger participants and also to older participants with lower storage capacity. Furthermore,

it correlated with individual storage capacity estimates only within the older group (Old high ≠ Old low = Young). These findings compare with previous neuroimaging studies reporting age-related activity increases that were associated with retained levels of performance (e.g., Cabeza et al., 2002; Fabiani et al., 2012). Among these, ERP investigations focused mainly on the 'P3' component, a centro-parietal positivity that is assumed to be generated within multiple areas of the fronto-parietal attention network (e.g., Knight, 1997; Makeig et al., 1999). In these studies, an augmented P3 was found only for elderly participants with high fluid processing abilities, which was interpreted to reflect compensation through enhanced attentional or executive control (e.g., Daffner et al., 2011; Riis et al., 2008). In younger individuals, specifically a right-distributed positivity has been linked to elaborated encoding of visuo-spatial information into vSTM (Müller & Knight, 2002; Polich et al., 1997). The present increase of right-central positivity only in elderly with high storage capacity suggests that these participants recruit additional resources to optimize their vSTM performance. A putative neural specification of such compensational mechanisms can be derived from NTVA. The model proposes that storage in vSTM is implemented as recurrent circular activity between thalamic, fronto-cortical, and posterior visual areas which initially coded the sensory information (Bundesen et al., 2011). In older age, the storage of visual object representations may be hampered by a decline in these posterior areas affecting the sustained activations of sensory neurons when stimulation itself has vanished (e.g., Faubert, 2002). However, elderly individuals with relatively high levels of storage capacity may be able to counteract this decrement to a certain degree by executive control mechanisms involved in vSTM storage, fostering, e.g., a deeper encoding of the stimulus material (Rypma & D'Esposito, 2000; Rypma et al., 2001). This interpretation is in accordance with fMRI studies showing that reduced activity in visual areas is compensated by increased frontal activation in high-performing elderly (e.g., Davis et al., 2008). In contrast, older participants with significant vSTM capacity reductions might not be able to call upon such reserve functions. For younger

participants, who do not suffer from compromised posterior cortical functions, maintenance of vSTM representations might be rather optimal without recruiting frontal control resources – and thus, they might not show any vSTM performance-related differences in the right central positivity.

Separability of processing speed and storage capacity in older age

Both TVA parameters, processing speed *C* and storage capacity *K*, were shown to decline with age (see also Habekost et al., 2012; McAvinue et al., 2012). However, not a common constraint seems to limit these abilities, in the sense of cognitive dedifferentiation with advancing age (Li et al., 2004). In fact, the inter-parameter correlation of *C* and *K* was smaller within the older than within the younger sample. Thus, the two parameters influence older individuals' visual attention capabilities rather more independently. In line with this, we replicated distinct electrophysiological markers related to processing speed on the one hand and storage capacity on the other in older individuals. Critically, additional correlates found exclusively in the older participant group, i.e., the anterior N1 in case of processing speed and the right-central positivity in case of storage capacity, were also distinct. These findings further strengthen the assumption of NTVA that the two general capacity parameters reflect discrete entities, which are supported by separate neural mechanism (Bundesen et al., 2005, 2011). Furthermore, our results imply that the distinctiveness of the two functions is preserved (or even increased) in older age.

Processing of non-attended letters

The ability to filter out irrelevant information is considered to be a critical determinant of interindividual differences and age-related decline in vSTM storage capacity (e.g., Jost et al., 2010; McCollough et al., 2007). In the present study, we therefore systematically controlled for the influence of filler items in the un-cued hemifield inherent in the lateralized

vSTM paradigm (e.g., Vogel & Machizawa, 2004) as a potential confound for the results on ERP correlates of storage capacity (and also processing speed). Specifically, we included trials from the EEG session in an extended, additional, fit to estimate the TVA top-down control parameter α, which expresses the relative weights of un-cued relative to cued letters (Kyllingsbæk, 2006)[9]. *Alpha*-values were overall low, indicating that most participants were able to use the cue highly effectively. In accordance with previous behavioral studies (McAvinue et al., 2012), older participants were nevertheless somewhat less effective than younger participants in allocating their available attentional weight to the target letters (95% vs. 98%). Critically, the identified ERP correlates of the two general capacity parameters were also found after excluding participants with relatively high α-values from the analyses. Thus, ERP differences marking age and/or interindividual differences in processing speed and storage capacity were verified within a sample of participants, whose distractibility by filler letters can be considered minimal. This implies that the identified electro-cortical markers are not attributable to differences in processing of the un-cued letters in EEG experiment but reflect genuine (attentional capacity) parameter changes.

3.2.6 Conclusions

In summary, we identified age-independent and age-related neural markers of distinct visual attention capacity parameters according to the formal TVA framework. Across age groups, interindividual differences in processing speed were associated with the posterior N1 response, which is assumed to reflect the efficiency of object discrimination processes. Interindividual and age differences in storage capacity were indexed by the magnitude of the CDA, which marks the amount of information hold in vSTM. In addition, we found distinct ERP correlates of both functions exclusively in the older sample. Only older individuals with

[9] Note that processing speed *C* and storage capacity *K* were estimated based on performance in the standard procedure using unilateral arrays in which the total attentional weight is allocated to the target letters

slower processing speed showed reduced anterior N1 amplitudes compared to fast elderly and all younger participants, indicating a selective decline in voluntary attentional guidance that slows categorization speed. Furthermore, only older participant with high storage capacity showed an enhanced right-central positive deflection, compared to low-capacity elderly and all younger participants, indicative of compensatory recruitment of attentional resources to retain high levels of vSTM performance in these participants. Taken together, our results demonstrate that distinct neural mechanisms determine visual attention abilities in older age, which depend on the availability and utilization of attentional control mechanisms to a larger degree that in younger age.

Author contributions

I.W., K.F., and T.T. designed the study. I.W. programmed and conducted the experiment, analyzed the data, and wrote the paper. M.D. programmed the TVA-fitting procedures and performed the analyses of the parameter alpha. K.F., H.J.M., and T.T. commented and revised the manuscript.

3.2.7 References

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IV. General Conclusions

4.1 Aim of the projects

Several theories of cognitive aging have claimed that a general limitation of attentional capacity accounts for a broad range of cognitive changes that occur with advancing age (e.g., Craik & Byrd, 1982). Furthermore, this limitation has been suggested to result from a central decrement of resources in the aging brain (e.g., West, 1996). While it is tempting to assume a single causal factor underlying the pattern of age-related changes in cognitive functioning, empirical findings from behavioral and neurocognitive research rather indicate that unitary models of cognitive aging lack specificity (e.g., Reuter-Lorenz & Park, 2010). Instead, multiple 'pools' of attention limitations may concur and explain the manifold pattern of cognitive changes in older age (Hartley, 1992; Wickens, 1980). The aim of the present PhD thesis was to specify the nature of diverse attentional resource limitations by disentangling several attentional components on the behavioral and neuronal level. More precisely, psychological paradigms that permit a fine-graded dissociation of attentional processes involved in a task were combined with ERPs, which allow separating brain activity that is related to these processes.

4.2 Aging and visual search

4.2.1 Key findings

In the first project, age-effects on different attentional components in a compound search task were electrophysiologically dissociated. Age-related slowing was demonstrated to originate at several stages in the processing stream: For older relative to younger participants, stimulus selection was slowed, analysis of stimulus features in vSTM was impaired, and selection and execution of the motor response was prolonged. In addition, intertrial analyses revealed that aging affected automatic and controlled processes in visual search differently: Weighting (or priming) of the search-relevant target dimension at the early stage of stimulus

selection and weighting of the motor response at the later stage of response execution was preserved in older age. In contrast, flexible S-R-mapping across trials on intermediate stages of S-R transmission was particularly impaired in older age.

4.2.2 Dissociating generalized slowing from specific factors

Our findings contribute to a central question in aging research, that is, to which extent age-related decline can be attributed to a general underlying factor and how specific factors contribute to this pattern (Fisk et al., 1992). In particular, there has been evidence for predominant age deficits in executively controlled processes (e.g., Castel et al., 2007; Mayr et al., 2001), while automatic processes were shown to be relatively preserved in older age (e.g., Kumada & Hibi, 2004; McCarley et al., 2004). However, proponents of uni-dimensional 'general slowing' accounts have argued that a higher degree of complexity simply leads to more pronounced age effects in tasks commonly employed to study executive functions, such as task-switching, dual-task paradigms, or task conditions that induce conflicts, compared to those assessing automatic processes, such as priming tasks (e.g., Cerella, 1980). In particular, age deficits are assumed to accumulate with the number of performed cognitive operations, and thus, to become more prominent with increasing numbers of operations involved. In the present design, the influence of general differences in task complexity on age effects could be ruled out by separating more automatic from controlled operations as well as from effects of general slowing within one single task.

In this way, the study of the first project demonstrated that age-related slowing in visual search – even when target selection is driven by a strong 'pop-out' bottom-up signal – already affected early allocation of attention to the target location. Slowing then pervaded throughout subsequent processing stages up to the production of the motor response. This finding appears to be in line with one-factor models, confirming that overall behavioral slowing indeed accrues across multiple stages in the processing stream (e.g., Brinley, 1965;

Salthouse, 1996). Possible unspecific deteriorations in the aging brain that may cause this general slowing are decelerated neural transmission due to reduced dendritic branching, less active synapses, reduction of particular neurotransmitters, or loss of myelin with advancing age (e.g., Reuter-Lorenz, 2002; Salthouse, 2000).

However, the study also demonstrated that general slowing does not fully explain the age effects that occur in visual search. The analyses of intertrial effects revealed that automatic repetition facilitation was supported by similar neural mechanisms in younger and older participants. In contrast, performance of the elderly suffered more when S-R associations had to be reconfigured across trials in comparison to younger adults. While priming or weighting processes are assumed to be largely independent from the availability of attentional resources, the flexible handling of S-R mappings across trial events is assumed to rely on resource demanding executively controlled processes (e.g., Hommel, 2004; Johnson et al., 2004). Thus, our findings also lend support to aging theories claiming that specific age deficits result from pre-dominant decrements in executive functions (e.g., West, 1996). The ERP modulations further indicated that this age deficit originated during S-R transmission processes, which are assumed to be controlled by fronto-parietal areas in the visual attention network (Madden, 2007; Pollmann et al., 2006). Therefore, our results are also in accordance with the assumption that age decrements stem from predominant structural and functional changes in fronto-cortical brain circuits (Raz et al., 2005; Resnick et al., 2003). One age-dependent alteration that might specifically impede S-R transmission processes in the elderly could be reduced connectivity between fronto-parietal areas that support visuo-motor transmission (e.g., Grieve et al., 2009). In addition, dopaminergic functioning is known to be affected by aging (Braver & Barch, 2002; Volkow et al., 2000). Recently, the efficiency of the dopaminergic system has been shown to be critical for retrieving S-R bindings (Colzato et al., 2011); its reduced efficiency in older age may also contribute to the specific deficit in S-R mapping processes.

In summary, the first study revealed general as well as specific resource limitations to contribute to the observable age-related changes in visual search performance. Age-related slowing affects processing throughout, but is not tenable as a unitary cause of decline. The involvement of processing components with high demands on attentional control, presumably relying on fronto-parietal areas within the visual attention network, leads to an additional, specific deficit in older age.

4.3 Distinct capacity limitations of visual attention

4.3.1 Key findings

In the second project, we identified neural correlates of the two general visual attention capacity functions proposed by (N)TVA, visual perceptual processing speed *C* and vSTM storage capacity *K*. ERP amplitudes were analysed according to individual performance levels, separately for each of the two parameters. In the initial study on younger participants, distinct ERP markers of individual differences in both functions were identified: The posterior N1 was smaller for participants with higher relative to lower processing speed. In contrast, the CDA was larger for participants with higher relative to lower storage capacity. In the second study, two age groups were compared with the same approach in order to investigate age-related changes in attentional parameters and neural markers of these processes. The previously identified ERP correlates of individual differences in processing speed and storage capacity were also validated in the older group. Furthermore, additional ERP components were found to index performance levels in each parameter only within the elderly sample: The anterior N1 was significantly reduced in older participants with lower processing speed levels relative to faster older participants and younger participants. The right-central positivity was enhanced in older participants with higher storage capacity relative to older participants with lower storage capacity and younger participants.

4.3.2 Neural markers of TVA parameters of attentional processing capacity

The results of the first study of the second project can be regarded as important pioneering work in several aspects. First, the identified neural correlates of processing speed *C* and storage capacity *K* provide direct empirical evidence for the NTVA assumption that the two parameters are related to distinct brain mechanisms (Bundesen et al., 2005, 2011). Moreover, our findings underline the specificity and validity of TVA-based assessment, which is currently the only way to achieve independent estimates of these two functions (Habekost & Starrfelt, 2009). Finally, they demonstrate the procedure's potential to integrate psychological and neurobiological processes within applied neuro-cognitive and clinical research in a highly specific manner.

In future studies, the present approach might be extended to examine further model assumptions. For instance, behavioral studies have demonstrated that internal states of the observer that can be experimentally manipulated, such as alertness (Matthias et al., 2010), arousal (Sørensen & Bundesen, 2011), or expectancy (Vangkilde et al., 2012), have a selective influences on TVA parameters. Furthermore, pharamacological studies have proven that processing speed *C*, but not storage capacity *K*, affected by psychostimulant drugs (Finke et al., 2010; Vangkilde et al., 2011). Combining ERPs with such within-subject manipulations could be used to investigate the neural mechanisms underlying intraindividual variations in attentional functions. In addition, the approach is particularly promising to unveil neural underpinnings of developmental- and pathology-related changes in attention abilities. Along these lines, we investigated the brain-behavior relationships that characterize attentional functioning of (healthy) older individuals in the second study.

4.3.3 Neural markers of age-related changes in TVA parameters

As expected, processing speed *C* and storage capacity *K* declined with age. This finding replicates the results of a number of studies showing deficits in mental speed and

visual span with aging (e.g., Salthouse, 1994, 1996). Both functions have been denoted as mediators of general cognitive abilities in older age (e.g., Verhaegen, 2011). What has been questioned is whether deficits in these two functions stem from decline in a single general limiting factor, and to what extent specific age-related changes differ from general interindividual differences in the functions (e.g., Kühn et al., 2011). The ERP results of the second study indicate that in older, similar to younger participants, individual differences in processing speed and storage capacity are related to the individuals' efficiency in discriminating object and upholding sustained activation of vSTM representations, respectively. In addition, two further mechanisms appearing to determine attention performance only in the older group were unveiled. First, deficient voluntary attentional weight setting within the first 100 ms after encountering information could be a critical factor for reduced encoding rates in older age. Second, elderly individuals who retain high levels of vSTM capacity seem to rely on the recruitment of additional resources for storage processes. Together, these findings indicate that the older brain is not simply less efficient than the younger one; rather, it undergoes reorganization processes that vary across aging individuals. In more detail, the specific age effects seem to result from age-dependent changes within attentional control functions supported by frontal-parietal areas of the attention network (Corbetta & Shulman, 2002). This is generally in accordance with aging theories proposing that executive functions mediated by frontal brain areas play a special role in older age (e.g., Cabeza, 2002; Raz et al., 2005). Furthermore, the effect of age-related changes in attentional control is not reducible to a unitary mechanism, but involves (at least) two distinct mechanisms supporting visual attention functions. Most interestingly, the integrity and potential for compensation within frontally-mediated control functions appears to be a critical determinant of whether attentional abilities decline with aging or are reserved in older individuals. Finally, the findings of the second study in the second project again validate the

conceptual advantage of the (N)TVA framework and exemplifie the virtue of applying the evolved approach to study attentional changes in special populations.

4.4 Multiple components of aging in visual attention

The present work demonstrates that unitary accounts to date may not suffice to explain cognitive aging. Rather, age-related changes in visual attention and their underlying brain processes appear to be multifaceted. The results highlight the value of the presently employed theory-driven neuro-cognitive approach to resolve this manifoldness. The combination of ERP measurements with established psychological paradigms based on theoretical frameworks of visual attention permitted to characterize the mechanisms underlying age-related changes in visual attention in a uniquely fine-graded manner. General and specific factors that decrease attentional functioning with aging were dissociated within the same participants and the same task; factors that are indivisible based on behavioral measures alone (e.g., Salthouse, 2000). Furthermore, the ERP data revealed that (quantitatively) behaviorally measured age-related reductions (e.g., of processing speed or visual capacity) are determined by qualitative changes in the aging brain. In particular, brain processes underlying separate key functions of attentional abilities were disentangled. Importantly, separate neural markers of age-invariant individual differences in these functions could be identified along with neural markers of declined and preserved abilities in older age. The identification of neural mechanisms underlying the integrity of attentional abilities in older age are especially relevant in the context of 'cognitive reserve' (Stern, 2002, 2009), meaning brain processes that support retained performance levels. The present results provide highly selective markers of cortical reorganization in support of attentional functions and emphasize the potential of brain plasticity as a critical determinant of cognitive functioning in aging individuals (Reuter-Lorenz & Park, 2010).

4.5 References

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Curriculum Vitae

PERSONAL INFORMATION

Name	Iris Wiegand
Date of birth	May 26th, 1985
Nationality:	German
Address:	Dietrich-Bonhoeffer-Str. 8 85567 Grafing b. München Germany
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EDUCATION

2010–2013	**PhD in Systemic Neurosciences** *Graduate School of Systemic Neuroscience* *LMU Munich* PhD thesis: Components of aging: Neurophysiological markers of age-related changes in visual attention (Supervision: Prof. H. J. Müller, PD Dr. K. Finke)	Munich Germany
2004 –2009	**Diploma in Psychology (1,0)** *Saarland University* Diploma thesis: Contributions of familiarity to associative recognition memory – an ERP study. (1,0) (Supervision: Prof. A. Mecklinger)	Saarbrücken Germany
1997–2004	**Abitur (1,8)** *Gymnasium Melle*	Melle Germany

WORK AND RESEARCH EXPERIENCES

January 2010 – December 2012	**Research Assistant** General and Experimental Psychology (Prof. H. J. Müller) Elite-Master-Program ‘MSc Neuro-Cognitive Psychology‘ *LMU Munich*	Munich Germany

March – December 2009	**Student Research Assistant** Experimental Neuropsychology Unit (Prof. A. Mecklinger) *Saarland University* International Research Training Group 'Adaptive Minds' (IRTG 1457)	Saarbrücken Germany
May 2007 – October 2008	**Student Research Assistant** Clinical Neuropsychology Unit (Prof. G. Kerkhoff) *Saarland University*	Saarbrücken Germany
January – July 2008	**Tutor** Brain & Cognition Unit (Prof. H. Zimmer) *Saarland University*	Saarbrücken Germany
November 2005 – December 2007	**Student Research Assistant** Brain & Cognition Unit (Prof. H. Zimmer) *Saarland Universit***y**	Saarbrücken Germany

PRESENTATIONS

December 2012	**Center of Excellent Cognitive Interaction Techonology – *Vision Science Colloquium*** Invited Talk: *Neural markers of interindividual and age differences in TVA parameters visual processing speed and vSTM*	Bielefeld Germany
July 2012	**Visual Search and Selective Attention Symposium – *VSSA 2012*** Poster: *ERPs dissociate TVA parameters of visual perceptual processing speed and vSTM capacity*	Holzhausen Germany
June 2012	**International TVA Network Meeting – *iTVA 2012*** Invited Talk: *Event-related potentials differentiate TVA parameters of general capacity*	Copenhagen Denmark
April 2012	**54. Tagung experimentell arbeitender Psychologen - *TeaP 2012*** Symposium: *Adult age differences in visual cognition*	Mannheim Germany

	Talk: *Adult age difference in visual search from perception to response*	
September 2011	**11th International Conference on Cognitive Neuroscience - *ICON 2011*** Poster: *Event-related potentials differentiate perceptual and short-term memory related TVA parameters*	Palma, Mallorca Spain
June 2011	**Seminar 'Neurofeedback – Klinische Anwendungsgebiete' - *Akademie bei König & Müller*** Lecture: *Neurofeedback bei Patienten mit erworbenen Hirnschädigung*	Würzburg Germany
March 2011	**53. Tagung experimentell arbeitender Psychologen - *TeaP 2011*** Poster: *Altersbedingte Verlangsamung in Visueller Suche: Eine neuro-chronometrische Analyse*	Halle (Saale) Germany
February 2011	**15th Ann. Meeting of the Biofeedback Foundation of Europe - *BFE Meeting 2011*** Poster: *EEG-Correlates of attention in brain-injured patients and healthy controls*	Munich Germany

PUBLICATIONS

Wiegand, I., Töllner, T., Müller, H. J., Finke, K. (in preparation). ERP markers of age-related changes in visual capacity – a TVA-based study. (PhD thesis)

Wiegand, I., Töllner, T., Habekost, T., Dyrholm, M., Müller, H. J., Finke, K. (under review). ERP correlates of visual processing speed and visual-short term storage capacity. (PhD thesis)

Wiegand, I., Müller, H. J., Finke, K., Töllner, T. (2013). Event-related potentials dissociate perceptual from response-related age effects in visual search. *Neurobiology of Aging. 34*, 973-985. (PhD thesis)

Wiegand, I., Bader, R., Mecklinger, A. (2010). Mulitple ways to the prior occurrence of an event: An electrophysiological dissociation of experimental and conceptually driven familiarity. *Brain Research,* 1360, 106-118.

Wiegand, I., Keller, I. (2009). EEG-Korrelate der Aufmerksamkeit bei Gesunden und Patienten mit Hirnschädigung. *Zeitschrift für Neuropsychologie,* 20, 4.

Summer/Autumn 2012	**Supervision Research Project: The role of context in visual search in schizophrenia (Tessa Rusch)** MSc Neuro-Cognitive Psychology (2nd/3rd Semester) *Charité, Department of Psychiatry and Psychotherapy, Berlin and LMU Munich (with Prof. P. Sterzer)*	Berlin/Munich Germany
Summer 2012	**Tutorial: Neuro-Cognitive Methods** MSc Neuro-Cognitive Psychology (2nd Semester) *LMU Munich*	Munich Germany
Summer 2012	**Supervision Masterthesis: Age-related modulations in perceptual grouping and attentional guidance during global and local search (Cornelja Starman)** MSc Neuro-Cognitive Psychology *LMU Munich (with PD Dr. M. Conci, Dr. T. Töllner)*	Munich Germany
Winter 2010/11	**Research Seminar: ERP studies of age-related changes in perceptual grouping** MSc Neuro-Cognitive Psychology (3rd Semester) *LMU Munich (with PD Dr. M. Conci, PD Dr. K. Finke)*	Munich Germany
Winter 2010/11	**Research Seminar: Parameter-based assessment of attentional changes in schizophrenia** MSc Neuro-Cognitive Psychology (3rd Semester) *Department of Psychiatry and Psychotherapy, LMU Munich (with PD Dr. K. Finke, PD Dr. K. Hennig-Fast)*	Munich Germany
Winter 2010/11	**Research Seminar: Aging and visual grouping** MSc Neuro-Cognitive Psychology (3rd Semester) *LMU Munich (with PD Dr. M. Conci)*	Munich Germany
Summer 2010	**Clinical Blockseminar: Neglect** MSc Neuro-Cognitive Psychology (2nd Semester) *Schön Klinik Bad Aibling (with Prof. Ingo Keller)*	Bad Aibling Germany
Summer 2010	**Tutorial: Neuropsychological Assessment**	Munich Germany

MSc Neuro-Cognitive Psychology (1st Semester)
LMU Munich

SCIENTIFIC TRAINING (SELECTED COURSES)

October 2012	**Summerschool: EEG and fMRI analyses with EEGLab and SPM** *Hanse-Wissenschaftskolleg* Prof. S. Debener and others	Delmenhorst Germany
June 2012	**ERP Bootcamp** *Center for Visual Cognition, University of Copenhagen* Prof. S. Luck	Copenhagen Denmark
February 2012	**Workshop: fMRI theory, application and practice** *Graduate School of Systemic Neuroscience* Dr. T. Stephan, Dr. V. Flanagin and others	Planegg-Martinsried Germany
June 2011	**Workshop: Theory of Visual Attention** *University of Copenhagen* Assoc. Prof. T. Habekost, Assoc. Prof. S. Kyllingsbæk and others	Copenhagen Denmark
May 2011	**Workshop: Human modeling** *Graduate School of Systemic Neuroscience* Prof. S. Glasauer u.a.	Martinsried Germany
Winter 2010/11	**Seminar: TMS theory and practice** *LMU Munich* Dr. P. Taylor	Munich Germany
October 2010	**Workshop: Brain oscillations and cognitive processes** *LMU Munich* Prof. W. Klimesch	Munich Germany
Summer 2010	**Seminar: Transforming numbers into objects: the basics of programming an experiment with MATLAB** *LMU Munich* PD Dr. M. Conci	Munich Germany

INTERNSHIPS

October 2008 – February 2009	**Schön Klinik Bad Aibling** *Clinical Internship: Neuropsychology* Research project: Neurofeedback in brain-injured patients with attention deficits Supervision: Prof. I. Keller	Bad Aibling Germany
February – March 2007	**Max-Planck Institute of Cognitive Brain Sciences** *Research Internship: Cognitive Neuropsychology Unit* Research project: Artificial grammar learning Supervision: Dr. J. Müller	Leipzig Germany

GRANTS

November 2010	**Full PhD-stipend (24 month)** *Elite Network Bavaria*
May 2009	**Student stipend for "Outstanding diploma thesis" (6 month)** *Psychology Department, Saarland University*

IT SKILLS

SPSS, MatLab, E-Prime, VisionAnalyzer, EEGLab, EEProbe, Brain Voyager, SPM, Citavi/Endnote, MSOffice, PowerPoint

LANGUAGE SKILLS

English (fluent), French (basic), Danish (basic)

List of publications

Wiegand, I., Finke, K., Müller, H. J., & Töllner, T. (2013). Event-related potentials dissociate perceptual from response-related age effects in visual search. *Neurobiology of Aging, 34*(3), 973-985.

Wiegand, I., Töllner, T., Habekost, T., Dyrholm, M., Müller, H. J., & Finke, K. (under review). Distinct neural markers of TVA-based visual processing speed and short-term storage capacity parameters.

Wiegand, I., Töllner, T., Dyrholm, M., Müller, H. J., & Finke, K. (in preparation). Neural markers of age-related decline and reserve in visual processing speed and visual short-term memory storage capacity.

List of author contributions

‘Event-related potentials dissociate perceptual from response-related age effects in visual search’

I.W., K.F., and T.T. designed the study, based on experimental procedures formerly designed by T.T.. I.W. programmed and conducted the experiment, analyzed the data, and wrote the paper. K.F., H. J.M., and T.T. commented and revised the manuscript.

‘Distinct neural markers of TVA-based visual processing speed and short-term storage capacity parameters‘

I.W., K.F., and T.T. designed the study. I.W. programmed and conducted the experiment, analyzed the data, and wrote the paper. M.D. programmed the TVA-fitting procedures and performed the analyses of the parameter alpha. K.F., H.J.M., T.T., T.H., and M.D. commented and revised the manuscript.

‘Neural markers of cognitive decline and reserve in perceptual processing speed and working memory storage capacity’

I.W., K.F., and T.T. designed the study. I.W. programmed and conducted the experiment, analyzed the data, and wrote the paper. M.D. programmed the TVA-fitting procedures and performed the analyses of the parameter alpha. K.F., H.J.M., and T.T. commented and revised the manuscript.

Prof. Hermann J. Müller (Head of the General and Experimental Psychology, LMU Munich)

Declaration

I hereby confirm that this dissertation ‘Components of aging: Neurophysiological markers of age-related changes in visual attention’ is the result of my own work and that I have only used sources or materials listed and specified in the dissertation. A full list of the references employed has been included. For parts of the work that contains or is based on co-authored manuscripts or published articles, my contributions to the article and of all co-authors are declared.

Munich, January 2013

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Iris Wiegand