# Neural markers of attentional parameters in the ageing brain

Graduate School of
Systemic Neurosciences
LMU Munich

**Dissertation der Graduate School of Systemic Neurosciences der**

**Ludwig-Maximilians-Universität München**

Submitted by **Natan Edward Napiórkowski**

**March 2019**

Supervisor

**Prof Dr. Hermann Müller**

Department Psychologie

Lehrstuhl Allgemeine und Experimentelle Psychologie

Ludwig-Maximilians-Universität München

First Reviewer: **Prof Dr. Hermann Müller**

Second Reviewer: **PD Dr. Kathrin Finke**

Third Reviewer: **PD Dr. Thomas Töllner**

External Reviewer **Prof. Veronica Mazza, PhD**

Date of Submission: March 25th 2019

Date of Defense : July 23rd 2019

## Abstract

The studies presented in the current PhD thesis aimed at investigating the neural correlates of distinct aspects of visual attention, i.e., spatial bias, efficiency of top-down control and visual processing speed and how they change with healthy ageing. The presented studies are theoretically grounded on Bundesen's Theory of Visual Attention, which provides a mathematical framework enabling quantifying various visual attention functions as the independent parameters of the model. A more recent neural interpretation of these attentional processes – NTVA – served as a basis for investigating attentional processing in combination with neurophysiological techniques. In the presented thesis, we combined TVA-based partial- and whole-report tasks with briefly presented letter arrays that enable mathematically independent estimations of the attentional parameters with simultaneous EEG recording. Extracting event-related lateralizations (ERL) from the signal provided fine-graded neurophysiological signatures of the attentional processes involved in the tasks.

In the first empirical study, we combined a partial report task with ERP measurement and aimed at investigating how attentional spatial bias and top-down control efficiency are reflected in the electrophysiological brain activity of healthy participants of between 20 and 35 years of age. We divided participants into groups with more and less efficient top-down control and left- and rightward spatial bias, respectively. First, an ERL component – the PCN wave – reflecting interindividual differences in top-down control efficiency was identified by comparing participants with more relative to less efficient top-down control. Participants with more, compared to less efficient top-down control showed higher PCN amplitudes. Second, we identified asymmetries in earlier visual ERLs reflecting the direction of the spatial bias by comparing participants with a bias

towards left or towards right hemifield. Our results show that these two distinct functions of attention are exclusively reflected by the amplitudes of the distinct ERLs.

In the second study, we aimed at investigating whether top-down control efficiency is affected by healthy ageing and whether it is similarly reflected in older adults by the amplitude of the lateralized components PCN and Ppc, as reported for younger adults. To pursue this goal we employed an identical methodology as in the first study to additionally test older adults ranging between 33 and 77 years of age. To control for a potential influence of (the amount of) cognitive reserve, we included crystallized IQ as a common proxy for cognitive reserve in the analyses. We divided participants into individuals with more relative to less efficient top-down control and lower versus higher level of cognitive reserve. We found comparable top-down control efficiency values across age groups and, furthermore, that across all age groups, participants with more efficient top-down control showed higher amplitudes of both the Ppc and the PCN waves. We further found that the amount of cognitive reserve modulated the relation between age, top-down control efficiency, and ERLs amplitudes. More precisely, only in participants with higher crystallized IQ Ppc amplitude was higher in participants with more efficient compared to less efficient top-down control. In contrast, in participants with lower crystallized IQ the PCN amplitude decreased significantly with age.

In the third study, we combined a whole report task with ERP assessment. We aimed at investigating whether and how visual processing speed is reflected in the neural activity of the brain as indexed by ERLs, and whether this potential relation is affected by healthy ageing. We assessed visual processing speed in a sample of participants ranging from 20 to 78 years of age. Participants were divided into groups with relatively low versus high visual processing speed. Data revealed that visual processing speed declines with age. Further, we identified two lateralized components indexing individual differences in visual processing speed: N1pc and PCN. Both components had increased amplitudes in participants with higher processing speed. Furthermore, amplitudes of the N1pc was increased and latency of the PCN was delayed in older, compared to younger, participants. These age-related changes in the components reflecting visual processing speed may suggest that younger versus older participants employ different mechanisms while performing the whole-report task. More precisely, younger participants may encode the entire display at the early stage of processing and then select relevant information, whereas older ones rather preselect relevant information during an initial phase.

The evidence collected across the three ERP studies provides valuable insights into the relation between efficiency of attentional functions, brain activity, and healthy ageing. We found that trajectories of age-related changes of distinct attentional functions are substantially different. Age also does not affect all electrophysiological correlates of functions of attention equally. Finally, our studies show that the relation between efficiency of attentional functions and their neurophysiological correlates is influenced by the amount cognitive reserve.

# Table of Contents

# Table of Figures

## Study 1: Age-dependent differences in visual processing speed and early, spatially selective processing: New insights from N1pc and PCN waves

## Study 2: Aging, efficiency of visual attentional selection and cognitive reserve: insights from event-related EEG lateralizations.

## Study 3: Age-dependent differences in visual processing speed and early, spatially selective processing: New insights from N1pc and PCN waves

**Abbreviations**

EEG - Electroencephalography

ERL - Event related lateralization

ERP – Event related potential

FIRM - Fixed-capacity Independent Race Model

fMRI - functional magnetic resonance imaging

MCI - Mild cognitive impairment

MWT-B Mehrfachwahl-Wortschatz-Intelligenz-Test B

N1pc - N1-posterior-contralateral

NTVA- neural Theory of Visual Attention

PCN – Posterior-Contralateral Negativity

PET - positron emission tomography

Ppc - Positivity-posterior-contralateral

TVA - Theory of visual attention

VSTM - Visual short-term memory

# 1. Introduction

## 1.1. Neural processes underlying functions of visual attention.

At any given moment the amount of visual information reaching our visual system exceeds the limited capabilities of the human brain to process each element separately and in sufficient detail by far (e.g. Broadbent, 1958). Thus, an ability to select only relevant information out of a great number of available, but irrelevant stimuli is necessary for the efficient functioning in the environment. This complex ability is called visual attention.

From a neurobiological perspective, processing information requires highly energy-demanding firing of neurons that influence the total amount of energy required by the brain (Attwell and Laughlin, 2001). The total amount of energy available for the brain at a given moment is basically constant and cannot be increased significantly in order to process more information (Clarke and Sokoloff, 1994). Therefore, the ability to efficiently reduce the amount of processed input by extracting its most relevant elements, while ignoring less relevant ones, is crucial for functioning. In the visual domain, visual selective attention is the function that controls the distribution of highly limited cognitive resources in order to maximize the efficiency of processing information relevant to the observer's states and goals (Allport, 1989; Desimone and Duncan, 1995; Posner and Petersen, 1990).

## 1.2. Theory of Visual Attention (TVA)

The scientific investigation of visual attention requires a coherent description (i.e. a model) of the functioning of the postulated attentional processes. Such a model must, in turn, permit formulating hypotheses and offer means to test them. Therefore, the three studies presented in the present thesis are theoretically grounded on the Theory of Visual Attention (TVA, Bundesen, 1990). TVA is a formal mathematical model of the basic mechanisms of visual attention that provides a computational framework enabling modelling various attentional components as mathematically independent parameters (Kyllingsbæk, 2006; Dyrholm et al., 2011). TVA was developed on the basis of earlier models describing visual attentional selection.

An important attempt to model the processes involved in attentional selection was a *choice model* proposed by Luce (1963). According to this model, the probability of selecting a given object (e.g. red letter appearing on a screen) is influenced by two mechanisms, perceptual similarity and decision bias. Formally, the probability of reporting an object *i* while stimulus *k* is being presented is given by:

$$P(k,i)=\frac{\eta(k,i)\beta_i}{\sum_{j=1}^{n}\eta(k,j)\beta_j} \tag{1}$$

where $\eta(k, i)$ denotes the measure of similarity of the reported object *i* to the presented object *k* and parameter $\beta_i$ represents a measure of the general bias towards identifying any presented objects as object *i*. The probability $P(k, i)$ is represented as a fraction of all other possibilities to make any other categorization. Each memory representation *j* (i.e. template of the stimulus) specifies its sensory features (e.g. colour, shape, size). The comparison of stimulus *k* against the memory template *j* provides a measure of a match between object and template: $\eta(k, j)$. In addition, an observer can be predisposed to generally assign any stimuli to the category *j*, which can be expressed by the value $\beta_j$

which is independent of the actual stimulus. In other words, performance in the task increases with the strength of the similarity of the reported object *i* to the presented object *k* and the general bias towards identifying any object as *i* (described by the numerator of the equation 1). On the other hand, performance decreases with the overall strength of similarities of the element *k* to all other *n* elements stored in the memory and biases towards reporting them (described by the denominator of the equation 1). Thus, the selection of an object is more probable if the object is similar to the representation of a target object and the observer is biased towards selecting objects from the particular category.

The choice model has been successfully used to predict performance in a partial report task (Bundesen et al. 1984, 1985; Bundesen 1987). In the partial report experiment participants are briefly presented with multiple objects (typically alphanumerical characters) and are asked to selectively report as many target objects as possible, while ignoring the distractors. Target and distractor objects can be defined by their properties such as location, colour, size or shape (e.g. Sperling, 1960; von Wright, 1968). The description of task performance accuracy (i.e. number of correctly reported target letters) provided by the choice model is based on three main assumptions. The first assumption is that performance in the partial report task reflects the number of target elements that successfully entered the visual short-term memory (VSTM) store. This buffer is characterized by its limited capacity K (see: Sperling, 1967), which is assumed to be independent from the type of the entering elements. The maximum capacity K of the VSTM store has been empirically shown to be 3 to 4 elements (Sperling 1960; Bundesen et al. 1984; Shibuya and Bundesen 1988; Luck and Vogel, 1997; Lee and Chun 2001). The second assumption of the choice model is that the duration of the stimulus exposure is long enough to fill up the VSTM store. Finally, the third assumption of the model is that each presented object has a certain attentional weight *w*. As long as the VSTM store is not entirely filled, the probability of a given object to be encoded is described by its attentional weight $w$ divided by the sum of weights of all other elements being processed (Luce, 1959). In case of a display of alphanumerical characters, where targets and distractors differ only in colour, one can also assume that all targets have the same weights $w_t$, and all distractors have the same weights $w_d$. The ratio of the distractor and target weights is termed parameter top-down control efficiency $\alpha$ and is one of the key parameters of the choice model:

$$\alpha = \frac{w_d}{w_t} \tag{2}$$

The parameter $\alpha$ describes the efficiency of attentional selection. A parameter value approaching 0 means that weights of distractors are significantly lower than those of targets and, therefore, that the probability of a distractor to be encoded into VSTM is low. Thus, the lower the parameter $\alpha$ value, the more efficient is top-down control. In contrast, a value of parameter $\alpha$ approaching 1 means that the weights of the targets and distractors are relatively equal and, therefore, that the probability to be encoded into the store is relatively comparable for targets and distractors. Thus, higher parameter $\alpha$ values indicate less selective processing.

Comparing attentional weights for the left and the right hemifield averaged across target and distractor objects, provides an estimate of the parameter spatial bias $w_\lambda$ reflecting the spatial distribution of attentional weights,. It can be expressed as:

$$w_\lambda = \frac{w_L}{w_L + w_R} \tag{3}$$

where $w_L$ and $w_R$ denote the attentional weights allocated to objects presented in the left and right visual field, respectively. If the spatial distribution of attention is balanced across hemifields, the parameter $w_\lambda$ equals 0.5. Values smaller than 0.5 indicate a bias towards the right side, values higher than 0.5 a bias towards the left.

A choice model is, however, a non-process model (see: Townsend and Ashby, 1982), i.e. it explains the results of target selection and provides accurate predictions for the partial report task results, but does not describe the temporal aspect of the selection process. Compared to this, the *race model,* which was developed to incorporate the temporal course of attentional selection, is wider in scope. Bundesen (1987) showed that a choice model can be derived from the simplified race model. In the race model, multiple objects in the visual field are competing to get encoded to the VSTM. According to a particular version of the race model, the Fixed-capacity Independent Race Model (FIRM, Shibuya and Bundesen, 1988), processing capacity is constant and also the VSTM store capacity is fixed and limited (similar as in the choice model). The FIRM model describes attentional selection as a process with two consecutive stages. First, an attentional weight *w* is assigned to each object in the visual field. The higher weight *w* represents stronger sensory evidence that the given object is a target (e.g. red letter in contrast to blue distractor letters). Second, the total processing capacity *C* available in the visual system is distributed among the processed objects proportional to their attentional weights. The process of encoding information into the VSTM begins with a short delay after the stimulus onset (denoted *t0*). Thus, the parameter *t0* is a measure of the threshold of conscious perception, i.e. the minimum effective stimulus exposure duration. As long as the encoding process is active, the time required to encode an element *x* into the VSTM is described in a probabilistic manner by an exponential distribution:

$$F(t) = 1 - \exp(-v_x * t) \tag{4}$$

where $v_x$ denotes the amount of processing speed allocated to the processed object *x* and *t* denotes time. An example of the exponential function described by the equation (4) is presented in Fig. 1.

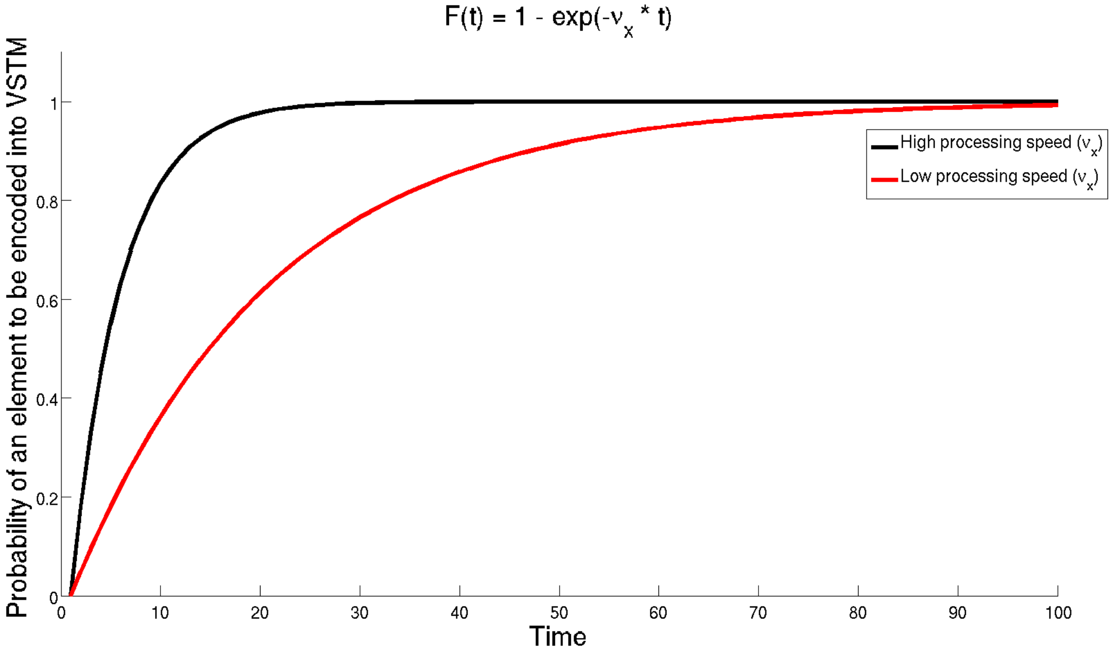


**Fig. 1. An example of the exponential function.** The function describes the probability of a visual element to be encoded into the VSTM. The probabilities are presented separately for high (black line) and low (red line) values of processing speed $v_x$.

The process of encoding information lasts until either all elements in the display are encoded (assuming that the number of elements is lower than the VSTM capacity *K*), the VSTM store is full, or the display time has elapsed.

Due to the incorporation of time in the model, the FIRM model provides an accurate description of performance accuracy in the task with variations of number of targets, number of distractors and of stimulus exposure durations. Modelling the probability distribution of the performance in a given task can be done by the estimation of five intentional parameters predicted by the model: *K* (VSTM store capacity), *C* (total processing capacity), *t0* (threshold of conscious perception), *α* (efficiency of attentional selection) and $w_\lambda$ (spatial bias).

Bundesen's Theory of Visual Attention is a computational model that integrates the choice model of Luce (1963) describing single object recognition with the race model of Shibuya and

Bundesen (1988) describing temporal aspect of attentional processing. More precisely, TVA links the 4 parameters of the FIRM model with two parameters of the choice model- $\eta$ (perceptual similarity) and $\beta$ (decision bias). According to TVA, selection and recognition are not distinct mechanisms, but occur simultaneously as two aspects of the same processing mechanism. All elements present in the visual field are processed in parallel in two stages. In the first stage each object is compared with representations stored in visual long-term memory. Based on the sensory evidence $\eta(x, j)$ that an object $x$ belongs to a category $j$ (within the set of all categories $R$), an attentional weight $w$ is attributed. The efficiency of this process is assumed to be independent from the number of processed elements. The outcome of that process depends also on the pertinence value $\pi_j$ of the category $j$:

$$w_x = \sum_{j \in R} \eta(x, j) \pi_j \tag{5}$$

In the second stage all objects are competing to be encoded into the VSTM store. As in the choice model, the capacity of the VSTM is assumed to be limited to $K$ elements and the race is terminated after the VSTM store is filled up. The processing rate $v(x,i)$ of an object $x$ is given by the equation (6):

$$v(x,i) = \eta(x,i) \beta_i \frac{w_x}{\sum_{z \in S} w_z} \tag{6}$$

where $\eta(x,i)$ denotes the sensory evidence that the given object $x$ belongs to the category $i$ and value $\beta_i$ denotes the perceptual decision bias of the category $i$ (see choice model), $S$ denotes the set of all elements being present in the visual field and $w_x$ and $w_z$ denote attentional weights of elements $x$ and $z$ respectively. Thus, the processing rate of an element $x$ is a fraction of the sum of the attentional weights of all elements being processed.

Broadbent (1971) has suggested that efficient attentional selection requires two distinct mechanisms to operate: one is filtering relevant information by its pertinence (i.e. selection of objects) and the second is pigeonholing based on the attentional bias (i.e. selection of features). In TVA these two processes are related to the two above-mentioned equations: (5) and (6). The filtering mechanism is based on the distribution of the attentional weights and is represented by the equation (5). If the pertinence value $\pi_j$ of a category $j$ is high compared to the pertinence value of the other categories, the selection probability of any object $x_j$ belonging to this category is increased proportionally to the value $\eta(x, j)$, which provides sensory evidence that the object $x$ belongs to the factorized category $j$. As a result, the processing of objects belonging to the category $j$ is prioritized at the expense of other objects. The pigeonholing mechanism is related to the perceptual bias value $\beta_i$. Assuming that the currently relevant category is the category $i$ (e.g. objects being red), the categorization of each element as belonging to the category $i$ is favoured if the bias associated with the category $i$ is proportionally higher than biases associated with all other categories. Therefore, an increased value $\beta_i$ in the rate equation (6) increases the processing rates of all objects belonging to the category $i$ (i.e. all red objects).

## 1.3. Neural circuits potentially involved in visual attention

The neural implementation of the mechanisms of attentional selection described by TVA is still subject of an ongoing debate. Desimone and Duncan (1995) proposed that the biased competition between visual objects takes place in two major processing streams within the cortex. Each stream leaves from the primary visual cortex (V1, striate cortex) that receives visual input. The first stream is a ventral pathway directed into the inferior temporal cortex, which is assumed to enable object recognition. The second stream is a dorsal pathway directed to the posterior parietal cortex. The dorsal stream is assumed to enable spatial perception and visuo-motor performance (Ungerleider and Mishkin 1982). More recently, a basic concept of TVA, i.e. a biased competition account of attention has been linked to the neuronal activity in the visual system by the 'Neural Theory of Visual Attention" (NTVA, Bundesen et al. 2005). In NTVA, neurons within the visual system are assumed to be specialized in representing distinct features and responding exclusively to one visual object at a time. The sum of activation related to processing an object is proportional to 1) the number of neurons in which the processed category is represented (represented by $\pi_j$ in the equation [5] and 2) to the firing rates of the neuron coding features of the processed object) represented by $\beta_i$ in the equation [6]. The filtering operates through dynamic remapping of the receptive neuronal fields in the cortex in order to dedicate more cells to the relevant categorization processing and less to the irrelevant one. The mechanism of pigeonholing is related to the multiplicative scaling of the activation level in the cells coding the given feature. Therefore, the categorization of a visual object is proportional to the total activation generated by the number of neurons (filtering) and the rate of firing of the individual neurons representing the categorization (pigeonholing).

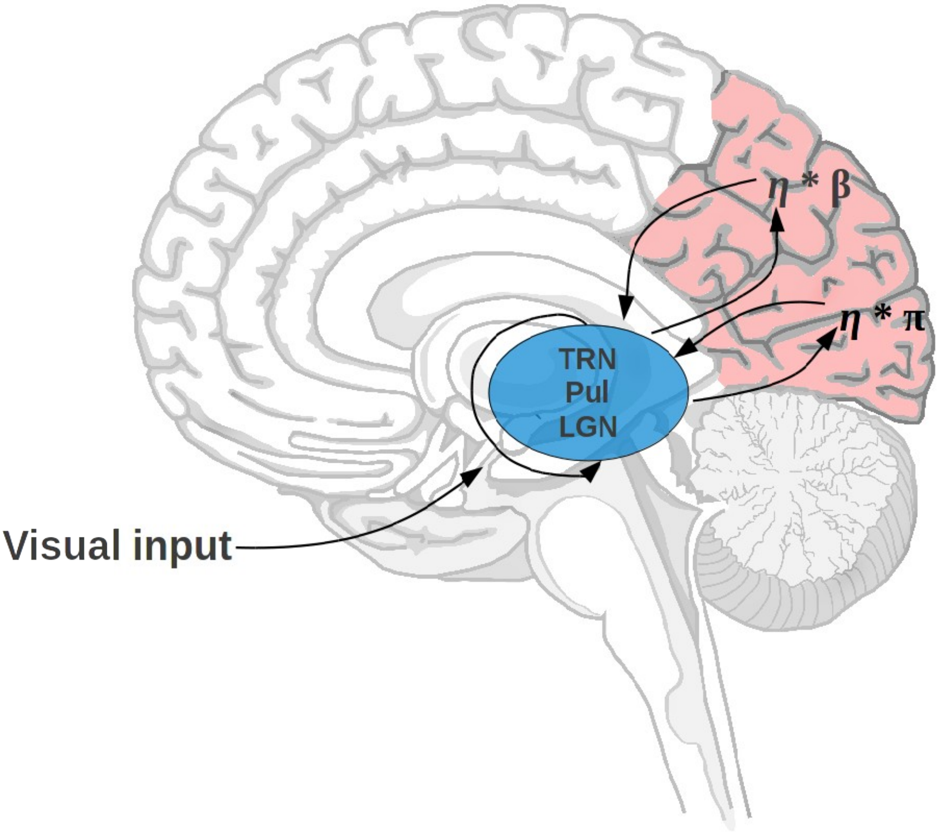


**Fig. 2. Scheme of the brain circuits involved in attentional selection proposed by NTVA**. Illustration adapted from: Bundesen et al. (2005). Key: TRN: Thalamic Reticular Nucleus; Pul: Pulvinar Nucleus; LGN: Lateral Genicular Nucleus. Image modified from Wikimedia Commons on the Creative Commons Attribution-Share Alike 3.0 license.

Although NTVA does not imply any particular neuroanatomical structures to be involved in information processing, some plausible localizations have been suggested. More precisely, the authors suggested that in the first (unselective) wave of processing the visual input from the retina is transmitted to the lateral geniculate nucleus (LGN) of the thalamus, traditionally viewed as a gateway receiving retinal information and projecting it to the striate and extrastriate areas of the visual cortex (Jones, 1985; Sherman and Guillery, 2001). Here, the η values are calculated, i.e. the sensory evidence that a processed object *x* has some particular features, and thus belongs to category *i*. The η values are then multiplied by the π values, i.e. pertinence values of the category *i* (see:

equation [5]). As a result, the neuronal activation related to a relevant object is amplified, and the activation related to an irrelevant object is being suppressed. The multiplied signal is subsequently transmitted to the pulvinar nucleus of the thalamus (Pul), where the attentional weights $w$ are computed. In the second (selective) wave of processing, the total cortical processing capacity is distributed proportionally to the attentional weights $w$ and therefore relevant objects are processed by more neurons than irrelevant ones. Here the $\eta$ values are multiplied by the $\beta$ values, i.e. bias associated with the category $i$ (see equation 6). According to NTVA, the products of the multiplication are transmitted to the thalamic reticular nucleus (TRN), which stores a visual short-term memory (VSTM) map. At this point, the processed objects are starting a race for encoding into the VSTM. The activation representing the winner categorization is then projected from the TRN back to the GLN cells involved in coding the winning categorization. This creates a positive feedback loop sustaining activation.

The prominent role of the visual cortex in attentional selection has been experimentally demonstrated by Hung, Driver and Walsh (2005). They applied repetitive transcranial magnetic stimulation (rTMS) to the visual areas in the posterior parietal cortex while participants were performing a TVA-based partial report task (participants were briefly presented with task-relevant targets and task-irrelevant digits distinguished by colour). It is generally assumed that TMS generates temporary disruptions in the cortical circuits and can thus be used to investigate the role of various cortical areas in cognitive processing (for review, see Walsh and Cowey, 2000; Walsh and Pascual-Leone, 2003). The results showed that interruption in the neuronal activity within right posterior parietal cortex affected top-down control efficiency. More precisely, the efficiency of selection was suppressed for the targets presented in the left (i.e. contralateral) hemifield and enhanced for the targets presented in the right (i.e. ipsilateral) hemifield. No such relation was observed for left parietal cortex suppression.

## 1.4. Estimation of TVA parameters

Reliable assessment of the TVA parameters can be obtained from the mathematical modelling of the report accuracy in two behavioural tasks: partial and whole report. In both tasks, the participant is briefly presented with arrays of letters and is asked to verbally report the presented letters. In the presented studies, the tasks were adapted for simultaneous EEG recording by including unmasked trials. This was done in order to avoid eliciting potentials in response to a mask onset that may confound the proceeding stimulus-related brain response. Additionally, in the whole report tasks, unilaterally presented target stimuli were symmetrically counterbalanced by equiluminous random characters in order to assure an equal physical stimulation across both hemifields.

The TVA parameters top-down control efficiency $\alpha$ and *spatial lateralization* $w_{lat}$ can be estimated by modelling accuracy in a partial-report task. In this task, participants were presented with either a) two red letters (targets), b) one red letter accompanied by a blue letter (distractor) or c) a single red letter. Participants were asked to report only the red letters and ignore the blue ones (see Fig. 3). Modelling performance accuracy across different partial-report conditions provides separate estimates of the attentional weights $w_i$ allocated to targets, distractors and to stimuli presented in the left and right hemifields. From these values, using equations [2] and [3], one can derive TVA parameters top-down control efficiency $\alpha$ and spatial lateralization $w_{lat.}$ The comprehensive description of the fitting procedure and available fitting software can be found in Kyllingsbæk (2006).

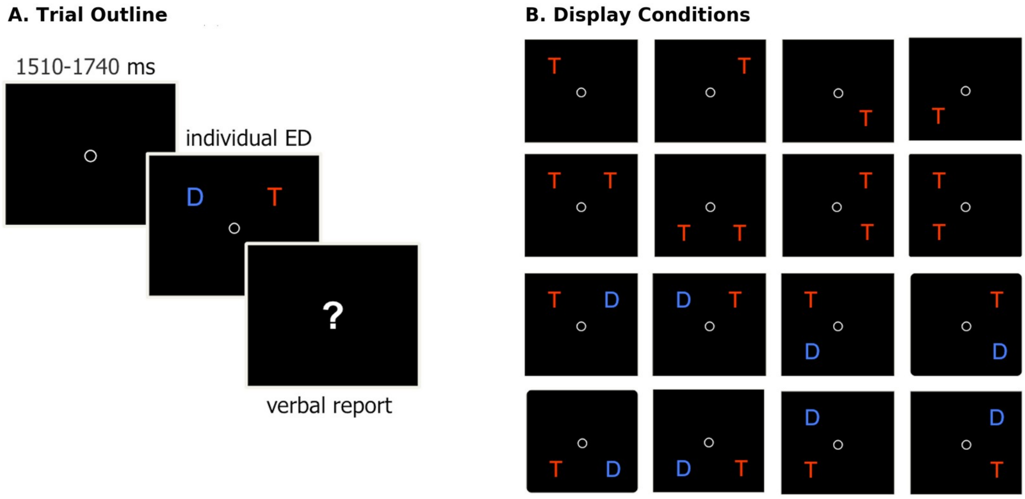


**Fig. 3. Example of the partial report task.** Fig. A depicts the trial outline used in the studies 1 and 2. The task consisted of 16 different conditions. Target letters (here symbolized by Ts) were red, whereas distractors (here Ds) were blue. Fig. B depicts 16 different configurations of stimuli used in the partial report. Targets were presented in red and distractors were presented in blue.

The estimates of the TVA parameters *t0, K,* and *C* can be derived from the report accuracy in a whole-report task. In the whole-report task a participant is presented with an array of letters and is asked to report as many of them as possible. The letters are displayed with varying exposure durations, typically ranging from 10 ms to 200 ms. An example of the task is presented in Fig. 4

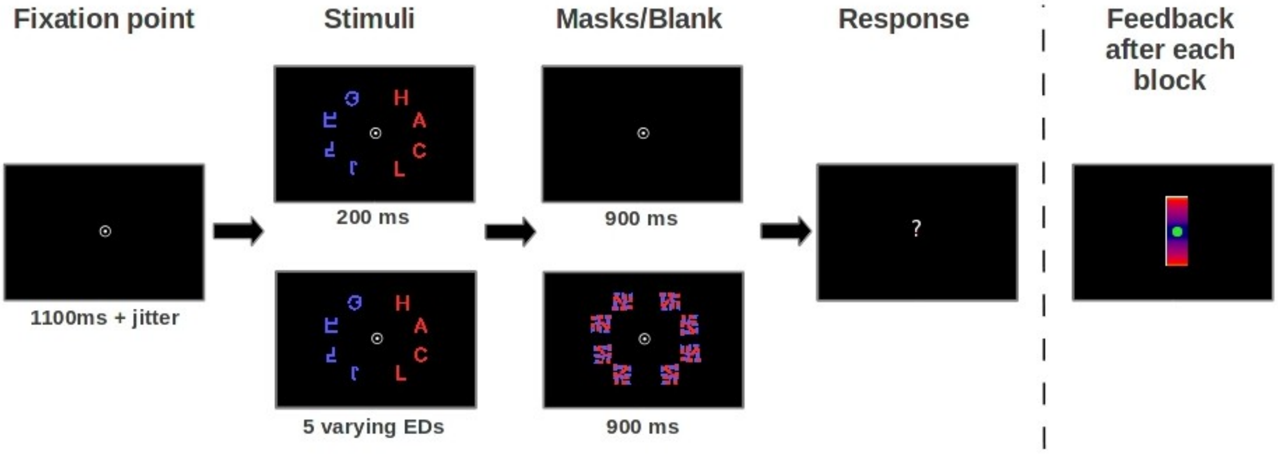


**Fig. 4. An outline of the whole report task.** In each trial, the participant was presented with 4 target letters on either the left or the right side of the display. On the other side, scrambled stimuli were presented in order to assure equal physical stimulation across hemifields. For each participant, 5 different exposure durations were adjusted. Stimuli were presented for these exposure durations were followed by masks. In addition, the conditions with the second shortest and the longest exposure duration were also presented without masking.

According to equation [4], the probability of an element to be encoded into the VSTM is described by an exponential function and increases with time. Thus, the report accuracy of multiple presented letters in the task can be modelled as an exponential function of the stimuli exposure duration (Bundesen 1990; Dyrholm, Kyllingsbæk, Espeseth et al., 2011; Kyllingsbæk 2006). An example of a curve fitted to the real data is presented in Fig. 5. The curve is characterized by three TVA parameters. The first parameter is the visual threshold for conscious perception $t0$ [s]. It is the value for which the number of encoded elements is 0, i.e. $F(t0) = 0$. The second parameter is the asymptote of the function, i.e. parameter $K$ [elements], which determines the maximum number of elements that can be stored in the VSTM. The third parameter is termed visual processing speed $C$ [1/s] and describes the slope of the curve at the point t0. This parameter describes the rate of visual information uptake i.e. number of visual elements encoded to the VSTM per second.

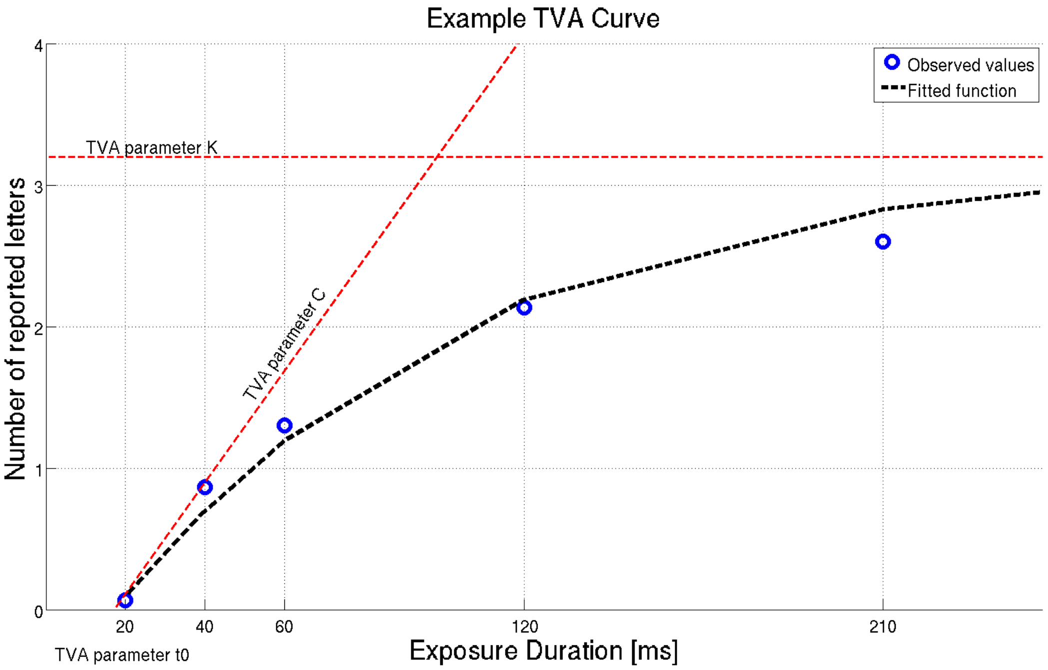


**Fig. 5. An example of the exponential TVA curve fitted to real data of a representative participant.** According to TVA, the accuracy in the whole-report task can be modelled as a function of exposure duration. This provides estimates of the key parameters of attention: visual perceptual threshold t0, which is a root of the fitted function, parameter VSTM storage capacity K, which denotes the asymptote of the function, and parameter processing speed C, which denotes the slope of the function at the point F(t) = 0.

## 1.5. Visual attention and the ageing brain

There is a general consensus that changes in cognitive performance, including attention, are normal processes that accompany healthy ageing (e.g. Harada et al, 2013). Many behavioural and neuroimaging studies showed a significant age-related decline in visual selective attentional abilities (Kok, 2000; Kim et al. 2007, Madden et al., 2005; Raz, 2000). Furthermore, it was shown that the severity of the decline strongly depends on the type of visual stimuli and the complexity of the task. For example, older adults exhibit particular difficulties in suppressing a reaction to salient, strongly attracting stimuli (McDowd, 1997; Mevorach, Humphreys and Shalev, 2006).

Hasher and Zacks (1988), for example, assumed the existence of a mechanism of attentional inhibition of irrelevant information. They suggest that the observable age-related impairment in various cognitive domains may result from an inability to reduce the interference from stimuli that are irrelevant for a current task. They proposed the "inhibitory deficit hypothesis" to explain this phenomenon. The fact that older adults, compared to younger ones, show this decreased ability to selectively focus on task-relevant stimuli has been interpreted to be related to a decreased ability to inhibit distracting information (Gazzaley et al. 2005; Clapp and Gazzaley, 2012). Effective inhibition of processing irrelevant stimuli enables an allocation of greater amounts of cognitive resources to process relevant ones. Therefore, an impairment of inhibition may lead to an overload of working memory with irrelevant information, which in turn reduces the amount of resources available to process relevant information.

On the other hand, Salthouse (1996) proposed the "processing speed hypothesis" which postulates that many cognitive deficits in older adults result from a decline in general processing speed of the central nervous system. This theory states that decreased speed of all mental operations in older adults leads to significantly increased time required to complete various cognitive tasks. Moreover, the increased time needed to process the given operation leaves less time for execution of other, subsequent, cognitive operations. In addition, as all operations require more time, the output generated during an earlier stage of processing may decay and become unavailable for a later stage. The "processing speed hypothesis" received strong support in numerous investigations (see Salthouse, 1996).

Age-related changes of attentional functions were also found in the studies based on TVA. These studies show that healthy ageing affects distinct parameters of attention with varying degrees. Habekost et al (2012) found a linear decrease of the TVA parameter visual processing speed C with age in older adults. Their result was supported by McAvinue et al (2012), who demonstrated that parameters of attention most prone to decline with age were visual processing speed C and short-term memory capacity K. A corresponding result was more recently found by Wiegand et al (2014) who showed that older, compared to younger adults, had significant decreased TVA parameters visual processing speed C and visual short-term memory capacity K. It seems that age-related changes in parameters of general attentional capacity C and K are characterized by different trajectories than changes of the parameter of attentional selectivity: top-down control efficiency α. Efficiency of top-down control shows some age-related decline in the youngest adults, but then remains stable with more advanced age. According to Espeseth et al (2014), top-down control efficiency becomes relatively stable from age of 30, whereas following McAvinue et al (2012) at the age of 50.

Although the majority of elderly people experience a decline in cognitive functioning, some of them seem to be able to preserve their cognitive capabilities. Katzman et al. (1988) reported 10 cases of women over 80 years who had advanced Alzheimer's disease in post-mortem examination, but presented normal cognitive functioning. Further studies confirmed this finding, reporting that between 25 and 67% of elderly people showing no cognitive impairment, actually have features of neurodegeneration (Crystal et al., 1988; Morris et al., 1996; Ince, 2001; Price and Morris., 1999; Mortimer et al. 2003).

Such discrepancy between the severity of neural degeneration and that of cognitive decline can be explained by the individual heterogeneity in the amount of cognitive reserve (Stern, 2002). According to the cognitive reserve concept, individuals differ in their neurobiological and cognitive resources. Only after these resources are exhausted by processes of neural damage, cognitive impairment becomes observable. The cognitive reserve is typically evaluated by education and crystallized IQ (mostly vocabulary-based) tests, and occupational attainment (Richards and Sacker, 2003; Stern, 2009). In accordance with the assumption that individuals with greater cognitive reserve are more efficient in withstanding neural decline and thus in remaining cognitively healthy, it was shown repeatedly that older adults with greater cognitive reserve have a later onset of cognitive decline and that they are less likely to manifest symptoms of clinical dementia (Artero, Touchon and Ritchie, 2001; Avlund, Damsgaard and Osler, 2004; Barber-Gerateau, et al. 1999; Fotenos et al., 2008; Li, Wu and Wen, 2000; Pereira, Yassuda, Oliveira and Forlenza, 2008; Scarmeas and Stern, 2003, Van der Elst, Van Boxtel, Van Vreukelen and Jolles, 2008; Zunzunegui, et al., 2006). Therefore, in ageing studies the relevance of cognitive reserve as a critical individual characteristic with a potentially modifying role is increasingly acknowledged.

To summarize, visual attention is not a single function, but rather a conglomerate of various functions that underlie many higher-order cognitive processes. These functions are influenced by age, although trajectories of age-related changes significantly differ across different parameters of attention and across subjects. Therefore, shedding more light onto the relation between age and changes in the efficiency attention may be enabled by a reliable measurement of attentional parameters, together with careful screening of participants that includes estimates of the amount of cognitive reserve.

### 1.6. EEG as a tool to measure neural underpinnings of attention

Theoretical models and experimental data point to the crucial role of extrastriate area in visual attentional processing. Therefore, studies measuring brain activity, such as EEG, related attentional processing typically focus on these area. Due to an excellent spatial resolution, modern neuroimaging techniques, such as functional magnetic resonance imaging (fMRI) and positron emission tomography (PET), have a prominent role in the neurocognitive sciences. However, hemodynamical responses to the brain activity are relatively slow, therefore neuroimaging methods usually do not enable tracking the time course of the brain processes on a time scale of less than a second. Therefore the main advantage of EEG is a high temporal resolution it provides. EEG allows recording brain activity with a precision reaching a fraction of a millisecond. Furthermore, given the fact that the brain tissue is highly conductive, delays between postsynaptic activity generating changes in the electrical field and the recorded signal are negligible (Nunez and Srinivasan, 2006). Many aspects of information processing within the brain seem to operate on the scale of tens of milliseconds, therefore despite its low spatial resolution, EEG and especially event-related potentials (ERP) are a widely used tool for measuring neural correlates of distinct cognitive processes (Luck, 2005a).

ERPs are extracted from the continuous EEG signal by averaging fragments of the signal time-locked to the investigated event (for example the display of a stimulus). With enough repetitions of the event, random noise unrelated to the event can be averaged out leaving the signal reflecting brain activity induced by the investigated event. An ERP waveform can be characterized by its amplitude, polarity and latency that may vary across different tasks and also between groups of subjects differing for example in age. It is generally assumed that the latency of the ERP component is related to the time course of a given cognitive process, whereas the amplitude reflects the number of neurons engaged in the ongoing process (e.g., Luck, Woodman and Vogel, 2000; Polich, 2007). Therefore, comparing latencies and amplitudes of the selected ERP components between different groups (e.g., between younger and older participants) can provide valuable information about stages of processing and their neural underpinnings.

Over the past 50 years of research on the neural basis of attention, i.e. since the early study of Eason, et al. (1969), various ERP components have been linked to various aspects of attentional selection. One of the most widely documented relations between visual attention and ERPs is the attentional modulation of the amplitudes of the P1 (first positive-going deflection) and the N1 (first negative-going deflection). Both components are most pronounced over the occipital lobe and their amplitudes increase for stimuli presented in the attended compared to the unattended location (see Hillyard, Vogel and Luck, 1998; Mangun, 1995). Idealized components elicited during presentation of stimuli in the attended (solid red line) and unattended (dashed black line) location are presented in the Fig. 6.

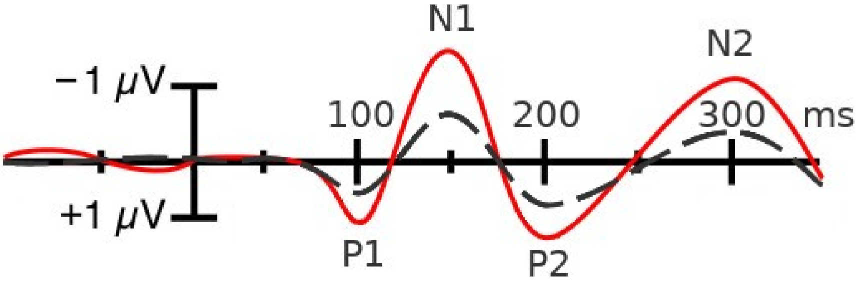


**Fig. 6. Idealized ERP waveforms.** The waveforms show the signal elicited during presentation of the stimulus in the attended (solid red line) and unattended (dashed black line) location.

The typical latency of the positive P1 component is 70-100 ms post stimulus (Luck, Woodman, and Vogel, 2000). The component was shown to be modulated by spatial attention (see review by Hillyard, Vogel and Luck, 1998) and there is a general consensus that the P1 component is related to processing suppression of the information presented at unattended locations. This may enable reducing interference and directing more attentional resources in order to process stimuli presented at the attended locations. In contrast, the later, negative N1 component typically peaks at 100-150 ms (Mangun and Hillyard, 1991). The N1 component amplitude was found to be elicited in discrimination and detection tasks (Hopf et al., 2002; Vogel and Luck, 2000). Thus, it is assumed to be modulated by cognitive demands of the discrimination task demands (Hillyard, Vogel and Luck, 1998; Luck, 1995, 1998; Luck et al., 1994; Vogel and Luck, 2000). Subsequent component is a positive deflection termed P2 with an usual latency of 180–320 ms poststimulus. Within visual domain it is interpreted as an index of mechanisms for selective attention, feature-based processing (based on i.e. colour, shape or orientation), and the early stage of encoding of a visual object (Luck and Hillyard, 1994). The later, negative, deflection is an N2 component peaking at 200-350ms post-stimulus, which is actually a family of components reflecting different cognitive processes. The posterior N2 is usually increased as a response to the display of less frequent target objects. Thus, it is interpreted as an index of the stimulus categorization process (Folstein and Petten, 2008).

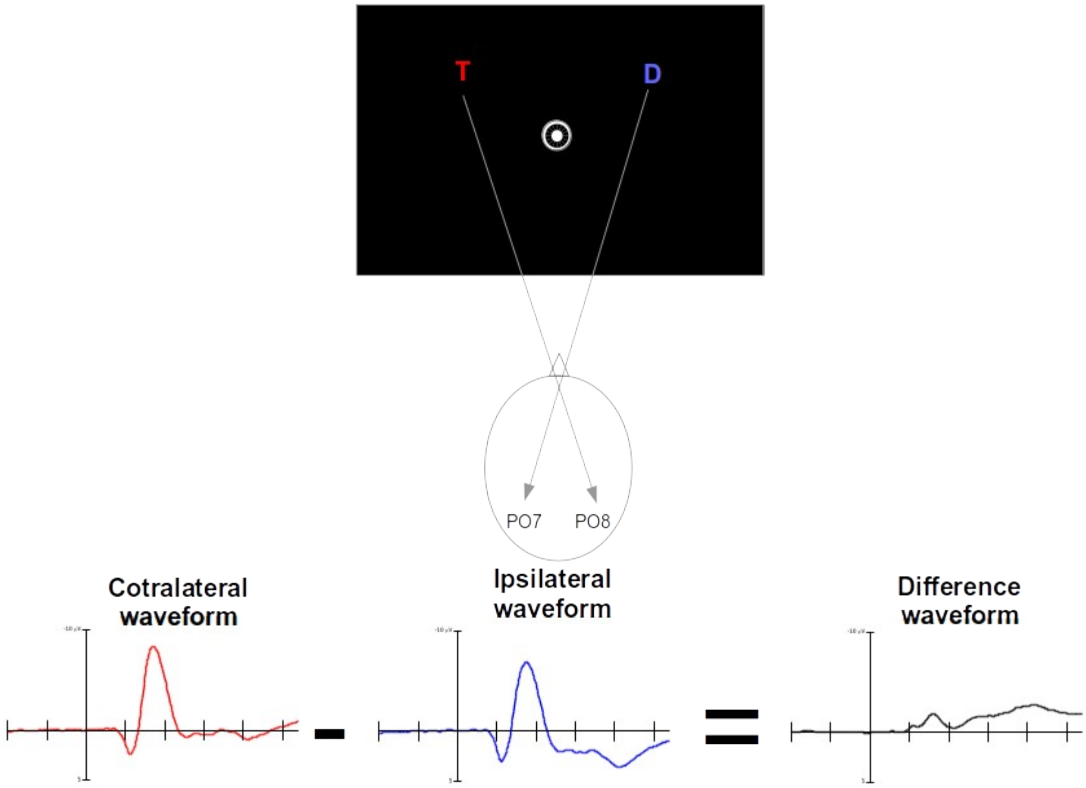


**Fig. 7**: **Example of the ERL computation.** The waveform recorded over the site ipsilateral to the attended target (blue) is subtracted from the waveform recorded over the contralateral site (red) resulting in a contra-ipsilateral difference waveform (black).

Due to the fact that the spatial allocation of attention modulates some ERP components, the lateralization of these ERPs (i.e. Event Related Lateralization, ERL) has been used as a valid marker of attentional processes (see: Eimer, 1996; Heinze, Luck, Mangun and Hillyard 1990; Hopf et al., 2000; Luck 2005b; Mazza, Turatto, Caramazza, 2009). In case of an experiment in which a participant is presented with a lateralized visual stimuli an ERL is computed as a difference in waveform over the hemispheres contralateral vs. ipsilateral to the visual hemifield in which the attended stimulus is presented (Corriveau et al., 2012; Luck, Woodman and Vogel, 2000; Wascher and Wauschkuhn, 1996) (see Fig. 7). Subtracting the signal recorded over the ipsilateral site from the signal recorded over the contralateral site enables subtracting out the information that is common for the processing of attended and unattended stimuli (Oostenveld, Stegeman, Praamstra and van Oosterom, 2003) leaving in the signal information related to the attentional processing of the lateral stimuli.

An early lateralized component, typically elicited over the lateral occipital sites, in the time interval of the N1 component is the so-called N1pc (N1-posterior-contralateral). It is assumed to reflect a process of an “initial orienting of attention” based on the physical features of the presented object (Wascher and Beste, 2010). A subsequent, but positive lateralized deflection is the Ppc (Positivity-posterior-contralateral). The Ppc has been suggested to reflect a process of a location-specific inhibition of the sensory information (Gokce et al., 2014). The most extensively studied and replicated lateralized component is the PCN component (Posterior-Contralateral Negativity; Ansorge and Heumann, 2006; Jaskowski, van der Lubbe, Schlotterbeck and Verleger, 2002; see also: Conci, Töllner, Leszczynski and Müller, 2011; Töllner, Conci and Müller, 2015) also called N2pc (N2-posterior-contralateral; Luck and Hillyard, 1994; Eimer, 1996). The PCN is a negative-going deflection elicited at the posterior electrodes with a typical latency between 175 and 300 ms post-stimulus (Töllner, Zehetleitner, Gramann and Müller, 2010, Töllner, Müller and Zehetleitner, 2011). There is a general agreement that the PCN amplitude reflects the process of attentional selection of task-relevant visual objects presented among task-irrelevant ones in visual space (Eimer, 1996; Luck and Hillyard, 1994; Woodman and Luck, 2001, 2003). As shown by a study combining different imaging methods (event-related magnetic fields, functional magnetic resonance imaging and event related potentials) the neural sources of the PCN wave are located in the lateral occipital cortex and in the visual V4 area (Hopf et al. 2006). The latency of the component is thought to indicate the transition from the pre-attentive sensory coding of the stimulus to the focal-attentional stage of selection (Töllner et al., 2010). A variability of the PCN latency has been reported in several studies. This demonstrates, that the timing of a target selection may be affected by various factors, for instance target set size (Wolber and Wascher, 2005), stimulus intensity (Brisson, Robitaille, and Jolicoeur, 2007), top-down processes (Töllner et al., 2011), or intertrial history (Töllner et al. 2008). Therefore, the amplitude of the PCN component may serve as an index of the amount of attentional resources being allocated, whereas latency may serve as an index of pre-attentive processing speed.

Methodology of event-related components have been also successfully used to identify the neural underpinnings of distinct attentional parameters as postulated by TVA. In their study, Wiegand et al. (2014) examined young participants with the TVA-based paradigm of whole report arrays of letters with simultaneous EEG recording. They showed that participants with higher compared to lower TVA parameter processing speed C had suppressed amplitudes of the visual N1. In a follow up study, Wiegand and colleagues (2014b) demonstrated that the relation between the N1 amplitude and visual processing speed was present also in older participants, despite significantly decreased processing speed in older compared to younger individuals. This suggested that mechanisms underlying age-related slowing of processing speed do not influence N1 component.

Event related components have also been shown to reflect age differences. Lorenzo-López, Amenedo and Cadaveira (2006) showed that in older participants, compared to younger, the PCN component was significantly delayed. This finding suggested that the allocation of attention is significantly slower in ageing individuals. Furthermore, the amplitude of the component was decreased in older participants compared to younger ones. This was interpreted as an index of decreased amounts of attentional resources devoted to process the target stimuli (Luck et al, 1997). Similarly, Wiegand et al. (2013) demonstrated that in a visual search task the PCN was elicited significantly later in older participants than in younger. This result suggests that the process of selection a task-relevant visual object requires more time in older than in younger adults. It is therefore assumed that age-related differences in ERPs reflect differences in the way the neural resources are engaged in the task. Thus, together with sensitive and appropriate behavioural measures, ERLs can provide valuable insights into age-related changes in distinct components of visual attention (Braver et al., 2009).

## 1.7. Summary

In summary, visual attention is a complex set of functions enabling effective functioning in the environment by selecting relevant elements out of the multitude of visual inputs. Also, this complex phenomenon is affected by ageing, although the nature of the specific changes and the degree to which functions of attention are declining with age is still a subject of debate. According to some researchers, age-related decline of higher-order cognitive functions may be attributed to an incapability to inhibit the selection of distracting stimuli. On the other hand, such decline may also be attributed to a decreased processing speed of the nervous system. Furthermore, neural underpinnings of attentional processes and their relation to age are still uncertain. Shedding more light on the nature of age-related changes in visual attentional functions and their neural correlates may be possible by grounding scientific studies in a coherent model such as Bundesen’s TVA and applying neurophysiological measurements.

# 2. Manuscript:

# Event-related EEG lateralizations mark individual differences in spatial and non-spatial visual selection.

Iris Wiegand*[1,2,3], Natan Napiorkowski*[4,5], Thomas Töllner[4,5], Anders Petersen[6], Thomas Habekost[6], Hermann Müller[4], Kathrin Finke[4,7]

[1]Max Planck UCL Centre for Computational Psychiatry and Ageing Research

[2]Center for Lifespan Psychology, Max Planck Institute for Human Development

[3]Visual Attention Lab, Brigham & Women's Hospital and Harvard Medical School

[4]General and Experimental Psychology, Department of Psychology, LMU Munich

[5]Graduate School of Systemic Neurosciences, LMU Munich

[6]Center for Visual Cognition, Department of Psychology, University of Copenhagen

[7]Hans-Berger Department of Neurology, Jena University Hospital

* IW and NN contributed equally to the work

Corresponding Author:

Iris Wiegand, PhD

Email: wiegand@mpib-berlin.mpg.de

Address: Max-Planck Institute for Human Development, Lentzeallee 94, 14195 Berlin, Germany

## 2.1. Abstract

Selective attention controls the distribution of our visual system's limited processing resources to stimuli in the visual field. Two independent parameters of visual selection can be quantified by modelling an individual's performance in a partial-report task based on the computational Theory of Visual Attention (TVA): i) *top-down control* $\alpha$, the relative attentional weighting of relevant over irrelevant stimuli and ii) *spatial bias* $w_\lambda$, the relative attentional weighting of stimuli in the left versus right hemifield. In this study, we found that visual event-related EEG lateralizations marked inter-individual differences in these two functions. First, individuals with better top-down control showed higher amplitudes of the *posterior contralateral negativity* (PCN) than individuals with poorer top-down control. Second, differences in spatial bias were reflected in asymmetries in earlier visual ERLs depending on the hemifield position of targets; specifically, individuals showed a positivity contralateral to targets presented in their prioritized hemifield and a negativity contralateral to targets presented in their non-prioritized hemifield. Thus, our findings demonstrate that two functionally different aspects of attentional weighting quantified in the respective TVA parameters are reflected in two different neurophysiological measures: the observer-dependent spatial bias influences selection by a bottom-up processing advantage of stimuli appearing in the prioritized hemifield. By contrast, task-related target selection governed by top-down control involves active enhancement of target, and/or suppression of distracter, processing. These results confirm basic assumptions of the TVA theoretical framework, complement the functional interpretation of ERL components in selective attention studies, and are of relevance for the development of neuro-cognitive attentional assessment procedures.

## 2.2. Introduction

At any given point, we can consciously process only a small proportion of the massive visual input we are exposed to. The cognitive function that deals with distributing our highly limited processing resources is visual selective attention (Desimone & Duncan, 1995). Top-down control over selection enables the observer to focus attention on objects that are relevant to immediate goals, while ignoring irrelevant distracters. Efficient top-down attentional control is thus critical for acting intelligently in our visual environment and has been proposed to account for individual differences in general fluid cognitive abilities (Kane, Poole, Tuholski, & Engle, 2006). Accordingly, impaired top-down control, for example under normal aging or clinical psychiatric and neurological conditions, causes difficulties in a variety of tasks (e.g., Bishop, 2008; Gold, Fuller, Robinson, Braun, & Luck, 2007; Madden, 2007; Parasuraman & Haxby, 1993). How attentional resources are shared among objects in the visual field is not only determined by the relevance of the object, but also their spatial locations (e.g., the visual hemifield). Marked spatial processing asymmetries are associated with attentional dysfunction following brain damage, such as hemispatial neglect (Corbetta, Kincade, Lewis, Snyder, & Sapir, 2005). In healthy subjects, the amount of attentional capacity allocated to the left and right hemifields is largely balanced. When sufficiently sensitive measures are applied in larger samples, a slight left-ward bias ("pseudo-neglect") is reliably observed on the group level (Bowers & Heilman 1980; Nicholls, Bradshaw, & Mattingly, 1999), and, in line with this, a left visual field advantage often manifests in lateralized attention tasks (Carlei & Kerzel, 2017; Śmigasiewicz, Asanowicz, Westphal, & Verleger, 2014; Verleger et al., 2009). At the single-subject level, however, side and degree of the spatial bias vary considerably among individuals, while being relatively stable within a given person. Accordingly, the spatial bias has been suggested to be a trait-like attribute (Benwell, Thut, Learmonth, & Harvey, 2013; Tomer et al., 2013) that potentially impacts the person's attentional performance (Bellgrove, Dockree, Aimola, & Robertson, 2004; Benwell, Harvey, Gardner, & Thut, 2013; Finke, et al., 2005; Matthias, Bublak, Costa, Müller, Schneider, & Finke, 2009). Together, spatial and non-spatial selection can be regarded as two fundamental features of the visual and fronto-parietal attention systems (Corbetta & Shulman, 2002; 2011), which constitute critical determinants of individual differences in visual cognitive abilities both under normal and clinical conditions.

Individual estimates of spatial and non-spatial attentional selection can be derived from parametric assessment based on the computational Theory of Visual Attention (TVA, Bundesen, 1990). TVA is closely related to the 'biased competition' account (Desimone & Duncan, 1995) and assumes that multiple objects in the visual field compete for access to a limited visual-short term memory (vSTM) store. An object's competitive strength depends on its attentional weight, which determines the fraction of the total processing capacity allocated to the object. An object will be selected and stored in vSTM when its encoding process is completed before the stimulus presentation terminates, given that vSTM has not yet been filled up. In a further development of the model, the processes have been interpreted on a neuronal level (NTVA, Bundesen, Habekost, & Kyllingsbæk, 2005; 2011). Specifically, the number of neurons representing an object categorization is assumed to be proportional to the attentional weight allocated to it and, thus, its probability of being selected.

TVA partitions attentional functions into distinct parameters that can be modelled based on an individual's accuracy in simple letter report tasks (Duncan, Bundesen, Olson, Humphreys, Chavda, & Shibuya, 1999). Specifically, selective attentional weighting is quantified in two parameters, i) top-down control α, the efficiency of selecting task-relevant target letters over task-irrelevant distracter letters, and ii) spatial bias wλ, the distribution of attention to letters in the left versus right hemifield.

That the two parameters can indeed be taken to reflect stable processing characteristics for a given individual is substantiated by high internal (> 0.9) and test-retest reliability (> 0.8) of the α and wλ parameters (Habekost, Petersen, & Vangkilde, 2014). The high reliability of the wλ estimates mirrors the high (test-retest) reliability of spatial bias measures derived from the landmark (or the line bisection) task (Benwell, Thut, et al., 2013), which is frequently used to quantify hemispatial processing asymmetries in healthy individuals and neglect patients (Harvey, Milner, & Roberts, 1995). Furthermore, TVA parameters have been demonstrated to selectively correlate with other neuropsychological tests measuring related functions. In particular, top-down control α was found to be related to interference in a Stroop task (Bäumler, 1985); and a stronger degree of spatial bias wλ,, that is absolute deviation from balanced processing regardless of direction (Dev(wλ)), was shown to be associated with poorer performance in a visuo-spatial scanning task (Zimmermann & Fimm, 1993), in which participants had to decide whether a ‘target’ square having a gap in the upper edge was present in a 5 x 5 matrix of squares having a gap either in the left, the right, or the lower edge (Finke, Bublak, Krummenacher, Kyllingsbæk, Müller, & Schneider, 2005) – indicative of a more general, stable tendency to prefer on side of space.

In this study, we aimed at identifying neurophysiological indices of individual differences in these two parameters by combining TVA-based assessment with recordings of event-related potentials (ERPs). ERPs can be used as online markers of several independent but overlapping subcomponents of visual attention in one task (Luck, 2005) and were suggested to reflect neurophysiological correlates of individual differences in latent cognitive traits (Cassidy, Robertson, & O’Connell, 2012; McLoughlin, Makeig, & Tsuang, 2014). In this respect, we previously demonstrated that ERPs marked inter-individual differences in the two distinct TVA parameters of visual capacity, processing speed C and storage capacity K (Wiegand, Töllner, Habekost, Dyrholm, Müller, & Finke, 2014; Wiegand, Töllner, Dyrholm, Müller, Bundesen, & Finke, 2014).

Specifically visual selection processes can be examined by means of event-related lateralizations (ERLs) over posterior-occipital sites (Luck, Woodman, & Vogel, 2000). Visual ERLs are computed as the difference in activity over the hemispheres contra- and ipsilateral to laterally presented stimuli. They are considered to reflect stimulus processing in visuo-topically organized extrastriate areas recurrently linked to higher-level fronto-parietal areas in the attention network (Eimer, 2015; Hopf et al., 2006). When a lateral target stimulus is presented together with a physically similar distracter stimulus in the opposite hemifield, a negativity contralateral to the attended target stimulus is elicited around 175-300 ms following its onset, referred to as Posterior Contralateral Negativity (PCN, or N2-posterior-contralateral; Eimer, 1996; Luck & Hillyard, 1994; Töllner, Rangelov, & Müller, 2012). The PCN amplitude is interpreted as reflecting the amount of attentional resources recruited to select a target in the presence of distracting stimuli (Töllner, Zehetleitner, Gramann, & Müller, 2012; Woodman & Luck, 2001). The component was suggested to subsume activations related to multiple mechanisms acting simultaneously to resolve this attentional competition, specifically: activity to enhance processing of the target plus activity to suppress processing of the distracters (Hickey, Di Lollo, & McDonald, 2009). In some studies, a positivity that precedes the PCN can be observed contralateral to the target (Corriveau, Fortier-Gauthier, Pomerleau, McDonald, Dell'Acqua, & Jolicoeur, 2012; Jannati, Gaspar, & McDonald, 2013). This Posterior Positivity Contralateral (Ppc) was suggested to reflect bottom-up processing differences between the target and distracter stimuli that may also contribute to selection (Gokce, Geyer, Finke, Müller, & Töllner, 2014; Wiegand, Finke, Töllner, Starman, Müller, & Conci, 2015).

To investigate electrophysiological correlates of TVA parameters of spatial and non-spatial selective attention, we recorded EEG while participants performed a partial-report letter task (Wiegand, Petersen, Finke, Bundesen, Lansner, & Habekost, 2017) in which subjects had to identify target letters and ignore distracter letters pre-specified with respect to colour. For each participant, we derived quantitative and independent TVA-based estimates of top-down control α and spatial bias wλ from their report accuracy under different display conditions (Fig. 1): a target letter was presented either alone, accompanied by another target letter, or accompanied by a distracter letter, in the same or the opposite hemifield. We analysed visual ERLs in response to target displays with a distracter in the opposite hemifield. ERLs were i) averaged across trials with targets in the left and right hemifields (PCN), to derive ERL correlates of parameter top-down control α; and ii) averaged separately for trials with a target in the left (and a distracter in the right) hemifield and a target in the right (and a distracter in the left) hemifield to derive ERL correlates of parameter spatial bias wλ. First, we hypothesized that the PCN, as a marker of resource allocation for visual selection, would mark individual differences in the parameter top-down control α. Specifically, we expected larger PCN amplitudes to indicate better top-down control over target selection. Second, we hypothesized that hemifield-specific ERLs might reveal asymmetries in the resource allocation to targets in the left versus right hemifield, which would be related to individual differences in the parameter spatial bias wλ.

## 2.3. Methods

*Participants*. Thirty-three healthy volunteers participated in the experiment. Two participants were excluded whose PCN amplitude deviated more than 3 standard deviations from the average amplitude of -1.88 μV. In the remaining sample of 31 participants, mean age was 26.74 years (SD: 4.60, range: 20-35 years; 16 male, 15 female). All participants had normal or corrected-to-normal vision and none of them reported colour blindness, any chronic eye disease, or any psychiatric or neurological impairments; also, none exhibited symptoms of depression (scores < 18 in Beck's depression inventory, Beck, Steer, & Brown, 1996) or anxiety (scores < 59 in the State-Trait Anxiety Inventory, Spielberger, Gorsuch, & Lushene, 1970). Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971). XX 28 of the participants had a right-hand dominance and 3 of the participants had a left-hand dominance. Written informed consent according to the Declaration of Helsinki II was obtained from all participants, and they received payment of 10€/h for their service. The study was approved by the ethics committee of the Department of Psychology, Ludwig-Maximilians-Universität München.

*Design and Procedure.* The PC-controlled experiment was conducted in a dimly lit, sound-attenuated and electrically shielded cabin. Stimuli were presented on a 24-inch monitor (800×600 pixel screen resolution; 100-Hz refresh rate). Participants were seated in a comfortable chair at a viewing distance of approximately 65 cm to the screen. The entire test session lasted approximately 2 hours, including completion of a demographic questionnaire as well as neuropsychological screening assessing visuo-motor speed, depression, anxiety, and verbal IQ. Tests were completed in random order before the experiment, followed by preparation of the EEG recording and, finally, the partial-report task, which took some 45 minutes to perform. Participants were given standardized written and verbal instructions, and they were presented with example displays on the screen to illustrate the task before the experiment started.

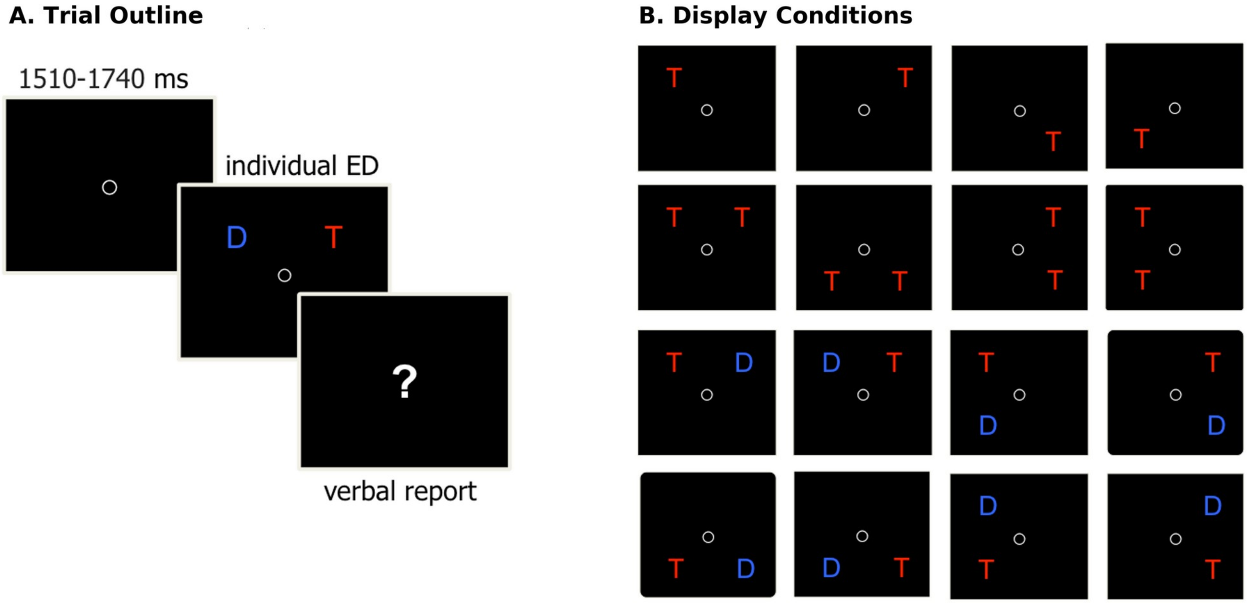


**Fig. 1: Task procedure and stimuli.** Trial outline of the partial-report task (A). 16 different display configurations presented in the partial report (B). Targets (“T”) were presented in red and distractors (“D”) were presented in blue.

In the partial-report task, on each trial (Fig. 1A), either a single target, two targets, or a target and a distracter were presented. Two letters were either presented vertically (unilateral display) or horizontally (bilateral display), but never diagonally, resulting in 16 different display configurations (Fig. 1B). A trial started with the presentation, for a variable duration (see below), of a white circle (diameter of 0.9o) with a white dot in the middle in the centre of the screen, which participants were instructed to fixate throughout the whole trial. Then, the letter array was presented on a black background for an exposure duration that was determined individually for each participant in a pre-test (see below). Participants’ task was to verbally report only the red target letters, and to ignore the blue distracter letters. The report could be performed in any (arbitrary) order and without emphasis on response speed. Participants were instructed to report only those letters they were 'fairly certain' of recognizing. The experimenter entered the responses on the keyboard and pressed a button to initiate the next trial. To avoid response preparation varying with build-up of temporal expectancy as time elapses (Vangkilde, Coull, & Bundesen, 2012), the inter-trial intervals (ITIs) were drawn from a geometrical distribution with a constant hazard rate of 1/5 and a range of 1510-1740 ms using time steps of 10 ms.

The experiment consisted of a total of 504 trials: 112 in the single-target condition, 112 in the dual-target condition, and 280 in the target-distracter conditions (112 unilateral, 168 bilateral displays). For the ERL analyses, only conditions in which the target and distracter appeared in opposite hemifields were relevant, while all of the 16 display conditions were important for the parameter fitting based on the behavioural data (Duncan et al., 1999). The experiment was divided into 14 blocks of 36 trials each. Conditions were balanced across blocks and each participant was presented with the same displays, though in a different random sequence. Letter stimuli were presented in Arial font size 16, with equal frequency at each of four possible display locations forming an imaginary square, with a distance of approximately 10 cm from the fixation circle, corresponding to a visual angle of 8.75°. Red target letters (CIE xyY: .534, .325, 3.25) and blue distracter letters (CIE xyY: .179, .118, 3.15) were of comparable luminosity and size (0.9° of visual angle). The letters presented on a given trial were randomly chosen from a pre-defined sub-set (ABDEFGHJKLMNOPRSTVXZ) without replacement.

*Determination of individual exposure durations.* Before the experimental session, a pre-test was conducted to familiarize participants with the partial-report task and determine the exposure duration

(ED) for the test individually for each participant, thus controlling for potential individual differences in task difficulty. First, 16 trials were run with an ED of 80 ms to acquaint the participant with the trial procedure. Then, an adaptive test procedure containing 24 trials followed, in which the ED was adapted stepwise based on performance in 12 dual-target trials: when the participant reported both targets correctly, ED was decreased by 10 ms; when the participant reported one letter correctly, the ED was kept at the current value; and when the participant reported no letter correctly, the ED was increased by 10 ms. Another 24 trials were then run using the ED identified by this procedure, with participants receiving feedback on their performance after the block. The ED thus determined was accepted for the test when performance ranged between 70% and 90% correct with single-target displays and exceeded 50% correct with dual-target displays (i.e. reached a level indicating that the participant was, in principle, able to identify more than one letter at the given exposure duration). Otherwise, the determination procedure was continued until the criterion was reached, which was the case for the majority of our participants.

Participants' final ED was 20.97 ms on average (range: 10-90 ms). Note that the individual TVA parameter estimates of top-down control α and spatial bias wλ are independent from the individual EDs. In any case, the EDs were sufficiently short to mostly prevent saccades during display exposure, which could have contaminated the ERLs (Luck, 2005). ERLs were previously shown to be unaffected by variations in short EDs up to 200 ms (Brisson & Jolicœr, 2007), and in fact, in the present study, EDs did not correlate with TVA parameter estimates or ERLs [all rs < .24, all ps > .17].

*Parameter estimation.* TVA parameters were derived by modelling individual performance accuracy across the different partial-report conditions (see Fig 1B) using a TVA-based algorithm with a maximum likelihood estimation procedure (see Dyrholm, Kyllingsbæk, Espeseth, & Bundesen, 2011, and Kyllingsbæk, 2006, for details). The parameters of main interest in the present study were the two TVA parameters related to selective attention. The top-down control parameter, α, reflects the task-related differences in weights for targets (wT) and distracters (wD), and is defined as the ratio wD/wT. Theoretically, perfect selection would imply that all attentional weight was on targets and none on distracters, resulting in $\alpha = 0$. By contrast, completely unselective processing would imply equally weighted target and distracter processing, resulting in $\alpha = 1$. Accordingly, lower α values indicate more efficient top-down control. The spatial bias parameter, wλ, reflects the spatial distribution of attentional weights across the left ($w_{left}$) and the right ($w_{right}$) visual hemifield and is defined as the ratio $w_{left}/(w_{left} + w_{right})$. A value of $w\lambda = 0.5$ indicates balanced weighting, a value of $w\lambda > 0.5$ a leftward bias, and a value of $w\lambda < 0.5$ a rightward spatial bias. In addition to the parameters related to selection, we estimated the sensory effectiveness, a, which is a measure of the total processing capacity (in number of letters) at a given exposure duration, independent of how attentional resources are divided across different objects in the visual field.

TVA parameters are considered latent parameters, that is, entities of the processing system operating at any instance. They are inferred from modelling the observed raw data (report accuracy) in those partial-report conditions assumed to be most influenced by the respective parameter. We verified the correspondence between parameters and raw performance by calculating selection indices, which we then correlated with the estimates derived from the model. Specifically, parameter α is estimated mainly from performance decrements in the target-distracter condition, relative to performance conditions without distracters; thus, we computed a 'target selection index' as the mean performance accuracy in the single-target and dual-target conditions divided by performance accuracy in the target-distracter condition ([0.5*ACC1T+0.5*ACC2T]/ACCTD). Parameter wλ is estimated mainly from performance in display conditions with targets presented bilaterally in both the left and the right visual hemifield; thus, we computed a 'spatial selection index' as the relative difference in correctly reporting targets in the right vs. left hemifield in the bilateral dual-target condition ($ACC_{left}/[ACC_{right} + ACC_{left}]$).

*EEG recordings and ERLs.* The EEG was recorded continuously from 64 active Ag/AgCl electrodes (ActiCAP system, Brain Products) using BrainAmp DC amplifiers (Brain Products). Sixty-three electrodes were mounted on an elastic cap (Falk Minow Service), with positions placed according to the international 10/10 system (American Electroencephalographic Society, 1994). One additional electrode was placed at the inferior orbit below the left eye in order to further control for blinks and saccadic eye activity. The impedances of all electrodes were kept below 5 kΩ, and regularly controlled every 4 blocks. All signals were recorded at a sampling rate of 1 kHz and filtered online with a 0.1- 250 Hz bandpass filter. Electrode FCz was used as online reference. During offline pre-processing, the raw data of each participant was first visually inspected to detect and manually remove artefacts of nonstereotypic noise (e.g., electromyographic bursts). We ran an infomax independent component analysis (Bell & Sejnowski, 1995) to identify and backtransform components representing ocular artefacts (Jung et al., 2000). After ICA inspection, the continuous EEG was low-pass filtered at 40 Hz (Butterworth zero phase filter, 24 dB/oct) and re-referenced to averaged mastoids (channels TP9/10). The EEG was segmented into 1000-ms epochs, ranging from 200 ms before to 800 ms after stimulus onset. The pre-stimulus interval was used for baseline corrections. Trials containing signals exceeding ±30 µV in channels at the outer left and right canthi of the eye (F9/F10) were marked as artefacts associated with residual eye-related activity and not included in the analyses (7% of all trials). Trials including voltage steps larger than ± 50 µV/ms and activity lower than ± 0.5 µV within intervals of 500 ms or signals exceeding ± 60 µV in any channel were marked as artefacts and removed from the analysis on an individual-channel basis.

We computed ERLs based on trials in which a target and a distracter letter were presented bilaterally (i.e., in opposite hemifields) on lateral parieto-occipital electrodes (PO7/PO8). Only trials on which target letter was reported correctly were included in the analyses. Note that, although wλ is estimated mainly from bilateral target displays in the TVA fitting, the latent spatial bias parameter is assumed to be also realized in the magnitude of the relative attentional weights to targets presented in the left compared to the right hemifield when a distracter is in the opposite hemifield, or no stimulus is in the opposite field. We chose bilateral target-distracter displays for the analyses because it is only in this condition that the sensory input is balanced across hemifields, with contra-vs.-ipsilateral hemispheric differences reflecting attention-related differences in target and distracter processing; by contrast, no reliable lateralization in ERPs can be measured in displays with targets in both hemifields.

ERLs were calculated by subtracting ERPs at electrodes ipsilateral from those at electrodes contralateral to the target, averaged over presentations in the upper and lower visual field. Time windows used for analyses were based on visual inspection of individual differences in grand-averaged ERLs. For the PCN analyses, we computed grand-average (contralateral-minus-ipsilateral) difference waves averaged across left and right targets ([(PO8-PO7left target) + (PO7-PO8right target)]/2), and extracted peak amplitudes (mean +/- 10 ms around the maximum deflection) in the 130-350 ms post-stimulus time window. For analysing hemifield asymmetries in the ERLs, we extracted mean amplitudes 140-200 ms post-stimulus from grand-averaged event-related (contralateral-minus-ipsilateral) difference waves on parieto-occipital electrodes separately for displays in which the target was presented in the left hemifield and the distracter in the right hemifield (PO8-PO7left target), and vice versa for trials in which the target was presented in the right hemifield and the distracter in left hemifield (PO7-PO8right target). We measured mean amplitudes, rather than peak amplitudes, because individual peaks could not be reliably determined, owing to the lower signal-to-noise ratio in the hemifield-specific ERLs as compared to the PCN (the latter being based on averaging across double the amount of trials).

*Statistical analyses.* First, we examined whether target selection was effective in our sample by a one-sample t-test testing whether α–values would be significantly lower than 1 (indicating unselective processing). Second, we tested whether there was a spatial bias to the left or right hemifield in our sample by a one-sample t-test against 0.5 (indicating balanced spatial weighting). We further confirmed that the correspondence between the performance pattern in the raw data and the parameter estimates by correlating individual α- and wλ-values with the target selection and, respectively, spatial selection indices computed from the observed performance data. To test the independence of the two parameters of selection, we computed Pearson correlations between the α and wλ estimates, and also between α and the general degree of spatial bias irrespective of direction (i.e., the deviation from balanced weighting, $w\lambda = 0.5$).

For the following examinations for individual differences, we split the sample twice into two groups: first, into groups with better vs. poorer top-down control according to the median value of α; second, into groups with left vs. right spatial bias according to the median value of wλ. The resulting differences between the respective groups in the parameter estimates and report accuracy in the relevant display conditions of the (partial-report) task were examined by t-tests.

We assumed that individual differences in the PCN would reflect the relative distribution of attentional weights among target and distracter letters, quantified as parameter α. We further hypothesized that individual differences in the left-right asymmetry of ERLs would be related to the observer-specific relative spatial distribution of weights between hemifields, quantified as parameter wλ. Finally, we assumed that these associations would be independent of each other, that is, individual differences in α would not be reflected in hemispheric asymmetries of the ERL, and individual differences in wλ would not be reflected in overall amplitudes of the PCN.

To test these hypotheses, we analysed the PCN in two one-way ANOVAs, one with the between-subject factor Top-down Control (better/poorer), and another with the between-subject factor Spatial Bias (leftward bias/rightward bias). We analysed hemifield-specific ERLs in two mixed ANOVAs, one with the within-subject factor Target Hemifield (left/right) and the between-subject factor Spatial Bias (leftward bias/rightward bias), and another with the within-subject factor Target Hemifield (left/right) and the between-subject factor Top-down Control (better/poorer). Significant interactions were followed-up by t-tests (Bonferroni corrected). Finally, we repeated the analyses with handedness as a covariate, as handedness has been suggested to co-vary with asymmetries in other cognitive and perceptual processes (Jewell & McCourt, 2000).

## 2.4. Results

*Behavioural data and model fit summary.* The model explained on average 80% (mean R2) of the variability in the observed mean scores, and the estimated parameters were comparable to previous TVA-based studies with young, healthy participants (Bundesen, 1998; Finke et al., 2005; Matthias et al., 2009). The overall performance accuracy was 79.84%, and the performance pattern between conditions was in line with TVA predictions and the group differences in top-down control α and spatial bias wλ (Fig. 2): Participants reported most letters correctly in the single-target condition, in which all attentional resources were expended on only one item, and performance was comparable across groups. For dual-letter displays, report performance (for one target in the display) was reduced more in the dual-target conditions compared with the target-distracter conditions, indicating that participants shared resources among the targets in the dual-target conditions, whereas they allocated more attentional weights to the targets than to the distracters in the target-distracter conditions. Paired-samples t-tests confirmed that, across all participants, mean accuracy was significantly lower in the dual-target conditions [Mean = 76.28, SD = 7.93] compared to both the single-target [Mean = 81.97, SD = 6.75] and target-distractor [Mean = 81.28, SD = 6.95] conditions [both t(30) > 6.1, both p < .001]. Individuals with poorer compared to better top-down control showed smaller performance differences between the conditions with and without distracters [Mean = 1.76, SD = 2.21 vs. Mean = 8.45, SD = 2.67 t(29) = 7.626, p < .001], indicating that they allocated relatively less attentional weight to distracters (Fig. 2A and 2B). Furthermore, individuals showed higher report accuracy for targets that occurred in their prioritized hemifield in bilateral display conditions (in which another stimulus appeared in the opposite hemifield), indicating that more attentional weight was allocated to the stimulus on the preferred side (Fig. 2 C and D). For individuals with a leftward bias, report accuracy was significantly higher for targets in the left than in the right hemifield [t(15) = 2.995, p = .009]. Conversely, for individuals with a rightward bias, there was a trend towards higher report accuracy for targets in the right versus the left hemifield [t(14) = -1.729, p = .106] (note that the degree of spatial bias was also higher in the leftward-bias group, see below).

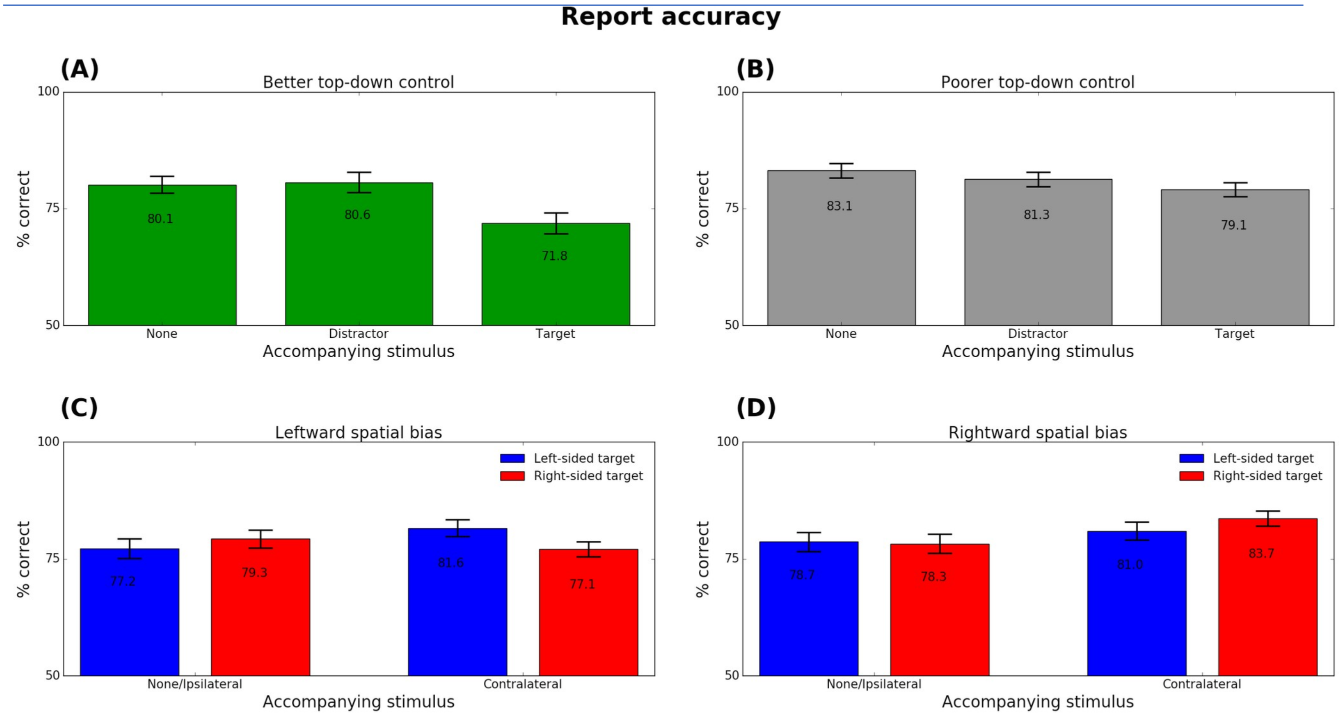


**Fig. 2. Report accuracy in the partial-report task.** Bars depict mean number of correctly reported target letters and standard errors of the means in different conditions of the partial report task. For groups of individuals with better top-down control (A) and poorer top-down control (B), performance is shown for conditions in which a target was presented without accompanying stimulus, in which a target was accompanied by a distracter, and in which are a target was accompanied by a second target. For groups of individuals with left-ward spatial bias (C) and right-ward spatial bias (D), performance is shown for conditions in which a target was presented either alone or with an accompanying stimulus in same (ipsilateral) hemifield and in which a target was presented with an accompanying stimulus in the opposite (contralateral) hemifield, separately for targets presented in the right hemifield (blue) and the left (red) hemifield.

The estimates of top-down control α indicated that target selection was effective (i.e., $\alpha < 1$) across the entire sample [Range = 0.17–0.67, Mean = 0.42, SD = 0.14, t(30) = -22.34, p < .001] (Fig. 3A). The estimates of spatial bias wλ indicated a slight, but non-significant leftward bias (i.e., $w\lambda > 0.5$) across the entire sample [Range = 0.39–0.68, Mean = 0.52, SD = 0.06, t(30) = 1.66, p = .107] (Fig. 3B). The groups split according to the median value of α, naturally, differed in their estimates of α [better top-down control Mean = 0.30, SD = 0.11 vs. poorer top-down control Mean = 0.53, SD = 0.07, t(29) = -7.443, p < .001], but not in their estimates of wλ [better top-down control Mean =

0.52, SD = 0.07 vs. poorer top-down control Mean = 0.52, SD = 0.05, t(29) = 0.021, p = .98]. Conversely, the groups split according to the median value of $w\lambda$ (0.51) differed in their estimates of $w\lambda$, [leftward bias: Mean = 0.56, SD = 0.04 vs. rightward bias: Mean = 0.47, SD = 0.03, t(29) = -5.942, $p < .001$], but did not differ in their estimates of $\alpha$ [leftward bias Mean = 0.43, SD = 0.15 vs. rightward bias Mean = 0.42, SD = 0.15, t(29) = 0.153, p = .88].

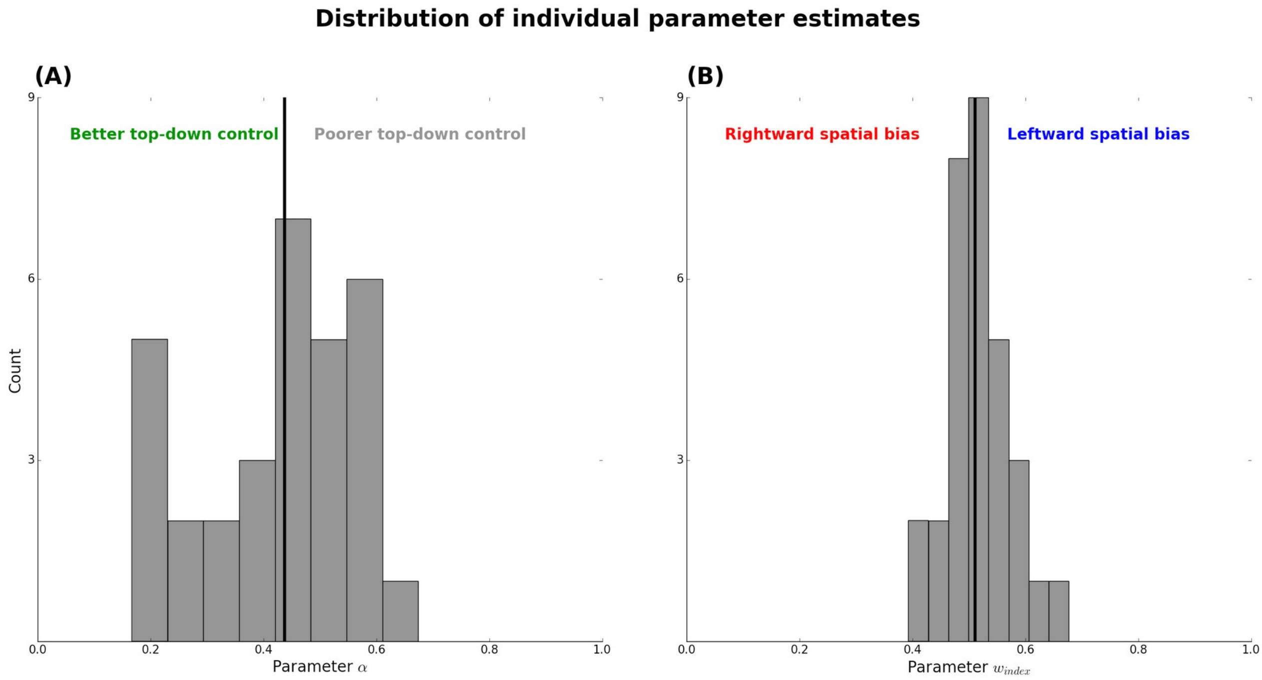


**Fig. 3 : Distribution of individual parameter estimates.** Histograms showing the distribution of individual values of top-down control $\alpha$ (A) and spatial bias $w_{\lambda}$ (B) for. The black lines indicate the median of the sample based on which participants were assigned to groups of better and poorer top-down control and to groups of leftward and rightward spatial bias, respectively.

Significant correlations between the parameter estimates and selection indices based on raw scores confirmed that the values derived from the modelling procedure corresponded to the pattern in the observed performance: top-down control $\alpha$ correlated with the target selection index [r(29) = .956, $p < .001$], and spatial bias $w\lambda$ correlated with the spatial selection index [r(29) = .736, p

< .001]. By contrast, α and wλ did not correlate significantly with each other [r(29) = -.076, p = .684]. And neither did α correlate with the spatial selection index [r(29) = .032, p = .866], nor did wλ correlate with the target selection index [r(29) = -.020, p = .914]. Top-down control α did also not significantly correlate with the degree of spatial bias Dev(wλ), regardless of direction [r(29) = -0.292, p = 0.111].

*TVA parameters and ERLs.* Characteristic visual potentials over parieto-occipital electrode sites were elicited in the bilateral target-distracter condition of the partial-report task, which were larger over the hemisphere contralateral to the hemifield in which a target letter was presented. The amplitudes of ERLs further varied with individuals' level of top-down control α and spatial bias wλ (Fig. 4 and 5).

The ANOVA on PCN amplitudes averaged across the hemifields with the between-subject factor Top-down Control revealed a significant effect of Top-down Control [F(1,29) = 5.72, p = .02]. Amplitudes were higher in individuals with better as compared to individuals with poorer top-down control (-2.21 µV vs. -1.57 µV) (Fig. 4B). The same analyses with the between-subject factor Spatial Bias revealed no significant effect of Spatial Bias [F(1,29) = 2.74, p = .11], indicating that the PCN was modulated by individual differences in parameter α, but not in parameter wλ (Fig. 4C). The ANCOVAs including handedness as a covariate revealed essentially the same results, with a significant effect of Top-down Control [F(1,28) = 5.437 p = .027], but not of Spatial Bias [F(1,28) = 2.610 p = .117], on PCN amplitudes.

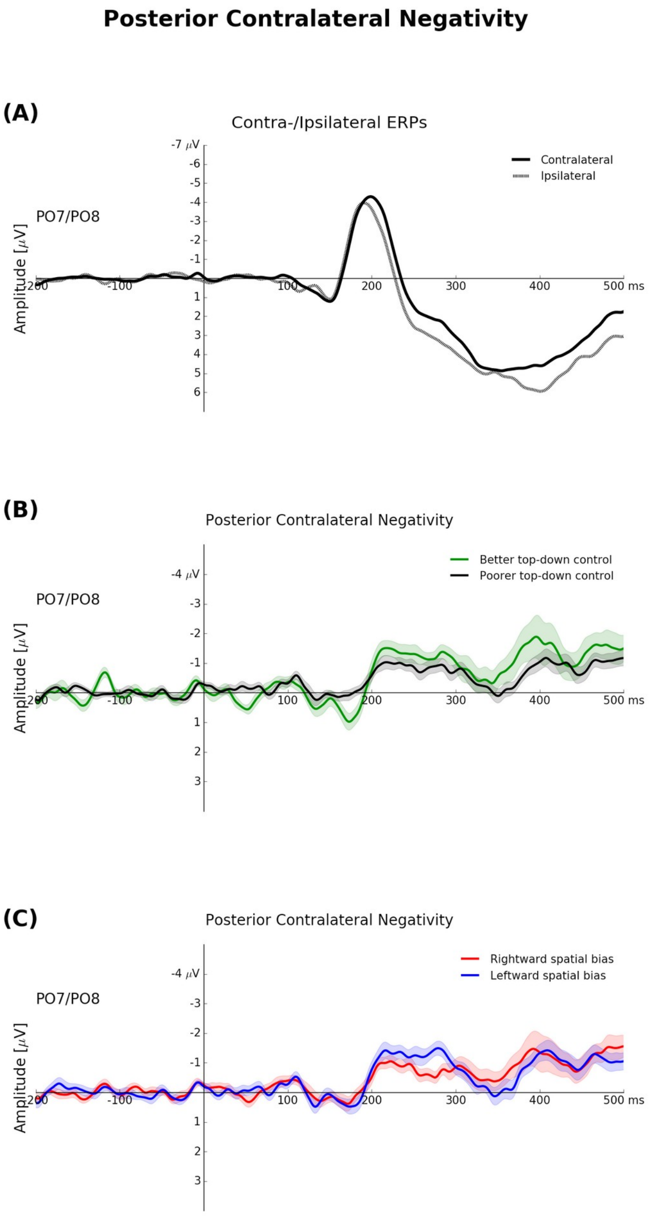


**Fig. 4: PCN**. ERPs contra- and ipsilateral to the target across all participants (A) and PCN (contra-minus-ipsilateral difference) in response to displays with bilateral target-distracter configurations averaged over left- and right-target displays at posterior-occipital electrodes, for groups of individuals with better top-down control (green line) and poorer top-down control (grey line) (B), and for groups of individuals with a leftward spatial bias (blue line) and individuals with a rightward spatial bias (red line) (C). Shaded areas represent standard error of the averaged waveforms.

The ANOVA on hemifield-specific ERLs with the between-subject factor Spatial Bias revealed a significant interaction between Spatial Bias and Target Hemifield [F(1,29) = 8.29, p = .007], showing that ERL lateralization to left vs. right targets varied with participants' prioritized hemifield (Fig. 5B5C and D). Post-hoc tests revealed that ERL amplitudes in response to right-target displays were negative in individuals with a left-ward spatial bias and positive in individuals with a right-ward spatial bias [-1.32 µV vs. 0.99 µV, t(29) = 2.897, p < .01], while ERL amplitudes in response to left-target displays were negative in individuals with a right-ward spatial bias and positive in individuals with a left-ward spatial bias [-0.72 µV vs. 1.69 µV, t(29) = -2.689, p = .012]. Two paired-samples t-tests revealed that amplitudes in response to right- and left-target displays differed significantly for the group of participants with a left-ward bias [t(15) = 2.799, p = .013], but not the group with a right-ward bias [t(14) = -1.377, p = .190].

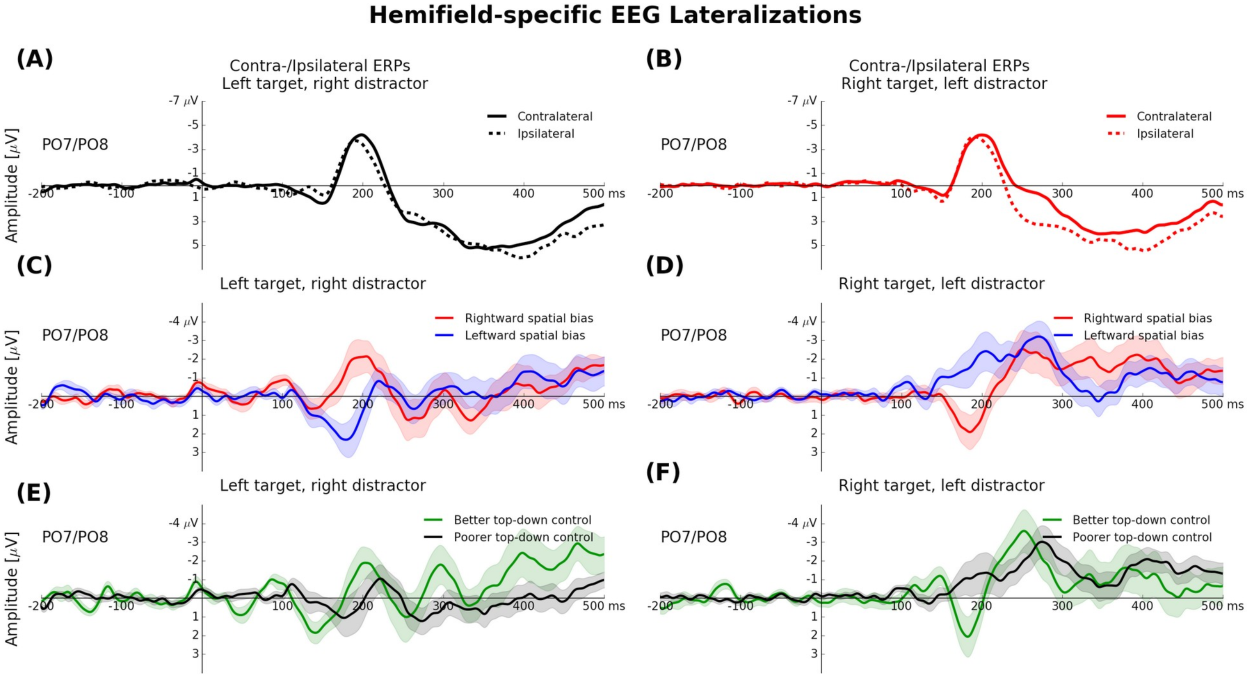


**Fig. 5: Hemifield-specific asymmetries in ERLs.** Grand-averaged ERPs across all participants contra- and ipsilateral to the target in response to displays with targets presented in the right hemifield and distracters in the left hemifield (A) and to displays with targets presented in the left hemifield and distracters in the right hemifield (B). ERLs (contra-minus-ipsilateral difference) are shown separately for groups of individuals with a rightward spatial bias (red lines) and leftward spatial bias (blue lines) in response to displays with targets presented in the right hemifield and distracters in the left hemifield (C) and to displays with targets presented in the left hemifield and distracters in the right hemifield (D) and for individuals with a better top-down control (green lines) and poorer top-down control (grey lines) in response to displays with targets presented in the right hemifield and distracters in the left hemifield (E) and to displays with targets presented in the left hemifield and distracters in the right hemifield (F).

The ANOVA on hemifield-specific ERLs with the between-subject factor Top-down Control did not reveal an interaction of Top-down Control and Target Hemifield [$F(1,29)<0.01$, $p = 0.96$] (Fig. 5C). Thus, the results indicate that hemispheric asymmetries in the ERL varied with individual differences in the parameter $w\lambda$, but not in the parameter $\alpha$. The ANCOVAs including handedness as a covariate revealed the same results: a significant interaction of Target Hemifield and Spatial Bias [F(1,28) = 15.634, p < .001], but not of Target Hemifield and Top-down Control [F(1,28) = 0.273, p = .606], on amplitudes of the hemifield-specific ERLs.

## 2.5. Discussion

We identified distinct ERL correlates of individual differences in TVA-based parameters of task-specific and hemifield-specific visual selection. First, the PCN varied with parameter top-down control α, but not with parameter spatial bias wλ. Second, hemifield-specific asymmetries in the ERLs varied with parameter spatial bias wλ, but not with parameter top-down control α.

*The PCN amplitude as a neural marker of individual differences in top-down control.* Parameter estimates of top-down control α showed that selection of task-relevant over -irrelevant objects was overall effective (i.e., targets received higher attentional weights than distracters), while this selection efficiency varied considerably among the individual participants (Fig. 3A). These inter-individual differences in top-down control were reflected in the PCN; specifically, individuals with more efficient top-down control exhibited larger PCN amplitudes in response to bilateral target-distracter displays compared to individuals whose task-related selection was less efficient.

The large majority of PCN studies investigated the component using variants of visual search tasks (Eimer, 2015; Töllner et al., 2012), and the mechanisms assumed to be reflected in the PCN have been interpreted in influential visual search models developed to explain search performance under varying target-distracter configurations (Found & Müller, 1996; Müller & Krummenacher, 2006; Wolfe, Cave, & Franzel, 1989; Wolfe, 1994, 2007). Within subjects, the PCN amplitude varies with the demands of top-down control in the task: it decreases when selection is made easier, for example, by eliminating or lowering the number of distracters (Luck & Hillyard, 1994); and it increases when selection becomes harder, such as in visual search for targets defined by feature conjunctions as compared to single features (Luck & Hillyard, 1995; Luck, Girelli, McDermott, & Ford, 1997). The PCN is sensitive to voluntary preparation, for example, when setting oneself to a target expected to be defined within a particular feature dimension – corroborating the component's association with task-dependent, top-down modulation of processing the selection-relevant target feature (Töllner, Zehetleitner, Gramann, & Müller, 2010; Töllner, Müller, & Zehetleitner, 2012).

Given these (and numerous other) reports of within-subject PCN variations resulting from experimental visual-search manipulations, the consensus view is that the component reflects a filtering mechanism subserving the selection of task-relevant stimuli, whereby the processing of targets is enhanced at the expense of distracters (Eimer, 2015; Luck, 2012). The PCN amplitude specifically is assumed to reflect the amount of attentional resources allocated to the task-relevant stimulus (Eimer et al., 1996; Luck & Hillyard, 1994; Töllner et al., 2008). Following this, we interpret the between-subject differences we found under constant selection demands in the partial-report task to indicate that individuals with better top-down control allocate relatively more of their available attentional resources to the task-relevant object, compared to individuals with poorer top-down control. In terms of TVA, this translates into a stronger competitive advantage of the target over the distracter in the selection process (Bundesen & Habekost, 2008).

(N)TVA (Bundesen 1990, Bundesen et al., 2005), as a more general theory of visual selection, has direct implications for visual search performance (Bundesen & Habekost, 2008) and provides a complementary theoretical background for interpreting the ERP modulations.[1]

---

[1] Guided Search and related models distinguish between an early stage of preattentive, capacity-unlimited parallel processing of simple sensory information, which is followed by a capacity-limited, serial selection process required for recognition of the selected items. TVA also envisages a first stage of preattentive parallel processing of the objects in the visual field (though not necessarily limited to simple sensory features), on which the computation of attentional weights is based. However, in contrast to the serial selection process in Guided Search, in TVA, the second stage of processing is assumed to be a parallel capacity-limited process that is biased by the outcome of the first processing stage (for details, see Bundesen & Habekost, 2008).

Specifically, the mechanisms assumed to be reflected in the PCN are reconcilable with the mechanism of attentional weighting which, on TVA, underlies top-down selection (Bundesen et al., 2005). TVA assumes that objects are selected by a "filtering" mechanism, in which attentional weights are computed for all objects in the visual field based on their current importance. The available processing resources are then distributed among objects according to their weights. As a result, objects with higher weights are processed faster and more likely to be selected, which, in terms of TVA, corresponds to being encoded into vSTM. In a partial-report situation (or, similarly, in visual search), in which stimuli fall into categories of targets and distracters, effective top-down control devotes relatively more visual processing resources to the behaviourally important target objects by assigning higher weights to them compared to less important distracter objects. The individual efficiency of this filtering process is reflected in the parameter estimate of top-down control α. In line with this, given its association with α, the PCN amplitude could be interpreted as a marker of the relative difference in the weighting of targets in one and distracters in the opposite hemifield, on an individual-subject level. NTVA further proposes that the distribution of neural resources according to the attentional weights is governed by higher-order cortical areas that project to visual areas via the pulvinar nucleus of the thalamus (Bundesen et al., 2005). In line with this proposed implementation of top-down processing, generator sources of the PCN have been identified within the ventral occipito-temporal cortex, where processing is influenced by top-down signals from frontal and parietal areas (Buschman & Miller, 2007; Hopf et al., 2002).

In order to integrate the results with other theoretical accounts of visual attention (Guided Search: Wolfe, 1994, 2007; Dimension-Weighting Account: Müller et al., 1995) and to test the generalizability of the association between PCN amplitudes and individuals' ability to effectively filter target and distracter information, testing the relationship between individual differences in performance in other selective attention tasks, specifically visual search, would be informative. In fact, there is accumulating evidence that PCN amplitudes are larger in individuals with faster as compared to slower response times in visual search tasks (Töllner, Conci, & Müller, 2015; Williams & Drew, 2017).

*Hemifield-specific ERL asymmetries are related to individual differences in spatial bias.* On the group level, parameter estimates of spatial bias, $w\lambda$, indicated largely balanced spatial weighting. However, a slight, non-significant, leftward “pseudoneglect” was found, which mirrors the rightward spatial bias found in patients with visual hemi-neglect in such TVA-based letter report paradigms (Duncan et al., 1999; Finke, Matthias, Keller, Müller, Schneider, & Bublak, 2012), albeit to a much lower degree. This finding in healthy individuals is common (Finke et al., 2005) and in accordance with the right-hemisphere dominance-hypothesis for visuo-spatial attention (Heilman & Van den Abell, 1980; Posner & Petersen, 1990). For single participants, however, sizable spatial biases to either left or the right hemifield were apparent (Fig. 3B). This implies that, on the individual level, attentional resources deployed to locations in the left and right hemifields are asymmetrical, and that the direction and degree of this asymmetry varies among individuals.

While inter-individual differences in spatial biases have previously been linked to other aspects of neural hemispheric asymmetries, such as white matter volume (Thiebaut de Schotten et al., 2011) and activity in the fronto-parietal attention network (Szczepanski & Kastner, 2013), our study is the first to link intrinsic hemifield asymmetries in spatial prioritization (or weighting) to asymmetries in ERLs marking visual selection processes. Typically, on the assumption that the visual system is organized contralaterally in a symmetrical fashion, left-right asymmetries in ERLs such as the PCN are rarely reported (Mazza & Pagano, 2017). However, by taking individual differences in spatial bias $w\lambda$ into account, we revealed potentially meaningful asymmetries in early EEG lateralizations elicited by correctly identified targets in the left versus right hemifield: individuals with a leftward bias exhibited a negative ERL in response to right-target displays, but, within the same time range, a positive ERL in response to left-target displays; conversely, individuals with a rightward bias showed a negative ERL in response to left-target displays, but a positive ERL in response to right-target displays.

A subdivision into negative and positive ERLs that co-occur in the broader PCN time range has previously been noted by Hickey et al. (2009). In particular, they proposed the PCN to reflect the summation of a positivity contralateral to the distracter (PD) that is related to a spatially-specific active suppression mechanism and a negativity contralateral to the target (NT) that is related to target selection. In the present study, we observed a negativity contralateral to the target (or positivity contralateral to the distracter) only when the target appeared in the individual's non-prioritized hemifield. This may be taken to indicate that more activity related to enhance target- ( or suppress distracter-) processing was engaged by our participants if the relevant information was presented at a non-favored location.[2]

---

[2] Recall that we analyzed only bilateral target-distracter displays. Accordingly, ERLs always reflected the summation of both components. Future studies may compare hemifield differences in ERLs as a function of individuals' spatial bias using displays with both laterally and vertically presented target and distracter stimuli, which permit the $P_D$ and $N_T$ to be distinguished (see Hickey et

Of note, the spatial bias-related asymmetry in ERLs occurred in a time window before the maximum deflection of the overall PCN (Fig. 3 and 4). Several recent studies have pointed out that the Ppc can precede the PCN with some display configurations (Corriveau et al., 2012; Jannati et al., 2013). The functional interpretation of the Ppc is still under debate. The component has been suggested to mark an early, attention-driven location-specific signal to a salient, task-relevant or irrelevant stimulus (Corriveau et al., 2012; Fortier-Gauthier, Dell'Acqua, & Jolicœur, 2013). This can be distinguished from the later Pd component that has been related to the active suppression of a salient distracter (Sawaki & Luck, 2013). While our study is the first to suggest the Ppc's relation to spatial attentional bias, the component has recently also been reported to be sensitive to individuals' attentional biases towards certain stimulus features; specifically, a processing advantage for targets coloured red over other target colours (Pomerleau, Fortier-Gauthier, Corriveau, Dell'Acqua, & Jolicœur, 2014), as well as to "global preference", that is, preferential processing of object configurations that form a global shape over non-shape configurations with otherwise equal physical features (Wiegand et al., 2015). In the present study, participants showed a Ppc for targets that appeared in their prioritized hemifield (recall that the target-distracter colour assignments and shapes were the same for all participants) associated with a processing advantage for stimuli in this over stimuli in the opposite hemifield. Accordingly, the Ppc might be regarded as a marker of bottom-up signals for selection strongly driven by intrinsic observer preferences, creating "subjective saliency" of the target in the prioritized compared to the stimulus in the contralateral hemifield. This early, rather automatic processing advantage may then bias the subsequent stage of target selection reflected by the PCN, which, in contrast, is strongly influenced by top-down processes of attentional

---

al., 2009).

control and marks task-related selection by actively enhancing target-related, or suppressing distracter-related, information (Gokce et al., 2014; Wiegand et al., 2015).

In terms of NTVA, the early spatial bias-specific asymmetry seen in the Ppc might reflect a bottom-up mechanism of spatial weighting generating a topographic priority map during some early, spatially specific processing wave – consistent with the view that the Ppc reflects laterally imbalanced activity to the most salient item on a salience map (Jannati et al., 2013). An individual's spatial bias would translate into higher weights for stimuli at locations in the preferred hemifield, compared to weights for stimuli in the opposite hemifield. As a consequence, stimuli at prioritized locations have a competitive advantage in the second processing wave of selection, in which resources are re-distributed according to weighting of both spatial and non-spatial features of stimuli in the visual field (Bundesen et al., 2005; Habekost & Bundesen, 2008).

Our results lend support to the notion that the spatial bias is a generalizable, trait-like characteristic of an individual's attentional system (Benwell, Thut et al., 2013). This, however, does not imply that spatial processing asymmetries are non-malleable. Rather, individual differences in (baseline) spatial biases can co-occur, or even interact, with task-dependent changes in spatial bias (Benwell, Harvey et al., 2013; Matthias et al., 2010). Of note, in TVA-based tests, letter stimuli are used, which may induce an asymmetry due to left-hemisphere dominance for processing verbal stimuli (Gross, 1972). In fact, TVA parameters processing speed C and vSTM storage capacity K measured in a letter whole-report paradigm are typically found to be slightly higher in the right than in the left hemifield (Brosnan et al., 2017; Kraft et al., 2015; Wiegand et al., in press). This indicates that stimulus material-dependent lateralizations become prominent in parameters of visual attention capacity. In fact, in a vSTM task with non-verbal stimuli, a left-hemifield advantage was found, at least for simple-feature stimuli (Sheremata, Bettencourt, & Somers, 2010; Sheremata & Shomstein, 2014). Importantly, in TVA, visual capacity is measured independently of the relative spatial distribution of available processing resources reflected in parameter wλ, with the latter typically revealing the slight leftward pseudo-neglect also in tasks that use letter stimuli (Finke et al., 2005). Similarly, a left-hemifield advantage is observed in rapid visual presentation tasks with letter stimuli, together with a stronger PCN over the right compared to left hemisphere, which was attributed to the right-hemispheric dominance for attention (Śmigasiewicz, et al., 2014; Verleger et al., 2009). In future experiments, task demands and stimulus material should be manipulated to systematically investigate whether and how those factors affect spatial bias, asymmetries in attention capacity, and hemifield-specific ERLs within individuals.

*Top-down control and spatial bias are independent aspects of visual selection.* TVA assumes that the relative weighting of objects for selection with respect to task relevance and spatial position are two independent processes, and accordingly the parameters reflecting those functions are estimated mathematically independently from each other, as well as independently of the overall available processing capacity. In accordance with this theoretical assumption, our study as well as previous reports yielded only small, non-significant correlations between the parameters top-down control and spatial bias (Finke et al., 2005; Habekost et al., 2014; Wiegand, Petersen, Bundesen et al., 2017). Furthermore, a double dissociation of the two functions has been demonstrated in brain-damaged patients (Bublak et al., 2005): a patient with a lesion in the inferior parietal region exhibited a rightward spatial bias and intact top-down control, whereas the opposite pattern, impaired top-down control in presence of balanced spatial processing, was found in a patient with a superior frontal lesion. In line with previous work (Wiegand, Töllner, Habekost et al., 2014; Wiegand, Töllner, Dyrholm, et al., 2014), here we further support TVA's independence assumption by showing distinct relationships between inter-individual differences in the model parameters and ERPs.

Apart from separating spatial and non-spatial selection processes, the TVA-based approach further permits those functions to be quantified independently of motor processes. Handedness has been shown to co-vary with asymmetries in other cognitive and perceptual processes, including spatial bias measured in the landmark task (Jewell & McCourt, 2000). However, the association between our TVA-based behavioural measures of spatial attentional processing asymmetries (and top-down control) and ERLs did not change when we included handedness as a covariate in the analysis. A crucial difference between the landmark task and TVA-based assessment is that the former requires hand responses, which is why the resulting measure of visual spatial bias might be more prone to be influenced by asymmetries in the motor system (Luh, 1995). In line with this view of differential motor involvement in spatial bias measures, recent neuroscientific studies indicate that asymmetries in frontal and parietal areas for visual spatial processing are unrelated to the degree of handedness (Badzakova-Trajkov, Häberling, Roberts, & Corballis, 2010; Szczepanski & Kastner, 2011). Similarly, handedness did modulate neither behavioural nor ERL hemifield asymmetries in a lateralized rapid serial visual presentation task (Śmigasiewicza, Liebrand, Landmesser, & Verleger, 2017).

## 2.6. Summary and Outlook

In the present study, we combined parametric assessment based on the computational TVA framework and visual ERLs, and established neuro-cognitive markers of individual differences in two distinct functions of selective visual processing: First, top-down control, quantified as parameter α, was related to the PCN amplitude, indicating that individuals with better top-down control engage more resources during attentional selection of task-relevant over irrelevant stimuli. Second, spatial bias, quantified as parameter wλ, was related to hemispheric asymmetries of visual ERLs depending on the target and distracter position in the display, indicating differences in early bottom-up visual processing of stimuli in an individual's more, relative to less, preferred hemifield. The presumed neuronal mechanisms underlying the activation pattern are in line with assumptions of NTVA and support the view that the two aspects of spatial and non-spatial attentional weighting reflect independent functions of the human visual processing system (Bundesen et al., 2005; 2011).

TVA provides a formal theoretical framework for the interpretation of linked cognitive and neurophysiological processes, grounded on basic research. Typically, ERPs are examined with regard to their variation with experimental conditions; thus, inferences are biased by the investigators' pre-assumptions about the hypothesized variation of cognitive processes and ERPs in a given task manipulation. The present inter-individual differences approach therefore augments our understanding of the linkage between cognitive processes and ERP deflections (Braver, Cole, & Yarkoni, 2010). Finally, TVA-based assessment provides a proven methodological apparatus for quantifying attentional functions in the normal populations, lifespan changes (McAvinue et al., 2012), and subtle and severe dysfunctions under various clinical conditions (Habekost, 2015). On this basis, the present approach offers a promising method for deriving individual neuro-cognitive trait-markers of attentional functions, as well as indices of age- and disease-related changes in these functions (Wiegand, Töllner, Dyrholm et al., 2014; Wiegand et al., 2016; Wiegand, Petersen, Bundesen, & Habekost, 2017).

## 2.7. Acknowledgements

This work was supported by a MOBILEX mobility grant (1321-00039B) from the Danish Council for Independent Research and European Union Marie Sklodowska-Curie COFUND actions (IW), the European Union's Horizon 2020 research and innovation programme under the Marie Sklodowska-Curie grant agreement no. 702483 (IW), the European Union's Seventh Framework programme for research, technological development, and demonstration under the Marie Sklodowska-Curie Initial Training Network grant agreement no. 606901 (KF, TT, HJM, TH, AP), a grant (FI 1424/2-1) of the German Research Foundation (KF), a Sapere Aude Grant (11-104180) from the Danish Council for Independent Research (TH), and the Graduate School of Systemic Neurociences (GSN) of the LMU Munich (NN). Thanks to Erika Kunstler for help with the data assessment.

# 3. Manuscript:

# Aging, efficiency of visual attentional selection and cognitive reserve: insights from event-related EEG lateralizations.

Natan Napiorkowski[1,2], Thomas Töllner[1,2], Iris Wiegand[3,4,5], Anders Petersen[6], Hermann Müller[4], Kathrin Finke[1,7]

[1]General and Experimental Psychology, Department of Psychology, LMU Munich

[2]Graduate School of Systemic Neurosciences, LMU Munich

[3]Max Planck UCL Centre for Computational Psychiatry and Ageing Research

[4]Center for Lifespan Psychology, Max Planck Institute for Human Development

[5]Visual Attention Lab, Brigham & Women's Hospital and Harvard Medical School

[6]Center for Visual Cognition, Department of Psychology, University of Copenhagen

[7]Hans-Berger Department of Neurology, Jena University Hospital

## 3.1. Abstract

Visual attentional functions are affected by ageing. Their decline was suggested to result from a decreasing efficiency of top-down control, i.e. a deficit in prioritizing relevant over irrelevant information. However, investigations of this assumption brought mixed results. In order to gain more information about the relation between healthy ageing and changes in the efficiency of attentional selection, we assessed top-down control efficiency using a partial-report task with briefly presented letter arrays based on Bundesen's Theory of Visual Attention in a sample of healthy participants divided into three age groups: youngest, middle and oldest. The task was combined with a simultaneous EEG recording to investigate whether potential age-related changes in top-down control efficiency are reflected by changes in the amplitudes of the lateralized components. Furthermore, we included a measurement of crystallized IQ, as a potential factor influencing age-related cognitive changes. We did not find changes in top-down control efficiency with ageing nor any relation to crystallized IQ. Electrophysiological data revealed that participants with more efficient top-down control showed larger amplitudes of the lateralized components Ppc and PCN. These results were in turn modulated by crystallized IQ: Ppc amplitude was related to top-down control efficiency only in participants with higher crystallized IQ, whereas PCN amplitude was related to age only in participants with lower crystallized IQ. Our results indicate that top-down control efficiency is basically preserved in normal ageing. Furthermore, the fact that the same ERP correlates, i.e. Ppc and PCN amplitudes, reflected top-down control efficiency across age groups indicated that top-down control is neurally implemented in a similar way in older healthy participants as in younger participants. We hypothesise that declining amplitudes of the described components might be indicators of the age-related cognitive decline. The fact that crystallized IQ modulated the

relationship between top-down control efficiency and both age and Ppc and PCN amplitudes indicates that cognitive reserve has a significant role for the way top-down control is implemented in ageing individuals.

## 3.2. Introduction

Normal ageing affects functions of visual attention (e.g. Craik & Salthouse, 2000; Carlson et al. 1995; Salthouse et al, 1989, Madden, 2007). Critically, there is an ongoing debate on the specific attention functions that decline with ageing. According to the ”inhibitory deficit hypothesis”, the underlying cause is less efficient top-down control, i.e. a reduced ability to prioritize relevant information while reducing interference from distracting information in older compared to younger adults (Hasher & Zacks, 1988). However, coherent evidence for this assumption is missing. On one hand, such inhibitory deficit could explain why older compared to younger adults show higher brain activity associated with distractor processing in fMRI studies (Gazzaley et al., 2005, 2007). On the other hand, it has been shown that older adults can effectively use top-down controlled strategies in various visual search tasks, which actually suggests at least some aspects of visual attentional control are preserved in normal ageing (Madden et al., 2004, 2005). For example, prefrontal cortical activation during the performance if visual attention tasks was found to be higher in older compared to younger adults. This suggested that older individuals may recruit preserved compensatory top-down control mechanisms in order to counteract age-related decrease of attentional capacity functions relying on more posterior parts of the brain, such as, e.g., visual processing speed (Cabeza, 1997; Madden, Whiting & Huettel, 2005).

One decisive advantage for the characterization of age-related changes in visual attention functions can be gained by use of psychophysical paradigms based on the computational Theory of

Visual Attention (TVA, Bundesen, 1990). As different parameters of visual attention can be quantified independently using TVA-based methodology, a high cognitive precision is achieved (see Habekost, 2015, for a review). In close relation to the 'biased competition' account of attention (Desimone & Duncan, 1995), TVA assumes that multiple objects presented in the visual field are processed simultaneously and compete to get encoded into a highly limited visual short-term memory store (see: Cowan, 2001; Sperling, 1960). Only objects that reach the store are assumed to get consciously represented and, thus, available for actions, such as, e.g. verbal report. The probability of an object to get access to the store depends on its processing rate, which, in turn, is determined by its relative attentional weight (w). When task-related selection is efficient, targets receive relatively higher attentional weights, and are, thus, processed faster, compared to distractors. TVA-based modelling of performance in a partial report task with briefly presented target and distractor letters (Duncan, et al., 1999) allows for a separate estimation of the attentional weights allocated to task-relevant targets on the one hand and task-irrelevant distractors on the other. Parameter top-down control $\alpha$ is defined as the ratio of distractor and target weights and provides a quantitative measure of how efficiently a given participant can prioritize targets over distractors.

With respect to pathological ageing, it has been reported that parameter top-down control as measured with TVA-based partial-report tasks is impaired in patients with Mild Cognitive Impairment at risk for Alzheimer's disease and, more so, patients with Alzheimer's disease (Redel et al, 2012). With respect to the influence of normal ageing on top-down control, two TVA-based studies have been published so far. Both used a CombiTVA task with intermingled partial and whole report trials, the latter including multiple target and no distractor items, allowing the additional assessment of attentional capacity parameters such as visual threshold, visual processing speed and visual short-term memory storage capacity (Vangkilde et al., 2011). Across these two studies (McAvinue et al. 2012; Espeseth et al. 2014), substantial and linear age effects were found only on attentional capacity parameters. In contrast, top-down control efficiency showed some age-related decline only in the very youngest groups and remained relatively stable up from the age of around 30 (Espeseth et al., 2014) and 50 (McAvinue et al. 2012), respectively, until the age of 80+ years. These results rather support the assumption of preserved top-down control in ageing individuals (Madden et al., 2004). However, average top-down control values in these studies generally indicated floor effects across the different adult groups that might result from the requirement to switch between whole and partial report trials. Hence, it is possible that floor effects prevented age effects from being shown in older adult groups.

A second decisive step in order to shed more light onto the relationship between top-down control and ageing can be accomplished by taking individual differences in cognitive reserve into account. Cognitive reserve is a construct that has been postulated to explain a non-linear relationship between brain damage and observed clinical symptoms. More precisely, a greater amount of cognitive reserve is assumed to denote a higher ability to use alternative brain networks or more efficient cognitive strategies in response to a cognitively demanding task. Thus, higher cognitive reserve is suggested to increase the probability of preserved cognitive performance in face of neurodegeneration (Stern, 2003). The amount of cognitive reserve is typically estimated by measures of educational attainment, such as crystallized IQ (Stern, 2002), which can be assessed with vocabulary tests (Cattell, 1971; Sumowski et al., 2010). Measures of crystallized IQ do typically not decline throughout the process of normal ageing (Stankov, 1988) and even during pathological neurodegeneration (Almkvist and Tallberg, 2009). Thus, they are seen as being good indicators of educational attainment across the life span.

A third mean to shed a closer light on the question of potential age-related changes in top-down control is the combination of the assessment of behavioural and neural indices of the efficiency of selection. According to the neural interpretation of TVA (NTVA, Bundesen et al., 2005) the biased distribution of attentional weights across objects is guided by higher-order cortical areas that project via the ventral visual processing stream, through the pulvinar nucleus of the thalamus, to visual areas (Bundesen et al., 2005). Importantly, a recent study combining electroencephalography (EEG) and TVA-based assessment (Wiegand et al., in press) identified the amplitude of the Posterior Contralateral Negativity (PCN), a lateralized event-related component with neural sources within the ventral stream (Buschman and Miller, 2007; Hopf et al., 2006), as a neurophysiological correlate of the individual efficiency of top-down control. More precisely, in this study, participants with more as compared to those with less efficient top-down control showed higher PCN amplitudes. The PCN is typically elicited 200-350 ms post-stimulus and is a marker of attentional resources recruited to select a relevant object in the presence of distractors (see: Eimer, 1996; Heinze, Luck, Mangun and Hillyard, 1990; Luck, 2005; Töllner et al., 2012; Woodman and Luck, 2001). Subsequent lateralized component, the Posterior Positivity Contralateral is a positive lateralized component typically elicited 160-270 ms post-stimulus and was recently suggested to reflect an early location-specific processes of distractor inhibition (Ppc, Corriveau et al., 2012; Jannati et al., 2013). Importantly, both PCN and Ppc, have been reported to be sensitive to normal ageing (e.g. Pagano et al., 2015; Van Der Lubbe & Verleger, 2002; Wiegand et al. 2015). Thus, as normal ageing is assumed to affect both, efficiency of top-down control and amplitudes of EEG components reflecting attentional selection and distractor inhibition, the question arises whether and how attentional top-down control in ageing individuals is related to the amplitudes of PCN and Ppc.

Combining these three means we aimed at investigating the relationship between ageing and top-down control efficiency. In the current study we tested 1) whether and how the efficiency of attentional top-down control is affected by normal ageing and/or by crystallized IQ and whether potential effects interact. Furthermore, we tested 2) whether the established neurophysiological correlates of top-down control are affected by aging and/or IQ and whether potential effects interact. To address these questions we combined a partial-report letter task with simultaneous EEG recording and measurement of crystallized IQ in a group of 83 healthy participants at the age of 20 to 77 years, divided into three age groups of comparable size. In the partial-report task participants had to report briefly presented targets (red letters) while ignoring distractors (blue letters). From report accuracy in different conditions (see: Figure 1) we derived the TVA parameter top-down control α for each participant, which we compared between youngest, middle and oldest participants divided into groups with relatively high and low crystallized IQ. To gain information concerning neural correlates of top-down control efficiency, we compared amplitudes of lateralized components PCN and Ppc between participants with better and poorer top-down control and higher and lower crystallized IQ.

## 3.3. Methods

**Table 1**.

Demographic information

| | Youngest participants | Middle participants | Oldest participants | Sig. $\chi^2$ or F |
|---|---|---|---|---|
| N | 28 | 27 | 28 | |
| Age [years] | 35.5 (3.8)<br><20-33> | 45.81 (7.56)<br><33-58> | 71.07 (4.06)<br><60-77> | p<0.001 |
| Sex (F/M) | 16/12 | 16/11 | 8/20 | p=0.038 |
| Education [years] | 12.57 (0.74)<br><10-13> | 12.81 (1.27)<br><9-13> | 11.82 (1.61)<br><9-14> | p=0.090 |
| Depression (BDI) | 4.79 (4.72)<br><0-17> | 6.5 (5.59)<br><0-18> | 5.36 (4.68)<br><0-18> | p=0.446 |
| State Anxiety (STAI) | 35.79 (9.04)<br><24-59> | 32.87 (10.85)<br><0-58> | 32.29 (7.21)<br><23-49> | p=0.311 |
| Trait Anxiety (STAI) | 34.79 (11.23)<br><0-57> | 34.57 (12.48)<br><0-67> | 31.89 (7.75)<br><20-51> | p=0.532 |
| Psychological distress (BSI) | 3.45 (3.13)<br><0.42-14.90> | 3.99 (2.63)<br><0.2-9.92> | 3.22 (1.90)<br><0.14-7.27> | p=0.554 |
| Sleep quality (PSQI) | 4.73 (1.28)<br><2-8> | 4.92 (1.66)<br><0.1-7.00> | 5.14 (1.55)<br><3-10> | p=0.603 |
| MMSE | --- | --- | 29.07 (0.90)<br><27-30> | --- |
| Executive functioning (TMT B/TMT A) | 2.34 (0.84)<br><1.25-5.78> | 2.31 (0.65)<br><1.28-4.15> | 2.33 (0.85)<br><0.83-3.98> | p=0.985 |

*Key: F-female; M-male; R-right handed, L- left handed; TMT – Trail Making Test; BDI – Beck Depression Inventory; STAI - State-Trait Anxiety Inventory; BSI - Brief Symptom Inventory; PSQI - Pittsburgh Sleep Quality Index; MMSE: Mini Mental State Examination.*

### Participants

Eighty-three native German speakers took part in the study. Participants were divided into three groups of comparable size, according to their age: 28 participants were allocated to the "youngest group" (aged 23 to 33 years), 27 to the "middle group" (aged 33.5 to 58 years) and 28 participants to the "oldest group" (aged 60 to 77 years). The experimental procedure was approved by the local ethics committee of the psychology department of the Ludwig-Maximilian-University, Munich. All participants provided written informed consent according to the Declaration of Helsinki II and received payment or course credits for taking part in the study. Before the experimental session participants filled out demographic surveys containing demographical information. Then, a further screening was carried out by a psychologist, consisting of an assessment of depression symptoms (Beck's depression inventory, BDI; Beck et al. 1996), anxiety symptoms (The State-Trait Anxiety Inventory, STAI, Spielberger et al., 1983), psychological distress (Brief Symptom Inventory, BSI, Derrogatis, 1993), sleep quality (The Pittsburgh Sleep Quality Index, PSQI, Buysse et al., 1983), visual search speed and executive functioning (Trail Making Test, TMT, Reitan, 1958), and, in the oldest group only, general cognitive status (Mini Mental State Examination, MMSE, Folstein et al., 1975). The demographic details are listed separately for each age group in the Table 1[3]. Age groups were matched with respect to educational level, mental health (BDI, STAI, BSI, PSQI) and executive functioning (TMT B/TMT A). However, sex distribution differed between groups and therefore sex was taken into account as a covariate in the statistical analyses. Criteria for exclusion from the study included a questionnaire report of history of psychiatric (e.g. anxiety disorder, schizophrenia, claustrophobia or depression) or neurological (e.g. brain injury, stroke, seizures, dementia) disorders, disorders leading to risk for mental decline (non-corrected hypertension, diabetes), non-correctable vision problems (e.g. colour blindness or glaucoma), intake of medication affecting cognitive

---

[3] Demographic data presented separately for participants of different age and IQ level is presented in the supplementary material.

performance or alcohol at the day of testing, and, in the screening, a BDI score >20 indicating current depression or a MMSE score < 27 indicating beginning neurodegeneration.

All participants were part of the Munich INDIREA[4] aging cohort, which consists of a sample of 108 healthy adults aged 19 to 78 years old who underwent functional and structural MRI and electroencephalography. For the current study, 4 participants were excluded from this original sample, according to the exclusion criteria listed above, 3 due to the BDI score and 1 participant due to the MMSE score. Furthermore, the data of further participants of whom behavioural and EEG data was recorded, was not used for further analyses. This was data of 14 participants who showed ceiling effect or floor effect in the partial report task i.e. performance above 90% or below 70% in the single target condition, 4 participants who showed excessive eye ocular artefacts in the EEG signal and 3 participants who showed extreme ERL amplitudes that deviated more than 3 standard deviations from the respective average.

### Partial-report paradigm

**Task.** The TVA-based partial-report task was similar to the task introduced by Duncan et al. (1999). Fig. 1 illustrates the sequence of stimuli presented in a single experimental trial. Participants were instructed to fixate on a central point displayed at the beginning of each trial and throughout stimulus presentation. Subsequently, an array of red (target) and blue (distractor) letters was briefly presented on a black background. In each trial participants could be presented either with a single target letter, two target letters or one target letter accompanied by one distractor letter. The task was to verbally report only the red targets while ignoring the blue distractors without order or speed constraints.

---

[4] Individualized Diagnostics and Rehabilitation of Attentional Disorders

Time for report was indicated by the appearance of a white question mark in the centre of the screen. The experimenter was present in the chamber throughout the whole testing procedure, sitting behind the participant, entering the letters reported by the participant on a keyboard and manually starting each trial by a key press. The duration of the letters' exposure was individually adjusted in a pre-test to ensure a comparable level of task difficulty across participants.

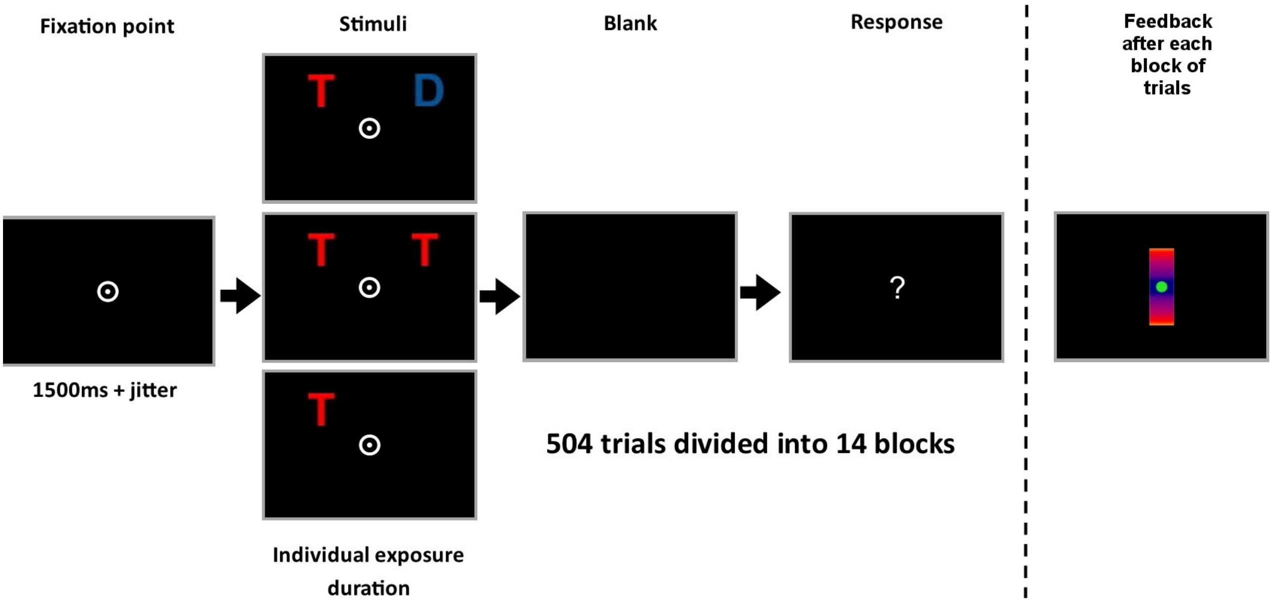


**Figure 1. Sequence of events in the partial report experiment.** Each trial started with a fixation point, followed by a brief display containing either a single target (red letter) letter, a target accompanied by another target or a target accompanied by a distractor (blue letter). This was followed by a display with a white question mark indicating time for reporting displayed red targets. (Note that the figure does not present the actual proportions of the used stimuli).

**Procedure.** At the beginning of the assessment all participants received standardized written and oral instructions with a presentation of the stimuli used in the experiment. Then 16 practice trials were presented with an exposure duration of 80 ms. This was followed by a procedure for adjusting the individual exposure duration, consisting of 24 trials (4 single target, 12 dual target, 8 target-distractor trials), with an initial exposure duration of 80 ms. If the participant reported both letters correctly in the dual target condition, exposure duration was decreased by 10 ms. If only one letter was reported correctly, exposure duration remained unchanged. If none of the letters was reported correctly, exposure duration was increased by 10 ms. Single target and target plus distractor conditions were additionally displayed. They were, however, not used for exposure duration adjustment, but simply for familiarizing the participant with the task. The adjustment procedure was followed by a performance check block with 24 trials (8 single target, 8 dual target, 8 target-distractor trials), presented for the previously adjusted duration. Following this, accuracy for single target, dual target and target-distractor display trials was separately calculated and displayed on the screen. If accuracy was within a range of 70 – 90% in the single target and above 50% in the dual target condition (i.e. on average more than one letter was reported correctly in the dual target condition), the experimenter started the testing phase of the partial report experiment. If the accuracy was either below or above this range, the experimenter manually adjusted the exposure duration and repeated the performance check procedure until the appropriate exposure duration was found. The number of trials with the different conditions was unequal, due to varying relevance with respect to the ERP assessment in our study. More precisely, 112 single target trials were presented equally often at the four different locations; 112 dual target trials were presented, with equal numbers of vertical and horizontal display trials. 280 target-distractor trials were presented. Out of these, 112 trials were vertical and 168 were horizontal target-distractor trials. Together, these were 16 different conditions containing the target equally often at all four possible locations, constituting 504 trials, divided into 14 blocks. The different experimental conditions were equally distributed across blocks of trials and were displayed in randomized order within the block.

After each experimental block the participant received a visual performance feedback in which the percentage of correctly reported letters out of all reported letters was displayed. To avoid too liberal or too conservative responses, participants were instructed to aim for correctness between 70 – 90%, indicated by a green colour coding of the desired range on an accuracy scale. Note that the feedback did not deliver information with respect to absolute performance. The total duration of the session was approximately two hours, including the questionnaires, EEG preparation, verbal instructions and approximately 45 minutes of testing procedure.

**Stimuli.** The central fixation point was a white circle of 0.9° in diameter, with a white dot in the centre, presented for a duration randomly drawn from 10 to 240 ms. The presented letters were randomly chosen out of the set: {A, B, D, E, F, G, H, J, K, L, M, N, O, P, R, S, T, V, X, Z} with the same letter appearing only once in a given trial. The red target letters (CIE xyY: 0.534, 0.325, 3.25) and blue distractor letters (CIE xyY: 0.179, 0.118, 3.15) were of comparable luminance and had a size of 0.9°. Letters were displayed horizontally or vertically, but never diagonally, at the corners of an imaginary square, with an edge length of 12.3° centred on the midpoint of the screen. The white question mark indicating time for reporting letters was 0.9° in diameter.

**Apparatus.** The task was conducted in a dimly lit and sound-attenuated chamber (Industrial Acoustics Company). To avoid distraction, the source of light was placed behind the participant. Stimuli were displayed against a black background on a 24" LED screen (resolution: 800 x 600 pixels, refreshing rate: 100 Hz), with a viewing distance of approximately 65 cm.

**Estimation of top-down control efficiency.** Modelling of the behavioural data was performed using the TVA computational model, implemented in the Matlab toolbox *libTVA* (Mads Dyrholm, www.machlea.com/mads/libtva.html). Detailed descriptions of the fitting procedure can be found in Kyllingsbæk (2006). Fitting individual raw datasets to the model described by the TVA provided estimates of attentional weights $w_i$ assigned to targets and distractors displayed at each of the four different locations used in the partial report experiment. Based on these values task-related weighting, described by parameter α, can be estimated. Parameter α reflects the efficiency of the top-down control and is derived as the ratio of attentional weights allocated to distractor objects $w_D$ to the weights allocated to target objects $w_T$:

$$\alpha = \frac{w_D}{w_T}$$

Thus, lower α values indicate more efficient top-down control and higher values, approaching 1, indicate rather non-selective processing. The parameter α is estimated based on the decrease of performance in the conditions where a target is accompanied by a distractor, relative to conditions without distractors. Thus, in order to verify the correspondence between the estimated parameter α and raw performance, we computed a target selection index (TSI) based on the accuracy raw scores. TSI was computed as mean performance accuracy in the single-target ($ACC_{1T}$) and dual-target conditions ($ACC_{2T}$) divided by performance accuracy in the target-distracter condition ($ACC_{TD}$).

$$TSI = \frac{0.5 * \left( ACC_{1T} + ACC_{2T} \right)}{ACC_{TD}}$$

**Crystallized intelligence measurement**

Assessment of the crystallized intelligence was accomplished using the German Multiple-Choice Vocabulary Test (MWT-B, Lehr, 1995), which can be used for measurement of premorbid IQ in clinical groups (Lehrl, Triebig and Triebig, 1995). In this test participants select one actual word given among four distractors (pseudo-words) in rows with increasing difficulty. Higher IQ is reflected by a higher number of correctly recognized words.

### EEG data acquisition

Electroencephalographic was recorded simultaneously with behavioural data from 64 active Ag/AgCl electrodes (actiCAP System, BrainProducts). Sixty-three electrodes were mounted on an elastic cap (Falk Minow Service), with positions matching the international 10-10 system (American Electroencephalographic Society, 1994). Saccadic eye activity was monitored by an additional VEOG electrode placed at the inferior orbit below the left eye. All electrodes' impedances were regularly controlled every 4 blocks of trials and were kept below 5 kΩ. The EEG signals were amplified using BrainAmp DC amplifier (BrainProducts) with sampling rate of 1 kHz, referenced to channel FCz, and online filtered using 250 Hz low pass filter.

During offline analysis the raw data of each participant was first visually inspected to detect and manually remove nonstereotypic noise (e.g., excessive electromyographic bursts). Then, the continuous signal was high-pass filtered at 0.1 Hz (Butterworth zero phase filter, 24 dB/oct). In order to identify and remove ocular artefacts (blinks and horizontal eye movements) an Infomax Independent Component Analysis (Bell and Sejnowski, 1995) was performed using the Brain Vision Analyzer II software (BrainProducts). After ICA inspection, the data was re-referenced to averaged mastoids (channels TP9/10) and filtered using 40 Hz low-pass filter (Butterworth zero phase, 24 dB/Oct). In the next step, the continuous EEG signal was segmented into 1000 ms epochs, ranging from 200 ms pre-stimulus to 800 ms post-stimulus onset. The pre-stimulus interval was used for baseline correction. Epochs containing signals exceeding ±30 µV in channels F9/10, likely indicating residual eye-related activity, were excluded from the analyses (7% of all trials). Trials including voltage steps greater than ± 50 µV/ms, activity lower than ±0.5 µV within intervals of 500 ms or signals exceeding ± 60 µV in any channel were also marked as artefacts and removed from the analysis on an individual-channel basis.

In order to isolate lateralized brain activity from non-lateralized ERPs, the waveforms at the posterior-occipital electrodes ipsilateral to the side of the target location were subtracted from the waveforms contralateral to the target ($[(\mathrm{PO8}–\mathrm{PO7})_{\mathrm{left\ target}} + (\mathrm{PO7}-\mathrm{PO8})_{\mathrm{right\ target}}]/2$). Peak amplitudes were manually determined as a mean value of ten samples before and after maximum positive deflection within the time range of 80 to 250 milliseconds post-stimulus for the Ppc and maximum negative deflection within the time window of 130 to 350 milliseconds post-stimulus for the PCN.

In the EEG analysis we used only trials in which target and distractor letters were displayed in opposite hemifields. In these conditions sensory input is balanced across hemifields, therefore contra-ipsilateral hemispheric differences reflect purely target-related processing differences. As parameter *top-down control α* reflects the ratio of target and distractor weights, we assumed that individual differences in top-down control would be reflected by differences in ERPs in these conditions.

**Statistical analyses**

To investigate the relation between age, crystallized IQ, top-down control efficiency and its neural correlates, participants within each age group were assigned to groups of participants having either more or less efficient top-down control based on the median split according to the TVA parameter α and participants having either relatively high or relatively low crystallized IQ based on a median split according to the MWT-B score.

**Raw data.** We performed a two way ANOVA on the accuracy level in the baseline single target condition with factors age group (levels: youngest, middle, oldest) and crystallized IQ level (levels: lower, higher) to ensure that the difficulty level was comparable across age groups.

**Theory of visual attention parameter estimates.** The correspondence between the empirical scores and the scores predicted by the TVA model was verified by correlation between the target selection index and parameter *α* separately for the different age and crystallized IQ groups. In addition, we computed the goodness of fit $R^2$ values that reflect the amount of variance in the raw performance that can be predicted by the individual TVA parameter estimates.

**Effects of age and crystallized IQ on top-down control efficiency.** To analyse the effects of age and crystallized IQ on top-down control efficiency, a two way ANOVA was used with the between-subjects factors age (levels: youngest, middle, oldest) and crystallized IQ level (levels: lower, higher). Subsequently, we calculated a two-way ANOVA on the target selectivity index with factors age group and crystallized IQ level in order to test whether the raw data pattern supports the results obtained by the analysis of the parameter top-down control efficiency α

**Effects of age and crystallized IQ on neural correlates of top-down control efficiency.** This was followed by the analysis of the effects of age and crystallized IQ on neural correlates of top-down control efficiency. We investigated two lateralized components: Ppc and PCN. Firstly we confirmed the existence of the lateralized components by using paired samples t-tests to compare the amplitudes of the Ppc and PCN components against the most positive and most negative deflection measured within the pre-stimulus time range. In the next step the effects of age, top-down control efficiency and crystallized IQ on the amplitudes of the components were investigated using three-way ANOVAs with the between-subjects factors age group (levels: youngest, middle, oldest), top-down control efficiency (levels: less efficient, more efficient) and crystallized IQ level (levels: lower, higher). Whenever appropriate the Greenhouse-Geisser correction for nonsphericity (Jennings and Wood, 1976) was applied. Due to unequal distribution of males and females across groups, all ANOVAs included sex as a covariate variable. Significant results of the ANOVAs were supplemented by Pearson correlation analyses in order to more closely investigate relations between examined variables. All statistical analyses were performed using IBM-SPSS Statistics (version 24, IBM, USA).

## 3.4. Results

### Raw data

Visual attentional top-down control (according to TVA) is a capability of prioritizing targets over distractors. Figure 2 presents the percentage of correctly identified target letters, separately for conditions where the target letter was presented without any other stimulus (None) or was accompanied by a distractor (D) or another target (T). Accuracy is presented separately for all age groups and for participants with relatively higher and lower crystallized IQ. As we were interested in top-down control across the visual fields, averaged values across left and right hemifields are resented.

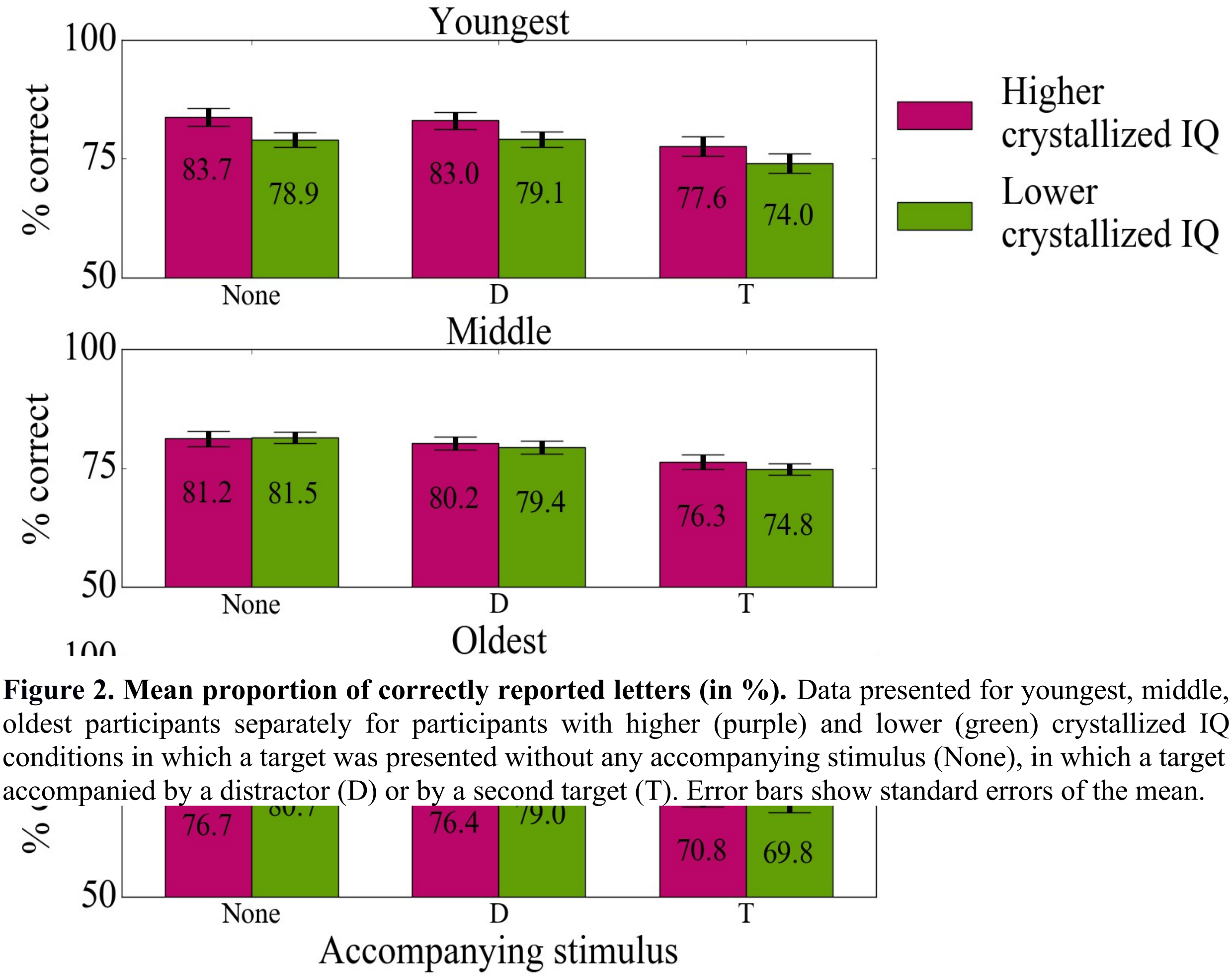


**Figure 2. Mean proportion of correctly reported letters (in %).** Data presented for youngest, middle, and oldest participants separately for participants with higher (purple) and lower (green) crystallized IQ for conditions in which a target was presented without any accompanying stimulus (None), in which a target was accompanied by a distractor (D) or by a second target (T). Error bars show standard errors of the mean.

The criterion of 70 – 90% accuracy in the single target baseline condition was reached in all age and IQ groups. The pattern of performance over different conditions was in accordance with predictions made by the TVA. Numerical value of accuracy was highest in the single-target condition, in which all attentional weights can be allocated to a single item. Compared to this, it was a bit reduced in the target-distractor condition and it was more reduced in the dual target condition, where weights had to be distributed across equally relevant stimuli. This pattern indicates that participants allocated more resources to target than to distractor stimuli.

### Theory of visual attention parameter estimates

From the estimates of the attentional weights obtained in the partial report task, we fitted the parameter efficiency of *top-down control α*. The highest estimate of top-down control was $\alpha = 0.74$, indicating that in the entire sample [M = 0.41, SD = 0.15] participants prioritized targets compared to distractors[5]. The parameter *top-down control α* correlated significantly with the target selection index in all age groups and in participants with lower and higher crystallized IQ, [all $r > 0.951$, all $p<0.001$], which confirms close correspondence between estimated parameters and report accuracy patterns. In order to assess the amount of variability in the report accuracy across the different experimental conditions explained by the model a mean goodness-of-fit $R^2$ measure was calculated separately for each age group and participants with lower and higher crystallized IQ. Across all groups the model explained at least 78% of the variability in the raw performance.

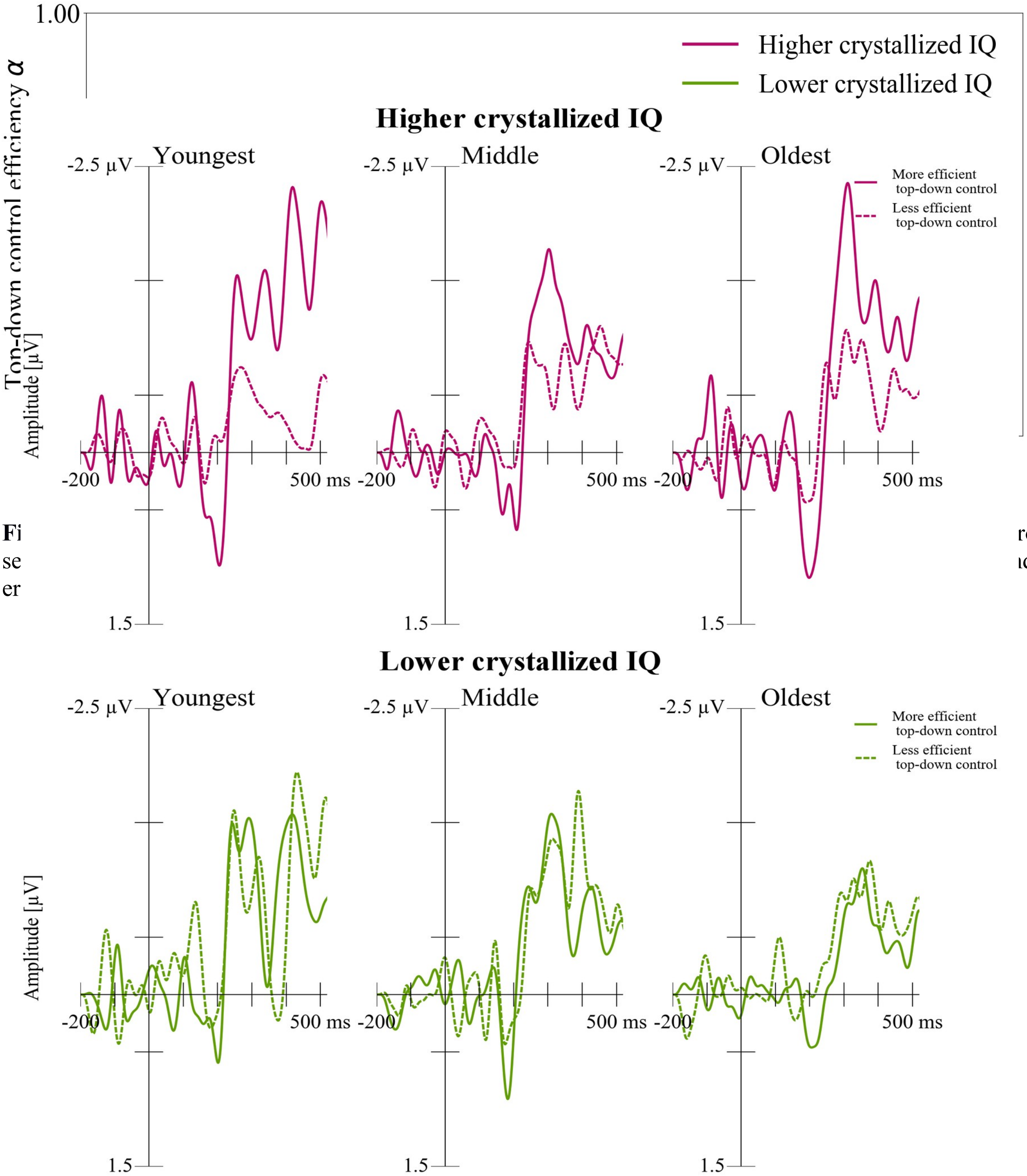
### Effects of age and crystallized IQ on top-down control efficiency

The two-way ANOVA on top-down control *α* with age group and crystallized IQ level as between-subjects factors revealed no significant effect of age, [$F(2,76)=3.043$, $p=0.054$] or crystallized IQ

---

[5] Note that more efficient top-down control is denoted by lower values of the TVA parameter. Parameter α value equal 1 denotes lack of selectivity.

[F(1,76)=0.084, p=0.773]. The interaction was also not significant [F(2,76)=0.391, p=0.678], see Figure 3. Thus, the efficiency of top-down control α was found to be relatively comparable across age groups. Furthermore, there was no indication that IQ level modulated top-down control across age groups. As a control analysis, we computed a two-way ANOVA on the target selectivity index with factors age group and crystallized IQ level. This analysis revealed no significant main effect of age, [F(2,76) = 2.532, p=0.086] or crystallized IQ [F(1, 76)=0.163, p=0.688]. The interaction of both factors was also not significant [F(2, 76) = 0.323, p=0.725]. This confirms that estimated parameter top-down control efficiency *α* is in good correspondence to the raw data.



**Fi** roup,
se ıdard
er

### Effects of age and crystallized IQ on neurophysiological correlates of top-down control efficiency.

**Posterior contralateral positivity (Ppc)** As revealed by a significant paired-samples t-test, the amplitude of the Ppc component was significantly larger than a maximal deflection measured within pre-stimulus time range [M=0.95 μV, SD=0.63 vs. M=0.78 μV, SD=0.35, t(82)=2.242, p=0.028], confirming the presence of this component.

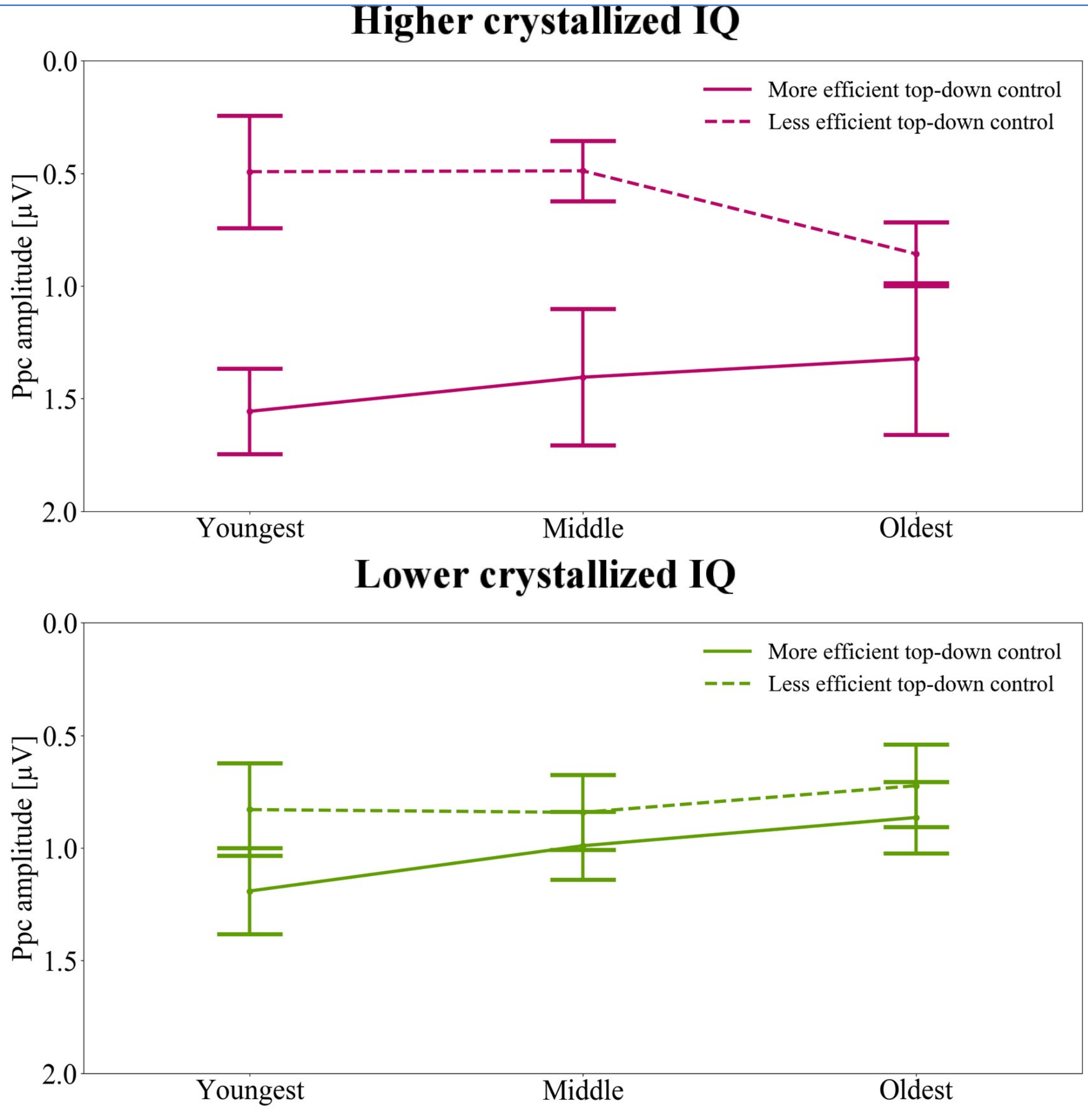


**Figure 5. Amplitudes of the Ppc components.** Amplitudes presented for youngest, middle and oldest participants separately for participants with more efficient (solid line) and less efficient (dashed line) top-down control. The top figure presents amplitudes averaged for participants with higher crystallized IQ. The bottom figure presents amplitudes averaged for participants with lower crystallized IQ.

Figure 5 presents Ppc amplitudes for younger, middle and older participants separately for participants with more and less efficient top-down control and with higher and lower crystallized IQ level. A three-way ANOVA on the amplitude of the Ppc component with the factors age group, top-down control efficiency and crystallized IQ revealed no significant main effects of age group [F(2,70)=0.168, p=0.846] or crystallized IQ [F(1,70)=1.058, p=0.307]. However, we found a significant main effect of top-down control efficiency: the amplitude of the Ppc component was larger in more efficient compared to less efficient participants [M=1.21 μV, SD=0.63 vs. M=0.70 μV, SD=0.52, F(1,70)=15.366, p<0.001]. No two-way or three-way interaction between age and top-down control efficiency was found. Thus, the effect of top-down control on the Ppc component was comparably found across all age groups. Furthermore, across all age groups, we found a significant interaction of top-down control efficiency and crystallized IQ [F(1,70)=5.080, p=0.027], see Figure 6. Separate post-hoc t-tests revealed that in participants with relatively high crystallized IQ, the Ppc amplitude was higher in participants with more efficient compared to less efficient top-down control [M=1.44 μV, SD=0.72 vs. M=0.62 μV, SD=0.53, t(40)=4.230, p<0.001]. No comparable difference was found in participants with relatively low crystallized IQ [t(39)=1.366, p=0.180]. None of the other interactions reached significance (all p>0.482).

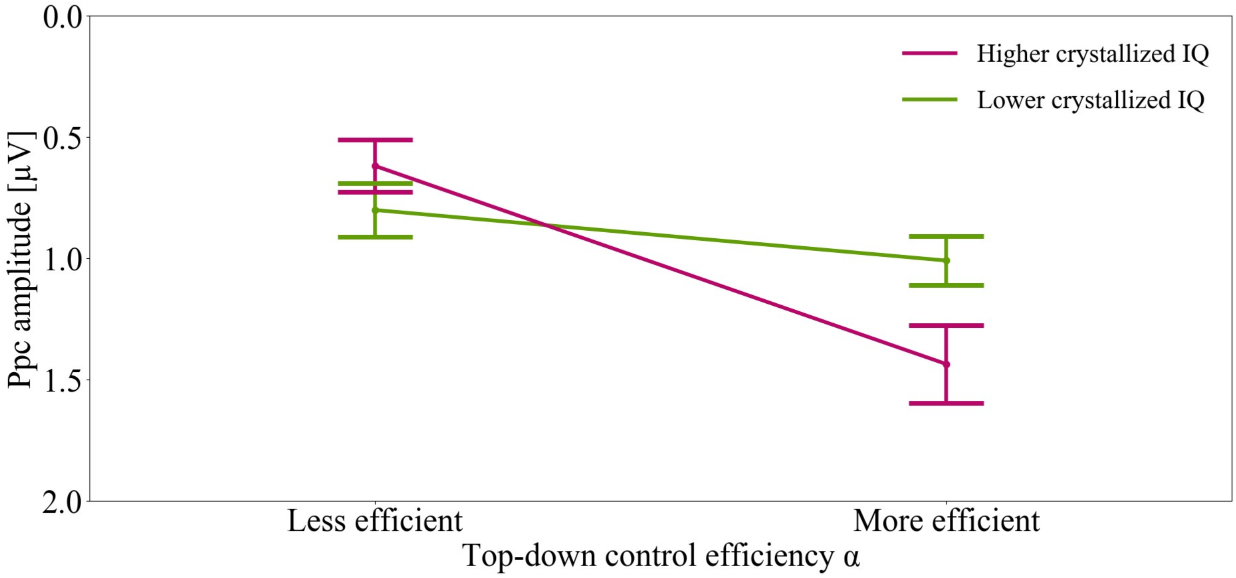


**Figure 6. Interaction of crystallized IQ and top-down control efficiency on the amplitude of the Ppc component**. Error bars show standard errors.

In order to further investigate the interaction between top-down control efficiency and crystallized IQ, we checked for a linear relationship between the amplitude of the Ppc component and top-down control efficiency separately in the groups with higher and lower crystallized IQ. A significant correlation was found only in the group with higher IQ, i.e. amplitude of the Ppc component increased significantly with efficiency of top-down control, [r=-0.567, p<0.001][6], but not in the group with lower IQ [r=-0.069, p=0.667], see: Figure 7.

---

[6] Note that a negative value of the Pearson r coefficient denotes positive correlation between top-down control efficiency and Ppc amplitude.

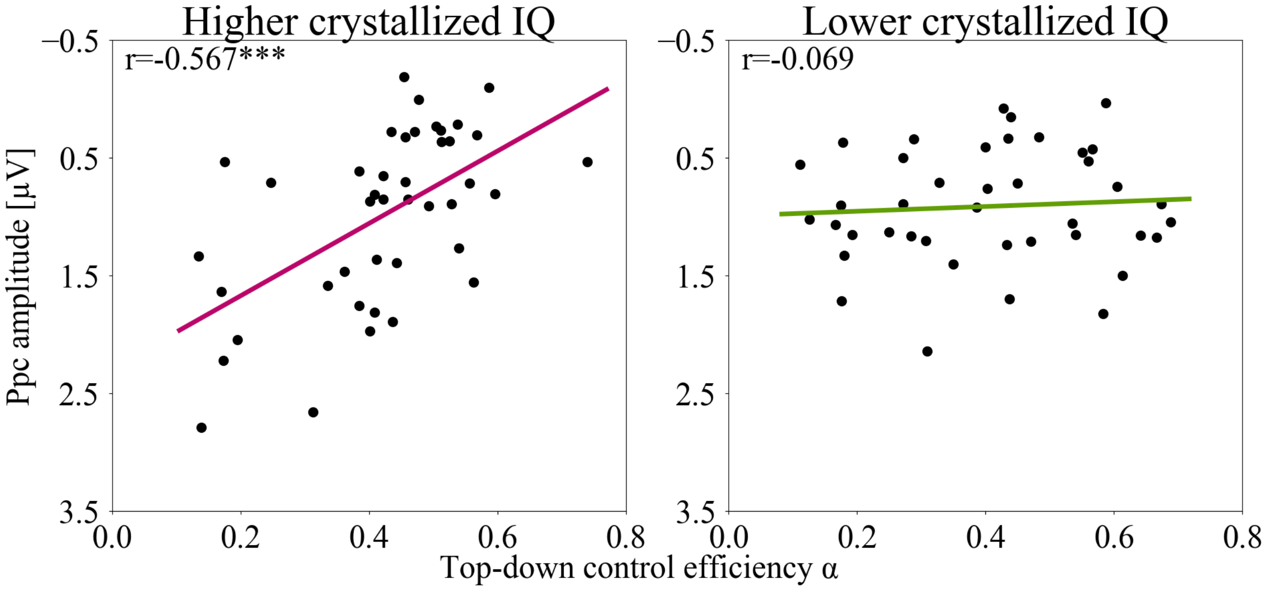


**Figure 7. Correlation between the amplitude of the Ppc component and top-down control efficiency α** Correlations presented for the high (left) and low (right) crystallized IQ group. *** p< 0.001

**Posterior contralateral negativity (PCN)** The amplitude of the PCN component was significantly larger than the maximal deflection measured within pre-stimulus time range as revealed by paired-samples t-test [M=-1.87 µV, SD=0.90 vs. M=-0.76 µV, SD=0.40, t(82)=-11.916, p<0.001], thereby confirming also the presence of the PCN in the present task.

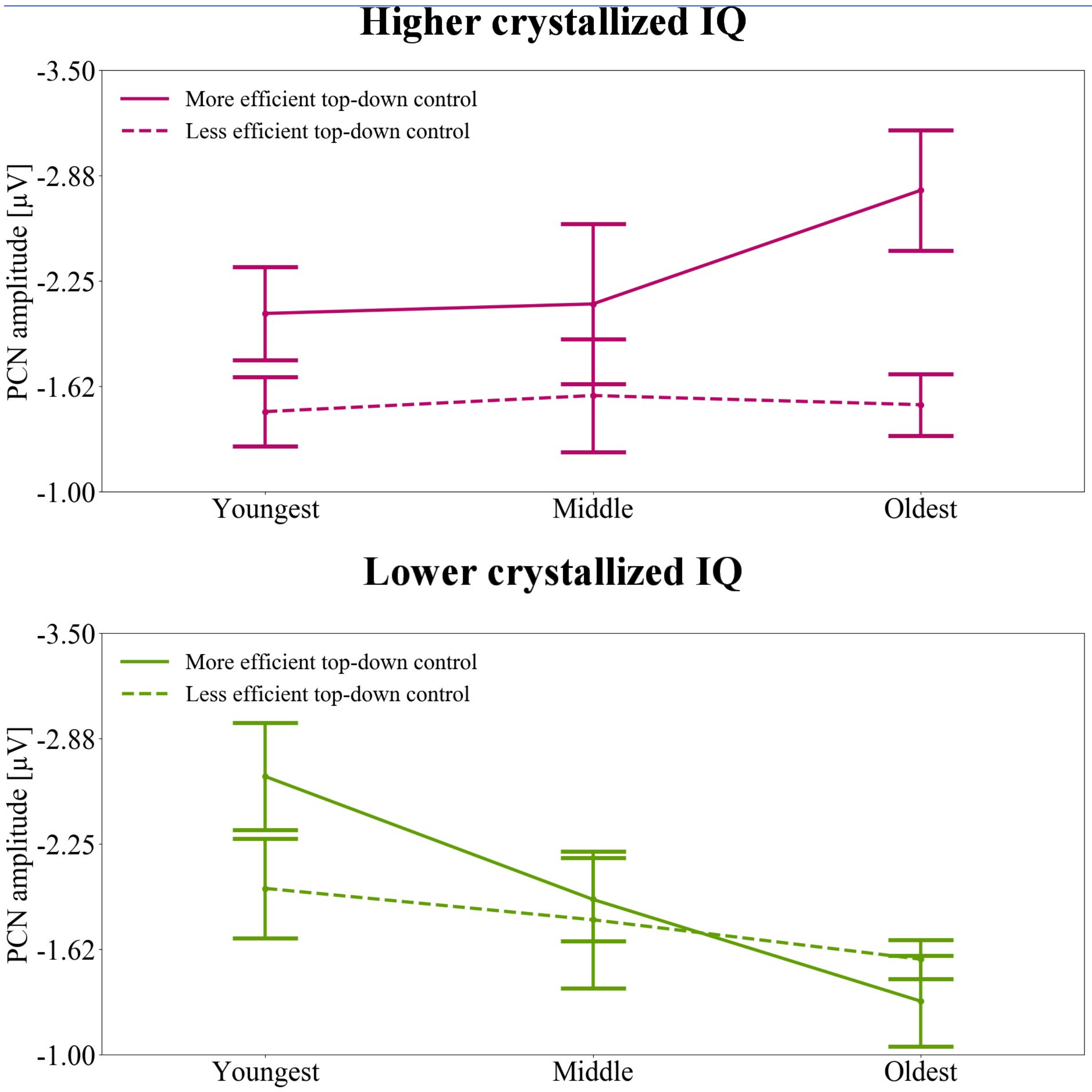


**Figure 8. Amplitudes of the PCN as a function of age, separately for participants with more (solid line) relative to less efficient (dashed line) top-down control.** The top figure presents amplitudes averaged for participants with higher crystallized IQ, he bottom figure presents amplitudes averaged for participants with lower crystallized IQ.

Figure 8 presents the PCN amplitudes for youngest, middle and oldest participants averaged separately for participants with more versus less efficient top-down control and with higher and lower crystallized IQ level. In the three-way ANOVA with the factors age group, top-down control efficiency and crystallized IQ, the main effect of top-down control efficiency was found to be significant [F(1,70)=5.781, p=0.019]. This indicates that the amplitude of the PCN component was larger in the participants with more efficient [M = -2.11 µV, SD = 0.99] compared to less efficient top-down control [M=-1.65 µV, SD=0.76]. Neither the main effects of age [F(2,70)=0.405, p=0.669] nor crystallized IQ [F(1,70)=0.289, p=0.587], nor the interaction of age with top-down control efficiency were significant [F(2,71)=0.203, p=0.816]. Thus, the modulation of the PCN amplitude by top-down control was evident across all experimental groups, and, thus, independent of age and IQ level. The interaction of age and crystallized IQ was significant [F(2,70)=3.712, p=0.029], see Figure 9.

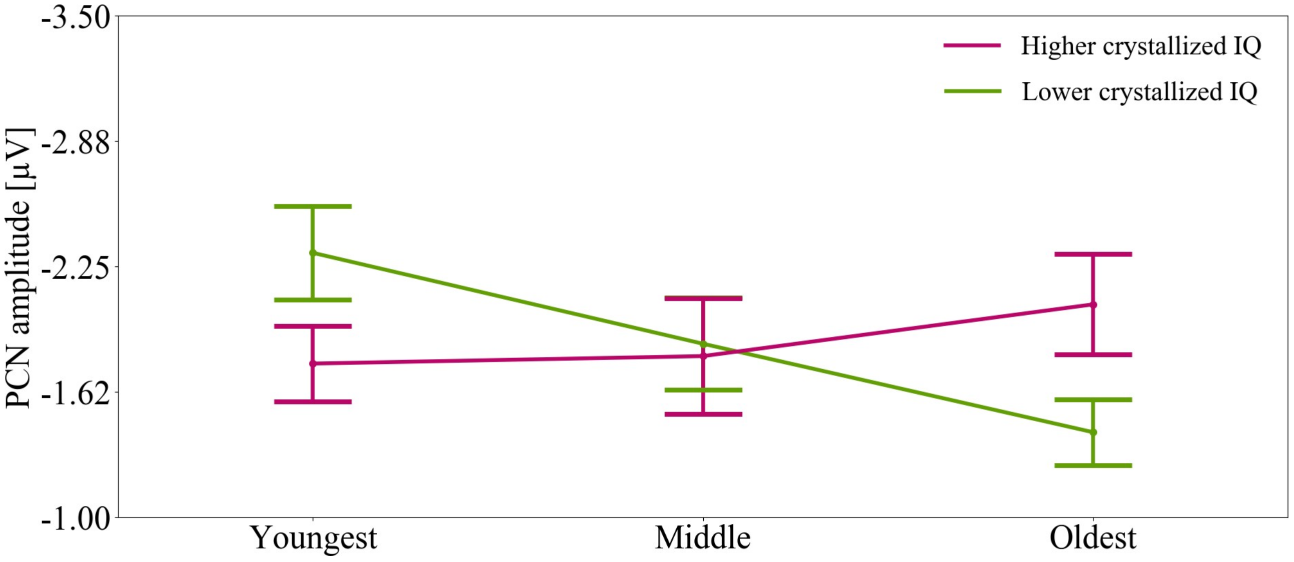


**Figure 9. Interaction of age and crystallized IQ on the amplitude of the PCN component.** Error bars represent standard errors.

The significant interaction was further analysed using separate ANOVAs for the relatively low and high crystallized IQ groups. In participants with lower crystallized IQ, there was a non-significant trend for a declining PCN amplitude with increasing age [F(2,37) = 2.615, p=0.087]. No such trend was found in participants with relatively high IQ [F(2,38) = 0.951, p=0.395]. In addition, in the oldest group, there was a marginal effect for a higher PCN in the group with relatively high compared to low IQ level [t(26) = 2.049, p = 0.051].

To follow up the result of a trend for a decreasing PCN with increasing age in participants with relatively low IQ level, we analysed whether a linear relationships between the PCN amplitudes and years of age would be found in these participants. We ran separate correlations for participants with relatively high and low IQ, across all experimental age groups. Indeed, we found that the amplitude of the PCN was significantly decreasing with age only in participants with relatively low crystallized IQ, [r=0.384, p=0.013], but not in the group with relatively high IQ [r=-0.098, p=0.539], see: Figure 10.

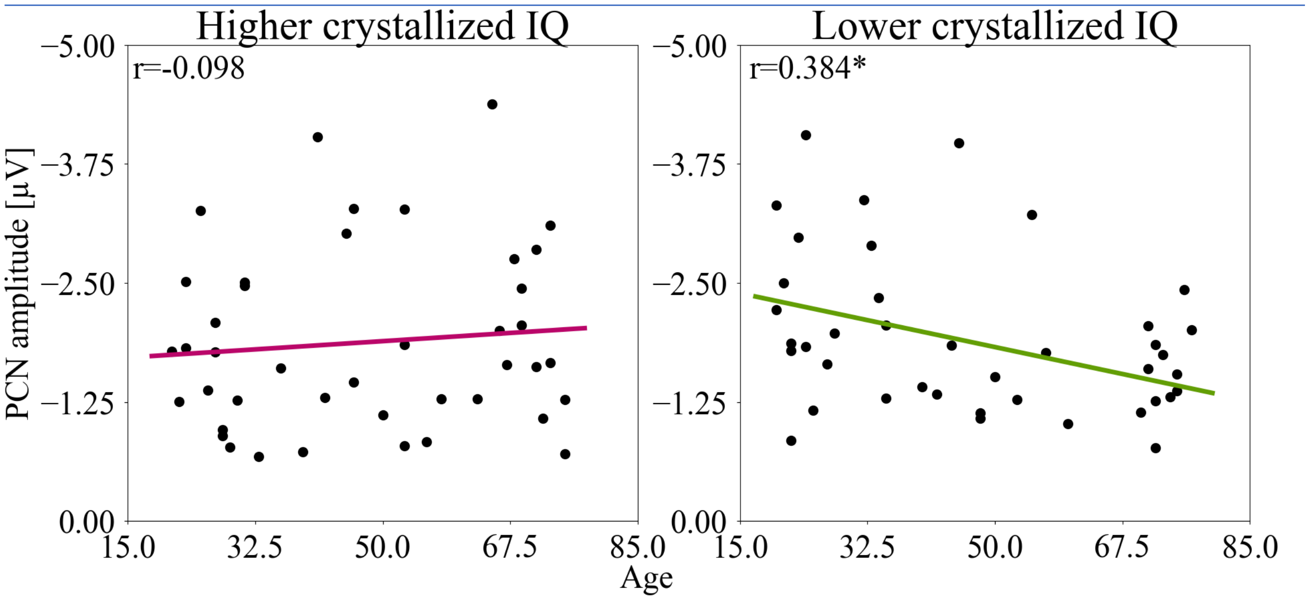


**Figure 10. Correlation between amplitude of the PCN component and age.** Correlation presented separately for participants with higher (left) and lower (right) crystallized IQ. *p<0.05

## 3.5. Discussion

In the current study we investigated whether and how top-down control efficiency was affected by healthy ageing and/or by the amount of cognitive reserve, or a mixture of both. Furthermore, we investigated whether electrophysiological correlates of top-down control previously established in young participants were affected by normal ageing and/or the amount of cognitive reserve and whether age and cognitive reserve interact with each other. In order to quantify the efficiency of top-down control and its electrophysiological correlates, we employed a TVA-based partial report task with simultaneous EEG recording in a sample of variable age. We assessed the amount of cognitive reserve by measuring crystallized IQ using the German MWT-B vocabulary test. To answer the questions concerning top-down control, we compared top-down control efficiency between the younger, middle and older participants, and between participants with relatively low and relatively high amount of cognitive reserve. Then, we compared behavioural and electrophysiological data between groups of different age, top-down control efficiency, and cognitive reserve level to answer the questions whether age and cognitive reserve modulate to the neurophysiological correlates of top-down control.

**Influence of age and cognitive reserve on top-down control efficiency.**

All participants included in the current study were able to prioritize task-relevant targets over task-irrelevant distractors (all participants had a value of the parameter $\alpha$ lower than 1). We found that efficiency of top-down control was neither affected by age nor by the amount of cognitive reserve. The latter result is in line with a study presented by Madden et al. (2005), who found that at least some forms of top-down control are preserved in ageing. Previous TVA studies showed age-related decline in participants younger than 30 (Espeseth et al., 2014) and younger than 50 (McAvinue et al. 2012) years old. In older participants, top-down control efficiency was shown to remain relatively stable. In our study, to add to the knowledge on the effects of top-down control on ageing, we carefully checked all participants for potential factors influencing cognition such brain injury, seizures, dementia, depression, anxiety disorder, psychological distress or sleep quality. Furthermore we also matched participants with respect to their educational background. Thus, participants included in the study had a relatively homogeneous sociodemographic status, are healthy and do not suffer from dementia or mild cognitive impairment indicating risk for dementia.

### Relation between ERLs, age, top-down control efficiency and cognitive reserve

We analysed amplitudes of two distinct lateralized components as established correlates of top-down control efficiency: Ppc and PCN. Both components were elicited by the presentation of target letter accompanied by a distractor letter in the opposite hemifields. We found that the amplitudes of both components were associated with top-down control efficiency and that this relation was equally present across the different age groups. This implies that the amplitudes of the PCN and Ppc may be considered as valid neural markers of visual top-down control efficiency in healthy participants across the lifespan.

in participants with a relatively high amount of cognitive reserve. As the Ppc component has been suggested to reflect an inhibitory mechanism (Gokce et al., 2014), we assume that higher Ppc amplitudes in participants with more efficient top-down control reflect more efficient inhibition of visual distractors, which in turn leads to more efficient selection of a task-defined targets during subsequent processing stages. The fact that we found such a relationship only in participants with relatively high amount of cognitive reserve may suggest that participants that differ in educational attainment employ different strategies for selection of relevant information. Of note, our results imply that, across all age groups, in participants with higher cognitive reserve early bottom-up driven processes contribute more to visual selection processes than in participants with low cognitive reserve.

Wiegand et al. (2017) previously identified the PCN amplitude as a neural correlate of the efficiency of top-down control. In the current study we showed that this relation is preserved in older age: more efficient top-down control was associated with a more pronounced negativity on the side contralateral to the target across all three age groups. While the absence of a main effect of age implied that healthy aging does not influence the PCN amplitude in general, a significant interaction suggests that aging separately affects the PCN in participants with low and high cognitive reserve. In participants with rather low cognitive reserve, the PCN amplitude was significantly affected by aging. A follow-up correlation analysis showed that the PCN amplitude decreased significantly with increasing age in this group. In participants with a rather high cognitive reserve, the PCN amplitude remained unchanged with increasing age. Recall that the PCN amplitude is thought to reflect the amount of attentional resources engaged to select a task-relevant object (e.g., Eimer et al., 1996; Luck and Hillyard, 1994; Töllner et al., 2012). Thus, we assume that, in participants with lower amount of cognitive reserve, ageing might be related to a reduced ability to efficiently distribute attentional resources towards the targets. This finding of a reduced component might be the first sign of decreasing selection efficiency in the neural system despite lack of behavioural consequences. Such changes might be detectable, but at even higher age.

In sum, age and the amount of cognitive reserve modulate the relationship between the efficiency of attentional top-down control and its neural correlates indexed by the ERLs. However, we did not find any differences in top-down control efficiency on the behavioural level between age groups. Thus, we propose that declining amplitude of the PCN might be a more sensitive indicator of the vulnerability to an age-related cognitive decline than the results of the behavioural task. Moreover, because the amount of cognitive reserve modulates the relation between age and the neurophysiological correlates of top-down control efficiency, it should be taken into account in ageing studies.

| | **Youngest participants** | | **Middle participants** | | **Oldest participants** | | **Sig. Mean effect of age** | **Sig. Mean effect of IQ level** | **Sig. Interaction** |
|---|---|---|---|---|---|---|---|---|---|
| | Lower crystallized IQ | Higher crystallized IQ | Lower crystallized IQ | Higher crystallized IQ | Lower crystallized IQ | Higher crystallized IQ | | | |
| **N** | 14 | 14 | 13 | 14 | 14 | 14 | | | |
| **Age [years]** | 24.5 (4.13)<br><20,33> | 26.5 (2.30)<br><21,31> | 45.08 (7.68)<br><34,57> | 46.5 (7.66)<br><33,58> | 72.36 (4.13)<br><60,77> | 69.79 (3.70)<br><63,75> | p<0.001 | 0.811 | 0.232 |
| **Sex (F/M)** | 10/4 | 6/8 | 7/6 | 9/5 | 5/9 | 3/11 | 0.038 | 0.325 | ---- |
| **Education [years]** | 12.43 (0.94)<br><10,13> | 12.71 (0.47)<br><12,13> | 11.77 (1.54)<br><9,13> | 12.57 (0.85)<br><10,13> | 11.64 (1.74)<br><9,14> | 12 (1.52)<br><9,13> | 0.088 | 0.084 | 0.713 |
| **Depression (BDI)** | 5.79 (4.51)<br><0,15> | 3.79 (4.89)<br><0,17> | 6.00 (5.80)<br><0,15> | 6.93 (5.59)<br><0,18> | 6.07 (4.62)<br><0,18> | 4.64 (4.81)<br><0,15> | 0.469 | 0.457 | 0.535 |
| **State Anxiety (STAI)** | 36.64 (8.69)<br><24,50> | 34.93 (9.64)<br><26,59> | 31.83 (14.82)<br><0,58> | 34.0 (3.82)<br><25,34> | 33.5 (6.67)<br><23,45> | 31.07 (8.72)<br><24,49> | 0.324 | 0.751 | 0.641 |
| **Trait Anxiety (STAI)** | 36.64 (8.45)<br><26,57> | 32.93 (13.54)<br><0,50> | 35.83 (16.39)<br><0,67> | 33.18 (6.57)<br><22,43> | 32.57 (6.93)<br><21,51> | 31.21 (8.72)<br><20,44> | 0.545 | 0.289 | 0.918 |
| **Psychological distress (BSI)** | 0.1 (0.01)<br><0.09,0.12> | 0.1 (0.01)<br><0.09,0.12> | 0.10 (0.01)<br><0.10,0.12> | 0.10 (0.01)<br><0.09,0.12> | 0.1 (0.01)<br><0.09,0.12> | 0.10 (0.01)<br><0.9,0.13> | 0.418 | 0.880 | 0.333 |
| **Sleep quality (PSQI)** | 5.08 (1.44)<br><3,8> | 4.38 (1.04)<br><2,6> | 5.09 (1.04)<br><3,7> | 4.76 (2.12)<br><0.1,7.0> | 4.93 (1.21)<br><3,7> | 5.36 (1.86)<br><3,10> | 0.607 | 0.567 | 0.384 |
| **MMSE** | ---- | ---- | ---- | ---- | 28.78 (0.80)<br><27,30> | 29.36 (0.93)<br><27,30> | ---- | 0.093 | ---- |
| **Speed of visual search (TMT A)** | 23.85 (9.89)<br><13.44,49.01> | 20.44 (5.68)<br><14.03,29.71> | 31.33 (9.65)<br><18.39,56.08> | 29.43 (14.97)<br><14.37,60.34> | 40.70 (8.49)<br><27.91,56.55> | 43.31 (10.24)<br><28.71,74.98> | p<0.001 | 0.691 | 0.516 |
| **Executive functioning (TMT B/TMT A)** | 2.12 (0.35)<br><1.25,3.17> | 2.56 (1.04)<br><1.53,5.78> | 2.1 (0.36)<br><1.52,2.64> | 2.51 (0.82)<br><1.28,4.15> | 2.54 (0.89)<br><1.15,3.98> | 2.12 (0.78)<br><0.83,3.77> | 0.984 | 0.387 | 0.071 |

**Table 2.** Demographic information presented for youngest, middle and oldest participants separately for participants with lower and higher crystallized IQ

*Key: F-female; M-male; R-right handed, L- left handed; TMT – Trail Making Test; BDI – Beck Depression Inventory; STAI - State-Trait Anxiety Inventory; BSI - Brief Symptom Inventory; PSQI - Pittsburgh Sleep Quality Index; MMSE: Mini Mental State Examination*

# 4. Manuscript:

## Age-dependent differences in visual processing speed and early, spatially selective processing: New insights from N1pc and PCN waves

*Natan Napiórkowski[1,2], Kathrin Finke[1,7], Hermann J. Müller [4], Iris Wiegand [3,4,5], Anders Petersen [6], and Thomas Töllner [1,2]*

[1]General and Experimental Psychology, Department of Psychology, LMU Munich

[2]Graduate School of Systemic Neurosciences, LMU Munich

[3]Max Planck UCL Centre for Computational Psychiatry and Ageing Research

[4]Center for Lifespan Psychology, Max Planck Institute for Human Development

[5]Visual Attention Lab, Brigham & Women's Hospital and Harvard Medical School

[6]Center for Visual Cognition, Department of Psychology, University of Copenhagen

[7]Hans-Berger Department of Neurology, Jena University Hospital

## 4.1. Abstract

Visual processing speed, i.e. the total amount of information being processed per second (Duncan et al. 1999) is one of the key components of Bundesen's Theory of Visual Attention (TVA; Bundesen, 1990). Recently, it has been shown that higher versus lower levels of processing speed are associated with the amplitude of the visual N1 (Wiegand et al. 2014a). However, it remains an open issue whether processing speed may also influence early, spatially selective processes as indexed by event-related lateralizations (ERLs). Here, we aimed at examining (i) whether interindividual differences in processing speed are reflected by ERLs, and (ii) whether the relation between processing speed and ERL waves is modulated by age. To quantify processing speed, we used a TVA-based whole-report task, with simultaneous recording of the electroencephalogram. We found that both N1pc and PCN waves index interindividual differences in processing speed, with enhanced amplitudes for participants with higher relative to lower levels of processing speed. In addition, N1pc waves were increased and PCN waves delayed for participants of older relative to younger age, suggesting that younger versus older participants employ different selection modes to solve the present whole-report task. While older participants seem to put more emphasis on pre-selecting, target information already during an initial orienting of attention phase (indexed by the N1pc), younger participants seem to encode the entire display during this early phase, which is then followed by a temporally less variable attentional selection process (indexed by the PCN).

## 4.2. Introduction

Visual processing speed is one of the key components of visual attention. In Bundesen's mathematical framework Theory of Visual Attention (TVA; Bundesen, 1990), processing speed is defined as the total amount of information being processed per second (Duncan et al. 1999). More specifically, TVA assumes that all objects in the visual field compete for getting encoded into visual short-term memory (vSTM), which is highly limited in storage capacity (see: e.g., Cowan, 2001; Luck & Vogel, 1997; Sperling, 1960). The core assumption of the theory is that all competing objects are processed simultaneously by the visual system, but at varying processing rates. In principle, the higher the rate of a given object, the higher is its probability of getting encoded into vSTM. The sum of all rates distributed among all objects being processed is depicted by the TVA parameter *processing speed C*. Individual estimates of the parameter *C* can be obtained by employing a simple psychophysical whole-report task. In this type of task, participants are briefly presented with an array of target objects (e.g., letters), with the instruction to verbally report as many of them as possible (see: Habekost, Petersen & Vangkilde, 2013). Such a design provides methodological advantages as the performance in the task can be dissociated from measures of motor processes. Notably, the latter may be a potentially confounding factor in, for example, ageing studies due to a general slowing of motor processes. An individual estimate of *C* can be derived by fitting the raw performance in the task as a function of stimuli exposure duration to the TVA model (a detailed formal description of the fitting procedure can be found in Kyllingsbæk, 2006).

More recently, a neural interpretation of TVA (NTVA, Bundesen et al. 2005) has suggested the neural mechanisms underlying processing speed. According to NTVA, processing speed of a perceived object is proportional to the number of neurons coding the object's features and to the firing rates of these neurons. Results of a recent EEG study by Wiegand et al. (2014a) were in accordance to this view: using a TVA-based whole report paradigm with simultaneous recording of event-related potentials (ERP), they showed that younger participants with higher compared to lower processing speed *C* exhibited reduced amplitudes of the visual N1 wave—a component associated with stimulus discrimination processes (Vogel and Luck, 2000). In a subsequent study, Wiegand et al. (2014b) showed that this relation between processing speed and the amplitude of the visual N1 was also preserved in older age participants, suggesting that age-specific mechanisms contributing to changes in processing speed are not modulating the N1 component.

Of note, Wiegand et al. did not investigate the relation between processing speed and early, spatially specific processes as indexed by event-related lateralizations (ERLs). That is, differences in electrophysiological activity that can be directly linked to attended, lateralized objects (activity obtained from the contralateral hemisphere) as opposed to objects that are not attended (activity obtained from the ipsilateral hemisphere) (see: Corriveau et al., 2012; Luck, Woodman, & Vogel, 2000; Wascher and Wauschkuhn, 1996). The difference between contra- and ipsilateral ERP activity provides direct information about target-related brain activity, as any target-unrelated activity that is common for attended and unattended objects will be cancelled out by the subtraction procedure. Thus, posterior ERLs have been shown to be particularly instructive for processes related to spatially selective attentional selection (e.g. Eimer, 1996; Woodman and Luck, 2003; Töllner, Conci, & Müller, 2015).

The aim of the current study was twofold: first, we aimed at examining whether interindividual differences in processing speed are reflected by early, spatially selective processes as indexed by ERLs; second, as processing speed has been shown to decline with age (Habekost et.al, 2012; Nielsen & Wilms, 2015; Wiegand et al. 2014b), we further aimed at investigating whether the relation between processing speed and ERL waves is modulated by healthy ageing. To assess these questions, we employed a TVA-based whole report paradigm, which was adapted for measuring lateralized components by presenting targets in the left or right visual hemifield. In order to test whether healthy ageing modulates the relation between processing speed and lateralized brain responses, we compared amplitudes and latencies of different ERLs (see below) between young, middle and older participants divided into subgroups with lower and higher TVA parameter *processing speed C*.

In the EEG analysis, we focused on three potential ERL candidates that may differentiate between high and low performers as a function of age. The first ERL candidate is a negative deflection typically observable in the time range of the P1/N1 (i.e. 100–200 ms post-stimulus), called N1-posterior-contralateral (N1pc). The N1pc is assumed to reflect weighting and competition of incoming sensory signals and an “initial orienting of attention” process (Wascher and Beste, 2010). Another ERL candidate, termed Positivity-posterior-contralateral (Ppc, Fortier-Gauthier et al., 2012; Leblanc, Prime, & Jolicœur, 2008), is a positive deflection usually observable in the time range 160-270 ms post-stimulus. The Ppc is usually elicited in fixed-feature search tasks (Jannati et al., 2013), and has been associated with a spatially specific inhibition process (Gokce, Geyer, Finke, Müller & Töllner, 2014; Wiegand et al. 2015). The third ERL wave that may be related to processing speed is the Posterior-Contralateral Negativity (PCN)[7]. The PCN is a negative-going deflection elicited over

---

[7] Note that the PCN wave is also referred to as N2-posterior-contralateral (N2pc; e.g., Luck, Fan and Hillyard, 1993). However, we prefer the term PCN because amplitude and timing of this ERL have been shown to be independent from the amplitude and latency of the non-lateralized N2 (see, e.g., Shedden and Nordgaard, 2001; Töllner et al., 2011a).

parieto-occipital areas in the time range approximately 200-350 ms post-stimulus. There is a general consensus that this component reflects focal-attentional selection of task-relevant objects in visual space (Eimer, 1996; Töllner et al., 2016; Woodman and Luck, 2001).

Based on the interpretation provided by the NTVA and the results of Wiegand et al. (2014a, 2014b), we expect that participants who allocate proportionally greater amount of attentional resources to the task-relevant red letters than task-irrelevant blue characters would elicit more pronounced contra-minus-ipsilateral asymmetry in EEG activity over visual sensory areas. Thus, the magnitude of this asymmetry should reflect the interindividual differences in processing speed. However, it is still not clear on which stage of processing one should expect this effect. Interindividual differences in processing speed might be related (i) to the initial orientation of attention as reflected by the N1pc, (ii) to spatially specific inhibition of distractor items as indexed by the Ppc, (iii) to the attentional selection of the target letters as marked by the PCN, or (iv) to a mixture between these alternatives.

## 4.3. Methods

**Table 1. Demographic information**

| | Young participants | Middle participants | Older participants | Sig.<br>$\chi^2$ or F |
|---|---|---|---|---|
| N | 32 | 29 | 33 | |
| Age | 26.16 (4.12)<br>20-34 | 46.83 (6.65)<br>35 - 58 | 71.03 (4.5)<br>60 - 78 | <0.001 |
| Sex (F/M) | 17/15 | 20/9 | 11/22 | 0.019 |
| Handedness Index | 0.63 (0.59)<br>-1 - 1 | 0.83 (0.46)<br>-0.8 - 1 | 0.84 (0.31)<br>-0.45 - 1 | 0.133 |
| Crystallized IQ (MWT-B) | 110.63 (14.16)<br>86 - 143 | 112.75 (14.99)<br>81 - 143 | 127,15 (10.29)<br>104 - 143 | <.0001 |
| Depression (BDI) | 4.28 (4.65)<br>0 - 17 | 6.50 (5.67)<br>0 - 18 | 5.24 (4.50)<br>0 - 18 | 0.225 |
| State Anxiety (STAI) | 34.73 (9.17)<br>23 - 59 | 34.39 (7.83)<br>14 - 58 | 31.81 (6.86)<br>23 - 49 | 0.285 |
| Trait Anxiety (STAI) | 34.68 (9.38)<br>20 - 57 | 36.29 (8.95)<br>24 - 67 | 31.64 (7.66)<br>20 - 51 | 0.107 |
| Psychological distress (BSI) | 0.30 (0.30)<br>0 - 1.43 | 0.43 (0.28)<br>0.4 - 1.08 | 0.32 (0.19)<br>0.02 - 0.72 | 0.104 |
| MMSE | --- | --- | 29.03 (0.88)<br>27 - 30 | --- |
| Processing speed (TMT A) | 22.09 (8.20)<br>10.40 - 49.01 | 30.96 (11.92)<br>14.37 - 60.34 | 42.38 (9,55)<br>27.91 - 74.98 | <0.001 |
| Executive functioning (TMT B) | 48.89 (18.24)<br>18.76 - 100.05 | 66.84 (27.29)<br>33.87 - 146.82 | 95.34 (29.69)<br>51.68 - 154.65 | <0.001 |

*Abbreviations: F, female; M, male; MWT-B, German Multiple-Choice Vocabulary Test; TMT, Trail Making Test; BDI, Beck Depression Inventory; STAI, State-Trait Anxiety Inventory; BSI,* Brief Symptom Inven*tory; MMSE, Mini Mental State Examination.*

*Participants***.** 32 younger, 29 middle and 33 older healthy adults were included in the study. All participants received payment or course credits for taking part in the study and provided written informed consent according to the Declaration of Helsinki II. The experimental procedure was approved by the Ethics Committee of the psychology department of the Ludwig-Maximilians-University. Participants were part of the Munich INDIREA[8] aging cohort, which consists of 108 healthy adults aged from 19 to 78 years old, who underwent behavioural assessment of memory, attention, and intelligence and received functional and structural MRI and electroencephalography. All participants were native German speakers and had normal or corrected to normal vision. Each participant was screened with an assessment of handedness (Edinburgh Handedness Inventory, Oldfield, 1971), crystallized IQ (Mehrfachwahl-Wortschatztest, Version B, i.e., Multiple Choice Vocabulary Intelligence Test, version B; Lehrl, 1977), anxiety (The State-Trait Anxiety Inventory STAI, Spielberger et al., 1983), psychological distress (Brief Symptom Inventory BSI, Derogatis, 1993), processing speed (Trail Making Test TMT, Reitan, 1958) and depression symptoms (Beck's depression inventory BDI; Beck et al. 1996). Older participants were additionally tested with the Mini Mental State Examination (MMSE, Folstein et al., 1975). The demographic data are summarized in Table 1. Exclusion criteria consisted of BDI score higher than 20 and MMSE score lower than 27 (in older participants), any neurological (e.g. brain injury, stroke, epileptic seizure) or psychiatric disorders (e.g. depression, anxiety disorder, schizophrenia), chronic eye diseases (e.g. colour blindness, glaucoma), intake of medication affecting cognitive performance and claustrophobia. In the current study, 5 participants withdrawn from the study, 3 participants were excluded due to depression symptoms (BDI score higher than 20), 1 participant due to dementia

---

[8] Individualised Diagnostics and Rehabilitation of Attentional Disorders

symptoms (MMSE score lower than 27), 3 participants due to vision problems and 2 participants due to excessive eye ocular artefacts in the EEG signal.

*Apparatus and stimuli.* Participants were tested in a sound-attenuated chamber (Industrial Acoustics Company) with a dim source of light placed behind the participant. Stimuli were presented on a 24" LED screen with resolution 800x600 pixels and refreshing rate of 100 Hz. Viewing distance was approximately 65 cm from the screen.

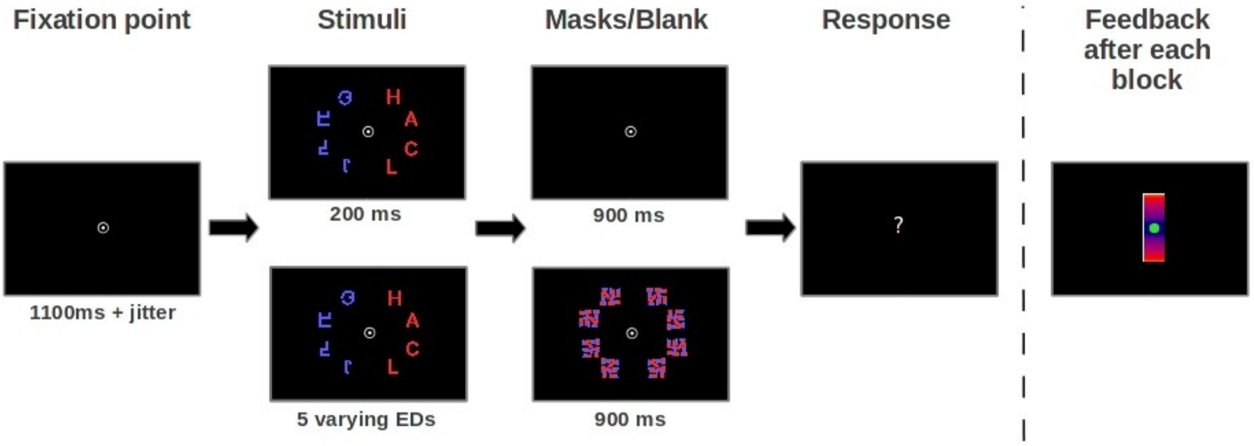


**Figure 1. Experimental procedure used for the assessment of the TVA parameter processing speed C.** Four red target letters arranged on a half-circle plane were presented either on the left or right side of the display and were physically counterbalanced with four blue, equiluminant characters. 5 individually adjusted exposure durations with masking were used. Additionally two conditions were unmasked: with the second shortest exposure duration and an exposure duration of 200 ms.

Fig. 1 illustrates the sequence of events being presented in a single experimental trial. At the beginning of each trial a fixation point (a white circle, size of 0.9° of the visual angle in diameter with a white dot in the centre) was presented in the centre of the display for a duration randomly drawn from 10 to 240 ms. Participants were instructed to fixate this point throughout the whole trial. Subsequently, an array of 4 red target letters (CIE xyY: [0.600, 0.327, 9.510]) was briefly presented on a black background. Presented letters were randomly chosen out of set: {A, B, D, E, F, G, H, J, K, L, M, N, O, P, R, S, T, V, X, Z}. Letters appeared on an imaginary semicircle with a radius of 5.27° of the visual angle either on the right or on the left side of fixation. To ensure balanced physical stimulation in both hemifields, target letters were accompanied with four, equiluminant, blue symbols (CIE xyY: [0.190, 0.143, 9.660]) displayed symmetrically on the side opposite to the targets. Diameters of letters and symbols were the same and equal to 1.3° of visual angle. The same letter and symbol appeared only once in a given trial. Participants were informed on which side of the display targets would be displayed at the beginning of each block of trials, and this side remained identical throughout the entire block. The target side in the first block was counterbalanced across participants (i.e. either left or right) and then alternated throughout the experiment. In five out of seven conditions used in the experiment the letter array was followed by a mask (see Fig. 1): eight red-blue scattered squares (size: 1.3º of visual angle) appearing at each stimulus location with a duration of 900 ms. In the remaining two unmasked conditions, stimuli were followed by a blank screen with a fixation point shown for 900 ms. After stimuli presentation a white question mark appeared in the centre of the screen, indicating the start of a verbal letter report. Participants were asked to report as many as possible red target letters in any order and without speed stress. After each block, participant received a visual performance feedback in which the percentage of correctly reported letters was displayed. To avoid too liberal or too conservative responses, participants were instructed to aim for correctness between 70% – 90%, indicated by green colour coding of the desired range on an accuracy chart presented after each block.

TVA parameter estimation delivers most precise fits if observations cover a broad range of performance including near-floor as well as near-ceiling performance. Therefore, the letter arrays were presented for five different, individually adjusted exposure durations with masking. In addition, two unmasked conditions were used: with the second shortest exposure duration and exposure duration of 200 ms. Due to the visual persistence, in the unmasked conditions the exposure durations are effectively prolonged compared to masked conditions (Sperling, 1960). Therefore, the five masked conditions and two unmasked conditions result in seven different effective exposure durations. Different experimental conditions were equally distributed across blocks of trials and were displayed in randomized order within the block.

The experimenter was present in the chamber throughout the whole testing procedure, sitting behind the participant in order to enter the letters reported by the participants and to manually start a new trial via key presses. The duration of each session was approximately two hours, including filling out of the questionnaires, EEG preparation, verbal instructions and approximately 45 minutes of testing procedure.

*Procedure.* Each session began with a presentation of written instructions and stimuli used in the experiment. This was followed by the procedure of adjusting the five individual exposure durations. The exposure adjustment phase consisted of twelve triples of trials divided into four blocks, resulting in a total of 48 trials. Each triple consisted of two trials that were not used for adjustment. These were either unmasked with exposure duration of 200 ms or masked with exposure duration of 250 ms. One trial in each triple was used for adjustment; this was masked and initially displayed for 80 ms. Each time the participant reported at least one letter in this trial, exposure duration was decreased by 10 ms until the lowest exposure duration was identified. Based on this value a set of additional 4 exposure durations was chosen from the predefined sets.

The testing phase consisted of 400 trials, equally distributed in 5 blocks with target letters presented on the left side, and 5 blocks with target letters presented on the right side. For each exposure duration we used 30 trials (15 for target letters displayed on each side) with exception of unmasked trials with exposure duration of 200 ms. These were presented 110 times on each side and were used for ERP calculations.

*EEG data acquisition.* The EEG data was continuously recorded using BrainAmp DC amplifiers (Brain Products) from 64 active Ag/AgCl electrodes (ActiCAP system, Brain Products). Sixty-three electrodes were placed on an elastic cap (Falk Minow Service) according to the international 10/10 system (American Electroencephalographic Society, 1994). In order to control for eye movements, we recorded the electrooculogram from electrodes placed at the outer canthi of the eyes and the superior and inferior orbits. Impedances at all electrodes were regularly controlled after each 4 blocks and kept below 5 kΩ. Signals were sampled at 1 kHz, online referenced to the electrode FCz and filtered with a 0.1- 250 Hz bandpass filter.

In the offline pre-processing, the raw data was first visually inspected in order to detect and remove nonstereotypic artefacts (e.g. electromygrahpic bursts). Then, the signal was filtered with a high-pass Butterworth zero phase filter (24 dB/oct) at 0.1 Hz. This was followed by an infomax independent component analysis (Bell and Sejnowski, 1995) to identify and remove components representing ocular artefacts (Jung et al., 2000). Subsequently, the data was filtered with a Butterworth zero phase, low-pass filter (24 dB/oct) at 40 Hz, and re-referenced to averaged mastoids (electrodes TP9/10). The continuous EEG was then segmented into epochs, each epoch ranging from 200 ms before to 500 ms after stimulus onset. The 200 ms pre-stimulus interval was used for baseline correction. Channels including voltage steps larger than ± 50 µV/ms, activity lower than ± 0.5 µV within intervals of 500 ms, or signals exceeding ± 60 µV in any channel were excluded on an individual-channel basis. On average, 16% of all trials were rejected using this procedure.

For the ERLs analysis, we selected unmasked trials with exposure durations of 200 ms. ERLs were computed as difference waves: ERP activity recorded over the hemisphere ipsilateral to the presented targets was subtracted from contralateral ERPs using the following formula: ([(PO8-PO7)$_{\text{left target}}$ + (PO7-PO8)$_{\text{right target}}$]/2). Subsequently, difference waves were grand-averaged across left and right targets. Amplitudes of the three candidate ERL waves were quantified by averaging 10 sample points (i.e. 10 ms) before and after the most negative deflection for the N1pc (120 – 210 ms post-stimulus) and the PCN (210 – 350 ms post-stimulus), and most positive deflection for the Ppc (160 – 270ms post-stimulus), respectively. Similarly, largest positive and largest negative deflections within the pre-stimulus baseline (-200 - 0 ms) were obtained in order to compare ERLs against baseline activity.

*Statistical analysis.* All statistical analyses were performed using IBM-SPSS Statistics (version 24, IBM, USA). Based on a median split of the TVA parameter *C*, participants within each age group were assigned to groups of participants having either relatively high or relatively low processing speed. To compare the amplitudes of each ERL wave against baseline (i.e., to validate that the respective ERL was reliably elicited), we calculated repeated-measures analyses of variance (ANOVAs) for the within-subjects factor time window (baseline vs. component) and for the between-subjects factor age group (younger vs. middle vs. older). Group differences in ERL amplitudes and latencies were tested using two-way ANOVAs for factors age group (younger vs. middle vs. older) and processing speed C-level (lower vs. higher). Whenever appropriate, Greenhouse-Geisser correction for non-sphericity was applied (Jennings and Wood, 1976). Post-hoc analyses were performed using Tukey's test. The association of the amplitudes and latencies of the tested components with age was assessed using Pearson's correlation. In order to control for the previously reported decline of the processing speed with age, association with the TVA parameter processing speed C was tested using partial correlation with age as a controlled variable.

## 4.4. Results

*Behavioural data.* The relatively high range of seven different effective exposure durations used in the present study generated a broad range of the number of correctly reported letters, defining probability distribution of performance as a function of exposure duration. Individual TVA parameters were derived by modelling raw performance accuracy in the whole report procedure using a maximum likelihood fitting algorithm (Kyllingsbæk 2006; Dyrholm et al. 2011). This procedure was implemented in a Matlab toolbox *libTVA* (Mads Dyrholm, http://www.machlea.com/mads/libtva.html). Mean scores obtained from TVA modelling showed a close correspondence to the empirically obtained mean values (mean goodness-of-fit: young: $R^2$=0.96; middle: $R^2$=0.96, older: $R^2$=0.94). TVA parameter *processing speed C* was significantly decreasing with age [r = -0.235, p = 0.022], replicating previous studies (e.g. Wiegand et al., 2014b), see Fig. 2.

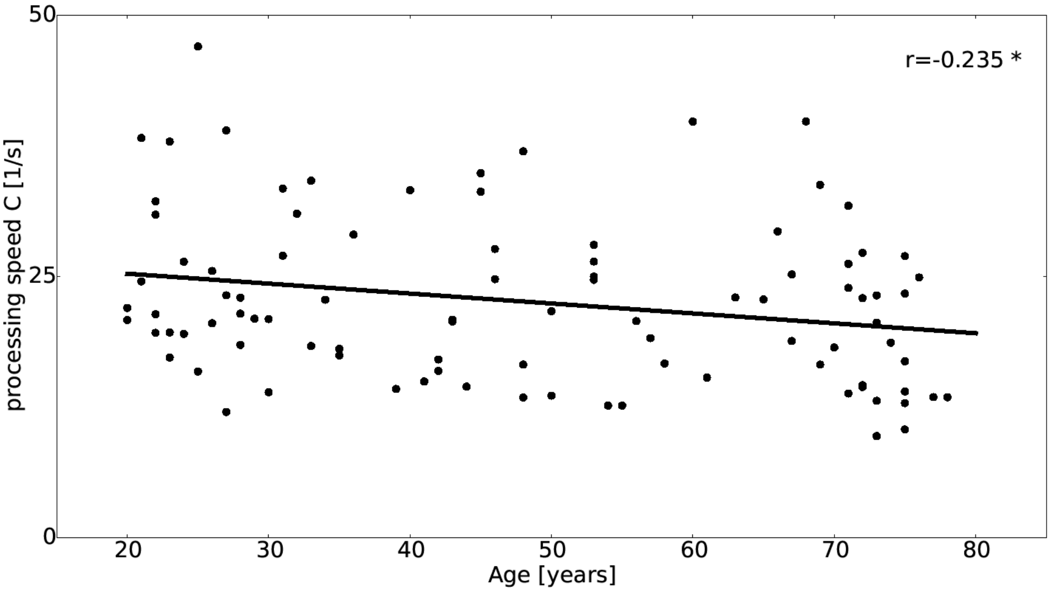


**Figure 2. Correlation between age and TVA parameter processing speed C.**

*Electrophysiological data.* Figure 3 presents grand-averaged event-related potentials elicited by unmasked target displays with exposure duration of 200 ms, recorded at channels PO7/8. The left panel presents waveforms recorded over the hemispheres contra- and ipsilateral to the target side. The right panel presents the corresponding (contralateral–ipsilateral) difference waveforms separately for participants with higher and lower TVA parameter processing speed C. For the N1pc time window, a clear negative-going deflection can be seen for older participants, which gradually decreases in amplitude for middle and younger age participants. In the younger group, a clear PCN wave was elicited, which appears to be less prominent for middle and older participants. This age-dependent PCN pattern is likely to result from increased trial-to-trial variance in older relative to younger participants, based on which the PCN appears to be more smeared in older age groups.

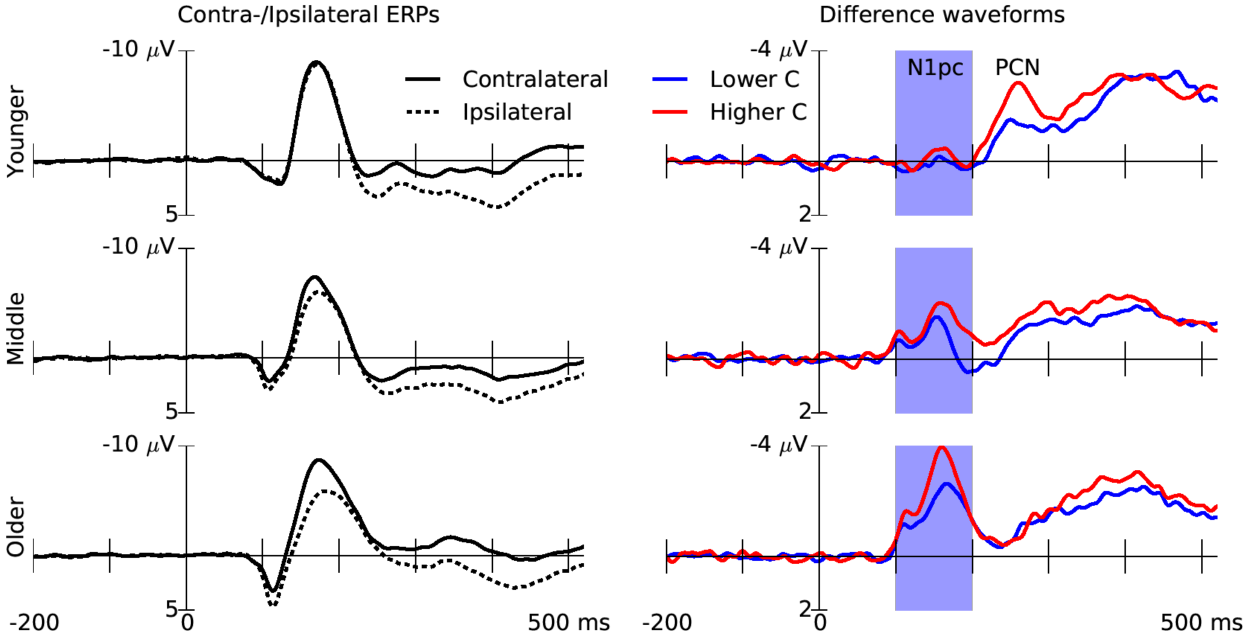


**Figure 3. Grand-averaged event-related brain potentials recorded from parieto-occipital electrodes (PO7/8) and grand-averaged separately for younger, middle and older participants.** Blue area marks N1pc time range. Left panel: Contralateral (solid line) and ipsilateral (dashed line) waveforms. Right panel: Difference waveforms compared between groups with lower (blue line) and higher (red line) processing speed C.

*N1-posterior-contralateral (N1pc).* The ANOVA testing the N1pc against baseline revealed the main effect of time window [F(1,91)=89.068, p<0.001] and age [F(2,91)=13,760, p<0.001] to be significant, indicating generally larger amplitudes for the N1pc time window relative to the baseline time window, and for older relative to younger participants. In addition, the interaction between both factors reached significance [F(2,91)=16.999, p<0.001], indicating that the N1pc was gradually increasing with age, whereas no such age-dependent difference was evident in the pre-stimulus time window.

In the next step, we tested whether the age-dependent N1pc effect was further modulated by processing speed C. The respective two-way ANOVA for the factors age and C-level revealed a significant main effect of age [F(2, 88)=16.455, p<0.001]: N1pc amplitudes were significantly higher in older participants [M=-3.81 µV, SD=2.03] than in middle [M=-2.21 µV, SD=1.84] and younger participants [M=-1.24 µV, SD=1.70]. N1pc amplitude was also larger in participants with higher as compared to lower processing speed C [M=-2.97µV, SD=2.33 vs. M=-1.89µV, SD=1.78] as confirmed by a significant main effect of C-level [F(1,88)=7.627, p=0.007]. Interaction between age processing speed was non-significant (p=0.764). Of note, N1pc amplitudes were significantly correlated with age [r(94)=-0.513, p<0.001], and a significant partial correlation between N1pc amplitude and processing speed C was also found [r(91)=-0.314, p=0.002] (see Fig. 4B and 4C).

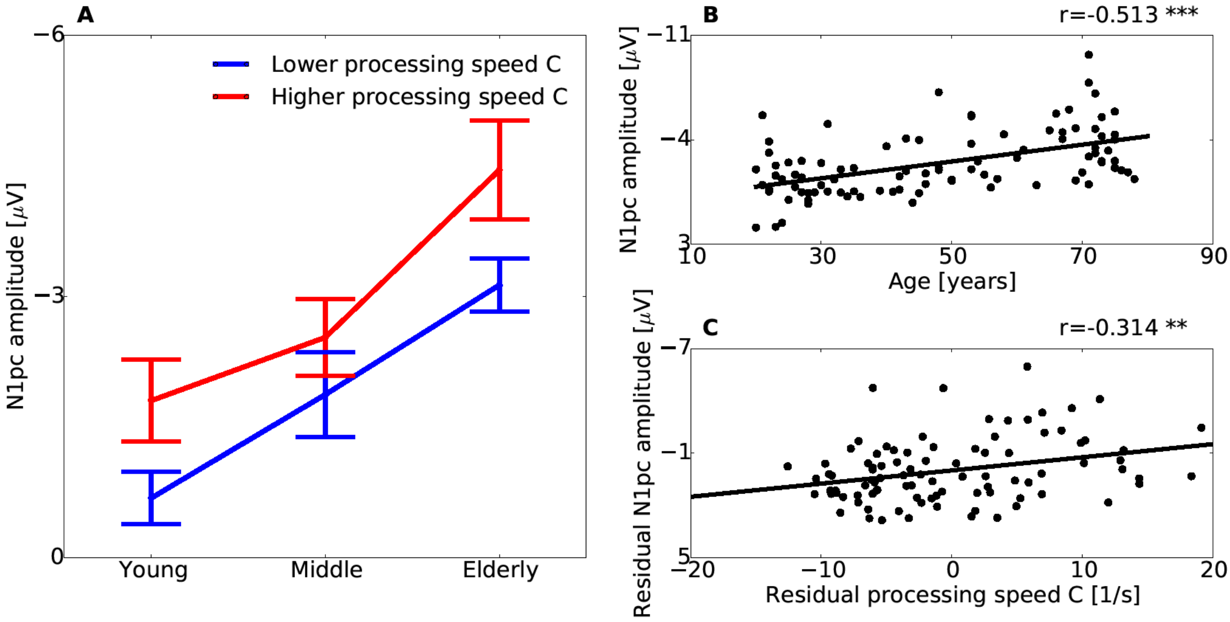


**Figure 4. Relation between the N1pc amplitude, age and processing speed C.** A) Mean amplitude of the N1pc component as a function of age group (young, middle, older) and C-level (lower, higher). Error bars show standard errors. B) Correlation between amplitude of the N1pc component and age. C) Correlation between residual N1pc amplitude and residual processing speed C when controlled for age. *** p<0.001, ** p<0.01.

The ANOVA calculated for the latency of the N1pc did not yield any significant results [all p>0.357]. The correlation of the N1pc latency with age and the partial correlation controlled for age with processing speed C were also far from significance [all p> 0.414].

*Positivity-posterior-contralateral (Ppc).* There was a significant main effect of time window [F(1,91)=7.835, p=0.003], which was driven by the counterintuitive pattern that the Ppc was significantly smaller in amplitude than baseline activation [M=0.22 µV, SD=1.32 vs. M=0.63 µV, SD=0.38]. While this pattern can be taken to indicate that there was no Ppc reliably triggered in the present data set, it is worth noting that this effect may be partly due to the preceding N1pc. The main effect of age reached significance [F(2,91)=3.583, p=0.032], indicating larger Ppc amplitudes for participants of older relative to younger age. The interaction of age and time window, on the contrary, was not significant [p=0.460].

The ANOVA for the factors age group and C-level did not yield any significant results [all p>0.130]. However, Ppc amplitudes significantly correlated with age [r(94)=-0.222, p=0.032] (see Fig. 5B), but not with processing speed as revealed by the partial correlation controlled for age between Ppc amplitude and C [r(91)=-0.168, p=0.107].

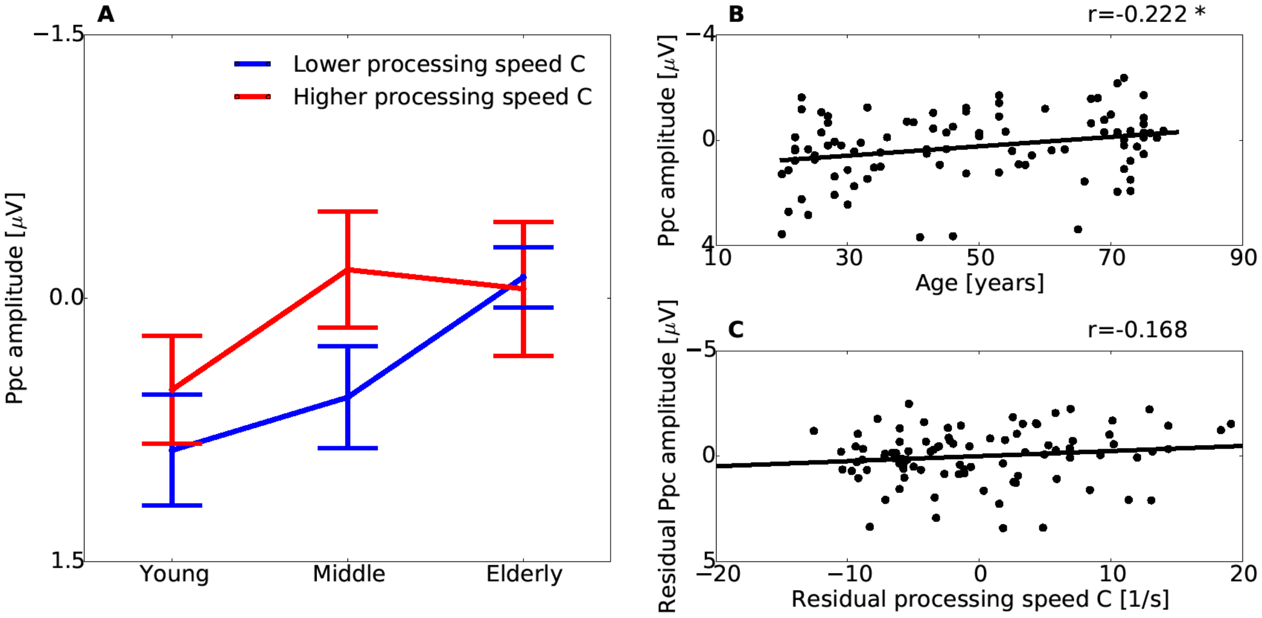


**Figure 5. Relation between the Ppc amplitude, age and processing speed C** A) Mean amplitude of the Ppc component as a function of age group (young, middle, older) and C-level (lower, higher). Error bars show standard errors. B) Correlation between amplitude of the Ppc component and age. C) Correlation between residual Ppc amplitude and residual processing speed C when controlled for age. * p<0.05.

The ANOVA on the timing of the Ppc did not yield significant results of age or C-level [all p>0.129]. The correlation between Ppc latency and age was found to be significant [r(94)=0.221, p=0.032], (see Fig. 6B). Partial correlation with processing speed C was not significant [r=0.054, p=0.607].

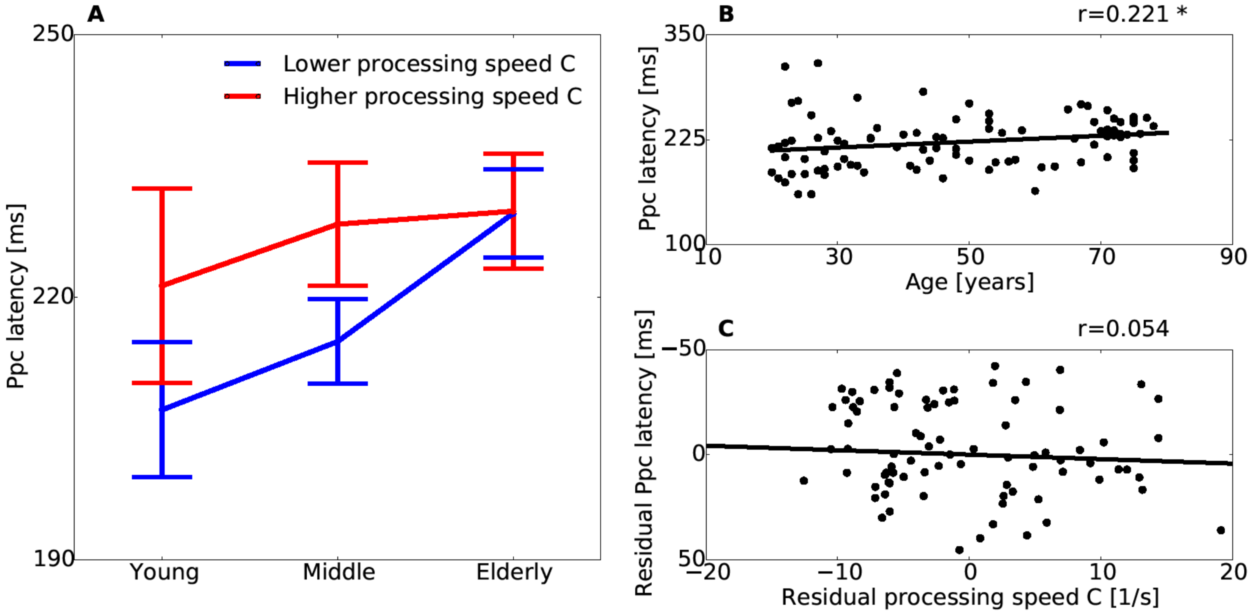


**Figure 6. Relation between the Ppc latency, age and processing speed C** A) Mean latency of the Ppc as a function of age group (young, middle, older) and C-level (lower, higher). Error bars show standard errors. B) Correlation between latency of the Ppc and age. C) Correlation between residual Ppc latency and residual processing speed C when controlled for age. * p<0.05.

*Posterior-Contralateral-Negativity (PCN).* Amplitudes of the PCN were significantly larger than baseline [M=-2.49 µV, SD=1.50 vs. M=-0.60 µV, SD=0.32], as confirmed by a significant main effect of time window [F(1,91)=158.483, p < 0.001]. The main effect of age group and the interaction between time window and age group did not approach significance [all p>0.121].

As revealed by the two-way ANOVA for the factors age and processing level C, participants with higher compared to lower processing speed C exhibited larger PCN amplitudes [M=-2.86, SD=1.80 vs. M=-2.10, SD=0.97, F(1,88)=6.517, p=0.012]. The main effect of age group and the interaction between C-level and age group, by contrast, were not significant [all p>0.122]. The correlation of PCN amplitudes with age was not significant [r = 0.111, p=0.289], but when controlled for age, the partial correlation of the PCN amplitude with processing speed C reached significance [r(91)=-0.262, p=0.011], showing that participants with higher processing speed had also larger PCN amplitude (see Fig. 7C).

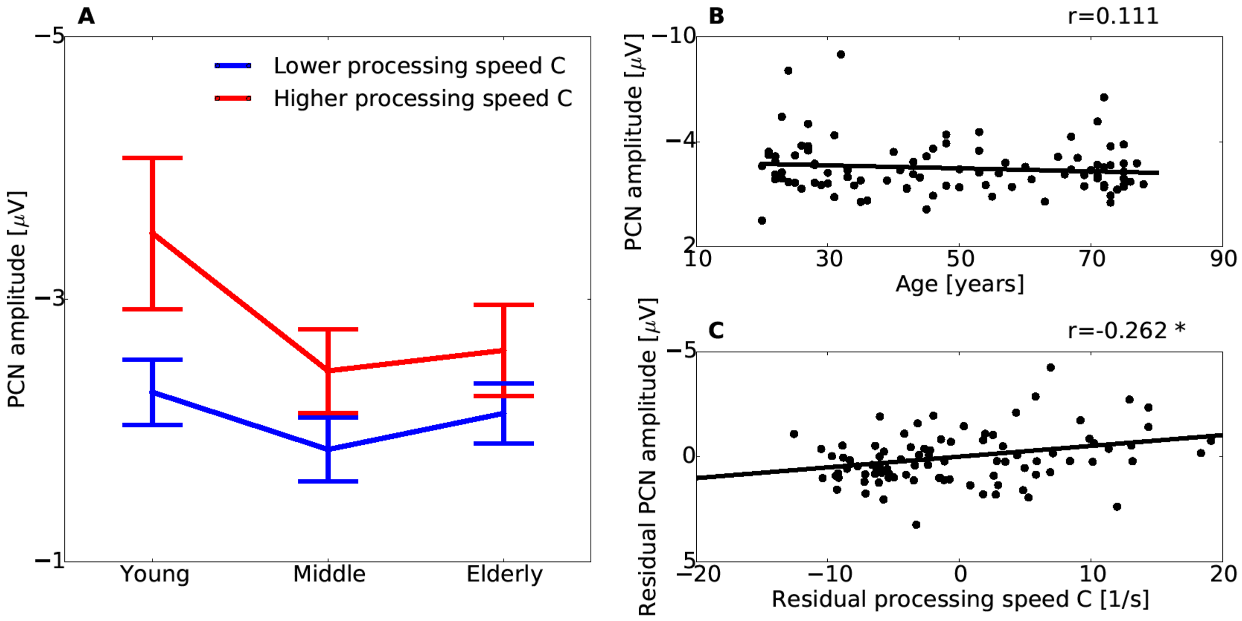


**Figure 7. Relation between the PCN amplitude, age and processing speed C.** A) Mean amplitude of the PCN component as a function of age group (young, middle, older) and C-level (lower, higher). Error bars show standard errors. B) Correlation between amplitude of the PCN component and age. C) Correlation between residual PCN amplitude and residual processing speed C when controlled for age. * p<0.05.

Analyses of the latency of the PCN yielded a significant main effect of age [F(2,88)=6.489, p=0.002] (see Fig. 7A). Post-hoc Tukey test revealed that, in younger participants, PCN waves were elicited significantly faster [M=292.34 ms, SD=42.95] than in older participants [M=324.18 ms, SD=30.90]. The main effect of C-level as well as the interaction were not significant [all p>0.362]. Further, PCN latency correlated significantly with age [r(94)=0.342, p=0.001], with increasing PCN latencies for participants of older relative to younger age (see Fig. 8B). Partial correlation controlled for age between PCN latency and processing speed C was not significant [r(91)=0.135, p=0.196], confirming that there was no relation between C and the PCN timing.

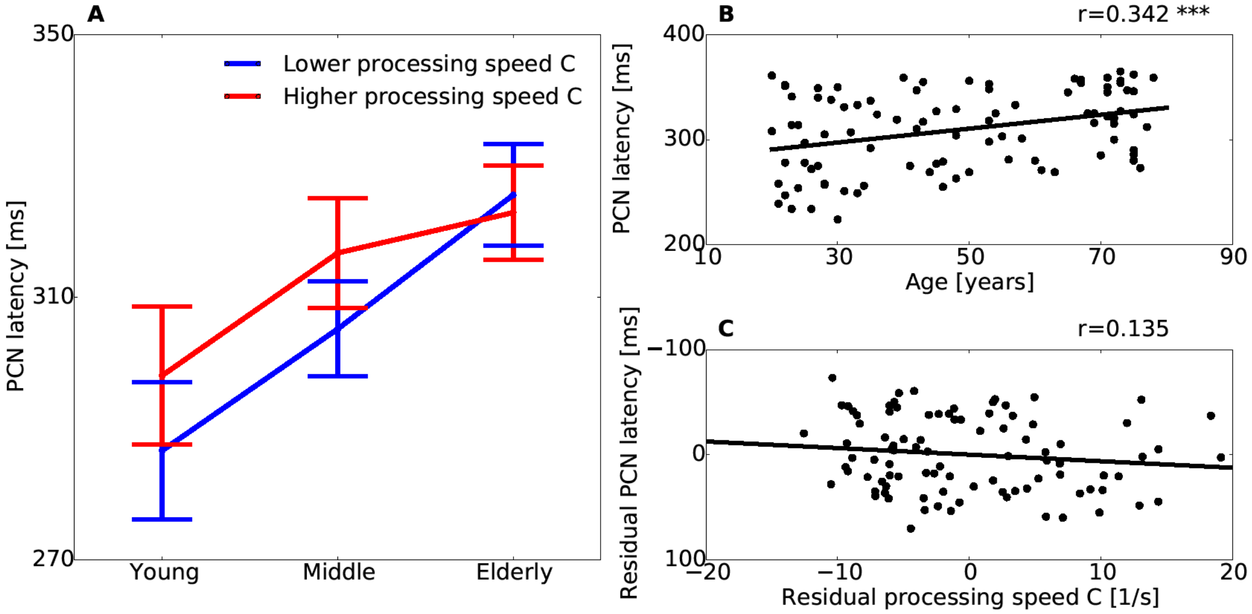


**Figure 8. Relation between the PCN latency, age and processing speed C.** A) Mean latency of the PCN component as a function of age group (young, middle, older) and C-level (lower, higher). Error bars show standard errors. B) Correlation between latency of the PCN component and age. C) Correlation between residual PCN latency and residual processing speed C when controlled for age. *** p<0.001.

## 4.5. Discussion

The aim of the present study was to investigate (i) the relation between interindividual differences in visual processing speed and early, spatially specific visual processing, and (ii) whether this relation depends on healthy ageing. In order to quantify processing speed, we adapted a TVA-based whole report task such that we could isolate event-related EEG lateralizations. In particular, we focused on three well-established ERL waves as potential candidates that may index interindividual differences in processing speed: N1pc, Ppc and PCN. To this end, we analysed the amplitudes as well as the timing of these ERLs between groups of lower versus higher processing speed as a function of healthy ageing (younger, middle and older).

The behavioural results showed a significant decline of visual processing speed with age, which is in accordance with age-related slowing observed in various other cognitive tasks (e.g. Bucur et al., 2008; Nielsen & Wilms, 2015; Salthouse, 1994). At the electrophysiological level, we found the amplitude of the N1pc being influenced by both processing speed and age: N1pc amplitudes were boosted in participants with higher as compared to lower processing speed, and enhanced for older relative to younger participants. The subsequent positive Ppc component, on the contrary, was not affected by processing speed, but exhibited age-dependent variations. As the age of the participants was increasing, Ppc amplitudes decreased while latencies slowed down. It is worth noting, however, that these effects have to be interpreted with caution as any differences observable for the Ppc might be directly caused, or confounded, by preceding N1pc differences. The third ERL wave of interest, the PCN, showed again a clear relation to processing speed: PCN amplitudes were larger for participants with higher relative to lower processing speed. While the latency of the PCN slowed down with age, no relation was evident between processing speed and the PCN timing.

### *Processing speed and age influence initial orienting of attention.*

While the exact process underlying the N1pc component is still subject to debate, an increasing body of studies suggests that this asymmetry during the P1/N1 time range can be associated with an initial attentional orienting response, which seems to be mainly driven by physical characteristics of bilateral stimulus arrays (Shedden and Nordgaard, 2001; Wascher and Beste, 2010, Sänger and Wascher, 2011). Wascher and Beste (2010), for example, showed that the N1pc can be observed in response to salient but task-irrelevant elements. In their study, a task-irrelevant orientation change (between two bar elements that were temporally separated by 50 ms) could occur at a location contralateral to a task-relevant luminance change (a black bar could be replaced by a white bar). When the contralateral orientation change was rather weak (using a length-to-width ratio of 1:1.35), the N1pc was elicited in response to the task-relevant location at which the luminance change occurred. When there was a high salient orientation change signal (using a length-to-width ratio of 1:2.41), by contrast, the N1pc was elicited in response to the location containing the task-irrelevant location. Based on this pattern, Wascher and colleagues proposed the idea that the N1pc may reflect an initial, saliency-driven attentional orienting response towards high salient stimulus elements.

Given that there were no manipulations of stimulus displays in the present study, our findings go beyond these previous reports by revealing that the N1pc amplitude is not exclusively linked to physical stimulus properties. Instead, we identified two additional inter-individual factors that determine the degree to which the N1pc is elicited: age and processing speed. In line with previous notions that varying N1pc amplitudes may reflect varying weighting and/or biasing of incoming sensory information (Wascher and Beste, 2010), an age-dependent increase in the N1pc may indicate that younger versus older participants employ different selection modes in the present whole-report task. As demonstrated by Figure 3, importantly, the present N1pc age effects derive from decreasing ipsilateral (instead of increasing contralateral) activity during the P1/N1 time range. Reduced ipsilateral activity may indicate that, in order to report target letters most efficiently, older participants may strategically de-allocate processing resources from the task-irrelevant distractor side, based on which the task-relevant target side may already be *pre-selected,* or biased, at this early processing level, before being attentionally selected at the subsequent stage (indexed by the PCN).

Such an early selection mode may be less necessary for younger participants as they have overall more attentional resources available—indexed by higher processing speed. That is, exposure duration of 200 ms (in the EEG trials) may provide sufficient time for younger participants to initially encode the entire display (the relevant and the irrelevant hemifield) during this early processing stage, leading to (more) comparable P1/N1 waves for both contralateral and ipsilateral hemifields. Spatial attentional selection of task-relevant objects may be then performed at the later stage, as reflected by faster and temporally less variable PCN waves.

Independent of this age effect, N1pc amplitudes were generally enhanced for participants with higher relative to lower processing speed. In line with the above outlined interpretation, this influence of processing speed may indicate that participants with higher processing speed are able to allocate a greater amount of processing resources to pre-attentive analyser units that code target information than participants with lower processing speed. As a result, the coding of task-relevant information is facilitated and the total amount of information being processed per second is increased (Duncan et al. 1999).

*Processing speed, age, and attentional selection.*

A second ERL that showed significant modulations owing to differences in processing speed and age was the PCN wave, which can be generally linked to attentional target selection in visual space (e.g. Eimer, 1996; Woodman and Luck, 2003; Töllner, et al., 2012). While participants with higher processing speed exhibited larger PCN waves than participants with lower processing speed, the timing of the PCN was systematically delayed as the age of the participants increased. As illustrated by Figure 4, the PCN is most pronounced in the younger group, less distinctive in the middle group, and even more smeared in the older group. Even though Fig. 3 gives the impression that PCN amplitudes were decreasing with age, differences between age groups in the PCN amplitude did not reach statistical significance. The absence of significant PCN amplitude effects may be caused by two reasons. First, because the PCN was triggered significantly later for older relative to younger participants (292 ms vs. 324 ms), it appears to partially overlap with the subsequent negative deflection (i.e., the SPCN)[9], based on which there may be no distinct PCN peak visible when calculating the grand-average waveforms for the older group (see Figure 4). Second, increased cross-trial variance in the older group may additionally lead to more spread out components in the grand-average waveforms and, thus, artificially reduced grand-average amplitudes.

The present findings replicate previous studies that reported age-dependent PCN modulations (e.g., Lorenzo-López et al., 2008; Wiegand et al., 2013, Pagano et al., 2016). Wiegand et al. (2013), for example, likewise observed delayed PCN waves for participants of older relative to younger age. Using a visual compound search task, participants in this study were instructed to report as fast as possible the orientation (vertical vs. horizontal) of a pop-out target, which was randomly defined by colour or shape. Accordingly, our findings demonstrate that age-dependent PCN timing effects can be generalized from 2-alternative-forced-choice visual search for singleton targets to whole report tasks, in which participants are instructed to select (and report up to) four colour-defined target letters without any time pressure.

Besides the influence of age, we found that the level of processing speed reliably modulated the elicitation of the PCN, thereby extending the list of interindividual factors that modulate attentional selection processes—including conditions of schizophrenia (Luck et al., 2006) and attention-deficit/hyperactivity disorder (Cross-Villasana et al., 2015). In particular, participants with higher processing speed exhibited larger PCN waves than participants with lower processing speed.

---

[9] For the sake of brevity, we refrained from discussing the SPCN in detail.

In most visual attention studies, enhanced PCN waves go along with facilitated behavioural performance. This relation has been demonstrated for various bottom-up and top-down-driven attention biases as, for example, physical salience (Brisson et al., 2007; Töllner et al., 2011), target and distractor expectancy (Töllner et al., 2010, 2015), or previous trial history (Töllner et al., 2008). When manipulating the salience of a pop-out target through varying the target orientation or the target colour relative to the orientation and colour of its surrounding distractors in visual search, for example, it has been shown that the PCN is gradually amplified for increasing relative to decreasing target-distractor similarity (Töllner et al., 2011). Following this and other reports, it has been proposed that the PCN can be used as neural measure of target salience/priority in tasks with bilateral, physically balanced stimulus arrays (Töllner et al., 2015). In the light of this proposal, the present results may indicate that enhanced PCN waves for participants with higher relative to lower processing speed may result from differences in early sensory tuning to task-relevant information, based on which target items will be processed with higher salience/priority. As a consequence, more attentional resources can be allocated to task-relevant items, thereby providing the basis for larger amounts of information being processed per second (Duncan et al. 1999).

*Conclusion.*

In the present EEG study, we identified the neural correlates of the attention parameter “processing speed” *C*, as defined by the well-established Theory of Visual Attention (Bundesen, 1990). We found that both N1pc and PCN waves index interindividual differences in *C*, and that this relation was independent of age. Furthermore, N1pc waves were markedly increased and PCN waves substantially slowed for participants of older relative to younger age. This ERL pattern suggests that younger versus older participants employ different selection modes to solve the present whole-report task. Older participants seem to put more emphasis on pre-selecting, or biasing, target information already during an initial orienting of attention phase (indexed by the N1pc), whereas younger participants seem to encode the entire display during this early phase, which is then followed by a temporally less variable attentional selection process (indexed by the PCN).

# 5. Summary and Discussion

## 5.1. Aim of the thesis

The main goal of the current PhD thesis was to shed more light on the relation between ageing and efficiency of visual attentional selection and visual processing speed and underlying neural activity of the brain. The presented work was theoretically grounded on the computational Theory of Visual Attention (TVA, Bundesen, 1990) and its more recent neural interpretation (NTVA, Bundesen, Habekost, & Kyllingsbæk, 2005; 2011). We performed three studies that combined TVA-based behavioural partial- and whole-report tasks with simultaneous EEG recording. During the experiments participants were asked to verbally report briefly presented targets (red letters). In the partial report task, targets were accompanied by distractors (blue letters) which participants were asked to ignore. The TVA-based fitting of report accuracy permitted a separate quantification of distinct attentional parameters postulated by TVA, whereas EEG provided information on the brain activity related to the attentional processes with excellent temporal resolution. In the analysis of the electroencephalographic data I focused on the event related lateralizations (ERLs) i.e. waveforms computed as a difference of the potentials contra- and ipsilateral to the presented target. In studies 1 and 2, we measured the amplitudes of the components elicited by displays in which the presented target was accompanied by a contralateral distractor. In study 3 we measured the amplitudes of components elicited by displays, in which the target letters presented in one hemifield were visually counterbalanced by meaningless characters in the other hemifield. Using such methodology we could measure brain potentials related to processing the target elements, leaving out any other, non-related activity. In the first study we aimed at identifying the neurophysiological underpinnings of the individual differences in two distinct parameters of attentional selection: top-down control efficiency and spatial bias. In the second study we aimed at investigating whether neural indices of top-down control efficiency change with healthy ageing and whether the potential relation between top-down control efficiency, age and brain activity is influenced by the individual amount of cognitive reserve (Stern, 2002). In the third study, we focused on investigating whether there is a relation between healthy ageing and individual level of visual processing speed, and whether and how this potential relation is reflected by the ERLs.

### Study 1: Event-related EEG lateralizations mark individual differences in spatial and non-spatial visual selection.

#### 1. Key findings

The first study contributed to a better understanding of how different parameters of attentional processing are reflected in brain activity. We tested young, healthy participants using a TVA-based partial report paradigm with simultaneous recording of ERLs. Performance in the task was mathematically modelled in order to obtain estimates of two distinct parameters of visual attentional selection: top-down control, quantified as TVA parameter $\alpha$, and spatial bias, quantified as TVA parameter $w_\lambda$. By comparing amplitudes of the ERLs in participants with better vs. poorer top-down control efficiency and left- vs. right-ward spatial bias we identified distinct lateralized components related to either of the parameters of attentional selection. More precisely, we demonstrated that differences in the efficiency of visual top-down control were reflected by the amplitude of the Posterior Contralateral Negativity (PCN), but not by the amplitudes of the hemifield-specific asymmetries. Conversely, interindividual differences in spatial bias were reflected by the differences in the amplitudes of the hemispheric asymmetries of visual ERLs, but they were not related to differences in the amplitudes of the PCN.

2. Implications and relations to other accounts.

We demonstrated that participants with more efficient top-down control elicited relatively larger amplitudes of the PCN than participants with less efficient top-down control. There is a general consensus among researchers that the PCN reflects brain activity involved in the process of filtering incoming visual information. This mechanism improves selection of relevant information by reducing processing of distracting information (Eimer, 2015; Luck, 2012). Specifically, the amplitude of the component is typically interpreted as an index of the amount of attentional resources involved in the processing of the given task-relevant visual object (Eimer et al., 1996; Luck & Hillyard, 1994; Töllner et al., 2008). However, in a large percentage of studies, changes in the amplitude of the PCN reflected changes in the difficulty of the task (e.g. Luck & Hillyard, 1994; Luck, Girelli, McDermott, & Ford, 1997) or changes in the saliency of the stimuli (e.g. Töllner et al., 2011). In the presented study the difficulty of the task was adjusted to be comparable across all participants and physical properties of the stimuli were kept constant throughout the entire experiment. Hence, the observed differences in the PCN amplitudes suggest that participants with more efficient top-down control allocate more attentional resources to relevant targets compared to the participants with less efficient top-down control. According to one of the main postulates of TVA, more efficient top-down control is a consequence of allocating relatively more attentional weights to the target and less to the distractor (Bundesen & Habekost, 2008). Thus, larger PCN amplitudes in participants with more efficient top-down control may be interpreted as a marker of more efficient distribution of attentional weights.

The direction of the spatial bias was reflected by the amplitude of the hemispheric asymmetries of visual ERLs, but did not correspond to the amplitude of the PCN. More precisely, we observed an enhanced negative ERL amplitude over the occipital site contralateral to the target. When the target letter was presented in the participants' non-prioritized hemifield, but not when it was presented in the prioritized hemifield. Furthermore, after we split participants into subgroups with rightward and leftward spatial bias according to the median value of the parameter spatial bias $w_\lambda$, we observed specific ERL patterns that differed between the groups: within the same time range, participants with rightward spatial bias showed a negative deflection in response to left-target displays and positive deflection in response to right-target displays. In turn, participants with leftward spatial bias showed a negative deflection in response to right-target displays and positive deflection in response to left-target displays.

The present results demonstrate that spatial and task related selection mechanisms are in fact two distinct processes that are associated with different brain activity. This result provides a strong support for the independence assumption postulated in the TVA, which assumes that the distribution of attentional weights of the processed objects according to their relevance for the task and their spatial location are independent from each other. This is reflected by mathematically independent modelling of parameters top-down control efficiency $\alpha$ and spatial bias $w_\lambda$.

**Study 2: Age related changes in neural marker of top-down control.**

1. Key findings

The second study aimed at investigating whether the relation between top-down control efficiency and its neural markers changes in healthy ageing. Participants of the study were also tested for the amount of cognitive reserve as a potential factor that might influence this relation. In this study we used the same partial-report task, TVA-based mathematical modelling of performance and simultaneous EEG recording as in the first study. In order to estimate the amount of cognitive reserve, we measured crystallized IQ using a *German Multiple-Choice Vocabulary Test* (MWT-B, Lehr, 1977). We tested healthy participants split into three age groups: younger (age 20 - 33), middle-aged (age 33 - 58) and older (age 60 - 77). We did not find evidence for changes in top-down control in aging individuals and did not find a significant relation between top-down control and crystallized IQ. Furthermore, analyses of electrophysiological data revealed that the relation between top-down control efficiency and PCN amplitude identified in the first study in younger participants is preserved also in ageing individuals. Furthermore, we demonstrated that in all age groups top-down control efficiency modulated the amplitude of the lateralized component Posterior Positivity Contralateral (Ppc), which precedes the PCN. Altogether, in all three age groups, participants with more efficient top-down control elicited larger Ppc and PCN amplitudes. Moreover, amplitudes of both lateralized components were not affected by age, but were revealed to be modulated by the amount of crystallized IQ. More precisely, we demonstrated that only in participants with relatively high, compared to relatively low crystallized IQ, the Ppc amplitude was higher in participants with more efficient compared to less efficient top-down control. Additional correlation analysis revealed that Ppc amplitude was linearly correlated with top-down control efficiency only in participants with relatively higher crystallized IQ, but not in participants with relatively lower crystallized IQ. The PCN amplitude showed a tendency to decline with age only in participants with lower crystallized IQ. A follow up correlation analysis showed that in participants with relatively lower crystallized IQ the amplitude of the PCN was significantly decreasing with age. In contrast, in participants with higher crystallized IQ the amplitude of the PCN remained unaffected by age.

## 2. Implications and relations to other accounts.

The presented findings provide new insights into more general questions on neural underpinnings of attentional selection. We demonstrated that the efficiency of top-down control is related to two well established markers of attentional processes: the Ppc and the PCN. Both components are thought to reflect two distinct aspects of processing of visual information. The Ppc is typically interpreted as a neural marker of a process of inhibition of task-irrelevant stimuli, which is considered to be a bottom-up driven mechanism (Gokce et al., 2014). The amplitude of the PCN component is widely interpreted as an index of the relative amount of attentional resources being allocated in order to process task-relevant stimuli (e.g., Eimer, 1996; Luck and Hillyard, 1994). Thus, our results showing a relation between top-down control efficiency and the amplitudes of the Ppc and the PCN are complementary with the existing literature. Furthermore, we demonstrated that the relation between top-down control efficiency and its electrophysiological correlates is modulated by healthy ageing and by the amount of cognitive reserve. Based on our finding that only in participants with higher amount of cognitive reserve the Ppc amplitude was correlated with top-down control efficiency, we suggest that participants may employ different strategies to select task-relevant information depending on the amount of their cognitive reserve. Participants with a higher amount of cognitive reserve may employ earlier and bottom-up driven mechanisms in order to facilitate subsequent selection. In contrast, we demonstrated that only in participants with lower levels of cognitive reserve the amplitude of the PCN was declining with age. Given that the PCN is assumed to reflect the relative amount of allocated resources to process the relevant as opposed to irrelevant information, we assume that in participants with lower, compared to higher, levels of cognitive reserve, the total amount of the available resources may decrease with age.

## Study 3: Age-dependent differences in visual processing speed and early, spatially selective processing: New insights from N1pc and PCN waves

### 1. Key findings

In the third study, we aimed at answering two questions. First, do ERLs reflect interindividual differences in visual processing speed. Second, is this potential relation affected by healthy ageing. In order to answer these questions we tested healthy participants from three age groups: youngest (age 20-34), middle (age 35-58) and oldest (age 60-78) using a TVA-based whole report task with simultaneous EEG recording. Individual estimates of the visual processing speed were obtained by modelling accuracy performance in the task. We demonstrated that visual processing speed can be linked to two distinct lateralized components: the N1pc and the PCN. Across all age groups, amplitudes of both components were increased in participants with higher, compared to lower, processing speed. However, the nature of the relation between each component and the processing speed level was also affected by age. In younger individuals, compared to older ones, the amplitude of the N1pc was decreased but its latency did not differ between age groups. In contrast, amplitude of the PCN did not show any relation to age, but its latency was shorter in younger than in older participants.

### 2. Implications and relations to other accounts.

The results presented in study 3 are reconcilable with other studies showing an age-related decline in processing speed (e.g. Espeseth, Vangkilde, Petersen et al., 2014; McAvinue, Habekost, Johnson et al., 2012). What our finding add to this picture is the fact that, on the neurophysiological level, the relation between age and processing speed decline is accompanied not only by quantitative, but rather qualitative changes of the lateralized components. More precisely, age-related decline of processing speed is not reflected by changes of a single ERL component, but it is rather reflected by changes in the overall characteristics of the evoked ERL waveform. We demonstrated that age not only affected the N1pc amplitude, but this enhancement was accompanied by a delay of the PCN latency. Functionally, N1pc amplitude is attributed to weighting of incoming sensory information (Wascher and Beste, 2010). Thus, significantly increased N1pc amplitude in older, compared to younger, adults may suggest, that these individuals, in face of lower amount of resources, preselect information during early stages of attentional processing. In contrast, younger participants showed faster PCN latencies, which suggests that in these individuals attentional selection of relevant elements may be performed at the later stage of processing. Together, our results imply that healthy ageing of the brain not necessary leads to a simple deterioration of the attentional functions, but it rather involves reorganization of the cognitive processes.

### 5.2. General conclusions from the projects

The presented studies demonstrate that the combination of testing methods based on well-established theoretical background with methodological advantages of electroencephalography may be particularly fruitful. TVA, which is a computational model, provides means to quantitatively and mathematically independently measure different parameters of visual attention, whereas the methodology of event-related potentials provides information on the brain activity with an excellent temporal resolution, crucial for disentangling functionally distinct processes.

The findings presented in the current thesis are in line with the interpretation postulated by NTVA, which suggests that distinct aspects of visual attentional functions are reflected by different neurophysiological markers. First, the functional interpretation of the PCN is reconcilable with the mechanism of allocating attentional weights to processed objects postulated by NTVA as a mechanism underlying top-down controlled selection (Bundesen et al., 2005). According to NTVA, a distribution of the attentional weights among the processed objects is the basis for the selection of the relevant objects in the visual field. In turn, attentional weights describe how the available neural resources are distributed among the processed objects. On the neural level, the distribution of the resources is assumed to be controlled by higher-order cortical areas located in striate and extrastriate cortical areas. Within these areas η values are computed, i.e. strength of evidence that the processed object belongs to a particular category, e.g. it is a target or distractor stimulus. Based on these values in a later stage of processing attentional weights ($w_i$) of the objects are derived (Bundesen et al., 2005). In line with this statement, it was shown in a study that combined different imaging methods (event-related magnetic fields and event related potentials) that the neural sources of the PCN component are located in the lateral occipital cortex and the visual V4 area (Hopf et al. 2006), which is a part of the extrastriate cortex – an area predicted by in NTVA. Thus, increased PCN amplitudes can be interpreted as an indirect measure of the relative distribution of attentional weights among task-relevant targets and irrelevant distractors.

Second, asymmetries of ERLs related to the direction of spatial attentional bias may reflect the mechanism of spatial weighting postulated by TVA. According to NTVA, attentional processing consists of two subsequent waves. The first wave is unselective. An attentional weight for each processed visual object is computed and stored in a saliency map located in the pulvinar nucleus. Objects being presented in the individual's preferred hemifield receive higher attentional weights compared to objects in the opposite hemifield, which is then reflected in the TVA parameter spatial bias $w_\lambda$. During the second, selective wave, the attentional weights $w_i$ serve as a basis for distribution of neural resources, i.e. number of neurons involved in processing of the visual information

(Bundesen et al., 2005). According to NTVA, task related and spatial selectivity are distinct and independent functions of visual attention. The findings of the studies 1 and 2 showing that TVA parameters spatial bias $w_\lambda$ and top-down control efficiency $\alpha$ were reflected by different lateralized components support the assumption, postulated by NTVA, that spatial and task-related aspects of attentional selection are in fact two independent functions of the visual processing system (Bundesen et al., 2005, 2011).

Finally, according to NTVA, the parameter visual processing speed C reflects the total amount of attentional weights allocated to process visual objects. As mentioned before, attentional weights guide the amount of resources engaged to process given visual information, i.e. the activity of the neurons within visual cortex. Total activity of cortical nerve cells is reflected by the amplitudes of the evoked potentials. Therefore increased N1pc and PCN amplitudes in participants with higher processing speed across all age groups can be interpreted as a neural marker of higher total amount of attentional resources allocated to process the target objects.

### 5.3. Outlook and future directions

The presented studies provide insights into the relation between attentional functions and neuronal activity. However, there are questions concerning changes of attention in an ageing brain that still remain unanswered and therefore the presented studies may serve as a starting point for further investigations. In order to gain more information on age-related changes in mechanisms of attention and their neural background one could employ further neuroimaging methods for measuring the neural correlates of the distinct attentional parameters and/or use different experimental designs.

**Longitudinal assessment.**

It is worth to note that study 2 and 3 compared independent groups of younger and older participants in a between-subjects manner. A longitudinal study seems to be the most adequate in order to link changes in functions of attention with the changes of neural activity in face of the neurodegenerative processes in the brain. A study of 34 MCI patients demonstrated that individuals who were diagnosed with dementia within 2.5 years from the date of the first assessment showed significantly poorer performance in a visual search task than patients who did not progress from MCI to dementia. Furthermore patients whose initial performance in the visual search task was particularly low had higher probability of developing dementia within the following 2,5 years (Tales et al., 2011). This suggests that visual attentional abilities decline with the progression of dementia. However, this study did not include the measurement of the brain activity. This was done in a more recent study investigating EEG correlates of the performance in the visual search task in younger and older participants. The study revealed that longer reaction times in older participants compared to younger were associated with age differences in the PCN (Wiegand et al. 2013). Based on the findings provided by the three aforementioned studies one can expect that a follow-up re-test study on our group of older participants may provide valuable results shedding more light onto the relation between distinct parameters of attentions and their neural underpinnings in the ageing brain.

**Examination of the consequences of pathological aging.**

Investigation of pathological ageing may also shed more light onto the neural mechanisms underlying attentional selection. It has been already demonstrated that top-down control efficiency is significantly decreased in patients with mild cognitive impairment (MCI) compared to healthy adults (Redel et al., 2012). However, Redel et al, did not collect electrophysiological data. In contrast, in the second study we demonstrated that in healthy adults the amplitude of the PCN is related to top-down control efficiency and in some individuals it declines with age, despite a general lack of age-related changes in top-down control efficiency on a behavioural level. However, we did not include patients with symptoms of neurodegeneration in the study. Therefore a question how declining top-down control efficiency in MCI patients is reflected by the PCN amplitude remains not answered. To address this issue one could propose a study that would combine a TVA-based assessment with an ERP methodology to test a patient group with symptoms of neurodegeneration. Preserved relation between top-down control efficiency and PCN amplitude may enable formulating a hypothesis that a decreased PCN amplitude in healthy adults may be predictive for pathological changes occurring in the brain.

**Employing further methods.**

As visual attentional processes occur within hundreds of milliseconds and are faster than temporal resolution of most neuroimaging methods such as fMRI or PET, a promising approach might be to employ methods with higher temporal resolution. Aside non-invasive electroencephalography, one of such methods is Transcranial Magnetic Stimulation (TMS), which has already been successfully used in the field of visual attention (for a review see: Taylor & Thut, 2012; Taylor, Walsh & Eimer, 2008). During the stimulation a very short impulse of a strong electric current is passed through the coil placed above the investigated cortical area inducing a rapidly-changing magnetic field that in turn induces an electric current in the cortical tissue (Walsh & Cowey, 2000) temporarily disrupting its functioning. Thus, TMS can be used to investigate whether there is a causal relation between functioning of a given cortical area and efficiency of a particular cognitive process. Using a single TMS impulse Fuggetta et al. (Fugetta et al., 2006) demonstrated that stimulation of the remote visual areas (right posterior parietal cortex) significantly impairs performance in the visual search task and eliminates the early phase of the PCN. Based on this finding, in a proposed TVA-based experiment with TMS stimulation one could formulate two main hypotheses: 1) stimulation of the V4 visual areas may affect the characteristics of the PCN elicited in a TVA-based task and 2) performance in the task may decline which would result in deterioration of TVA parameters. In particular, this decline could be related to an impairment in top-down control efficiency caused by the TMS stimulation. Linking induced changes in the top-down control efficiency with changes of the PCN may improve our understanding of neural underpinnings of attentional selection.

## 5.4. Conclusion

The current PhD thesis contributes to our understanding of the relation between ageing, the efficiency of attentional functions and their neural underpinnings. More precisely, the combination of electroencephalography with well-established paradigms based on the mathematical framework of the Theory of Visual Attention permitted us to demonstrate that 1) task-related and spatial attentional selection can be distinguished by different patterns of associated neural activity, 2) age-related changes in the brain activity reflecting attentional selection can be observed even when the changes on the behavioural level are not yet present and 3) age-related decline in visual processing speed is accompanied by use of different strategies in order to encode information in younger and older individuals. We also demonstrated that the amount of cognitive reserve is an important factor modulating the brain-behaviour relationship and should, therefore, be considered in ageing studies.

# 6. References

Allport, D. (1989). Visual attention. In P. M., *Foundations of cognitive science* (pp. 631–682). Cambridge: MIT Press.

Almkvist, O., & Tallberg, I. M. (2009). Cognitive decline from estimated premorbid status predicts neurodegeneration in Alzheimer's disease. *Neuropsychology, 23*(1), 117.

American Electroencephalographic Society (1994). Guideline thirteen: American Electroecephalographic Society guidelines for standard electrode position nomenclature. Journal of Clinical Neurophysiology, 11, 111-113.

Ansorge, U., & Heumann, M. (2006). Shifts of visuospatial attention to invisible (metacontrast-masked) singletons: Clues from reaction times and event-related potential. *Advances in Cognitive Psychology, 2*, 61-76.

Artero, S., Touchon, J., & Ritchie, K. (2001). Disability and mild cognitive impairment: A longitudinal population-based study. *International Journal of Geriatric Psychiatry, 16*, 1092-1097. doi:10.1002/gps.477

Attwell, D., & Laughlin, S. B. (2001). An energy budget for signaling in the grey matter of the brain. *Journal of Cerebral Blood Flow Metabolism*, 1133–1145.

Avlund, K., Damsgaard, M. T., & Osler, M. (2004). Social position and functional decline among non-disabled old men and women. *European Journal of Public Health, 14*, 212-216.

Badzakova-Trajkov, G., Häberling, I. S., Roberts, R. P., & Corballis, M. C. (2010). Cerebral asymmetries: complementary and independent processes. PloS one, 5(3), e9682.

Barberger-Gateau, P., Fabrigoule, C., Rouch, I., Letenneur, L., & Dartigues, J. F. (1999). Neuropsychological correlates of self-reported performance in instrumental activities of daily living and prediction of dementia. *The Journals of Gerontology. Series B, Psychological Sciences and Social Sciences, 54*, 293-303.

Bäumler, G. (1985). Farbe-Wort-Interferenztest (FWIT) nach J. R. Stroop. Göttingen: Hogrefe.

Beck, A. T., Steer, R. A., & Brown, G. K. (1996). Manual for the Beck Depression Inventory-II. San Antonio, TX: Psychological Corporation.

Bell, A. J., & Sejnowski, T. J. (1995). An information maximization approach to blind separation and blind deconvolution. *Neural Comput, 7*(6), 1129–1159.

Bellgrove, M. A., Dockree, P. M., Aimola, L., & Robertson, I. H. (2004). Attenuation of spatial attentional asymmetries with poor sustained attention. Neuroreport, 15(6), 1065-1069.

Benwell, C. S., Harvey, M., Gardner, S., & Thut, G. (2013). Stimulus-and state-dependence of systematic bias in spatial attention: additive effects of stimulus-size and time-on-task. Cortex, 49(3), 827-836.

Benwell, C. S., Thut, G., Learmonth, G., & Harvey, M. (2013). Spatial attention: differential shifts in pseudoneglect direction with time-on-task and initial bias support the idea of observer subtypes. Neuropsychologia, 51(13), 2747-2756.

Bishop, S. J. (2008). Neural mechanisms underlying selective attention to threat. Annals of the New York Academy of Sciences, 1129(1), 141-152.

Bowers, D., & Heilman, K. M. (1980). Pseudoneglect: effects of hemispace on a tactile line bisection task. Neuropsychologia, 18(4), 491-498.

Braver, T. S., Cole, M. W., & Yarkoni, T. (2010). Vive les differences! Individual variation in neural mechanisms of executive control. Current opinion in neurobiology, 20(2), 242-250.

Braver, T. S., Paxton, J. L., Locke, H. S., & Barch, D. M. (2009). Flexible neural mechanisms of cognitive control within human prefrontal cortex. *Proceedings of the National Academy of Sciences of the United States of America, 106*(18), 7351–7356.

Brisson, B., & Jolicoeur, P. (2007). The N2pc component and stimulus duration. Neuroreport, 18(11), 1163-1166.

Brisson, B., Robitaille, N., & Jolicoeur, P. (2007). Stimulus intensity affects the latency but not the amplitude of the N2pc. *NeuroReport, 18*, 1627–1630.

Broadbent, D. E. (1958). *Perception and Communication.* London: Pergamon.

Broadbent, D. E. (1971). *Decision and stress.* London: Academic Press.

Bublak, P., Finke, K., Krummenacher, J., Preger, R., Kyllingsbæk, S., Müller, H. J., & Schneider, W. X. (2005). Usability of a theory of visual attention (TVA) for parameter-based measurement of attention II: Evidence from two patients with frontal or parietal damage. Journal of the International Neuropsychological Society, 11(7), 843-854.

Bublak, P., Redel, P., Finke, K., 2006. Spatial and non-spatial attention deficits in neurodegenerative diseases: assessment based on Bundesen's theory of visual attention (TVA). Restor. Neurol. Neurosci. 24, 287–301.

Bucur, B., Madden, D. J., Spaniol, J., Provenzale, J. M., Cabeza, R., White, L. E., & Huettel, S. A. (2008). Age-related slowing of memory retrieval, contributions of perceptual speed and cerebral white matter integrity. *Neurobiol. Aging, 29*, 1070-1079.

Bundesen, C. (1987). Visual attention: Race models for selection from multielement displays. *Psychological Research/Psychologische Forschung, 49*, 113–121.

Bundesen, C. (1990). A theory of visual attention. Psychological Review, 97(4), 523-547.

Bundesen, C. (1998). A computational theory of visual attention. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 353(1373), 1271-1281.

Bundesen, C., & Habekost, T. (2008). Principles of visual attention: Linking mind and brain. Oxford: Oxford University Press.

Bundesen, C., Habekost, T., & Kyllingsbæk, S. (2005). A neural theory of visual attention: bridging cognition and neurophysiology. *Psychol. Rev., 112*, 291-328. doi:10.1037/0033-295X.112.2.291

Bundesen, C., Pedersen, L. F., & Larsen, A. (1984). Measuring efficiency of selection from briefly exposed visual displays: A model for partial report. *Journal of Experimental Psychology: Human Perception and Performance, 10*, 329 –339.

Bundesen, C., Shibuya, H, & Larsen, A. (1985). Visual selection from multielement displays: A model for partial report. In M. I. Posner & O. S. M. Marin (Eds.), *Attention and performance XI* (pp. 631-649). Hillsdale, NJ: Erlbaum.

Buschman, T. J., & Miller, E. K. (2007). Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. Science, 315(5820), 1860-1862.

Buysse, D. J., Reynolds, C. F., Monk, T. H., Berman, S. R., & Kupfer, D. J. (1989). The Pittsburgh Sleep Quality Index: a new instrument for psychiatric practice and research. *Psychiatry research, 28*(2), 193-213.

Cabeza R., 2002, Hemispheric asymmetry reduction in older adults: The HAROLD model. Psychology and Aging, 17:85–100.

Carlei, C. & Kerzel, D. (2017): Stronger interference from distractors in the right hemifield during visual search, Laterality: Asymmetries of Body, Brain and Cognition, DOI: 10.1080/1357650X.2017.1327539

Carlson, M. C., Hasher, L., Zacks, R. T., & Connelly, S. L. (1995). Aging, distraction, and the benefits of predictable. *Psychology and aging*(10), 427–436.

Cassidy, S. M., Robertson, I. H., & O'Connell, R. G. (2012). Retest reliability of event-related potentials: Evidence from a variety of paradigms. Psychophysiology, 49(5), 659-664.

Cattell, R. B. (1971). *Abilities: Their structure, growth, and action.* New York: Houghton Mifllin.

Clapp, W. C., & Gazzaley, A. (2012). Distinct mechanisms for the impact of distraction and interruption on working memory in ageing. *Neurobiol. ageing, 33*, 134-148. doi:10.1016/j.neurobiolageing.2010.01.012

Clarke, D. D., & Sokoloff, L. (1994). Circulation and energy metabolism of the brain. In G. J. Siegel, B. W. Agranoff, R. W. Albers, & P. B. Molinoff, *Basic Neurochemistry* (pp. 645-660). New York: Raven.

Conci, M., Töllner, T., Leszczynski, M., & Müller, H. J. (2011). The time-course of global and local attentional guidance in Kanizsa-figure detection. *Neuropsychologia, 49*, 2456-2464.

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. Nature Reviews Neuroscience, 3(3), 201-215.

Corbetta, M., & Shulman, G. L. (2011). Spatial neglect and attention networks. Annual Review of Neuroscience, 34, 569-599.

Corbetta, M., Kincade, M. J., Lewis, C., Snyder, A. Z., & Sapir, A. (2005). Neural basis and recovery of spatial attention deficits in spatial neglect. Nature Neuroscience, 8(11), 1603-1610.

Corriveau, I., Fortier-Gauthier, U., Pomerleau, V. J., McDonald, J., Dell'Acqua, R., & Jolicoeur, P. (2012). Electrophysiological evidence of multitasking impairment of attentional deployment reflects target-specific processing, not distractor inhibition. International Journal of Psychophysiology, 86(2), 152-159.

Cowan, N. (2001). The magical number 4 in short-term memory: a reconsideration of mental storage capacity. *Behav. Brain Sci, 24*(1), 87–114.

Craik, F. I., & Salthouse, T. A. (2000). *The handbook of aging and cognition.* Hillsdale: Erlbaum.

Cross-Villasana, F., Finke, K., Hennig-Fast, K., Kilian, B., Wiegand, I., Müller, H. J., & Töllner, T. (2015). The speed of visual attention and motor-response decisions in adult attention-deficit/hyperactivity disorder. *Biological psychiatry, 78*(2), 107-115.

Crystal, H., Dickson, D., Fuld, P., & et al. (1988). Clinico-pathologic studies in dementia: nondemented subjects with pathologically confirmed Alzheimer's disease. *Neurology, 38*, 1682–1687.

Derogatis, L. R. (1993). *BSI Brief Symptom Inventory: Administration, Scoring, and Procedure Manual (4th Ed.).* Minneapolis, MN: National Computer Systems.

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annu Rev Neurosci, 18*, 193-222.

Duncan, J., Bundesen, C., Olson, A., Humphreys, G., Chavda, S., & Shibuya, H. (1999). Systematic analysis of deficits in visual attention. *Journal of Experimental Psychology: General* (128), 450 – 478.

Dyrholm, M., Kyllingsbæk, S., Espeseth, T., & Bundesen, C. (2011). Generalizing parametric models by introducing trial-by-trial parameter variability: The case of TVA. *Journal of Mathematical Psychology, 55*(6), 416-429.

Eason, R., Harter, M., & White, C. (1969). Eff ects of attention and arousal on visually evoked cortical potentials and reaction time in man. *Physiology and Behavior, 4*, 283 – 289.

Eimer, M. (1996). The N2pc as an indicator of attentional selectivity. *Electroencephalography and Clinical Neurophysiology, 99*, 225-234. doi:10.1016/0013-4694(96)95711-9

Eimer, M. (2014). The neural basis of attentional control in visual search. Trends in Cognitive Sciences, 18(10), 526-535.

Eimer, M. (2015). EPS Mid-Career Award 2014: The control of attention in visual search: Cognitive and neural mechanisms. The Quarterly Journal of Experimental Psychology, 68(12), 2437-2463.

Electrode Position Nomenclature Committee. (1994). Guideline thirteen: guideline for standard electrode position nomenclature. *J. Clin. Neurophysiol, 11*, 111-113.

Espeseth, T., Vangkilde, S. A., Petersen, A., Dyrholm, M., & Westlye, L. T. (2014). TVA–based assessment of attentional capacities–associations with age and indices of brain white matter microstructure. *Frontiers in psychology*, *5*, 1177.

Finke, K., Bublak, P., Dose, M., Müller, H.J., Schneider, W.X., 2006. Parameter-based assessment of spatial and non-spatial attentional deficits in Huntington's disease. Brain 129, 1137–1151.

Finke, K., Bublak, P., Krummenacher, J., Kyllingsbæk, S., Müller, H. J., & Schneider, W. X. (2005). Usability of a theory of visual attention (TVA) for parameter-based measurement of attention I: Evidence from normal subjects. Journal of the International Neuropsychological Society, 11(07), 832-842.

Finke, K., Matthias, E., Keller, I., Müller, H. J., Schneider, W. X., & Bublak, P. (2012). How does phasic alerting improve performance in patients with unilateral neglect? A systematic analysis of attentional processing capacity and spatial weighting mechanisms. Neuropsychologia, 50(6), 1178-1189.

Finke, K., Schwarzkopf, W., Müller, U., Frodl, T., Müller, H. J., Schneider, W. X., . . . Riedel, M. (2011). Disentangling the adult attention deficit hyperactivity disorder endophenotype: parametric measurement of attention. *Journal of Abnormal Psychology, 120*(4), 890–901.

Folstein, J. R., & van Petten, C. (2008). Influence of cognitive control and mismatch on the N2 component of the ERP: a review. *Psychophysiology, 45*, 152–170.

Folstein, M. F., Folstein, S. E., & McHugh, P. R. (1975). "Mini-mental state". A practical method for grading the cognitive state of patients for the clinician. *Journal of Psychiatric Research, 12*, 189-198.

Fortier-Gauthier, U., Moffat, N., Dell'Acqua, R., McDonald, J. J., & Jolicœur, P. (2012). Contralateral cortical organisation of information in visual short-term memory: Evidence from lateralized brain activity during retrieval. *Neuropsychologia, 50*, 1748-1758. doi:10.1016/j.neuropsychologia.2012.03.032

Fortier-Gauthier, U., Dell'Acqua, R., & Jolicœur, P. (2013). The "red-alert" effect in visual search: Evidence from human electrophysiology. Psychophysiology, 50(7), 671-679.

Fotenos, A. F., Mintun, M. A., Snyder, A. Z., Morris, J. C., & Buckner, R. L. (2008). Brain volume decline in ageing: evidence for a relation between socioeconomic status, preclinical Alzheimer disease, and reserve. *Archives of neurology, 65*, 113-120.

Found, A., & Müller, H. J. (1996). Searching for unknown feature targets on more than one dimension: Investigating a "dimension-weighting" account. Attention, Perception, & Psychophysics, 58(1), 88-101.

Fuggetta, G., Pavone, E. F., Walsh, V., Kiss, M., & Eimer, M. (2006). Cortico-cortical interactions in spatial attention: a combined ERP/TMS study. *Journal of Neurophysiology*, *95*(5), 3277-3280.

Gazzaley, A., & D'esposito, M. (2007). Top-down modulation and normal aging. *Annals of the New York Academy of Sciences, 1097*(1), 67-83.

Gazzaley, A., Cooney, J. W., Rissman, J., & D'Esposito, M. (2005). Top-down suppression deficit underlies working memory impairment in normal ageing. *Nat. Neurosci., 8*, 1298-1300.

Gokce, A., Geyer, T., Finke, K., Müller, H. J., & Töllner, T. (2014). What pops out in positional priming of pop-out: insights from event-related EEG lateralizations. *Frontiers in psychology*, *5*, 688.

Gold, J. M., Fuller, R. L., Robinson, B. M., Braun, E. L., & Luck, S. J. (2007). Impaired top–down control of visual search in schizophrenia. Schizophrenia Research, 94(1), 148-155.

Gross, M. M. (1972). Hemispheric specialization for processing of visually presented verbal and spatial stimuli. Attention, Perception, & Psychophysics, 12(4), 357-363.

Habekost, T. (2015). Clinical TVA-based studies: a general review. *Frontiers in psychology*, *6*, 290.

Habekost, T., Petersen, A., & Vangkilde, S. (2013). Testing attention: comparing the ANT with TVA-based assessment. *Behav. Res. Methods, 46*, 81-94. doi:10.3758/s13428-013-0341-2.

Habekost, T., Vogel, A., Rostrup, E., Bundesen, C., Kyllingsbæk, S., & Garde, E. (2012). Visual processing speed in old age. *Scand. J. Psychol, 54*, 89-94. doi:10.1111/sjop.12008.

Harada, C. N., Love, M. N., & Triebel, K. (2013). Normal Cognitive ageing. *Clin Geriatr Med., 29*(4), 737–752. doi:10.1016/j.cger.2013.07.002

Harvey, M., Milner, A. D., & Roberts, R. C. (1995). An investigation of hemispatial neglect using the landmark task. Brain and Cognition, 27(1), 59-78.

Hasher, L., & Zacks, R. T. (1988). Working memory, comprehension, and ageing: a review and a new view. In G. H. Bower, *The Psychology of Learning and Motivation* (pp. 193-225). San Diego: CA: Academic Press.

Heilman, K. M., & Van Den Abell, T. (1980). Right hemisphere dominance for attention. The mechanism underlying hemispheric asymmetries of inattention (neglect). Neurology, 30(3), 327-327.

Heinze, H. J., Luck, S. J., Mangun, G. R., & Hillyard, S. A. (1990). Visual event-related potentials index focused attention within bilateral stimulus arrays. I. Evidence for early selection. *Electroencephalography and Clinical Neurophysiology, 75*(6), 511-527.

Hickey, C., Di Lollo, V., & McDonald, J. J. (2009). Electrophysiological indices of target and distractor processing in visual search. Journal of Cognitive Neuroscience, 21(4), 760-775.

Hillyard, S. A., Vogel, E. K., & Luck, S. J. (1998). Sensory gain control (amplification) as a mechanism of selective attention: Electrophysiological and neuroimageing evidence. *Philosophical Transactions of the Royal Society: Biological Sciences, 353*, 1257 – 1270.

Hopf, J. M., Boelmans, K., Schoenfeld, A. M., Heinze, H. J., & Luck, S. J. (2002). How does attention attenuate target–distractor interference in vision? Evidence from magnetoencephalographic recordings. *Brain Res. Cogn. Brain Res., 15*(1), 17-29.

Hopf, J. M., Luck, S. J., Boelmans, K., Schoenfeld, M. A., Boehler, C. N., Rieger, J., & Heinze, H. J. (2006). The neural site of attention matches the spatial scale of perception. Journal of Neuroscience, 26(13), 3532-3540.

Hopf, J. M., Luck, S. J., Girelli, M., Hagner, T., Mangun, G. R., Scheich, H., & Heinze, H. J. (2000). Neural sources of focused attention in visual search. *Cerebral Cortex, 10*(12), 1233-1241.

Hung, J., Driver, J., & Walsh, V. (2005). Visual selection and posterior parietal cortex: effects of repetitive transcranial magnetic stimulation on partial report analyzed by Bundesen's theory of visual attention. *Journal of Neuroscience*, *25*(42), 9602-9612.

Ince, P. (2001). Pathological correlates of late-onset dementia in a multicenter community-based population in England and Wales. *Lancet, 357*, 169–175.

Jannati, A., Gaspar, J. M., & McDonald, J. J. (2013). Tracking target and distractor processing in fixed-feature visual search: evidence from human electrophysiology. *Journal of Experimental Psychology Human Perception and Performance, 39*, 1713-1730.

Jaskowski, P., van der Lubbe, R. H., Schlotterbeck, E., & Verleger, R. (2002). Traces left on visual selective attention by stimuli that are not consciously identified. *Psychological Science, 13*, 48-54.

Jennings, J. R., & Wood, C. C. (1976). he ε-adjustment procedure for repeated-measures analysis of variance. *Psychophysiology, 13*, 277-278.

Jones, E. G., 1985, The Thalamus. Plenum Press. New York.

Jung, T. P., Makeig, S., Westerfield, W., Townsend, J., Courchesne, E., & Sejnowski, T. J. (2000). Removal of eye activity artifacts from visual event-related potentials in normal and clinical subjects. *Clinical Neurophysiology, 111*(10), 1745-1758.

Kane, M. J., Poole, B. J., Tuholski, S. W., & Engle, R. W. (2006). Working memory capacity and the top-down control of visual search: Exploring the boundaries of "executive attention". Journal of Experimental Psychology: Learning, Memory, and Cognition, 32(4), 749-777.

Katzman, R., Terry, R., DeTeresa, R., & et al. (1988). Clinical, pathological,and neurochemical changes in dementia: a subgroup with preserved mental status and numerous neocortical plaques. *Ann Neurol, 23*, 138 –144.

Kim, S., Hasher, L., & Zacks, R. T. (2007). Ageing and a benefit of distractibility. *Psychonomic Bulletin & Review, 14*(2), 301-305.

Kok, A. (2000). Age-related changes in involuntary and voluntary attention as reflected in components of the event-related potential (ERP). *Biological Psychology, 54*(1-3), 107-143.

Kraft, A., Dyrholm, M., Kehrer, S., Kaufmann, C., Bruening, J., Kathmann, N.,... & Brandt, S. A. (2015). TMS over the right precuneus reduces the bilateral field advantage in visual short term memory capacity. Brain Stimulation, 8(2), 216-223.

Kyllingsbæk, S. (2006). Modeling visual attention. *Behavior Research Methods, 38*, 123-133.

Leblanc, E., Prime, D. J., & Jolicoeur, P. (2008). Tracking the location of visuospatial attention in a contingent capture paradigm. *Journal of Cognitive Neuroscience, 20*, 657-671. doi:10.1162/jocn.2008.20051.

Lee, D., & Chun, M. M. (2001). What are the units of visual short-term memory, objects or spatial locations? *Perception and Psychophysics, 63*, 253-257.

Lehr, S. (1977). Mehrfachwahl-Wortschatz-Intelligenztest MWT-B. Manual. *Straube-Verlag, Erlangen*.

Lehrl S, Triebig G, Fischer B (1995) Multiple choice voca bulary test MWT as a valid and short test to estimate premorbid intelligence. Acta Neurol Scand 91(5):335–345

Lehrl, S., (1995). Mehrfachwahl-Wortschatz-Intelligenztest (MWT-B) (Multiple Choice Vocabulary Intelligence Test). Perimed-Spitta, Balingen.

Li, C. Y., Wu, S. C., & Wen, S. W. (2000). Longest held occupation in a lifetime and risk of disability in activities of daily living. *Occupational and Environmental Medicine, 57*, 550-554.

Lorenzo-López, L., Amenedo, E., & Cadaveira, F. (2008). Feature processing during visual search in normal ageing: electrophysiological evidence. *Neurobiology of ageing, 29*, 1101-1110.

Luce, R. D. (1959). *Individual choice behavior.* New York: Wiley.

Luce, R. D. (1963). Detection and recognition. In R. D. Luce, R. R. Bush, & E. (. Galanter, *Handbook of mathematical psychology* (pp. Vol. 1, pp. 103–189). New York: Wiley.

Luck, S. J. (1995). Multiple mechanisms of visual-spatial attention: Recent evidence from human electrophysiology. *Behavioural Brain Research, 71*, 113-123.

Luck, S. J. (1998). Sources of dual-task interference: Evidence from human electrophysiology. *Psychological Science, 9*, 223-227.

Luck, S. J. (2005). An introduction to the event-related potential technique. Cambridge, MA: MIT press.

Luck, S. J. (2005). The operation of attention—millisecond by millisecond—over the first half second. In H. Ogmen, & B. G. Breitmeyer, *The first half second: The microgenesis and temporal dynamics of unconscious and conscious visual processes.* Cambridge: MA: MIT Press.

Luck, S. J. (2012). Electrophysiological correlates of the focusing of attention within complex visual scenes: N2pc and related ERP components. In: S. J. Luck & E.S. Kappenmann (Eds.). The Oxford handbook of event-related potential components, pp. 329-360. Oxford: Oxford University Press.

Luck, S. J. (2012). Event-related potentials. *APA handbook of research methods in psychology*, *1*, 523-546.

Luck, S. J., & Hillyard, S. A. (1994). Electrophysiological correlates of feature analysis during visual search. *Psychophysiology*, *31*(3), 291-308.

Luck, S. J., & Hillyard, S. A. (1994). Spatial filtering during visual search: evidence from human electrophysiology. *J. Exp. Psychol. Hum. Percept. Perform.*, 1000–1014.

Luck, S. J., & Hillyard, S. A. (1994). Spatial filtering during visual search: evidence from human electrophysiology. Journal of Experimental Psychology: Human Perception and Performance, 20(5), 1000-1014.

Luck, S. J., & Hillyard, S. A. H. (1995). The role of attention in feature detection and conjunction discrimination: An electrophysiological analysis. International Journal of Neuroscience, 80(1-4), 281-297.

Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature, 390*, 279-281.

Luck, S. J., Fan, S., & Hillyard, S. A. (1993). Attention-related modulation of sensory-evoked brain activity in a visual search task. *Journal of Cognitive Neuroscience, 5*(2), 188-195.

Luck, S. J., Fuller, R. L., Braun, E. L., Robinson, B., Summerfelt, A., & Gold, J. M. (2006). The speed of visual attention in schizophrenia: Electrophysiological and behavioral evidence. *Schizophrenia research*, *85*(1), 174-195.

Luck, S. J., Girelli, M., McDermott, M. T., & Ford, M. A. (1997). Bridging the gap between monkey neurophysiology and human perception: An ambiguity resolution theory of visual selective attention. Cognitive Psychology, 33(1), 64-87.

Luck, S. J., Hillyard, S. A., Mouloua, M., Woldorff, M. G., Clark, V. P., & Hawkins, H. L. (1994). Effects of spatial cuing on luminance detectability: Psychophysical and electrophysiological evidence for early selection. *Journal of Experimental Psychology: Human Perception and Performance, 20*, 887-904.

Luck, S. J., Woodman, G. F., & Vogel, E. K. (2000). Event-related potential studies of attention. *Trends in Cognitive Sciences, 4*, 432-440.

Luh, K. E. (1995). Line bisection and perceptual asymmetries in normal individuals: What you see is not what you get. Neuropsychology, 9(4), 435.

Madden, D. J. (2007). Aging and visual attention. Current Directions in Psychological Science, 16(2), 70-74.

Madden, D. J., Whiting, W. L., & Huettel, S. A. (2005). Age-related changes in neural activity during visual perception and attention. In R. Cabeza, L. Nyberg, & D. C. Park, *Cognitive neuroscience of ageing: Linking cognitive and cerebral ageing* (pp. 157-185). New York: NY: Oxford University Press.

Madden, D. J., Whiting, W. L., Cabeza, R., & Huettel, S. A. (2004). Age-related preservation of top-down attentional guidance during visual search. *Psychology and Aging, 19*, 304–309.

Madden, D.J., Whiting,W.L., Spaniol,J., Bucur, B. (2005). Adult age differences in the implicit and explicit components of top-down attentional guidance during visual search. Psychology and Aging, 20, 317–329.

Mangun, G. R. (1995). Neural mechanisms of visual selective attention. *Psychophysiology, 32*, 4–18.

Mangun, G. R., & Hillyard, S. A. (1991). Modulations of sensory-evoked brain potentials indicate changes in perceptual processing during visual-spatial priming. *Journal of Experimental Psychology: Human perception and performance, 17*(4), 1057.

Matthias, E., Bublak, P., Costa, A., Müller, H. J., Schneider, W. X., & Finke, K. (2009). Attentional and sensory effects of lowered levels of intrinsic alertness. Neuropsychologia, 47(14), 3255-3264.

Mazza, V., & Pagano, S. (2017). Electroencephalographic asymmetries in human cognition. In: L. Rogers, G. Vallortigara. Lateralized Brain Functions. Methods in Human and Non-Human Species, pp. 407-439. Springer.

Mazza, V., Turatto, M., & Caramazza, A. (2009). Attention selection, distractor suppression, and N2pc. *Cortex, 45*(7), 879-890.

McAvinue, L. P., Habekost, T., Johnson, K. A., Kyllingsbæk, S., Vangkilde, S., Bundesen, C., & et al. (2012). Sustained attention, attentional selectivity,and attentional capacity across the lifespan. *Atten. Percept. Psychophys.* (74), 1570–1582. doi:10.3758/s13414-012-0352-6

McDowd, J. M. (1997). Inhibition in attention and ageing. *Journals of Gerontology Series B: Psychological Sciences and Social Sciences, 52*, 265-273.

McLoughlin, G., Makeig, S., & Tsuang, M. T. (2014). In search of biomarkers in psychiatry: EEG-based measures of brain function. American Journal of Medical Genetics Part B: Neuropsychiatric Genetics, 165(2), 111-121.

Mevorach, C., Humphreys, G. W., & Shalev, L. (2006). Opposite biases in salience-based selection for the left and right posterior parietal cortex. *Nature Neuroscience, 9*, 740-742.

Morris, J. C., Storandt, M., McKeel, D. W., & et al. (1996). Cerebral amyloid deposition and diffuse plaques in “normal” ageing: evidence for presymptomatic and very mild Alzheimer’s disease. *Neurology, 46*, 707–719.

Mortimer, J. A., Snowdon, D. A., & Markesbery, W. R. (2003). Head circumference, education and risk of dementia: findings from the Nun study. *J. Clin. Exp. Neuropsychol., 25*, 671–679.

Müller, H. J., & Krummenacher, J. (2006). Locus of dimension weighting: Preattentive or postselective?. Visual Cognition, 14(4-8), 490-513.

Nicholls, M. E., Bradshaw, J. L., & Mattingley, J. B. (1999). Free-viewing perceptual asymmetries for the judgement of brightness, numerosity and size. Neuropsychologia, 37(3), 307-314.

Nielsen, S., & Wilms, I. (2015). Cognitive aging on latent constructs for visual processing capacity: a novel structural equation modeling framework with causal assumptions based on a theory of visual attention. *Front. Psychol., 5*, 1596.

Nunez, P. L., & Srinivasan, R. (2006). *Electric fields of the brain: The neurophysics of EEG (2nd ed.).* Oxford: Oxford University Press.

Oldfield, R. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia, 9*, 97-113.

Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia, 9(1), 97-113.

Oostenveld, R., Stegeman, D. F., Praamstra, P., & van Oosterom, A. (2003). Brain symmetry and topographic analysis of lateralized event-related potentials. *Clinical neurophysiology*, *114*(7), 1194-1202.

Pagano, S., Fait, E., Brignani, D., & Mazza, V. (2016). Object individuation and compensation in healthy aging. *Neurobiology of aging*, *40*, 145-154.

Pagano, S., Fait, E., Monti, A., Brignani, D., & Mazza, V. (2015). Electrophysiological correlates of subitizing in healthy aging. *PloS one*, *10*(6), e0131063.

Parasuraman, R., & Haxby, J. V. (1993). Attention and brain function in Alzheimer's disease: A review. Neuropsychology, 7(3), 242-272.

Pereira, F. S., Yassuda, M. S., Oliveira, A. M., & Forlenza, O. V. (2008). Executive dysfunction correlates with impaired functional status in older adults with varying degrees of cognitive impairment. *International Psychogeriatrics, 20*, 1104-1115. doi:10.1017/S1041610208007631.

Polich, J. (2007). Updating P300: an integrative theory of P3a and P3b. *Clin. Neurophysiol., 118*, 2128–2148.

Pomerleau, V. J., Fortier-Gauthier, U., Corriveau, I., Dell'Acqua, R., & Jolicœur, P. (2014). Colour-specific differences in attentional deployment for equiluminant pop-out colours: evidence from lateralised potentials. International Journal of Psychophysiology, 91(3), 194-205.

Posner, M. I., & Petersen, S. E. (1990). The attention system of the human brain [Review]. *Annu Rev Neurosci, 13*, 25-42.

Price, J. L., & Morris, J. C. (1999). Tangles and plaques in nondemented ageing and "preclinical" Alzheimer's disease. *Ann. Neurol., 45*(3), 358-368.

Raz, N. (2000). Ageing of the brain and its impact on cognitive performance: Integration of structural and functional findings. In F. M. Craik, & T. A. Salthouse, *The Handbook of ageing and Cognition* (pp. 1-90). Mahwah: NJ: Erlbaum.

Redel P., Bublak P., Sorg C., Kurz A., Förstl H., Müller H. J., Schneider W. X., Perneczky R., & Finke K. (2012). Deficits of spatial and task-related attentional selection in mild cognitive impairment and Alzheimer's disease. Neurobiology of ageing. 33(1), 195. e27.

Reitan, R. M. (1958). Validity of the Trail Making Test as an indicator of organic brain damage. *Percept Motor Skills, 8*, 271-276.

Richards, M., & Sacker, A. (2003). Lifetime antecedents of cognitive reserve. *Journal of Clinical and Experimental Neuropsychology, 25*, 614-624.

Salthouse T.A. (1996), The processing-speed theory of adult age differences in cognition. *Psychol Rev,* 103:403– 428.

Salthouse, T. A. (1994). The aging of working memory. *Neuropsychology, 8*, 535-543.

Salthouse, T. A., Mitchell, D. R., Skovronek, E., & Babcock, R. L. (1989). Effects of adult age and working memory on reasoning and spatial abilities. *Journal of experimental psychology Learning, memory, and cognition* (15), 507–516.

Sänger, J., & Wascher, E. (2011). The influence of extrinsic motivation on competition-based selection. *Behavioural brain research, 224*(1), 58-64.

Sawaki, R., & Luck, S. J. (2013). Active suppression after involuntary capture of attention. Psychonomic bulletin & review, 20(2), 296-301.

Scarmeas, N., & Stern, Y. (2003). Cognitive reserve and lifestyle. *Journal of clinical and experimental neuropsychology, 25*, 625-633.

Shedden, J. M., & Nordgaard, C. L. (2001). ERP time course of perceptual and postperceptual mechanisms of spatial selection. *Cognit Brain Res, 11*, 59-75.

Sheremata, S. L., Bettencourt, K. C., & Somers, D. C. (2010). Hemispheric asymmetry in visuotopic posterior parietal cortex emerges with visual short-term memory load. Journal of Neuroscience, 30(38), 12581-12588.

Sheremata, S., & Shomstein, S. (2014). Hemifield asymmetries differentiate VSTM for single-and multiple-feature objects. Attention, Perception, & Psychophysics, 76(6), 1609-1619.

Sherman, S. M., and Guillery, R. W., 2001, Exploring the Thalamus, Academic Press, San Diego.

Shibuya, H., & Bundesen, C. (1988). Visual selection from multielement displays: Measuring and modeling effects of exposure duration. *Journal of Experimental Psychology: Human Perception and Performance, 14*, 591-600.

Society, A. E. (1994). Guideline thirteen: guideline for standard electrode position nomenclature. *J. Clin. Neurophysiol.*(11), 111-113.

Sperling, G. (1960). The information available in brief visual presentations. *Psychol Monogr Gen Appl*(74), 1–29.

Sperling, G. (1967). Successive approximations to a model for short term memory. *Acta Psychologica, 27*, 285-292.

Spielberger, C. D., Gorsuch, R. L., & Lushene, R. E. (1970). Manual for the state-trait anxiety inventory. Palo Alto, CA: Consulting Psychologists Press.

Spielberger, C. D., Gorsuch, R. L., Lushene, P. R., Vagg, P. .., & Jacobs, A. G. (1983). Manual for the State Trait Anxiety Inventory (Form Y).. *Consulting Psychologists Press*.

Stankov, L. (1988). Aging, Attention, and Intelligence. *Psychology and Aging, 3*(1), 59-74.

Stern, Y. (2002). What is cognitive reserve? Theory and research application of the reserve concept. *Journal of the International Neuropsychological Society* (8), 448–460.

Stern, Y. (2003). The concept of cognitive reserve: a catalyst for research. *Journal of clinical and experimental neuropsychology*, *25*(5), 589-593.

Stern, Y. (2009). Cognitive Reserve. *Neuropsychologia, 47*(10), 2015-2028. doi:10.1016/j.neuropsychologia.2009.03.004

Sumowski, J. F., Wylie, G. R., Chiaravalloti, N., & DeLuca, J. (2010). Intellectual enrichment lessens the effect of brain atrophy on learning and memory in multiple sclerosis. *Neurology, 74*(24), 1942-1945.

Szczepanski, S. M., & Kastner, S. (2013). Shifting attentional priorities: control of spatial attention through hemispheric competition. Journal of Neuroscience, 33(12), 5411-5421.

Śmigasiewicz, K., Asanowicz, D., Westphal, N., & Verleger, R. (2014). Bias for the left visual field in rapid serial visual presentation: Effects of additional salient cues suggest a critical role of attention. Journal of cognitive neuroscience, Journal of Cognitive Neuroscience, 27(2), 266-279.

Śmigasiewicz, K., Liebrand, M., Landmesser, J., & Verleger, R. (2017). How handedness influences perceptual and attentional processes during rapid serial visual presentation. Neuropsychologia, 100, 155-163.

Tales, A., Bayer, A. J., Haworth, J., Snowden, R. J., Philips, M., & Wilcock, G. (2011). Visual search in mild cognitive impairment: A longitudinal study. *Journal of Alzheimer's Disease*, *24*(1), 151-160.

Taylor, P. C. J., & Thut, G. (2012). Brain activity underlying visual perception and attention as inferred from TMS–EEG: A review. *Brain Stimulation: Basic, Translational, and Clinical Research in Neuromodulation*, *5*(2), 124-129,

Taylor, P. C., Walsh, V., & Eimer, M. (2008). Combining TMS and EEG to study cognitive function and cortico–cortico interactions. *Behavioural brain research*, *191*(2), 141-147.

Thiebaut de Schotten, M. T., Bizzi, A., Dell'Acqua, F., Allin, M., Walshe, M., Murray, R., Williams, S.C., Murphy, D.G., & Catani, M. (2011). Atlasing location, asymmetry and inter-subject variability of white matter tracts in the human brain with MR diffusion tractography. Neuroimage, 54(1), 49-59.

Töllner T, Gramann K, Müller HJ, Kiss M, Eimer M. 2008. Electrophysiological markers of visual dimension changes and response changes. J Exp Psychol Hum Percept Perform. 34:531--542.

Töllner, T., Conci, M., & Müller, H. J. (2015). Predictive distractor context facilitates attentional selection of high, but not intermediate and low, salience targets. *Human Brain Mapping, 36*, 935-944.

Töllner, T., Conci, M., Müller, H. J., & Mazza, V. (2016). Attending to multiple objects relies on both feature-and dimension-based control mechanisms: Evidence from human electrophysiology. *Atten Percept Psychophys, 78*, 2079–2089.

Töllner, T., Gramann, K., Müller, H. J., Kiss, M., & Eimer, M. (2008). Electrophysiological markers of visual dimension changes and response changes. Journal of Experimental Psychology: Human Perception and Performance, 34(3), 531.

Töllner, T., Müller, H. J., & Zehetleitner, M. (2011). Top-down dimensional weight set determines the capture of visual attention: Evidence from the PCN component. *Cerebral Cortex*, *22*(7), 1554-1563.

Töllner, T., Rangelov, D., & Müller, H. J. (2012). How the speed of motor-response decisions, but not focal-attentional selection, differs as a function of task set and target prevalence. Proceedings of the National Academy of Sciences, 109(28), E1990-E1999.

Töllner, T., Zehetleitner, M., Gramann, K., & Müller, H. J. (2010). Top-down weighting of visual dimensions: Behavioral and electrophysiological evidence. Vision Research, 50(14), 1372-1381.

Töllner, T., Zehetleitner, M., Gramann, K., & Müller, H. J. (2011). Stimulus saliency modulates pre-attentive processing speed in human visual cortex. PLoS One, 6(1), e16276.

Tomer, R., Slagter, H. A., Christian, B. T., Fox, A. S., King, C. R., Murali, D., & Davidson, R. J. (2013). Dopamine asymmetries predict orienting bias in healthy individuals. Cerebral Cortex, 23(12), 2899-2904.

Townsend, J. T., & Ashby, F. G. (1982). Experimental test of contemporary mathematical models of visual letter recognition. *Journal of Experimental Psychology: Human Perception and Performance, 8*, 834 – 864.

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. Mansfield, *Analysis of visual behavior* (pp. 549 –586). Cambridge: MA: MIT Press.

Van der Elst, W., Van Boxtel, M. P., Van Breukelen, G. P., & Jolles, J. (2008). A large-scale cross-sectional and longitudinal study into the ecological validity of neuropsychological test measures in neurologically intact people. *Archives of Clinical Neuropsychology, 23*, 787-800. doi:10.1016/j.acn.2008.09.002.

Van der Lubbe, R. H., & Verleger, R. (2002). Aging and the Simon task. Psychophysiology, 39(1), 100-110.

Vangkilde, S., Coull, J. T., & Bundesen, C. (2012). Great expectations: Temporal expectation modulates perceptual processing speed. *Journal of Experimental Psychology: Human Perception and Performance* (38), 1183–1191. doi:10.1037/a0026343

Verleger, R., Sprenger, A., Gebauer, S., Fritzmannova, M., Friedrich, M., Kraft, S., & Jaśkowski, P. (2009). On why left events are the right ones: neural mechanisms underlying the left-hemifield advantage in rapid serial visual presentation. Journal of Cognitive Neuroscience, 21(3), 474-488.

Vogel, E. K., & Luck, S. J. (2000). The visual N1 component as an index of a discrimination process. *Psychophysiology, 37*, 190-203.

von Wright, J. M. (1968). Selection in visual immediate memory. *Quarterly Journal of Experimental Psychology, 20*, 62-68.

Walsh, V., & Cowey, A. (2000). Transcranial magnetic stimulation and cognitive neuroscience. *Nature Reviews Neuroscience*, *1*(1), 73.

Walsh, V., & Pascual-Leone, A. (2003). *Transcranial magnetic stimulation: a neurochronometrics of mind*. MIT press.

Wascher, E., & Beste, C. (2010). Tuning perceptual competition. *J. Neurophysiol, 103*, 1057–1065.

Wascher, E., & Wauschkuhn, B. (1996). The interaction of stimulus- and response-related processes measured by event-related lateralizations of the EEG. *Electroencephalogr Clin Neurophysiol, 99*, 149-162.

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 ageing*, *34*(3), 973-985.

Wiegand, I., Finke, K., Töllner, T., Starman, K., Müller, H. J., & Conci, M. (2015). Age-related decline in global form suppression. *Biological psychology*

Wiegand, I., Hennig-Fast, K., Kilian, B., Müller, H. J., Töllner, T., Möller, H. J., Engel, R.R., & Finke, K. (2016). EEG correlates of visual short-term memory as neuro-cognitive endophenotypes of ADHD. Neuropsychologia, 85, 91-99.

Wiegand, I., Lauritzen, M., Osler, M., Mortensen, E.L., Rostrup, E., Rask, L., Richard, N., Horwitz, A., Benedek, K., Vangkilde, S., Petersen, A., (in press). EEG correlates of visual short-term memory in older age vary with adult lifespan cognitive development. Neurobiology of Aging, epub ahead of print. doi: 10.1016/j.neurobiolaging.2017.10.018

Wiegand, I., Napiorkowski, N., Töllner, T., Petersen, A., Habekost, T., Müller, H. J., & Finke, K. (2017). Event-related Electroencephalographic Lateralizations Mark Individual Differences in Spatial and Nonspatial Visual Selection. *Journal of cognitive neuroscience*, (Early Access), 1-16.

Wiegand, I., Petersen, A., Bundesen, C., & Habekost, T. (2017). Phasic alerting increases visual attention capacity in younger but not in older individuals. Visual Cognition.

Wiegand, I., Petersen, A., Finke, K., Bundesen, C., Lansner, J., & Habekost, T. (2017). Behavioral and brain measures of phasic alerting effects on visual attention. Frontiers in Human Neuroscience, 11, 176.

Wiegand, I., Töllner, T., Dyrholm, M., Müller, H. J., Bundesen, C., & Finke, K. (2014). Neural correlates of age-related decline and compensation in visual attention capacity. *Neurobiol. Aging, 35*, 2161–2173.

Wiegand, I., Töllner, T., Habekost, T., Dyrholm, M., Müller, H. J., & Finke, K. (2014a). Distinct neural markers of TVA-based visual processing speed and short-term storage capacity parameters. *Cereb. Cortex, 24*, 1967-1978.

Williams, L., & Drew, T. (2017). Electrophysiological Correlates of Individual Differences in Visual Search. Journal of Vision, 17(10), 1140-1140.

Wolber, M., & Wascher, E. (2005). The posterior contralateral negativity as a temporal indicator of visuo-spatial processing. *Journal of Psychophysiology, 19*, 182-194.

Wolfe, J. M. (1994). Guided search 2.0 a revised model of visual search. Psychonomic bulletin & review, 1(2), 202-238.

Wolfe, J. M., Cave, K. R., & Franzel, S. L. (1989). Guided search: an alternative to the feature integration model for visual search. Journal of Experimental Psychology: Human perception and performance, 15(3), 419.

Woodman, G. F., & Luck, S. J. (1999). Electrophysiological measurement of rapid shifts of attention during visual search. Nature, 400, 867–869.

Woodman, G. F., & Luck, S. J. (2001). Serial deployment of attention during visual search. *Journal of Vision*, *1*(3), 103-103.

Woodman, G. F., & Luck, S. J. (2003). Dissociations among attention, perception, and awareness during object-substitution masking. *Psychol. Sci., 14*, 605-611.

Woodman, G. F., & Luck, S. J. (2003). Serial deployment of attention during visual search. *Journal of Experimental Psychology: Human Perception and Performance*, *29*(1), 121.

Zimmermann, P. & Fimm, B. (1993). Test for Attentional Performance (TAP). Herzogenrath: Psytest.

Zunzunegui, M. V., Nunez, O., Durban, M., de Yébenes, M. J. G., & Otero, Á. (2006). Decreasing prevalence of disability in activities of daily living, functional limitations and poor self-rated health: a 6-year follow-up study in Spain. *Ageing clinical and experimental research,* 18(5), 352-358.

# 7. Acknowledgements

I wish to express my appreciation to many people who supported me with their help, advice and patience. First of all, I would like to express my deep gratitude to my first supervisor Hermann Müller, without whom I wouldn’t have the opportunity to join the General and Experimental Psychology Unit at LMU Munich and who was always there for us when we needed his advice. I am also most grateful to Kathrin Finke, Thomas Töllner and Christian Sorg for their support, thoughtful guidance and valuable suggestions that I could always count on. Thanks go as well to Alexander Svojanovsky, Manfred Jaschke and Monika Nörr from Brain Products for helpful meetings and wise advice for the future.

Finally, last but by no means least, I would like to thank Julia Neitzel, Adriana Ruiz Rizzo, Aurore Menegaux and Melanie Penning not only for all the fruitful meetings and discussions, but more importantly for making these 3 years a truly great human experience.

# 8. Curriculum Vitae

| | |
|---|---|
| Name: | Natan Napiórkowski |
| Nationality | Polish |

### Education

| | |
|---|---|
| 2014-present | PhD studies at Graduate School of Systemic Neurosciences, Ludwig-Maximilians Universität, Munich, Germany<br>• Investigating the relationship between efficiency of attention and its correlates in EEG signals in healthy adults at different age levels. |
| 2011 | Master's degree at University of Warsaw, Faculty Of Psychology,<br>• Subject: Psychology, specialization *Neuropsychology*. |
| 2012 | Bachelor's degree at the Faculty of Physics at the University of Warsaw.<br>• Subject: *Applications of Physics in Biology and Medicine*, specialization *Neuroinformatics*. |

### Professional Experience

| | |
|---|---|
| 2014-2017 | Employee of BrainProducts GmgH, Munich, Germany, as a member of a European Marie-Curie Research Fellowship Programme funded training network: Individualised Diagnostics & Rehabilitation of Attention Disorders (INDIREA). |
| 2016 | INDIREA Bootcamp: Neuropsychology, Neurophysiology & Rehabilitation.<br>• The bootcamp covered knowledge on cutting-edge techniques in brain monitoring and stimulation. |
| 2015 | Participation in BCI-Live project.<br>• Developing software for EEG based Brain-Computer Interface designed for patients suffering locked-in syndrome. |
| 2015 | INDIREA Bootcamp: *Neurocomputational Modelling* at Universitat Pompeu Fabra, Barcelona.<br>• The bootcamp covered basic principles of modelling as well as specific worked examples applied to whole-system behaviour, fMRI, EEG, and single neuron responses. |
| 2015 | INDIREA Bootcamp*: Introduction to the EEG & ERP Methodology* at Ludwig Maximilians University, Munich.<br>• The bootcamp provided an introduction to EEG signal analysis and ERP methodology used in the field of neuroscience. |

2014 INDIREA Bootcamp: Introduction to MRI at Otto Von Guericke University Magdeburg

- Bootcamp covered principles of MRI analysis and its applications in cognitive and clinical neuroscience research

2014 INDIREA Bootcamp: *TVA and psychophysical testing*, the Center for Visual Cognition, University of Copenhagen.

- Topic of the bootcamp was Theory of Visual Attention (TVA) and its applications.

2014 INDIREA bootcamp: *Attention – from neurons to cognition and the lab to bedside*, at Department of Experimental Psychology, University of Oxford.

- During the bootcamp different approaches and methods of studying attention were presented.

2014 Participation in a course: *EEG Data Analyses in Cognitive Science*, at the Center for Visual Cognition, University of Copenhagen.

- The course covered advanced issues of the EEG signals analysis.

2013 Steve Luck's ERP Bootcamp at Université Catholique de Louvain, Belgium,

- The bootcamp covered principles of EEG signal analysis and ERP methodology

2013 Research internship at Université Catholique de Louvain, Belgium.

- Conducting EEG research on motor imagery and performing complete EEG data analysis,

2012 Student practice at Faculty of Physics at the University of Warsaw, Poland,

- Designing and constructing an eyetracker based communicator for a patient suffering from late staged Multiple Sclerosis

2012 Talk describing own project: *Human-Computer interface based on EOG signals, with use of neural network algorithm* on the *Neuromania* conference in Torun, Poland,

2011 Practice in the Department of Neurosurgery, Banacha Hospital, Warsaw, Poland

- Performing diagnosis of patients suffering from brain injuries.

2011 The annual practice of rehabilitation with patients suffering from neurological diseases at Faculty Of Psychology,

- Weekly meetings with patients. Conducting rehabilitation sessions.

| | |
|---|---|
| 2010 | Practice in the Department of Neurology, John Paul II Hospital, Grodzisk Mazowiecki, Poland<br>• Learning methods of diagnosis and rehabilitation of patients suffering from neurological disorders. |

# 9. List of publications

**Wiegand, I., Napiórkowski, N.,** Töllner, T., Petersen, A., Habekost, T., Müller, H. J., & Finke, K. (accepted). Event-related EEG lateralizations mark individual differences in spatial and non-spatial visual selection. Journal of Cognitive Neuroscience.

**Napiórkowski, N.**, Finke, K., Müller, H., Wiegand, J., Petersen, A., Töllner, T., (2017), Event-related EEG lateralizations as neural measures of visual processing speed. Poster presented at the Working Memory Symposium, Munich, Germany.

**Napiórkowski, N.**, Töllner, T., Müller, H.J., Peterson, A, Wiegand, I., & Finke K. (2016). Electrophysiological markers of top-down control in younger and older participants. Poster presented at the annual meeting of the Society for Neuroscience (SfN), Nov 12, San Diego, USA.

**Napiórkowski, N.** (2012), *Eyetracking as a cheap assistive technology*. Poster presented at *Neuronus* conference in Cracow, Poland.

Gögler, N., Willacker, L., Funk, J., Strube, W., Langgartner, S., Napiórkowski, N., ... & Finke, K. (2017). Single-session transcranial direct current stimulation induces enduring enhancement of visual processing speed in patients with major depression. European archives of psychiatry and clinical neuroscience, 267(7), 671-686.\

Finke, K., Napiorkowski, N., Wiegand, I., Petersen, A., Müller, H. J., & Töllner, T. (2017). S142 Attention parameters and ERP correlates in aging individuals. *Clinical Neurophysiology*, *128*(9), e224.

Haupt, M., Sorg, C., Napiórkowski, N., & Finke, K. (2018). Phasic alertness cues modulate visual processing speed in healthy aging. Neurobiology of Aging.

Künstler, E. C., Penning, M. D., Napiórkowski, N., Klingner, C. M., Witte, O. W., Müller, H. J., ... & Finke, K. (2018). Dual task effects on visual attention capacity in normal aging. *Frontiers in psychology*, *9*.

# 10. Eidesstattliche Versicherung / Affidavit

Hiermit versichere ich an Eides statt, dass ich die vorliegende Dissertation 'Neural markers of attentional parameters in the ageing brain' selbstständig angefertigt habe, mich außer der angegebenen keiner weiteren Hilfsmittel bedient und alle Erkenntnisse, die aus dem Schrifttum ganz oder annähernd übernommen sind, als solche kenntlich gemacht und nach ihrer Herkunft unter Bezeichnung der Fundstelle einzeln nachgewiesen habe.

I hereby confirm that the dissertation 'Neural markers of attentional parameters in the ageing brain' is the result of my own work and that I have only used sources or materials listed and specified in the dissertation.

Munich, March 25th 2019

Natan Napiórkowski

# 11. Declaration of author contributions

**Study 1**

**Authors:** Iris Wiegand, Natan Napiorkowski, Thomas Töllner, Anders Petersen, Thomas Habekost, Hermann Müller, and Kathrin Finke

The author of this thesis is the shared first author of this manuscript together with I.W. I.W., K.F., and T.T. designed the study. A.P. programmed, whereas N.N. conducted the experiment and analysed the data. I.W. wrote the manuscript. N.N., K.F., H.M.,T.H., A.P. and T.T. commented and revised the manuscript as well as the response to reviewers and the revised version of the manuscript.

**Study 2**

**Authors:** Natan Napiorkowski, Thomas Töllner, Iris Wiegand, Anders Petersen, Hermann Müller, and Kathrin Finke

The author of this thesis is the first author of this manuscript. I.W., K.F., and T.T. designed the study. A.P. programmed, whereas N.N. conducted the experiment, analysed the data and wrote the manuscript. N.N., K.F., H.M., A.P. and T.T. commented and revised the manuscript before submission.

**Study 3**

**Authors:** Natan Napiórkowski, Kathrin Finke, Hermann J. Müller, Iris Wiegand, Anders Petersen, and Thomas Töllner

The author of this thesis is the first author of this manuscript. I.W., K.F., and T.T. designed the study. A.P. programmed, whereas N.N. conducted the experiment and analysed the data. N.N.

and T.T. wrote the manuscript. N.N., K.F., H.M., A.P. and T.T. commented and revised the manuscript before submission.