FEATURE ARTICLE

Distinct Neural Markers of TVA-Based Visual Processing Speed and Short-Term Storage Capacity Parameters

Iris Wiegand1,2, Thomas Töllner1, Thomas Habekost3, Mads Dyrholm3, Hermann J. Müller1,4 and Kathrin Finke1,5

1Department of Psychology, Ludwig-Maximilians-Universität München, Munich 80802, Germany, 2Graduate School of Systemic Neurosciences, Ludwig-Maximilians-Universität München, Planegg-Martinsried 82152, Germany, 3Center for Visual Cognition, Department of Psychology, University of Copenhagen, DK-1353 CopenhagenK, Denmark, 4Department of Psychology, Birkbeck College, London WC1E 7HX, UK and 5Neuro-Cognitive Psychology und Center for Interdisciplinary Research, University Bielefeld, 33615 Bielefeld, Germany

Address correspondence to Iris Wiegand, Department of Psychology, General and Experimental Psychology, Ludwig-Maximilians-University Munich, Leopoldstr. 13, D-80802 Munich, Germany. Email: iris.wiegand@psy.lmu.de

An individual’s visual attentional capacity is characterized by 2 central processing resources, visual perceptual processing speed and visual short-term memory (vSTM) storage capacity. Based on Bundesen’s theory of visual attention (TVA), independent estimates of these parameters can be obtained from mathematical modeling of performance in a whole report task. The framework’s neural interpretation (NTVA) further suggests distinct brain mechanisms underlying these 2 functions. Using an interindividual difference approach, the present study was designed to establish the respective ERP correlates of both parameters. Participants with higher compared to participants with lower processing speed were found to show significantly reduced visual N1 responses, indicative of higher efficiency in early visual processing. By contrast, for participants with higher relative to lower vSTM storage capacity, contralateral delay activity over visual areas was enhanced while overall nonlateralized delay activity was reduced, indicating that holding (the maximum number of) items in vSTM relies on topographically specific sustained activation within the visual system. Taken together, our findings show that the 2 main aspects of visual attentional capacity are reflected in separable neurophysiological markers, validating a central assumption of NTVA.

Keywords: cognitive efficiency, contralateral delay activity, individual differences, theory of visual attention, visual N1

Interindividual differences across a broad range of different tasks have been suggested to reflect variations in a set of fundamental abilities or processing resources (e.g., Deary 2000; Conway et al. 2003). In the visual system, 2 such key functions jointly determine an individual’s capacity for processing information: First, visual processing speed, the amount of visual information that can be processed within a certain time (Duncan et al. 1999; Deary et al. 2010). Second, the capacity limit of visual short-term memory (vSTM), the maximum number of objects that can be perceived at one point in time (Sperling 1960; Cowan 2001).

A mathematical framework for disentangling these general capacity parameters is provided by the theory of visual attention (TVA, Bundesen 1990). A unique feature of TVA is the explicit modeling of the parameters visual processing speed $C$ and vSTM storage capacity $K$. In close relation to the biased competition model of Desimone and Duncan (1995), TVA assumes a race among objects in the visual field that are processed in parallel and compete for selection. An individual encountering multiple visual elements will encode up to $K$ objects into vSTM in the order of which they completely process. Storage capacity $K$ refers to the individual maximum capacity of vSTM, with accords with the assumption, shared with other models, that only a limited maximum number of visual object representations can be maintained at any given time; in young, healthy individuals, this number averages about 3–4 objects (e.g., Luck and Vogel, 1997; Cowan 2001; Vogel and Machizawa 2004). The theory’s neural interpretation (NTVA; Bundesen et al. 2005, 2011) further suggests distinct brain mechanisms underlying visual processing speed on the one hand and storage capacity on the other. The speed of visual categorizations (in TVA, the categorization of an object is synonymous to its encoding into vSTM) is determined by both the sensory strength of competing objects and attentional biases of the observer. At the single-cell level, encoding speed is assumed to be proportional to both the number and firing rates of neurons that code for specific features of the objects in the visual field. In contrast, the number of objects stored in vSTM depends on activity in neurons coding the $K$ “winner” elements that are sustained via recurrent thalamocortical feedback loops (Bundesen et al. 2005).

The 2 functional components can be quantified for a particular individual using a simple psychophysical “whole-report” task. Mathematically independent estimates can be derived by modeling the amount of information that can be consciously perceived and reported from a briefly presented visual display as a function of exposure duration (a detailed formal description of the equations can be found in Bundesen (1990)). This way, it is possible to control for the influence of individual differences in processing speed $C$ (and also visual perceptual threshold $t_C$; see Parameter Estimation section) on the estimate of storage capacity $K$, in contrast to, for example, change detection paradigms (e.g., Luck and Vogel, 1997). Empirically, however, $C$ and $K$ typically correlate moderately across individuals (e.g., Finke et al. 2005; Habekost and Starrfelt 2009). This indicates that both parameters might be influenced by a shared general cognitive efficiency factor (perhaps related to intelligence), but it also implies that they reflect distinct processing components to a certain extent. Psychophysical, pharmacological, and patient studies support this functional separability. First, enhancement of phasic alertness by the use of warning cues has been shown to influence processing speed $C$, but not storage capacity $K$ (Matthias et al. 2010). Second, the psychostimulant methylphenidate enhances processing speed in lower performing individuals (Finke et al. 2010), and the cholinergic neurotransmitter...
nicotine slows processing speed (Vangkilde et al. 2011), whereas storage capacity is not affected by either drug. Finally, behavioral TVA-based assessment of different patient groups has revealed a double dissociation: While adult dyslexics exhibited a significantly reduced processing speed but a preserved storage capacity compared with normal matched individuals (Stenneken et al. 2011), the reverse pattern was found in adult attention-deficit hyperactivity disorder patients who displayed a deficit in storage capacity with preserved processing speed (Finke et al. 2011). However, in patients with circumscribed acquired brain lesions, reductions of processing speed and storage capacity typically co-occur (Duncan et al. 2003; Bublak et al. 2005). This covariance indicates that the 2 functions depend on partly overlapping neural structures that probably include areas in the extrastriate, parietal, and frontal cortices as well as the basal ganglia (Habekost and Starrfelt 2009). Lesion size might be a critical confounding factor here, with larger lesions increasing the probability of impairments in both components (Peers et al. 2005).

A more appropriate way to disentangle distinct brain processes underlying the 2 components might be the examination of healthy individuals’ brain activity measured while they are performing a visual attention task. In particular, it has been argued that assumptions about basic parameters of attention and working memory may be validated by an individual-difference approach establishing associations and dissociations between cognitive measures and neurophysiological measures (Vogel and Awh 2008; Rypma and Prabhakaran 2009). Such neurophysiological indices could be identified by means of event-related potentials (ERPs), which have been proven to provide online markers of multiple independent but overlapping subcomponents of cognition engaged in 1 task (Luck 2005). Recently, based on their reliability across repeated measurements and tasks, ERPs have even been designated as neuronal trait markers of individual cognitive abilities (Cassidy et al. 2012).

To identify potential correlates of the attention capacity parameters postulated by NTVA, we focused on ERP components that are known to mark cognitive operations involved in visual attention and vSTM processing. The early visual P1 and N1 are candidate components for depicting individual differences in the visual processing speed parameter. Amplitudes of P1 and N1 components elicited by a visual stimulus are typically enhanced when selective attention is directed to this stimulus (e.g., Heinze et al. 1990; Luck et al. 1990; Hilliard et al. 1998), which has been generally interpreted as attention-related facilitation of visual processing. More specifically, the effect on the visual P1 has been associated with enhanced sensory stimulus coding by selective attention (Johannes et al. 1995; Gramann et al. 2010). In addition to this, the amplitudes of the visual N1 are assumed to index object discrimination processes within the attentional focus (Vogel and Luck 2000). In particular, the N1 response has been shown to increase with increasing difficulty of the required visual discriminations (Tanaka et al. 1999; Kiefer 2001). However, the specific mechanism(s) underlying effects of experimental manipulations on the N1 are as yet not well understood (e.g., Vogel and Luck 2000). Thus, we assume that relating ERP deflections to interindividual performance differences under constant experimental conditions may provide further insight into the functional role of early visual components. Specifically, we hypothesize that under task conditions with controlled (constant) levels of difficulty the amplitudes of the N1 reflect the relative amount of an individual’s limited attentional resources required for object discrimination. According to TVA, this efficiency of resource allocation determines the rate of information uptake, and therefore, might be related to individual differences in processing speed C (Bundesen and Habekost 2008) (it should be noted that this definition of processing speed is at variance with previous ERP approaches which rather focused either on the point in time at which the waveforms of 2 conditions start to differ in an component-independent manner (e.g., Thorpe et al. 1996), or on component timing differences (e.g., Töllner and Rangelov et al. 2012; Töllner, Zehetleitner, and Gramann et al. 2011)). In attempting to identify electrophysiological correlates of the individual storage capacity K, we focused on “delay activity” (McCollough et al. 2007) subsequent to stimulus presentation. The overall delay activity is assumed to reflect vSTM maintenance as well as more general, nonmonomorphic processes, such as arousal or response preparation; that is, its amplitude has been related to the general amount of resources required to retain visual information (Rushkin et al. 1995; Meckliner and Pfeiffer 1996; LaBerge 1997). Processes more directly related to vSTM storage can be isolated in tasks with lateralized presentation of to-be-attended (and stored) information in bilateral stimulus arrays (Klaver et al. 1999). Calculating the difference between activity contra- and ipsilateral to the attended hemifield cancels out the task-general activity (Gratton 1998). The amplitude of the resulting difference wave, the contralateral delay activity (CDA: Vogel and Machizawa 2004; also referred to as sustained posterior contralateral negativity [SPCN]; Joliceur et al. 2006), systematically increases with the number of objects that have to be maintained and level off when the individual vSTM capacity limit is reached. A correlation between the CDA and TVA parameter K, an estimate of individual vSTM capacity limit unconfounded by individual differences in processing speed and perceptual threshold, would validate the components functional interpretation as a general marker of vSTM capacity.

In the present study, we aimed to test and validate the assumption of neurally distinct attentional capacity mechanisms by identifying electrophysiological correlates of visual processing speed C and storage capacity K using a standard behavioral whole-report task (see Duncan et al. 1999; Finke et al. 2005). Note that TVA parameter K can also be measured from change detection paradigms (Kyllingsbæk and Bundesen 2009) used in many other (ERP) studies of vSTM (e.g., Luck and Vogel 1997; Vogel and Machizawa 2004). However, only the whole-report paradigm permits parameter C to be quantitatively estimated within one-and-the-same procedure. We assessed estimates of each participant’s parameters. Letters were used as objects, and the task was to report as many letters as possible per stimulus array. Additionally, we recorded the EEG of the same participant sample during a cued “EEG report” task that allowed for analyses of lateralized and nonlateralized ERP components (Fig. 1). In the EEG report, the task was to report as many letters as possible from the cued hemifield while ignoring the letters presented in the uncued hemifield. Participants were assigned to groups based on a median split of their attentional parameter estimates derived from the standard behavioral procedure (see Table 1).
statistical tests of the high versus low performer group differences.

and low performers (based on a median split for parameters visual processing speed and delay activity of high and low performers with regard to parameter was tested by comparing amplitudes of the P1, N1, C200, P200, and N200 ERP components whereas storage capacity relates to CDA capacity parameters C1 and C2, respectively), along with statistical tests of the high versus low performer group differences.

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

Experimental Procedures

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

Experimental Design

Setup and Task
Participants completed 2 test sessions: first the standard TVA whole report and 5–10 days later the EEG report task (in TVA terms, the task in the EEG experiment is a (spatially cued) partial report, in which targets are selected from among distracters. However, we chose the neutral term “report” here, since in the classical lateralized vSTM paradigm (e.g., Vogel and Machizawa 2004), stimuli in the uncued hemifield are not necessarily considered as distracters (see Parameter Estimation section for a systematic analysis of attentional weights allocated to uncued letters, which we performed to resolve this ambiguity)) (Fig. 1). Daytime of testing, testing chamber, equipment, viewing distance, background and stimulus type, size, positions, and luminance were the same in both sessions. The PC-controlled tests were conducted in a dimly lit room with stimuli presented on a 17-in. monitor (1024 × 768 pixel screen resolution; 70-Hz refresh rate) and viewed at a distance of 65 cm. Participants were instructed to report as many letters as possible from a briefly presented array with 4 target letters. They were told to report only those target letters that they were fairly certain to have recognized. The verbal report was performed without stress on response speed. The experimenter entered the responses on the keyboard and started the next trial. Letters were chosen from a prespecified set {ACEH-JOPRSTWX}. Participants fixated on a central white cross (0.7° of visual angle in size) on a black background. Four letters (1.1° in size) appeared at positions on an imaginary circle with a radius of 2.5° of visual angle around central fixation.

<table>
<thead>
<tr>
<th>Parameter estimates</th>
<th>All participants (n = 22)</th>
<th>High performers (n = 11)</th>
<th>Low performers (n = 11)</th>
<th>F-values(^a)</th>
</tr>
</thead>
<tbody>
<tr>
<td>K</td>
<td>Median (range)</td>
<td>Mean</td>
<td>Mean</td>
<td>(F_{20,1} = 26.11)</td>
</tr>
<tr>
<td>3.44 (2.31–3.84)</td>
<td>3.61</td>
<td>2.99</td>
<td>(P &lt; 0.001)</td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>Median (range)</td>
<td>Mean</td>
<td>Mean</td>
<td>(F_{20,1} = 28.27)</td>
</tr>
<tr>
<td>30.80 (17.53–90.04)</td>
<td>64.6</td>
<td>24.5</td>
<td>(P &lt; 0.001)</td>
<td></td>
</tr>
</tbody>
</table>

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

\(^a\)Group differences were examined by ANOVA's with the between-subject factor C-level (high vs. low processing speed) and K-level (high vs. low storage capacity).

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

Prior to the parameter assessment procedure, we identified the most appropriate individual exposure durations in a pretest consisting of 24 masked trials. The presentation time at which a participant could report, on average, 1 letter per trial correctly (i.e., 25% report accuracy) was chosen as intermediate exposure duration, together with a shorter (half as long) and a longer (twice as long) exposure duration (mean intermediate exposure duration: 54.9 ms; range: 24–90 ms). In this way, we ensured maximum reliability of parameter estimation by obtaining a broad range of performance scores (dependent on exposure duration) for each individual, from around perceptual threshold to asymptotic vSTM storage performance. Note that the (variation in) exposure durations provide(s) a means for optimal TVA-based modeling of an individual's performance score, rather than being a determinant of the TVA parameters themselves.

In each trial, the fixation cross was presented for 300 ms, then a blank screen of 100 ms, which was followed by the letter array. The letter array consisted of 4 isoluminant letters, randomly chosen to be either red or green. All 4 letters were presented either on the left or the right side of central fixation. A given letter appeared only once in each trial display. In half of the trials, the letter array was followed by a mask with a duration of 500 ms at each stimulus location, which consisted of a square box outline filled with a “+” and an “x” overlaid (1.2° in size). Exposure durations were effectively prolonged in unmasked compared with masked conditions, owing to visual afterimage persistence (Sperling 1960): The combination of the presence/absence of masks with 3 exposure durations (short, intermediate, long) resulted in 6 different “effective” exposure durations. Exposure duration (short, intermediate, long), masking (masked, nonmasked), and letter array hemifield (left, right) varied randomly, resulting in 12 conditions equally frequent across 6 blocks of 40 trials each. The first block consisted of 40 practice trials, and data were modeled based on the 200 remaining trials, including at least 16 trials of each condition.

Report Procedure in the EEG Experiment

In the EEG experiment, the classical whole-report paradigm was adapted to be suitable for analyzing lateralized and non-lateralized ERP components. To ensure a balanced physical stimulation in both hemifields on each trial, we presented 2 letter arrays bilaterally, with the to-be-attended hemifield indicated by a 100% valid arrow precue, with the cued side varying randomly from trial to trial (based on the classical lateralized vSTM paradigm, e.g., Vogel and Machizawa 2004). The same letter was presented only once in a given trial display, either as to-be-reported target letters (cued hemifield), or as task-irrelevant filler letters (uncued hemifield). To aid target letter selection (in face of the presentation of additional stimuli), target and filler letters were different in color, that is: either all target letters were green and all filler letters red, or vice versa, in a randomly changing fashion. Each trial started with the central fixation cross presented for 100 ms. An arrow cue displayed for 200 ms was immediately followed by the (nonmasked) letter array presented for 200 ms. The cue prompted participants to effectively allocate their attention to the cued hemifield. The short time period between cue and array onset was chosen to keep the probability that participants move their eyes to the indicated hemifield low. A delay of 900 ms with a blank screen following stimulus presentation was included in order to measure visual maintenance. After the delay a question mark appeared in the center, prompting the verbal report (Fig. 1). After a practice block of 16 trials, EEG recording was started and a total of 240 trials were run.
Parameter Estimation

The accuracy of letter report as a function of effective exposure duration derived in the standard procedure was modeled according to TVA using a maximum likelihood fitting procedure (Kyllingsbæk 2006; Dyrholm et al. 2011). The modeling was based on estimating 4 parameters defining the psychometric function depicted in Figure 2 (see also Bundesen 1990): 1) parameter $t_0$, the minimal effective exposure duration (in ms) below which information uptake from the display is assumed to be zero; 2) parameter $\mu$, the persistence of the visual afterimage on unmasked trials (i.e., effective exposure prolongation in ms, estimated from performance differences between unmasked and masked trials); 3) parameter $C$, the visual processing speed, the “fixed capacity” sum of speed values across stimulus positions (estimated as number of elements processed per second); and 4) parameter $K$, the storage capacity (estimated as the expected value of the maximum number of elements that can possibly be represented simultaneously in vSTM). $C$ reflects the slope of the exponential psychometric (growth) function at its origin $t_0$, and $K$ reflects the asymptote of the function. In the current study, parameters $t_0$ and $\mu$ were mainly estimated to obtain valid estimates of the 2 parameters of focal interest, $C$ and $K$. Estimates of $t_0$ and $\mu$ did not significantly differ between participants with higher and lower processing speed $C$ and between participants with higher and lower storage capacity $K$ [all $F < 1.40$, $P > 0.25$].

An additional measure of top-down control, parameter $\alpha$, defined as the fraction of processing capacity allocated to the fillers, was estimated by an additional parameter fitting procedure in which trials from the EEG session (Report Procedure in the EEG Experiment section), in addition to trials form the standard experiment (Standard Whole Report Procedure section), were included in the model. A low $\alpha$-value (close to zero) indicates a good ability to prioritize task-relevant objects in the processing. An $\alpha$-value of zero would imply that the participant was able to use the spatial cue to completely “filter out” the fillers. An $\alpha$-value significantly higher than zero would indicate imperfect top-down control, with filler letters potentially interfering with the report of the cued target letters. We systematically examined, on the individual participant level, whether attentional resources were allocated to filler items by testing the significance of $\alpha$ (i.e., whether letters presented as fillers on the uncued side in the EEG paradigm received a significant amount of attentional weight) by means of Likelihood Ratio tests (the fits of two models were compared. One model treated fillers as “distractors” that competed for vSTM storage but were not to be reported, the second model assumed fillers as absent. Note that all analyses involving parameters $C$ and $K$ were based on the fitting including only trials of the standard procedure. The distractor model used one extra degree of freedom per fit, and the test was to see if this resulted in a significantly better fit).

EEG Data Acquisition

The EEG was recorded from 64 active Ag/AgCl electrodes (actiCap System, Brain Products, Munich), placed according to the International 10/10 system (American Electroencephalographic Society 1994). EEG and EOG were amplified by BrainAmp amplifiers (BrainProducts, Munich) using a 0.1- to 250-Hz bandpass filter. The data was sampled at 1 kHz, and filtered offline with a 0.5 Hz high-pass filter (Butterworth zero phase, 24 dB/Oct). All electrodes were recorded with reference to FCz, and re-referenced offline to averaged mastoids. Horizontal eye movements were registered from electrodes F9 and F10 and vertical eye movements were recorded from Fp1 and an electrode placed beneath the left eye. An Infomax Independent Component Analysis (Bell and Sejnowski 1995), as implemented in the Brain Vision Analyzer software (BrainProducts, Munich), was run to identify and backtransform ocular artifacts (blinks and horizontal eye movements; see also Jung et al. 2000). To further control for any remaining activity potentially related to horizontal eye movements shifts in the individual segments, we discarded all trials in which the signal exceeded ±30 $\mu$V in the channels F9/F10. Trials with artifacts — defined as any signal exceeding ±60 $\mu$V on any of the electrodes, and bursts of electromyographic activity (permitted maximal voltage steps/sampling point of 50 $\mu$V) — were excluded from the averages. Before the EEG was segmented into epochs for ERP analyses, the signal was filtered with a 40 Hz low-pass filter (Butterworth zero phase, 24 dB/ Oct).

For the ERP analysis, EEG epochs of 1400 ms (from 400 ms before onset of the letter array to 1000 ms after), were averaged separately for attend-left and attend-right conditions. Baseline correction was based on the 400–200 ms predisplay period (i.e., the 200 ms that preceded the cue). To examine potential relationships between TVA parameters and ERP components, we focused on early visual components (P1, N1) and delay activity over posterior areas. Time windows for analyses on mean amplitudes were derived from visual inspection of the grand-average potentials of these components (Table 2).

Table 2

<table>
<thead>
<tr>
<th>Component</th>
<th>Time window (ms)</th>
</tr>
</thead>
<tbody>
<tr>
<td>P1</td>
<td>80–110</td>
</tr>
<tr>
<td>N1</td>
<td>120–150</td>
</tr>
<tr>
<td>Contralateral delay activity</td>
<td>450–600</td>
</tr>
<tr>
<td>Overall delay activity</td>
<td>600–800</td>
</tr>
</tbody>
</table>

Difference waves were calculated by subtracting ipsilateral from contralateral activity (relative to the attended hemifield) at lateral electrodes.

Statistical Analyses

Participants were classified according to their parameter estimates derived in the standard procedure. Based on median splits of the $C$- and $K$-values, they were assigned to groups of 1) participants having either a relatively high or a low processing speed $C$, and 2) participants having either a relatively high or a low storage capacity $K$. The relationships between the estimated TVA parameters and the ERP components were examined by separate ANOVAs contrasting participants with regard to their $C$-level (high processing speed/low processing speed) and their $K$-level (high storage capacity/low storage capacity). To examine topography and lateralization, we
further included the within-subjects factors attended hemifield (left/right), electrode position (left/central/right), and electrode site (P/PO/O) in the ANOVAs. In case of a significant interaction of attended hemifield and electrode position, we examined lateralized ERPs by calculating difference waves, quantified by subtracting ERPs at electrodes ipsilateral from those at electrodes contralateral to the attended array. For the sake of brevity, we only report significant main effects and interactions including the factors C-level and K-level. Significant main effects and interactions were examined using pairwise post hoc contrasts. Owing to the fact that median splits are dichotomizations of continuous variables, information about the continuity of the relationship between TVA parameters and electrophysiological responses is somewhat limited (e.g., McCallum et al. 2002). Thus, potential associations between parameter estimates and ERPs revealed by the ANOVAs were re-examined by calculating Spearman correlation coefficients between individual C-values and K-values, and the mean amplitudes at electrodes where the effect of group differences in the respective parameter was maximal.

Results

Parameter Estimation

For each subject, the accuracy of letter report as a function of effective exposure duration was modeled by a TVA-based function representing the best fit of the data according to the maximum likelihood method (Kyllingsbæk 2006; Dyrholm et al. 2011) (Fig. 2).

The efficiency of selection guided by the cue was assessed by estimating an attentional weight index \( a \) to the uncued hemifield using the trials of the EEG experiment in addition to the trials of the standard experiment. On the group level, the hypothesis of perfect cue-guided selection (i.e., that \( a = 0 \)) was rejected (\( \chi^2(22) = 308.9; P < 0.01 \)). Individual Likelihood Ratio tests revealed that for 12 of the participants, objects on the uncued side received a significant amount of attentional weight (\( P < 0.05 \)). On average, however, \( a \)-values were very low (indicative of highly efficient selection) with a mean of 0.04 (range: 0.00–0.27), that is, on average only 2% of the participants’ processing capacity was allocated to the not-to-be-attended side (an \( a \)-value of 1.00 would indicate a 50/50 split of processing capacity between cued and uncued objects).

Overall, there was a close correspondence between the theoretically and the empirically obtained mean scores. Goodness-of-fit measures averaged across all participants showed that 95% of variance in the observed scores was accounted for by the maximum likelihood fit (\( R^2 \) [\( n = 22 \)] mean: 0.95; range: 0.82–0.99). Estimates of the TVA parameters processing speed \( C \) and storage capacity \( K \) were significantly correlated across participants (\( r = 0.57; P = 0.006 \)).

Event-Related Potentials

The onset of the stimulus array elicited visual P1 and N1 components, with the latter showing substantially higher amplitudes in individuals with lower processing speed \( C \) when compared with those with higher processing speed \( C \) (see Fig. 3a). Delay activity started around 300 ms after the stimulus onset and persisted until the end of the retention period as a more negative-going deflection over recording sites contralateral to the attended hemifield. This lateralization, particularly within a relatively earlier time range, was more pronounced for the individuals with higher storage capacity \( K \) compared with those with lower storage capacity \( K \) (see Fig. 4b). In contrast, overall delay activity, strongest over occipital sites within a relatively later time window in the retention period, was larger in individuals with lower storage capacity \( K \) compared with those with higher storage capacity \( K \) (see Fig. 5).

P1

The ANOVAs (see Statistical Analyses section) of the P1 amplitudes contrasting participants with higher and lower processing speed did not yield a significant main effect of C-level (\( F_{1,20} = 0.05; P = 0.82 \)), and no significant interactions involving this factor (all \( F < 1.44; all P > 0.25 \)). Thus, there was no evidence of a P1 modulation by individuals’ level of processing speed.

The analogous ANOVA including the factor K-level also did not reveal a significant main effect (\( F_{1,11} = 0.02; P = 0.88 \)) or interactions involving this factor (all \( F_{2,40} < 1.99; F_{2,30} < 1.71; all P > 0.15 \)).

N1

The ANOVA of the N1 amplitudes comparing participants with higher and lower processing speed revealed a main effect of C-level to be significant (\( F_{1,20} = 5.50; P = 0.03 \), as well as the interaction of C-level and Electrode Site (\( F_{2,40} = 5.04; P = 0.01 \)). These effects were due to the N1 being more pronounced for participants with lower compared with higher processing speed and that these individual differences were more marked at occipital (\( F_{1,20} = 6.85; P = 0.02 \)) compared with parieto-occipital (\( F_{1,20} = 4.82; P = 0.04 \) and parietal electrode sites (\( F_{1,20} = 3.31; P = 0.08 \) (Fig. 3). This relationship was confirmed by a significant correlation between individual C-values and N1 amplitudes (\( r = 0.44; P = 0.04 \)) (Fig. 5).

In contrast, the analogous ANOVA involving the factor K-level did not yield a main effect (\( F_{1,20} = 2.16; P = 0.16 \)) or any interactions (all \( F < 1.64; all P > 0.30 \)) with this factor. Individual K-values did not correlate significantly with N1 amplitudes (\( r = 0.31; P > 0.15 \)).

Analyses performed on N1 peak latencies (as recommended by 1 anonymous reviewer revealed no significant differences according to differential levels of individuals’ performance in terms of processing speed C, storage capacity K, and perceptual threshold \( l_0 \) (all \( F_{2,40} < 3.0; all P > 0.10 \)); N1 latencies also did not correlate with individual TVA parameter values (all \( r < 0.30; all P > 0.20 \)).

(Early) Contralateral Delay Activity

The ANOVA comparing delay activity of participants with higher and lower storage capacity in the 450–600 ms time window revealed a significant interaction of electrode side and attended hemifield (\( F_{2,40} = 28.46; P < 0.001 \)): activity was higher contralateral to the attended hemifield for all participants. Furthermore, there was a significant interaction between electrode site, attended hemifield, and K-level, (\( F_{2,40} = 4.07; P = 0.05 \)), indicating that this lateralization varied with individual storage capacity. A follow-up ANOVA on CDA amplitudes revealed the difference between contra- and ipsilateral activity to be larger in participants with higher compared with lower storage capacity.
Figure 3. Event-related potentials (nonlateralized). (a) Grand-averaged ERPs at occipital-central electrodes comparing high performers (black line) and low performers (gray line). Left: Participants assigned to groups with high and low processing speed C. Right: Participants assigned to groups with high and low storage capacity K. (b) Topographic maps of the difference in activity between participants with high and low processing speed C (left) and, respectively, participants with high and low storage capacity K (right), in the time range of the visual N1 (upper maps) and that of delay activity (bottom maps).

Figure 4. Lateralized event-related potentials. (a) Grand-averaged ERPs ipsi- and contralateral to the attended hemifield, comparing high performers (black line) and low performers (gray line). Left: Participants assigned to groups with high versus low processing speed C. Right: Participants assigned to groups with high versus low storage capacity K. (b) Difference waves comparing participants with high and low processing speed C and, respectively, participants with high and low storage capacity K. The topographic map (center) depicts the mean difference of activity when participants attended to the right hemifield versus when they attended to the left hemifield, in the time range of the contralateral delay activity.
storage capacity ($F_{1,20} = 4.60; P = 0.04$). Individual $K$-values were significantly negatively correlated with CDA amplitudes ($r = -0.47; P = 0.03$), confirming that the degree of lateralization systematically increased with storage capacity (Fig. 5).

In contrast, the analogous ANOVA comparing participants with higher and lower perceptual processing speed did neither yield a main effect of $C$-level on overall delay activity ($F_{1,20} = 0.26; P = 0.62$), nor a main effect of $C$-level on CDA amplitudes ($F_{1,20} = 0.01; P = 0.93$), nor any interactions involving the factor $C$-level (all $F < 1.74$; all $P > 0.05$). Individual $C$-values were not significantly correlated with CDA amplitudes ($r = -0.17; P = 0.44$).

(Late) Delay Activity
The ANOVA comparing delay activity of participants with higher and lower storage capacity in the 600–800 ms time window revealed a significant main effect of $K$-level ($F_{1,20} = 6.83; P = 0.02$): overall (nolateralized) negativity was higher for individuals with lower compared with higher storage capacity. Again, a significant interaction of electrode site and hemisphere ($F_{2,40} = 49.10; P < 0.001$) demonstrated that attention-related lateralization across all participants persisted into this late time period. In contrast to the earlier time window, $K$-level did not interact with electrode site and attended hemisphere ($F_{2,40} < 1.44; P = 0.25$). $K$-values were significantly positively correlated with delay activity in this late time window ($r = 0.45; P = 0.04$), corroborating that overall activity increased with lower individual storage capacity (Fig. 5).

The analogous ANOVA comparing participants with higher and lower processing speed did neither yield to a main effect of $C$-level ($F_{1,20} = 0.35; P = 0.56$) nor any interactions involving this factor (all $F < 1.37$; all $P > 0.25$). Again, individual $C$-values were not correlated with overall delay activity ($r = 0.25; P = 0.26$).

Effects of Top-Down Control in the EEG Experiment
To control for the influence of attentional weight potentially (mis-)allocated to fillers on the uncued side in the EEG experiment, we additionally contrasted ERP components of participants with imperfect and perfect top-down control ($\alpha > 0 \ [n = 12] \ vs. \ \alpha = 0 \ [n = 10]$. We found no significant main effects of $\alpha$-level or interactions with $\alpha$-level for any of the analyzed ERP components, (all $F < 1.74$; all $P > 0.15$).

Individual $\alpha$-values were also not correlated with amplitudes of any of the analyzed ERP components (all $P > 0.25$).

Discussion
We identified distinct ERP correlates of 2 central capacity parameters of visual attention, visual processing speed $C$ and vSTM storage capacity $K$, that were mathematically disentangled based on the formal TVA (Bundesen 1990). Interindividual differences in visual processing speed were reflected in reduced posterior N1 amplitudes for participants with higher relative to lower encoding rates. In contrast, interindividual differences in storage capacity were related to posterior delay activity after the perceptual stimulation had expired. More specifically, participants with higher storage capacity exhibited a stronger CDA in the early phase of the retention interval, whereas they showed a weaker longer lasting overall negativity when compared with participants with lower storage capacity.

ERP Correlates of Visual Perceptual Processing Speed $C$
The association between the TVA parameter visual processing speed $C$ and N1 amplitudes is compatible with basic assumptions of NTVA. According to NTVA, faster visual information processing is associated with increased activity in specific populations of neurons that represent the properties of the attended objects. Initially, this may seem to be at variance with our finding of larger ERP amplitudes in slower individuals. However, ERPs reflect the summated activity of large numbers of synchronously firing cortical nerve cells, thus, amplitudes do not necessarily depict highly specific neuronal activity in single neurons (Bundesen and Habekost 2008). Rather, they reflect the general amount of neural resources activated during a cognitive process (Luck 2005), with (potentially less specific) activation of many neurons manifesting in higher ERP amplitudes. Cognitive efficiency theories (e.g., Vernon 1983), in fact, predict a reversed relationship between amplitude and performance level, as we found it in the present study. Less activation in higher compared with lower performing individuals is interpreted to indicate more efficient brain functioning associated with high cognitive abilities (e.g., Haier et al. 1988; Rypma et al. 2002). Processing speed is assumed to be one of several basic determinants of general processing efficiency, that is, if cognitive operations can be performed quickly, resource allocation may be minimized and
performance maximized (e.g., Neubauer 1997; Deary et al. 2010). Accordingly, the present ERP variations indicate that lower N1 amplitudes index faster object categorization processes. This interpretation is also reconcilable with previous ERP studies and bears implications for the component’s general functional role.

The N1 has generally been related to visual discrimination processes within the focus of attention (Hillyard et al. 1998; Vogel and Luck 2000), that is, its amplitude can be assumed to index the (relative) amount of attentional resources required for successfully discriminating a given visual stimulus. Accordingly, in higher as well as lower performing individuals, the component’s enhancement by selective attention (Luck et al. 1990; Hillyard et al. 1998) may reflect an increased recruitment of resources when attention is directed to to-be-discriminated stimuli. Likewise, increased N1 amplitudes for more difficult compared with easer discrimination tasks (e.g., Tanaka et al. 1999; Kiefer 2001) would reflect that object categorization requires a relatively greater investment of attentional resources and proceeds more slowly under these conditions. Accordingly, with discrimination demands being constant, enhanced N1 amplitudes for participants with lower relative to higher perceptual processing speed suggest that faster performing individuals need to invest a relatively smaller amount of their available neural resources during early object processing; slower performing participants, by contrast, may require stronger attentional enhancement of cortical activity for discriminating the visual stimuli (e.g., Egner and Hirsch 2005), perhaps in order to compensate (at least in part) for their perceptual slowing. Similarly, additional neuronal activity involved in nonspecific visual processing may de-crease slower individual’ signal-to-noise ratio; that is, they may expend more (limited) attentional weight on internally generated, task-irrelevant activity in the visual cortex (Bundesen and Habekost 2008). By contrast, categorization might be sped up in faster processing individuals by their effective application of stored internal templates that closely match the currently presented stimuli (Bundesen et al. 2011). In line with this, the N1 response to novel stimuli, for which no pre-experimental templates exist, has been found to decrease with increasing numbers of stimulus repetitions (Groh-Bordin et al. 2007). Furthermore, the N1 is less pronounced when the similarity between objects that have to be classified is reduced (Tanaka et al. 1999; Töllner et al. 2009; Tokudome and Wang 2011). Thus, N1 amplitudes may signify the quality of (acquired) activated or the competition between internal object representations (Curran et al. 2002).

Interestingly, older individuals, whose visual processing speed is known to be reduced (Habekost et al. 2012; McAvinue et al. 2012), show augmented visual N1 amplitudes relative to younger individuals in many visual tasks (Kutas et al. 1994; Yordanova et al. 2004). Congruent with our interpretation, the age-related N1 enhancement has been suggested to reflect a stronger (compensatory) recruitment of attentional resources that elderly need for discrimination operations (DeSanctis et al. 2008; Finnigan et al. 2011), presumably for successful activation of internal templates, even under relatively low task demands. Admittedly, though, further work is required to specify the precise relationship between within-subject N1 effects and the speed of categorization processes between participant groups. Future studies may directly investigate the effects of, and potential interactions between, interindividual and intraindividual factors on ERPs by incorporating within-subject manipulations into the present approach.

**ERP Correlates of Visual Short-Term Memory Storage Capacity K**

The relationship established between TVA parameter storage capacity K and ERP delay activity are in line with the neural mechanisms proposed by NTVA and substantiates previous EEG findings relating the CDA to individuals’ vSTM capacity. In particular, NTVA assumes that vSTM storage relies on spatiotopically organized sustained activity, implemented via recurrent feedback loops between the thalamus and sensory neurons in visual cortical areas (Bundesen et al. 2005). The posterior-contralateral distribution (relative to the hemifield of encoded information) of the delay activity associated with storage capacity K supports the visuotopic organization of this recurrent activation. As suggested previously, delay activity during retention periods arises from thalamocortical activation (Birbaumer et al. 1990; LaBerge 1997). The present findings demonstrate that the overall delay activity and the lateralized proportion of this activity are dissociable with respect to their relationship to individual differences in vSTM limits: Overall nonlateralized activity was higher in participants with lower storage capacity; conversely, CDA amplitudes were larger in participants with higher storage capacity. This dissociation suggests that individuals with comparatively high storage capacity are characterized by efficient neural recruitment, that is, instantaneous CDA specifically associated with the storage of attended information, while minimizing later additional unspecific activity. The latter may involve un-profitable remote activity, processing of extraneous noise, or strategic compensational mechanisms during a time period in which the vSTM representation would already have started to decay. It should be noted that, theoretically, verbal rehearsal strategies (in addition to visual maintenance) could have been applied during the delay period in the EEG experiment. However, in previous ERP studies focusing on verbalization of to-be-memorized visual items, the employment of verbal strategies was associated with delay activity over frontal areas in a later time period not starting before about 1.5-s poststimulus presentation (Rushkin et al. 1997; Bosch et al. 2001). Thus, it seems unlikely that verbal rehearsal contributed to the earlier, posterior delay activity revealed in the present study.

Previously, the relationship between CDA and interindividual differences was disclosed by varying load conditions in change detection paradigms (e.g., Vogel et al. 2005; McCollough et al. 2007). In particular, the individual vSTM limit was associated with the relative point at which the CDA reached an asymptote; for example, participants with relatively low storage capacity reached the CDA asymptote already at low vSTM loads, whereas the CDA amplitude increased further with increasing loads for participants exhibiting higher storage capacity. Thus, typically, correlations were found between individual behavioral vSTM capacity measures and the relative increase of the CDA amplitude from lower loads (e.g., 2 items) to higher loads (e.g., 4 items) (e.g., Vogel et al. 2005; McCollough et al. 2007). By contrast, a straightforward correlation between the CDA and TVA-based estimated storage capacity K was demonstrated in the present study,
even despite the relatively long temporal gap (of 5–10 days) between parameter assessment and EEG recordings. Presumably, the highly reliable estimation of the individual TVA parameter \( K \) enabled us to establish this systematic relationship. Generally, this finding further supports that the CDA marks the latent storage capacity limit underlying visual operations in various tasks. In fact, a CDA is also elicited in other visual attention tasks requiring vSTM, such as attentional blink (Jolicour et al. 2006) and visual search (Perron et al. 2009; Wiegand et al. 2013). Recently, its amplitudes have been shown to correlate with individuals’ performance and reliance on vSTM in visual search (Luria and Vogel 2011). Taken together with the present results, this confirms the CDA as a general marker of individuals’ ability to maintain attended information in vSTM.

Furthermore, we controlled for a critical confound by estimating storage capacity independently of visual processing speed outside of the EEG experiment (i.e., in the TVA whole report experiment). Usually, vSTM performance and ERPs are assessed under conditions of a single, constant presentation time of the to-be-encoded stimulus array (e.g., Vogel and Machizawa 2004; but see Luria et al. 2010; Sander et al. 2011). Thus, interindividual differences in perceptual processing speed potentially influence both storage capacity measures and CDA amplitudes. Stimulus presentation in vSTM tasks may mostly suffice to fill up vSTM to capacity, and, overall, will not substantially affect the magnitude of the CDA (Luria et al. 2010). However, when participants are compared according to their individual speed level as in the present study, the brief presentation times necessary for ERP examination may lead to systematic underestimations of the maximum storage capacity especially for the group of lower performing participants. By quantifying parameter estimates of the 2 components based on the standard procedure with varying exposure durations, confounding effects of differences in processing speed on measures of vSTM capacity and the CDA could be ruled out. Critically, the present approach is therefore particularly suitable to investigate differences between groups of normal (young, healthy) individuals at different capability levels and, in a prospective sense, also in special populations with known reductions in processing speed, such as aging individuals or patient groups.

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

**Processing of Nonattended Letters**

The combination of TVA-based parameter assessment with ERPs further contributes to an ongoing discussion about the impact of filler items inherent in the lateralized vSTM paradigm (e.g., Arend and Zimmer 2011). Previous studies measuring the CDA have usually not systematically assessed whether objects in the not-to-be-attended hemifield receive attentional weight that could potentially influence behavioral vSTM measures and EEG responses. However, the ability to filter out irrelevant information is a critical determinant of interindividual differences in vSTM limits and CDA amplitudes (e.g., Vogel et al. 2005). The present approach enabled us to control for this potential influence of letters in the uncued hemifield. Storage capacity \( K \) was estimated based on performance in the standard procedure using unilateral arrays when the total attentional weight could be allocated to the target letters. Including trials from the EEG session in an extended fit permitted us to estimate the relative weights of cued and uncued letters for each participant, expressed in the TVA top-down control parameter \( a \) (Kyllingsbæk 2006). The results indicate that participants allocated the largest part of their available attentional weight (98%, on average) to the cued (target) letters. ERP activity did not differ between individuals with perfect and imperfect top-down control. This makes it unlikely that the processing of letters on the nonattended side accounted for individual differences in CDA amplitudes. Thus, in the present study, attentional resources allocated to the filler letters appeared to be of negligible impact. However, the general (usually implicit) assumption that items on the uncued side in a lateralized vSTM paradigm simply serve as fillers becomes questionable in the face of a measurable amount of attentional weight that is (mis-)allocated to letters on the uncued side, at least for some of the participants. In particular, in aging or clinical populations of individuals who suffer from a deficit in top-down attentional control, fillers may have a significant distracting impact and this should thus be taken into account when interpreting behavioral as well as electrophysiological responses (e.g., Töllner and Müller HJ et al. 2012).

**Conclusions**

In the present study, we used an interindividual differences approach to provide electrophysiological evidence for the neural independence of 2 distinct latent visual attention capacity parameters formally implemented in the neural theory of visual attention (NTVA; Bundesen et al. 2005, 2011): First, faster perceptual processing speed was associated with reduced (i.e., more efficient) brain activity during early object discrimination. Second, higher storage capacity was associated with a larger amount of delay activity specifically related to vSTM processing, while overall unspecific activity was less negative.

The identified ERP correlates of the 2 TVA parameters may be regarded as general neural efficiency measures of separate fundamental abilities and, thus, as a promising tool in the study of brain mechanisms underlying individual differences in more complex behavior (Neubauer 1997; Vernon 1983; Cassidy et al. 2012). Furthermore, if comparable reliability of the ERP correlates could be proven in different age groups and patient populations, they may have the potential to serve...
as neural markers disclosing age- and disease-related changes in attentional functions. These might then be used to quantify brain–behavior relationships in recovery, pharmacological treatment, and rehabilitation training in a highly sensitive manner.

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**Notes**

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**References**


Vernon PA. 1983. Speed of information processing and general intelligence. Intelligence. 7:53–70.


