



# Time-resolved neuroimaging of visual short term memory consolidation by post-perceptual attention shifts



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## ABSTRACT

Post-perceptual cues can enhance visual short term memory encoding even after the offset of the visual stimulus. However, both the mechanisms by which the sensory stimulus characteristics are buffered as well as the mechanisms by which post-perceptual selective attention enhances short term memory encoding remain unclear.

We analyzed late post-perceptual event-related potentials (ERPs) in visual change detection tasks (100 ms stimulus duration) by high-resolution ERP analysis to elucidate these mechanisms. The effects of early and late auditory post-cues (300 ms or 850 ms after visual stimulus onset) as well as the effects of a visual interference stimulus were examined in 27 healthy right-handed adults.

Focusing attention with post-perceptual cues at both latencies significantly improved memory performance, i.e. sensory stimulus characteristics were available for up to 850 ms after stimulus presentation. Passive watching of the visual stimuli without auditory cue presentation evoked a slow negative wave (N700) over occipito-temporal visual areas. N700 was strongly reduced by a visual interference stimulus which impeded memory maintenance. In contrast, contralateral delay activity (CDA) still developed in this condition after the application of auditory post-cues and was thereby dissociated from N700.

CDA and N700 seem to represent two different processes involved in short term memory encoding. While N700 could reflect visual post processing by automatic attention attraction, CDA may reflect the top-down process of searching selectively for the required information through post-perceptual attention.

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## Introduction

Memory is stored in separate ways, i.e. precategorical sensory memory, short term memory and long term memory (Atkinson and Shiffrin, 1971). Visual sensory memory (or iconic memory; Neisser, 1967) is thought to be able to keep a huge amount of information, but only for a very limited time span (Averbach and Coriell, 1961; Sperling, 1963). In contrast, the capacity of visual short term memory (VSTM) is strictly limited, holding no more than 3 or 4 objects at the same time (Luck and Vogel, 1997; McCollough et al., 2007; Woodman et al., 2001). Attention plays an important role in increasing the efficiency of short term memory encoding. Iconic memory can be enhanced by cueing (Averbach and Coriell, 1961), when attention is selectively switched to task relevant parts of a non-selective pre-processing trace

*Abbreviations:* (f)VSTM, (fragile) visual short time memory; ERP, event-related potentials; CDA, contralateral delay activity; RI, retroactive interference; vPINV, visual post imperative negative variation; rHF, lHF, right, left hemifield; TMS, transcranial magnetic stimulation.

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(Gegenfurtner and Sperling, 1993). Vogel et al. (2005) have pointed out that post-perceptive retro cues (given after the offset of a stimulus) may not support visual perception, but will enhance the post-perceptive encoding of the perceived information using different processing pathways (Herrero et al., 2009; Mangun, 1995; Vogel et al., 2005). During the maintenance of visual stimulus characteristics in sensory memory, attention will reduce memory load to those relevant items which should be memorized, so that VSTM capacity is not exceeded during memory encoding (Delvenne, 2005; Luck and Ford, 1998). The timing of the post-cue presentation is important (Vogel et al., 2005). Late post perceptual cues may have less or no effect when the time span of sensory memory is exceeded over 500 ms (Averbach and Sperling, 1961; Coltheart, 1983; Luck and Hollingworth, 2008). However, recent studies have shown that subjects could also benefit from later post perceptual cues (Makovski, 2012; Sligte et al., 2008; Vandenbroucke et al., 2011).

An intermediate memory state termed fragile visual short term memory (fVSTM) was differentiated from durable VSTM with less capacity (Fougnie et al., 2010; Luck and Vogel, 1997; Vogel et al., 2005). It is believed to have a higher storage capacity than VSTM and be longer lasting than sensory memory, as well as being easily overwritten by new stimuli (Matsukura and Hollingworth, 2011). Recent studies using

transcranial magnetic stimulation (TMS) support this theoretical concept. When TMS was applied to the right dorsolateral prefrontal cortex, VSTM was impaired but not fVSTM (Sligte et al., 2011).

In this study we challenge the question by which mechanisms the sensory characteristics of visual stimuli are maintained and consolidated during VSTM encoding by post-perceptive attention focusing. If a memory representation was available during sensory memory and fragile VSTM, post-perceptive attentional processes could act on this memory representation during stimulus post-processing. This process could allow more durable VSTM encoding which is not so easily overwritten by new stimuli. We aimed to find ERP correlates of the sensory memory, respectively of the fragile VSTM representations of the visual stimuli that had to be memorized as well as ERP correlates of the attentional post-processing after post-perceptive cues which pointed towards the relevant items to be encoded. We hypothesized that both ERP correlates for sensory memory representation and post-perceptive attentional processing during VSTM encoding should show a certain topographic overlap because post-perceptive attentional processing should be based on the available sensory memory representation.

In order to address post-perceptive attentional processing and VSTM encoding and maintenance, we assessed contralateral delay activity (CDA) as a possible ERP correlate. CDA is a slow cortical potential during VSTM tasks and starts about 200 ms after a side cue, which indicates which visual hemifield needs to be attended and persists throughout a retention phase of about one second (McCollough et al., 2007). It consists of a negativity over the hemisphere contralateral to the attended visual hemifield (relative to the ipsilateral hemisphere). CDA can be modulated by memory load (up to 4 objects per hemifield) (Delvenne, 2005; Klaver et al., 1999a; Luria and Vogel, 2011; Vogel and Machizawa, 2004). CDA could be a highly specific, neurophysiological correlate for VSTM representations and could provide information about maintenance, selection and retrieval during a memory task (Ikkai et al., 2010; Klaver et al., 1999b; Ruchkin et al., 1992). However, CDA has been examined in many study designs with visual cues preceding the visual memory task (Cowan, 2001; Cowan et al., 2005; Fougny and Marois, 2011; Herrero et al., 2009; Ikkai et al., 2010; Luria and Vogel, 2011; McCollough et al., 2007). Recent literature also investigated CDA development using visual retro-cues (Eimer and Kiss, 2010; Tollner et al., 2014, 2015; Williams and Woodman, 2012). In this study we examined CDA expression using auditory retro-cues during stimulus post-processing of visual memory item tasks.

Our second target parameter was a slow negative wave called N700, which is elicited over bilateral occipito-parietal areas after passive visual stimulation. It is most likely reflecting visual post-perceptual processing of information in higher visual areas (V2–V5) (Bender et al., 2010). N700 or visual post imperative negative variation (vPINV) occurs during the interval of 450–1000 ms, with a peak about 700 ms after stimulus onset (Allison et al., 1999; Bender et al., 2004b, 2008). In this study we challenged the hypothesis that the visual post-processing shown by N700 could be identical with the visual sensory memory trace upon which later attentional processes could act during CDA. Topographical similarities between N700 and CDA as well as their time courses suggested this hypothesis. Selective attention and memory encoding during CDA could make use of the N700-related stimulus post-processing when a post-cue is used. Post-perceptive attention could act on a transient representation in fragile VSTM which is displayed by the N700 potential. Slow wave ERP could image real-time processes of neuronal information encoding and memory consolidation.

We pursued the following aims in a series of experiments: First, we tried to replicate previous results (Bender et al., 2008, 2010) indicating that a visual N700 amplitude is elicited by automatic attention attraction during the passive watching of short visual stimuli (Experiment 1). Furthermore, we tested how intentional memory maintenance and post perceptual attention shifts affects N700 amplitude. We hypothesized that N700 would be increased bilaterally, when the subjects tried to

keep visual items in short term memory which were equally distributed over both visual hemifields (Experiment 2). In the third experiment we tried to analyze how the visual N700 was affected and how lateralized slow potentials (CDA) would develop when attention was focused by auditory post-perceptive cues which pointed towards the right or left visual hemifield (reducing memory load by half). Those post-perceptive auditory cues were applied at two different latencies, before and after the N700 peaks at 650 ms, to test whether attention is relevant for memory performance and CDA would develop “out of” the N700 potential (experiments 3 and 4). An early cue was given so subjects could extract the cue information before the N700 peak, and a late cue was given to analyze if subjects also benefitted when the N700 peak was already over. We hypothesized that CDA amplitude would correlate with and depend on the negativity which was elicited during N700.

In our final experiment (Experiment 5) we investigated the effects of an interfering visual stimulus on N700 and CDA. If a second stimulus of the same modality is presented in a short time interval after the first visual stimulus it can cause retroactive interference (RI) or the impairment of memory consolidation of the target stimulus (Breitmeyer and Ogmen, 2000; Bugmann and Taylor, 2005; Turvey, 1978). RI effects are not only caused by capacity overloading (Awh et al., 1998; Oh and Kim, 2004; Woodman and Luck, 2004) but also the encoding, maintenance and retrieval of the first visual stimulus in VSTM is disturbed when a second stimulus is encoded simultaneously (Cowan et al., 2005; Cowan and Morey, 2007). According to the concept of fVSTM, a second stimulus, which is presented after the perception of the first, could ‘overwrite’ the perceptual trace of the target stimulus in fVSTM if both stimuli are similar (Sligte et al., 2008). We challenged the hypothesis that an interfering stimulus could evoke a N700 potential even if it was intentionally ignored (if N700 was a passive sensory memory trace based only on prolonged activation elicited by perception). Additionally, an interfering stimulus could reduce N700 amplitude of the first visual stimulus, because previous studies had shown that shorter interstimulus intervals diminished N700 (Bender et al., 2006). In this case we hypothesized that CDA would be reduced as well, if CDA reflected the top-down controlled activation of the relevant parts of the unselective visual activation during N700.

Finally, the effects of the interference stimulus could help to elucidate the meaning of CDA further. CDA could represent a purer measure of memory than behavioral data if it directly reflected the neuronal activity related to memory storage. In this case, CDA should be reduced when interference effects impaired memory performance. However, CDA could also represent the process of selection or searching for the required information when post cues are presented (Eimer and Kiss, 2010). In this case CDA could still persist without major changes even despite strong interference effects when subjects performed an unsuccessful search of the required information. This question about the nature of CDA is crucial for the understanding and the use of CDA in neuropsychological studies.

In fact, as the reader will see in the following, we found a dissociation of the effects of the interference stimulus on N700 and CDA: N700 was strongly reduced by the visual interference stimulus which impeded memory maintenance, while CDA still developed in this condition after the application of auditory post-cues. Thus N700 could reflect visual post processing by automatic attention attraction, while CDA may reflect the top-down process of searching selectively for the required information through post-perceptual attention.

## Materials and methods

### Subjects

27 adult, healthy, right-handed ( $96.7 \pm 7.1\%$ ; according to the Edinburgh Handedness Inventory; Oldfield, 1971) young volunteers (16 females, 11 males, mean age  $26.3 \pm 2.9$  years;  $18.5 \pm 2.7$  years of

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