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Abstract

Introduction

Visual Working Memory (vWM) is a set of processes for short-term maintenance and manipulation of visual information. It is believed to be at the core of many higher level cognitive phenomena, such as fluid intelligence, reasoning and comprehension. Consequently, vWM is thought to underlie an important portion of variation in general cognitive performance, both in healthy individuals and in different clinical populations. Despite its central role, vWM is marked by a highly limited capacity, 3-4 items on average, posing an important research question on how this capacity can be used efficiently.

It is known that vWM capacity can be successfully controlled at the encoding phase by resisting task-irrelevant distractors. However, the mechanisms enabling adaptation to changing tasks and goals and dynamic removal of no-more-relevant vWM content during the maintenance phase are less known. In this study we aimed to investigate two possible mechanisms of task-irrelevant item elimination: Within a single visual hemifield and of the whole visual hemifield.

Methods

Two independent experiments comprising a set of five experimental conditions were designed based on a bilateral change-detection task with a retro-cue. Behavioral vWM capacity index K and an ERP marker, the Contralateral Delay Activity (CDA), were used as primary tools to probe into dynamic vWM content elimination during the maintenance phase. Both classic and mass univariate approaches were used to quantify CDA differences in different conditions.

Results & Discussion

Behavioral and ERP results confirmed successful elimination of memory items from the irrelevant visual hemifield after a retro-cue. However, this effect was not observed in conditions requiring item elimination within a single hemifield. Moreover, behavioral index K indicated that the single-hemifield conditions were unexpectedly difficult for the participants. The CDA provided additional proof that the difficulties were due to the cue processing or retrieval inference. This was a novel and surprising finding, as both color and directed-remembering retro-cues have been shown to successfully reduce vWM load. We argue that the observed detrimental effect of the retro-cue could be explained within the framework of feature integration theory.

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1. Introduction

Visual Working Memory (vWM) is a cognitive system that can temporarily maintain a highly limited amount of visual information in an active state for quick recall, integration and manipulation (Drew & Vogel, 2009). While some definitions of vWM tend to focus more on its storage properties (e.g. Curtis & D'Esposito, 2003; Fukuda & Vogel, 2009; Leonard et al., 2012; Sauseng, Griesmayr, Freunberger & Klimesch, 2010), the others accentuate its control processes (e.g. Drew, McCollough & Vogel, 2006; Emrich, Al-Aidroos, Pratt & Ferber, 2009; Gao et al., 2009) which underlie the conceptual separation of visual short term memory (vSTM) and vWM (Section 1.1.).

Traditionally, working memory research was dominated by verbal paradigms, however, there has been an explosion in visual WM research for the last twenty years (Luck & Vogel, 2013), significantly contributing to the growth of the field. According to D'Esposito and Postle (2015), there were 18.224 WM related PubMed citations and 1.580.000 Google Scholar search results in 2014. In August 2017 these numbers expanded to 42.474 PubMed citations and around 4.750.000 Google Scholar search results, with approximately one (in PubMed) to three (in Google Scholar) quarters of these results referring to visual WM.

There is a number of reasons for this growing and sustained interest in vWM. First, more and more is understood about the role of vWM in high-level visual information processing, such as integration of binocular visual input into coherent scene (Gao et al., 2009), or integration of retinal images separated by saccadic eye movements (Emrich et al., 2009; Luck & Vogel, 2013). Second, the role of vWM, as an "online workspace" for representing and manipulating task-relevant information has been repeatedly established (Luria, Balaban, Awh & Vogel, 2016). This property of "keeping relevant information in mind" (Baddeley, 2010; Howard et al., 2003) has placed vWM at the core of other cognitive functions (Luria et al., 2016; Ma, Husain & Bays, 2014), complex behaviors (Howard et al., 2003) and temporary extended tasks (Leonard et al., 2012). Finally, by considering the implication of vWM in a broad range of cognitive functions, vWM became a valuable gateway to understanding cognitive impairments in a range of neurodegenerative and psychiatric disorders (Section 1.3), as well as individual differences in cognitive processing in healthy adults (Section 1.2).

The growing body of knowledge and findings has naturally led to the development of new theoretical frameworks explaining the nature of vWM and its most notable feature, the

limited capacity (Sections 1.4. and 1.5.). Without a doubt, the increase in the number of vWM studies heavily relied on the development of new vWM markers and measurement methods (Section 1.6). These novel tools allow more reliable and precise probing into different vWM properties and sub-processes, revealing a complex and fascinating system of mechanisms for dynamic control of vWM capacity (Section 1.7.).

1.1. Disambiguation of short-term and working memories

The line separating working memory (WM) and short-term memory (STM) is often blurred, as they both span through a similar temporal window and are both marked by a highly limited capacity.

In general, the concept of STM is an older one dating back to the notion of primary-memory in W. James *Principles of Psychology* (as cited in Cowan, 2008, p. 323). In this seminal work, James (1890) defined the key hallmarks of short-term memory, such as maintenance of the representations in an active state, accessibility to conscious mind and limited temporal duration. Similar definitions of STM were first taken over by influential XX century cognitive psychologists, such as Atkinson and Shiffrin (1968), and then handed over to a new generation of memory researchers (Cowan, 2008).

A notion of working memory was first introduced by Miller, Galanter and Pribram in 1960 (as cited by Cowan, 2008, p. 325). It was defined as a memory that is used to manage plans and complex behaviors, where a plan was described as any hierarchical process that can control the order in which a sequence of operations is to be performed (Miller, Galanter & Pribram, 1986). Miller et al. (1986) argued that this complex hierarchical system, a plan, must be kept in a special state in order to coordinate its different parts and sequencing, and to remember it while it is being executed. He reasoned that for this purpose humans would need a type of "quick-access, working memory" (Miller et al., 1986, p. 65) which most likely resides in the frontal lobes.

However, it was due to the influential theory of Baddelay and Hitch (1974) that the concept of working memory started to dominate cognitive psychology and related disciplines. They used WM as an umbrella term for multiple cognitive systems working together, where the STM was just one of its components next to information manipulation and executive processes. This notion of WM as STM with additional control mechanisms is still prevailing (Aben, Stapert & Blokland, 2012), with such processes as sustained attention, information flow control, access to long-term memory, re-organization, integration, and suppression of

information being identified as possible WM control mechanisms (Sauseng et al., 2010).

Despite the separate history and conceptual differences, there still is a practical overlap of the two terms due to different operational definitions in various research laboratories. Aben et al. (2012) defined 7 groups of different interaction models of STM and WM, ranging from complete overlap to closed-loop systems. Moreover, many researchers use one term or another based on personal preference or, sometimes, as synonyms.

Nevertheless, it is generally accepted that these two constructs can and should be dissociated from each other as they are measured using different tools – simple span or complex span tasks –, and correlate with other cognitive faculties to different extents (Aben et al., 2012; Cowan, 2008).

1.2. WM relation to individual differences in higher cognition

As early as in 1960, Sperling reported that people on average could report only 4.3 items from a briefly presented memory set with an inter-subject variability ranging from 3.8 to 5.2 items. Surprisingly, intra-subject variability was extremely low, almost a constant, across a variety of different stimuli he used. Similarly, a few years earlier, Miller (1956) reviewed and reported limited WM capacities for a range of modalities, such as taste or different parameters of sound. Thus, it has been long established that WM capacity is highly limited, yet it is marked by large and stable individual differences. This stability of individual WM capacity, combined with simple and straightforward measurement methods, makes it a valuable gateway in understanding WM implications in other cognitive functions.

Visual WM is not an exception, as it is marked by capacity limitations similar to those in other modalities, from 1.5 to 5 (Vogel et al., 2005) or 6 (Cowan, 2001) items, which, nevertheless, are stable within an individual. In addition, vWM capacity has been repeatedly shown to correlate with, most notably, fluid intelligence (Fukuda, Vogel, Mayr & Awh, 2010; Heitz, Unsworth & Engle, 2005; Kane & Engle, 2002; Unsworth, Fukuda, Awh & Vogel, 2014), accounting for 43 % of individual differences in global fluid intelligence and 46 % of individual differences in overall performance on a broad battery of cognitive tasks (Luck & Vogel, 2013). In addition to intelligence, vWM capacity has been shown to correlate with attentional control, academic performance, reading comprehension, mathematical abilities, acquisition of a second language, and many other tasks (Drew & Vogel, 2009; Perez & Vogel, 2012).

In general, vWM tasks, such as Corsi block-tapping (Kessels, Zandvoort, Postma, Kappelle

& Haan, 2000) or change detection (Luck & Vogel, 1997), perform better than vSTM tasks, such as simple recall task, in explaining individual variance in other cognitive functions and aptitudes (Cowan, 2008). However, the debate over the underlying mechanisms of this superiority is still ongoing. There have been several approaches to solve this question by means of deconstructing vWM into short-term storage and executive components. Based on this, some researchers have reported that the STM component is the crucial one in explaining individual variability in intelligence measures (Colom, Shih, Flores-Mendoza & Quiroga, 2006; Fukuda et al., 2010). However, there is a well-established opposite view stating that the beneficial explanatory power of vWM primarily comes from its executive component, namely, better attentional control (Kane & Engle, 2002; Linke, Vincente-Grabovetsky, Mitchell & Cusack, 2011).

Better attentional control is believed to improve interference control, maintenance of task-goals and resistance to distractors. Moreover, it has been shown that high-capacity individuals are better at antisaccadic tasks and more resistant to "cocktail-party" effect, both tasks requiring attentional control (Conway, Cowan & Bunting, 2001; Drew & Vogel, 2009). Finally, in their pioneering work, Vogel and Machizawa (2004) showed that low-capacity and high-capacity individuals most likely differ in their resistance to distractors rather than in actual vWM storage space, as low-capacity individuals seem to be more susceptible to involuntary capture from target-resembling distractors. The individual differences in vWM capacity and attentional processes have also been reported to be reflected by differences in functional connectivity between prefrontal cortex, basal ganglia and parietal cortex, as measured with functional Magnetic Resonance Imaging (fMRI) (Luck & Vogel, 2013).

The importance of understanding the relation between vWM and other cognitive domains goes beyond that of simple curiosity or basic research. vWM capacity is an important limiting factor on a child's learning rate, hence, early screening for low vWM capacity could help to identify children at risk of subsequent academic difficulties (Astle et al., 2014; Baddeley, 2010). Moreover, it is possible that timely vWM training could also benefit healthy elderly and some clinical populations (Buschkuehl et al., 2008; Klingberg, 2010).

1.3. Visual WM impairments in clinical populations

As a consequence of visual WM being implicated in higher cognitive functions, its impairments have been reported in many neurodegenerative and psychiatric disorders. Probably the largest body of knowledge comes from vWM research in schizophrenia. It has

been established that schizophrenia patients have vWM deficits that can account for about 40% of the variance in their broad intellectual function (Luck & Vogel, 2013). Initially, the nature of these deficits had been attributed to possibly defective top-down and bottom-up attentional control. However, it has been recently established that despite the broad range of cognitive impairments, general attentional processes and memory precision are surprisingly intact in schizophrenia (Gold et al., 2006; Gold et al., 2010). Additional research revealed that attentional deficits in schizophrenia can only be observed in the presence of highly salient distractors (Hahn et al., 2010), leading to the hypothesis that the nature of vWM impairments in schizophrenia lies with a tendency to hyper-focus on a small number of items or salient distractors (Luck & Vogel, 2013). This is an excellent example how vWM research can help unravel the pathological mechanisms of a disease, as well as dissociating them from vWM mechanisms in suboptimally performing yet healthy individuals (Leonard et al., 2012).

Luria et al. (2016) in his review indicates that different vWM deficits have been reported in other clinical populations as well. For instance, Parkinson's disease patients were reported to have both impaired filtering efficiency (resistance to distractors), as well as reduced general vWM capacity (Lee et al., 2010). Similarly, filtering efficiency showed different temporal dynamics in healthy elderly, accounting for reduced WM capacity in the older age (Jost, Bryck, Vogel & Mayr, 2010). Lower electrophysiological vWM capacity markers have been observed in the Amyotrophic Lateral Sclerosis (ALS) patient group, though they showed no cognitive or behavioral impairment (Zaehle et al., 2013). In addition, vWM capacity seems to be reduced in people at risk of developing mild cognitive impairment (MCI), hence acting as a possible biomarker for early detection of neurodegenerative disorders (Newsome, Pun, Smith, Ferber & Barense, 2013). Finally, certain vWM deficits can be even observed in healthy overly anxious individuals, thus revealing its prevalent role both in clinical and psychological disorders (Miller & Bichsel, 2004; Shackman et al., 2006).

1.4. Working memory theories

It is customary to frame any research into a theoretical system that facilitates formation of thought and hypothesis. Working memory is not an exception, as there are several well-established yet competing theoretical models regarding its nature and working mechanisms. The first and oldest of such frameworks is the multicomponent WM model developed by Baddeley and Hitch in 1974, where WM is conceptualized as a complex system comprising

storage and processing functions. This model has been challenged by the state-based theories which define WM not as a separate system but rather as a continuous part of either information processing or unitary memory systems.

1.4.1. Multicomponent working memory model

The multicomponent WM model was designed by Baddeley and Hitch (1974) in their attempt to resolve dead ends in the at-the-time dominant dual memory model by Atkinson and Shiffrin (1968). The dual model postulated that the memory system comprises short-term memory (STM) and long-term memory (LTM), and that the flow of information from the STM to the LTM is an automatic passive process, given long enough STM maintenance (Baddeley, Eysenck & Anderson, 2015). However, based on accumulating findings, Baddeley and Hitch argued that simple unitary STM is insufficient in either explaining information transfer from STM to LTM or in outlining the role of STM in broader cognitive functioning (Baddeley, 2010; Baddeley et al., 2015; Baddeley, Kopelman & Wilson, 2003). Therefore, they proposed a complex system for short-term information storage and manipulation, termed Working Memory. Their WM comprised a central executive (attentional control system) and two independent subsidiary storage systems: phonological loop for acoustic or speech-based items, and visuospatial sketchpad for visually and/or spatially encoded items (Baddeley, 2010; Baddeley et al., 2015). Later, in an attempt to accommodate increasingly complex and conflicting research findings, the model expanded to include an episodic buffer (Baddeley, 2000; Baddeley, 2002). The episodic buffer was assumed to have a limited capacity, similarly to the phonological loop and visuospatial sketchpad. However, differently from the other two short-term storage systems, it was hypothesized to be multimodal in its nature, hence, able to integrate and manipulate information coming from different short-term storages or LTM. The content of the episodic buffer was described as accessible through awareness, placing it at the core of human consciousness (Baddeley, 2000; Baddeley, 2002).

According to the multicomponent WM model, the storage function of visual WM would depend on the visuospatial sketchpad, while its processing and control functions would be implemented by the episodic buffer and the central executive. The capacity limits of the vWM would be determined by the limits of the visuospatial sketchpad, while the processing limits would primarily come from the episodic buffer.

The multicomponent WM model had an enormous influence on WM research between 1985

and 2005 (D'Esposito & Postle, 2015), stimulating new hypotheses and a flow of findings. Although its importance in recent years has been diminished by newer models, it still remains one of the most elegant and productive theoretical frameworks of WM.

1.4.2. State-based working memory models

The state-based models argue that WM is an emergent phenomenon of a broader information processing or unitary memory system rather than a separate modular cognitive construct (D'Esposito & Postle, 2015). The arguments in favor of the state-based models mostly come from the overlapping functions of WM and selective attention (Awh, Vogel & Oh, 2006), as well as from the involvement of early perceptual cortical regions in short-term maintenance (Harrison & Tong, 2009; Lee, Kravitz & Baker, 2013).

1.4.2.1. Working memory and attention

Historically, cognitive constructs of attention and WM have been closely linked (Perez & Vogel, 2012; Vogel & Awh, 2008) and most WM theories would include attentional processes to a certain extent. This is not surprising since both phenomena are plagued by very similar capacity limits and are involved in the control of information processing (Awh et al., 2006; Mayer et al., 2007). This high similarity of the two constructs naturally led to an ongoing debate on whether attention and WM can be dissociated or actually they are the same complex phenomenon (Awh et al., 2006).

On the dissociation side of the debate, it has been pointed out that attention and WM are involved in different stages of information processing, namely, attention works at the perceptual stage as a "gatekeeper" directing relevant information to WM, whereas WM is involved in short-term information maintenance and processing, as well as active interfacing with LTM (Awh et al., 2006). Additional support for dissociation between WM and attention comes from numerous experimental findings indicating both separate functional mechanisms (Fougnie & Marois, 2006; Maxcey-Richard & Hollingworth, 2013), as well as underlying neuroanatomical structures or electrophysiological markers (Luck, 2014; Mayer et al., 2007). Finally, WM studies in patient populations, most notably vWM studies in schizophrenia, allow to clearly dissociate the two phenomena (Gold et al., 2006).

At the core of the "same-phenomenon" side of the debate lies the doubt as to the parsimony of a complex attention-WM system, where both phenomena would have overlapping

functions and limitations. The proponents of the epiphenomenal view of WM argues that all the core features of WM, such as information control mechanisms and limited capacity, can be explained by well-established knowledge about attention (D'Esposito & Postle, 2015; Postle, 2006; Kane & Engle, 2002).

The most influential and well-known state-based WM theory with attention at its core belongs to American psychologist Nelson Cowan. Essentially, his model comprises activated portions of unitary long-term memory and a focus of attention (FoA) (Cowan, 2001). Cowan provides a set of convincing arguments to state that the only capacity limited system among mental faculties is FoA, which would cause the information processing bottleneck in perception and short-term storage. The activated parts of LTM, on the other hand, are limited by the temporal decay function, lasting 2 to 30 seconds, and by inference from other perceptual or LTM items. According to Cowan, only the contents of FoA are accessible to awareness, making the assumptions of WM involvement in consciousness quite different from those of the multicomponent model (Cowan, 2001; Cowan, 2008; Cowan, 2011).

Despite the solid argumentation, the activation model of Cowan has been repeatedly challenged. For instance, Zhang and Luck (2009) argue that vWM does not manifest temporal decay function, as hypothesized by Cowan, but rather exhibits a sudden termination of items in its scope. Besides, Baddeley (2010) argues that Cowan's theory can be easily incorporated into the multicomponent model as a sub-theory explaining the relationship between the attentionally limited central executive and capacity limited episodic buffer.

1.4.2.2. Sensory recruitment theories

A further state-based theory has been proposed by another American psychologist Brad R. Postle (2006). He argues that working memory is an emergent property of the nervous system resulting from its potential to represent multimodal information by the flexibly deployable attention. Accordingly, attention is responsible for the coordinated recruitment of brain systems involved in perception, representation and action control. Short-term retention of any information, therefore, is related to sustained neural activity in the same brain regions that are responsible for managing that information in non-WM situations as well. Moreover, attention-based recruitment is a rather automatic process activating all available mental codes corresponding to an item when representing it in WM.

The sensory recruitment theory is far from being as well-known as those of multicomponent or attentional activation. Nevertheless, recent findings in neuroimaging and electrophysiological studies based on Multivariate Pattern Analysis (MVPA) provide some strong support to this theory (Postle, 2015). According to these studies, maintenance of visual information in visual WM tasks is accomplished in the early visual areas that have been "overseen" for decades due to the lack of sustained elevated activity (Harrison & Tong, 2009; Lee et al., 2013). Moreover, anatomical areas that were traditionally identified as vWM neural substrates, namely intraparietal sulcus (Todd & Marois, 2004), were not shown to contain representations of visual items (Harrison & Tong, 2009), striking a significant blow to many prominent more modular theories of vWM or its capacity. Consequently, the concept of sensory recruitment is likely to be incorporated into any novel vWM model or theory in the future.

1.5. Visual working memory capacity models

The most established and investigated property of vWM is its highly limited capacity. The average vWM capacity is estimated to be only about 3 to 4 items, though individual differences range from 1.5 to 5 (Vogel et al., 2005) or 6 (Cowan, 2001). Moreover, the individual capacity limits show some striking temporal stability and reliability across a range of different visual stimuli (Luck & Vogel, 1997). The reasons for such a stern limitation of vWM capacity are still unknown, though the speculations range from mathematical models to complex computational neuroscientific accounts (Cowan, 2001).

As a consequence, it is not surprising that vWM capacity has long been an intriguing subject stimulating such seminal works as those by Sperling (1960) or Miller (1956), as well as promoting the development of many influential theoretical models.

At the moment, the research of vWM capacity limits is dominated by two competing theoretical frameworks: discrete slot and continuous resource. Both models are supported by a vast body of research and literature, and any new evidence in favor of one model is usually followed by additional findings in favor of the other. As a result of this theoretical dichotomy, some newer vWM capacity models of dual, model-free or oscillatory nature have recently emerged.

1.5.1. Discrete-slot model

The origin of the discrete-slot visual WM capacity model can be traced back to a seminal paper of Luck and Vogel (1997). In a series of behavioral experiments, they explored vWM capacity for different visual features, such as color, orientation and size, as well as for their conjunctions. Although they applied a vast set of control studies trying to find any way to falsify their findings, all results pointed to the groundbreaking conclusion: visual WM capacity is limited, on average, to 3–4 integrated object percepts. Essentially, their model was based on the "all-or-nothing" principle: vWM can retain all information about 3 to 4 items, and any information about other items will be outside the scope of vWM (Fukuda, Awh & Vogel, 2010). Appropriately, their model has been termed *discrete-slot*, as any item in vWM would need to occupy one of the 3 to 4 available slots.

Solid support to this new model followed from many sides. First, the discovery of an electrophysiological vWM capacity marker, the Contralateral Delay Activity (CDA), which showed highly similar load sensitivity and dynamics to behavioral measurements (Vogel & Machizawa, 2004; Vogel et al., 2005). The CDA enabled reliable and sensitive probing into the maintenance phase of vWM with a high temporal resolution. Second, in the same year, Todd and Marois (2004) reported a load sensitive BOLD activation in bilateral intraparietal and intraoccipital sulci. Both electrophysiological and hemodynamic response markers reached asymptotic values at around 3–4 retained items and were highly correlated with individual vWM capacity limits.

Although the discrete slot model is fascinating by its simplicity and elegance, it has been struggling to accommodate the growing body of contradictory findings. The majority of these findings has come from studies manipulating visual information load and resolution, pointing to the fact that a simplistic "all-or-nothing" discrete-slot model cannot suitably accommodate complex visual items.

Another recent blow to the model has come from the multivariate pattern analysis studies of fMRI and EEG data, which showed that vWM maintenance is mostly performed by the early visual areas, hence, the previously believed load-sensitive role of CDA and intraparietal sulcus in vWM capacity is questionable (Harrison & Tong, 2009; LaRocque, Lewis-Peacock, Drysdale, Oberauer & Postle, 2013). However, some other studies do provide evidence for vWM maintenance expanding from visual areas to the parietal cortex as well (Christophel, Hebart & Haynes, 2012).

Despite the recent challenges, the discrete-slot framework has successfully demonstrated its

capability to change and adapt, thus it remains one of the most dominant models of vWM capacity.

1.5.2. Continuous resource model

The discrete slot model has been repeatedly challenged by the continuous resource vWM capacity model. According to this framework, vWM capacity is a highly limited resource, yet one that can be flexibly divided among all the items in a memory set (Bays & Husain, 2008; Ma et al., 2014). As a consequence, an increasing number of to-be-remembered items would be encoded with increasing internal noise and would lead to a decrease in performance in vWM tasks. The sources of this noise are cumulative and come from inherently noisy representations, gradual error accumulation over maintenance time, errors in binding objects to their features, interference from the probe set and similar (Ma et al., 2014). One of the core contributions to the continuous resource model came from the study of Alvarez and Cavanagh (2004). They used 5 stimuli classes of different complexity ranging from simple colors to shaded 3D cubes to show that vWM capacity was highly correlated with information load embedded in the stimuli. They obtained average vWM capacity measures from 1.6 to 4.4, depending on the stimuli complexity, and came to the conclusion that vWM is limited by the total amount of storable visual information rather than the number of discrete items.

An additional key contribution came from the study conducted by Bays and Husain (2008) who challenged the discrete slot model by shifting from a change-detection to a recall paradigm. Recall tasks usually are based on delayed-estimation method and employ a continuous response scale, for instance, a color-wheel in a task that requires remembering some colored squares (Luck & Vogel, 2013). The continuous response scale allows obtaining a distribution of response errors around the actual target value. The standard deviation, or width, of this distribution then corresponds to the precision with which an item was encoded (Bays & Husain, 2008; Luck & Vogel, 2013; Ma et al., 2014). Bays and Husain (2008) used continuous recall task both with colors and orientations and found that the recall precision dropped with every new item added to vWM, but there was no sharp cut off at the set size of 4, as predicted by the discrete slot model. In addition, while the discrete-slot model assumes that all the items within vWM capacity will be remembered with the same detail, P.M. Bays and M. Husain showed that the precision dropped significantly even with small memory sets, especially between one and two memory item sets.

Finally, it was demonstrated that precision of the stored item can be modulated by its salience or goal relevance at a cost of poorer memory for other stimuli in the set (Ma et al, 2014). These findings further supported the premise that vWM capacity can be dynamically and flexibly distributed among memory set items.

Nevertheless, these convincing findings were challenged by the discrete slot model supporters who showed that decreased performance with increased stimuli complexity can be attributed to the increased similarity between the test and probe items. They argued that the increased number of errors stem out from a failure in comparing test and probe arrays rather than a failure in storing a limited number of items (Vogel & Awh, 2008).

1.5.3. Dual models

A growing body of research and findings supporting both discrete-slot and continuous resource models has led to the development of a novel dual approach to vWM capacity.

The dual vWM models first emerged from the discrete-slot proponents in an effort to explain and incorporate findings regarding stimuli complexity and resolution. These models postulated the existence of two independent mechanisms controlling vWM capacity: a discrete capacity for a limited number of items, and a continuous flexible one for item resolution.

The interaction and underlying mechanisms of these two systems have not been consensually defined yet. For instance, Allon, Balaban and Luria (2014) proposed in their dual model that each visual hemifield is constrained by a discretely limited capacity, in accordance to the discrete-slot model, but at the same time, that within each visual hemifield, the memory resources are being shared in a continuous and flexible manner. Fukuda et al. (2010), on the other hand, proposed a two-factor model where the capacity – limited by the number of items – and resolution – limited by the information load – are two independent vWM properties. Similarly, Gao et al. (2009) in his dual approach to vWM capacity used a notion of two independent capacity mechanisms. He argued that a fixed number of representations can be stored only in a coarse form, while the capacity for fine-detail information about stimuli is limited separately.

Despite the lack of general consensus regarding dual vWM models, their use has been growing and they are likely to transform into one of the dominant vWM capacity theories in the future.

1.5.4. Computational oscillatory hypothesis

A rather different approach to a limited vWM capacity comes from a large body of electrophysiological studies in humans and animals. Tackled by computational neuroscientists, these studies inspired vWM models based on neural networks with recurrent feedback loops (Luck & Vogel, 2013). These types of models can easily accommodate notions of persistent memories, observed elevated neural activity and generated oscillatory patterns.

One of the strongest line of support to computational vWM capacity models comes from repeatedly observed oscillatory signatures in vWM tasks. First, load sensitive sustained phase synchrony between frontoparietal and visual areas has been observed in alpha, betta and gamma ranges (Howard et al., 2003; Palva, Monto, Kulashekhar & Palva, 2010). Moreover, this synchrony could successfully predict individual vWM capacity (Palva et al., 2010). Second, vWM maintenance is marked by suppressed activity in a broad range of frequency bands, from theta/low alpha (5–9 Hz) up to high gamma (50–150 Hz) (Palva, Kulashekhar, Hämäläinen & Palva, 2011). However, load-sensitive increase in theta activity in frontal regions (Jensen & Tesche, 2002; Sauseng et al., 2010), as well as increase in gamma power (Lisman & Jensen, 2013) have been also reported.

Although it is broadly accepted that different neural oscillations reflect different vWM processes, the precise role of each oscillatory activity is still debated. It is hypothesized that attentional and executive vWM processes may rely on alpha, beta and gamma activities, while the maintenance is underlain by theta and gamma oscillations (Palva et al., 2011).

Taking into account all these findings, Lisman and Buzsáki (2008) proposed a powerful computational vWM capacity model based on theta-gamma coupling (Lisman, 2010; Lisman & Jensen, 2013). According to this model, each item from a memory set is encoded by a different (though possibly overlapping) neural population. To avoid interference, each of these neural populations fires at different gamma cycles. To ensure the temporal stability of the representations, all of these gamma cycles are embedded at a different phase of a theta cycle. As a result, with each repeated oscillation of one theta cycle, a series of gamma cycles will recur. It has been estimated that one theta cycle can contain up to 7 gamma cycles (Lisman & Buzsáki, 2008), though 3 to 4 is a more likely estimation (Fukuda et al., 2010). Similar frequency coupling, yet between 32 Hz and 3 Hz, has been observed in prefrontal cortices of monkeys memorizing 2 items. The information about each item was encoded at

significantly different phases of the low frequency oscillation, providing additional support to an argument that this could be a mechanism enabling disambiguation of information in STM (Siegel, Warden & Miller, 2009).

Theta-gamma coupling is a highly attractive hypothesis that was embraced by different more theory-driven vWM capacity models (e.g. Luck & Vogel, 2013; Ma et al, 2014). It is argued that the role of this coupling mechanism could extend from vWM to any type of interregional transmission of multi-item messages (Lisman & Jensen, 2013). Nevertheless, more research is necessary, as the model keeps struggling to translate findings from highly precise single-unit animal recordings to lower precision findings in humans (Fukuda et al., 2010).

1.6. Visual WM capacity measurement

Over the years, limited STM and, later, WM capacity has been established for a variety of different stimuli, such as visual, auditory, tactile and similar. However, the precise estimates would vary substantially depending both on the stimulus modality and used paradigm. Therefore, it is not surprising that an effort to standardize WM capacity measurements emerged decades ago. One of the first attempts was made by Miller in 1956 who had been inspired by the at-the-time dominant information theory. He used a bit as the smallest memory capacity unit corresponding to the binary differentiation of two stimuli. However, a bit as a measurement unit seemed to overestimate the capacity measures and led to a large variation in capacity estimates.

A big step forward in standardization of vWM capacity measures was made by Luck and Vogel (1997) in their formative study, where they popularized the capacity index K for a change-detection task. It was followed by the error distribution-based capacity estimates for continuous recall tasks. Finally, an electrophysiological vWM capacity marker, the Contralateral Delay Activity (CDA), has been developed and used to both assess vWM capacity and its dynamic control.

1.6.1. Behavioral measurements

The most commonly used behavioral vWM capacity measurement is the index K. It was popularized by S. Luck and E. Vogel together with their discrete-slot vWM capacity model in 1997. Essentially, the index K is an estimate of the difference between responding to the

actual change (hit rate) and mistakenly perceived change (false alarm), adjusted to the size of the memory set. There are two formulas for the estimation of K that are often used arbitrarily by different research groups (Rouder, Morey, Morey & Cowan, 2011).

As Rouder et al. (2011) summarizes, the Pashler's variant of the formula is appropriate to use in the whole-display variant of the change-detection task. In a whole-display task, both the to-be-remembered memory set and the test probe have the same number of items, noted as N. In this task, the observer has to decide if any of the items from the set of size N has changed:

$$K = N\left(\frac{Hit\ Rate - False\ Alarm}{1 - False\ Alarm}\right)$$

The Cowan's variant of the formula, according to Rouder et al. (2011), should be used in a single-probe variation of the change detection task. In this task, the observer is presented with a memory set of N items, however, the test probe consists only of one item. In this case, the observer has to decide whether that one item was present in the initial memory set or not:

$$K = N(Hit\ Rate - False\ Alarm)$$

In general, single-probe based K yields a higher vWM capacity estimate, therefore, it is of crucial importance to use the appropriate K formula in order to avoid inflation of the estimates.

Behavioral index K can be applied to various change-detection tasks. However, growing popularity of the continuous resource vWM capacity model and delayed recall tasks required a novel way to measure vWM capacity. In recall tasks, both the stimuli and the response are on a continuous scale, therefore a binary accuracy measurement (correct/incorrect) is replaced by a more appropriate measurement of distance: how close to the correct target value is the response (Luck & Vogel, 2013).

In continuous recall tasks, observer responses are modelled by two distributions: a uniform distribution for the out-of-memory items which corresponding to random guessing, and a normal distribution of answers around the actual value of the memory item (Bays & Husain, 2008; Luck & Vogel, 2013; Ma et al., 2014). Consequently, a more precise internal

representation of the memory item would lead to a smaller standard deviation of the response distribution.

It is argued that this sum of two distributions is a more appropriate and accurate model for response behavior (Ma et al., 2014). Moreover, it allows to define the probability of an item being held in memory. The vWM capacity estimate, in this case, is this probability multiplied by the set size (Luck & Vogel, 2013).

Although probability-based capacity estimates were developed by the proponents of the continuous resource vWM model, they have been adopted also by the discrete-slot and dual model supporters (e.g. Zhang & Luck, 2011). In these cases, it is argued that the uniform random distribution reflects the discrete memory slots, while the normal distribution reflects the separate vWM storage mechanism for resolution.

1.6.2. Electrophysiological measurements: Contralateral Delay Activity

It has been long known that every endogenous and exogenous stimulus leaves an electrophysiological print. Under certain conditions, these prints are large enough to be recorded on the scalp by electroencephalogram (EEG). Event-related potentials (ERPs), time-locked voltage fluctuations in response to a stimulus, have been established for a vast range of processes and stimuli, constituting a large field on its own. Therefore, it is not surprising, that EEG was introduced into vWM research early in the theoretical formation of this phenomena.

From the beginning, it has been noted that vWM tasks are accompanied by a Negative Slow Wave (NWS) at temporal-parietal electrode sites (Drew, McCollough & Vogel, 2006; Luck, 2014). The amplitude and topography of this slow ERP component could be modulated by different properties of the task, such as stimulus type or difficulty. However, the NWS was notoriously difficult to interpret, as it potentially reflects a variety of different processes, such as attention, effort, or general level of arousal (Drew et al., 2006; Luck, 2014).

In 2004 Vogel and Machizawa came up with an idea how to overcome the shortcomings of the NWS. They used a modified bilateral change-detection task with two sets of stimuli presented on each side of the screen. A preceding cue indicated the relevant side of the screen that the observer was asked to memorize. Vogel and Machizawa applied a well-known contralateral control method (Gratton, 1998), which utilizes the lateralized organization of the visual system. According to Gratton (1998), experimental variance in visual experiments may be explained by the main effect of condition, hemisphere, and their

interaction. The interaction term can be isolated by subtracting the electrical activity in the ipsilateral brain hemisphere from the contralateral one. As a result, all non-lateralized activity, such as early visual processing, noise and some endogenous variables are cleaned away from the process of interest.

Subsequently, a vWM-related ERP component was isolated and termed Contralateral Delay Activity (CDA) due to its contralateral organization and presence during the vWM maintenance phase (Vogel & Machizawa, 2004). The CDA is a slow negative wave emerging at around 200–275 ms after the onset of a memory set, following the N2pc component (Emrich et al., 2009; Perez & Vogel, 2012; Vogel & Machizawa, 2004). It reaches its maximum amplitude at around 450 ms after the onset of the memory set and remains present up to the probe, slowly decreasing due to the increasing activity at the ipsilateral electrodes. The CDA has a posterior and lateral distribution with maximum amplitude over P3/4, PO3/4, P7/8, O1/2 and PO7/8 electrode sites (Perez & Vogel, 2012).

The locus of the CDA generator is unknown, although the posterior distribution is consistent with the fMRI identified IPS (Perez & Vogel, 2012). Until recently, the underlying mechanism of the CDA was believed to be the asymmetric oscillatory activity in the alpha range (Jensen, van Dijk & Mazaheri, 2010; van Dijk, van der Werf, Mazaheri, Medendrop & Jensen, 2010), however, lately, this theory has been challenged (Nikulin, Linkenkaer-Hansen, Nolte & Curio, 2010).

Luria et al. (2016) notes that activity similar to the CDA has been observed in non-vWM paradigms as well. Depending on the context, it receives a variety of names, such as Contralateral Negative Slow Wave (CNSW), Posterior Contralateral Negativity (PCN) or Contralateral Search Activity (CSA). As a result, a CDA-like activity is believed to reflect more general vWM function than that of simple maintenance.

The most important property of the CDA is its sensitivity to memory load. It has been shown that the CDA amplitude increases monotonically with a memory set but reaches asymptotical amplitude at around 3–4 items, similarly to the behavioral capacity estimates (Vogel & Machizawa, 2004; Vogel, McCollough & Machizawa, 2005). The CDA has been shown to reflect object identity rather than spatial location (Gao et al., 2011), yet it is also sensitive to object complexity (Gao et al., 2009). Moreover, this ERP component reflects the same individual differences as behavioral capacity measurements, making it a valuable tool in correlational studies. Most importantly, the CDA allows dynamic online monitoring of the number of items in vWM, thus opening the door to the investigation of vWM capacity control mechanisms.

1.7. Dynamic control mechanisms of visual WM capacity

It has been commonly accepted that vWM capacity is a key bottleneck in visual information processing. As a result, researches have long been interested in mechanisms and strategies that would allow using this extremely limited yet highly important system in an efficient way (Awh et al., 2006). Possible vWM capacity control mechanisms have been studied and proposed for two vWM stages, namely, encoding and maintenance.

One way to use vWM capacity efficiently relies on encoding only task relevant information. Vogel et al. (2005) probed this possible control mechanism with a variation of change-detection task. In the task, he used memory sets that consisted of 2 and 4 items (baseline conditions), and a memory set that consisted of 2 to-be-remembered items and 2 to-be-ignored distractors. The behavioral memory capacity index K was used to divide the participants in low-performance, or low-capacity, and high-performance, or high-capacity, groups. The average CDA activity in each group revealed an intriguing picture. In the low-capacity group the CDA amplitude in the distractor condition was very close to the CDA amplitude in the baseline condition of 4 items, whereas in the high-capacity group it was close to the CDA amplitude in the baseline condition of 2 items. The authors interpreted this as a strong evidence that the low-performance group did not actually has a smaller vWM capacity but rather a poorer resistance to task-irrelevant stimuli that would take up their vWM space. Based on this study, they introduced filtering efficiency (FE) as an important index of vWM capacity control at the encoding stage.

Efficient encoding during vWM tasks may be sufficient in well-defined and simplistic laboratory settings, however, in real life situations there is a necessity for control mechanisms that would allow updating vWM content dynamically. One of such mechanisms, appending new items into vWM during the maintenance phase, has been reported by Vogel et al. (2005). He showed that both low-performance and high-performance groups were able to append new memory items, however, the low-performance group could not resist appending task-irrelevant items.

As more and more has been learned about remembering in vWM, its antagonist, forgetting, has come to the research spotlight. In many models it is assumed that the contents of vWM can be eliminated either by passive temporal decay or by overwriting them. However, Zhang and Luck (2009) showed that vWM representations do not exhibit passive decay behavior but rather a sudden termination. This finding has stimulated further interest in the

mechanisms of vWM content elimination.

The ability to actively remove partial content from vWM capacity has been studied with paradigms employing retro-cues. Essentially, these tasks first present a memory set followed by a cue (the retro-cue) indicating which part of the memory set should be remembered or forgotten. Behavioral results indicate that retro-cues have a significantly positive effect on performance (Maxcey-Richard & Hollingworth, 2013; Maxcey & Woodman, 2014; Williams, Hong, Kang, Carlisle & Woodman, 2013), with directed-remembering cues working slightly better than directed-forgetting cues (Williams & Woodman, 2012). This beneficial effect was established both for spatial and color cues (Pertzov, Bays, Joseph & Husain, 2013), as well as both for items in a single visual hemifield (Kuo, Stokes & Nobre, 2012) and in the entire visual field (e.g. Williams & Woodman, 2012).

Electrophysiological recordings during the vWM tasks confirmed behavioral results. It has been shown that bilateral memory sets followed by a lateralized retro-cue lead to the emergence of the CDA (Eimer & Kiss, 2010; Maxcey & Woodman, 2014; Williams & Woodman, 2012). This strongly indicates that the observers were able to dynamically shift their attention and memory resources from the entire visual field to a single hemifield. Kuo et al. (2012), on the other hand, used the CDA to probe forgetting in a single hemifield. He demonstrated a significant reduction in the amplitude of the CDA, accompanied by the significantly improved behavioral performance after retro-cueing the upper or lower quadrant in one side of the screen.

The precise underlying mechanisms of active content elimination are not clear. It is speculated that retro-cues may lead to a higher fidelity representation of the remaining items and to a lower probability of sudden termination of these representations (Ma et al., 2014; Pertzov et al., 2013; Williams et al., 2013).

1.8. Research question and hypotheses

The goal of this study was to investigate dynamic elimination of task-irrelevant memory representations as one of the vWM capacity control mechanisms. The study focused on two possible mechanisms: discarding representations within a single-hemifield, and discarding an entire visual hemifield (i.e. elimination of all representations from one hemifield).

To this purpose, the study accommodated 5 experimental conditions divided among two experiments, which enabled key comparisons and hypotheses testing:

Keep 2: Participants are asked to remember orientations of 2 rectangles on the cued side of the screen and keep both of them throughout the trial. This is a baseline condition used to define the individual CDA amplitude with a small memory load of two items.

Keep 4: Participants are asked to remember orientations of 4 rectangles on the cued side of the screen and keep all of them throughout the trial. This is a baseline condition used to define the individual CDA amplitude with a large memory load of four items.

Drop 2: Participants are asked to remember orientations of 2 rectangles on the cued side of the screen. The retro-cue indicates one item that should be maintained for the probe. This is an experimental condition designed to probe the change in the CDA amplitude when compared to Keep 2. This change is associated with elimination of the task-irrelevant representation within a single hemifield.

Drop 4: Participants are asked to remember orientations of 4 rectangles on the cued side of the screen. The retro-cue indicates two items that should be maintained for the probe. This is an experimental condition designed to probe the change in the CDA amplitude when compared to Keep 2 and Keep 4. This change is associated with elimination of the task-irrelevant representations within a single hemifield.

Cue-after-target (CAT): Participants are asked to remember orientations of 2 rectangles on the left and 2 rectangles on the right side of the screen. The retro-cue indicates 2 items that should be maintained for the probe, either on the left or on the right side of the screen. This is an experimental condition designed to probe the change in the CDA amplitude when compared to Keep 2. This change is associated with elimination of the entire task-irrelevant visual hemifield.

Based on the abovementioned conditions, 2 sets of the hypotheses were formulated:

Hypothesis 1: Elimination within a single-hemifield (Figure 1):

The null hypothesis (H0): After the retro-cue, the average CDA amplitude in the Drop 2 and Drop 4 conditions will not be significantly different from the average CDA amplitude in baseline conditions Keep 2 and Keep 4, indicating no significant reduction in vWM load that would be expected to follow the elimination of task-irrelevant representations.

The alternative hypothesis (H1): After the retro-cue, the average CDA amplitude in Drop 2 and Drop 4 conditions will be significantly smaller from the average CDA amplitude in baseline conditions Keep 2 and Keep 4, indicating significant reduction in vWM load that would be expected to follow the successful elimination of task-irrelevant representations.

The average behavioral capacity index K in conditions Drop 2 and Drop 4 is expected to be the same as in conditions Keep 2 and Keep 4, respectively, as it should only be influenced by the initial memory set size (2 or 4) which is the same for both types of tasks.

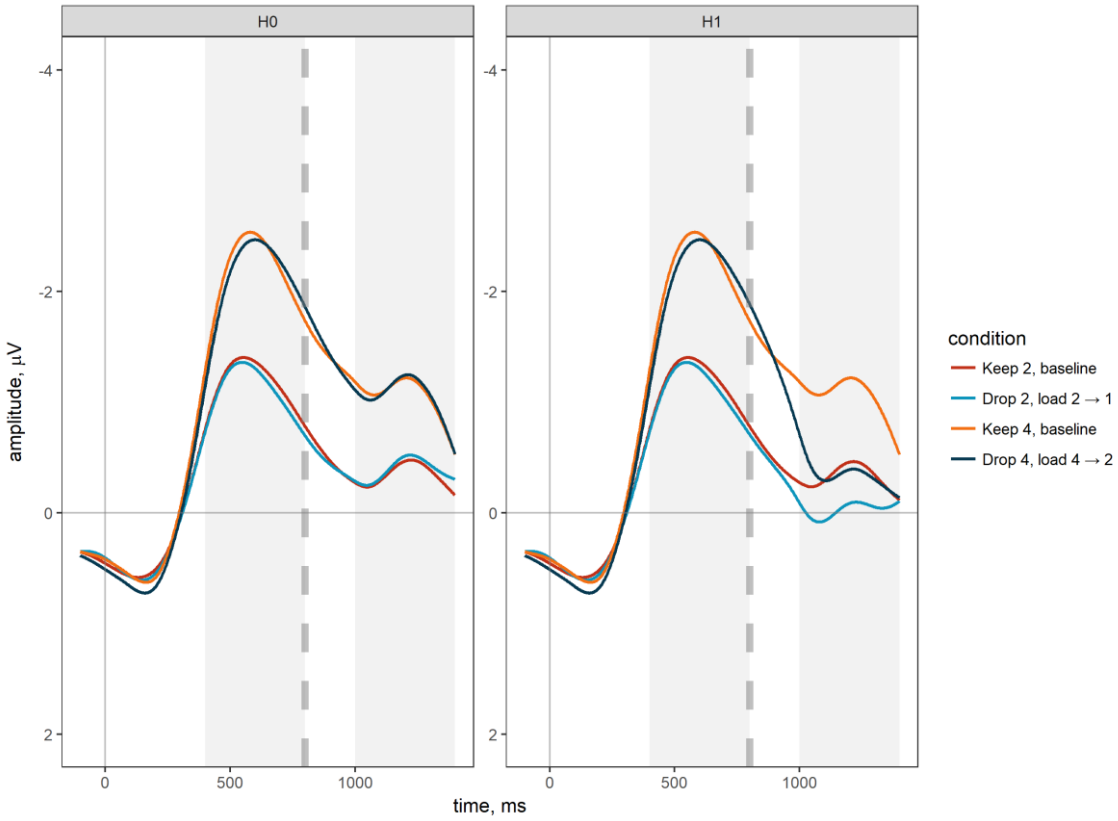

Figure 1. Null and alternative hypotheses regarding average CDA amplitude changes following elimination of task-irrelevant memory representations within a single hemifield. The gray dashed line indicates the onset of the retro-cue.

Hypothesis 2: Elimination of an entire visual hemifield (Figure 2):

The null hypothesis (H0): After the retro-cue, the average CDA amplitude in the Cue-after-target condition will not be significantly different from the average baseline EEG activity, indicating no significant lateralization of the internal memory representations that would be expected to follow the elimination of an entire visual hemifield.

The alternative hypothesis (H1): After the retro-cue, the average CDA amplitude in the Cue-after-target condition will significantly decrease from the baseline and will reach the average amplitude in the baseline condition Keep 2, indicating significant lateralization of the internal memory representations that would be expected to follow the successful elimination of an entire visual hemifield.

The average behavioral capacity index K in Cue-after-target condition is expected to be the

same as in a baseline condition Keep 4, as it should only be influenced by the size of the initial memory set, which is 4 in both conditions.

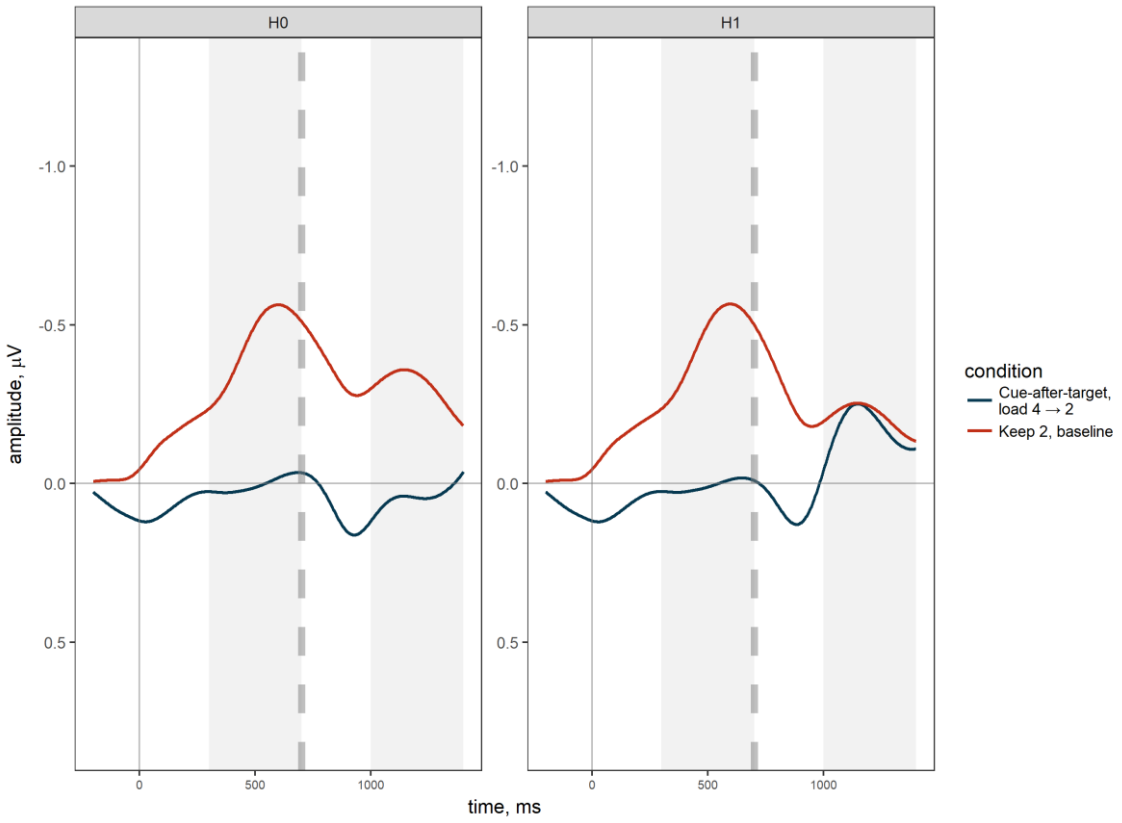

Figure 2. Null and alternative hypotheses regarding average CDA amplitude changes following elimination of an entire visual hemifield. The gray dashed line indicates the onset of the retro-cue.

Experiment 1 was designed to test the single-hemifield hypothesis and comprised four experimental conditions: two baseline conditions (Keep 2 and Keep 4) and two test conditions (Drop 2 and Drop 4).

Experiment 2 was designed to test both the whole-hemifield hypothesis and a single-hemifield hypothesis with a slightly changed task design and timing. It comprised four experimental conditions: two baseline conditions (Keep 2 and Keep 4), as well as Cue-after-target and Drop 4 conditions.

2. Methods

2.1. Experiment 1

Participants

Twenty-four female participants (23 right-handed) with an average age of 20.0 years (*SD* = 4.17) were recruited at Faculty of Arts, University of Ljubljana, between February and June, 2016. The participants received academic credits for their participation. The experiment was approved by the Faculty of Arts Ethics Committee at Faculty of Arts, University of Ljubljana, all participants were informed about the purpose and procedure of the experiment, and signed an informed consent form prior to participation.

EEG recordings and preprocessing

EEG recordings were performed with a 64 channel actiCAP® (Brain Products GmbH) and Brain Vision Recorder system (version 1.20.0701, © 2000–2014 Brain Products GmbH). FCz was used as a reference channel. The data was filtered with a low cutoff time constant of 10 s and a high cutoff of 250 Hz, and sampled at 500 Hz. During recordings, electrode impedance was kept below 25 kΩ as recommended by the manufacturer (Brain Products GmbH, 2013).

The recordings were performed in a separate EEG-dedicated room. Participants were sitting in a comfortable armchair with a stimulus presentation screen (BenQ XL2420T, © BenQ Corporation) around 1.1 meters in front of them. A response box (RB-540, © Cedrus Corporation) was used to perform the task. The participants were monitored, but not recorded, through a video camera (LifeCam Studio, © Microsoft Corporation) to ensure communication.

EEG data was preprocessed using a MATLAB-based (©MATLAB, The MathWorks, Inc) in-lab pipeline with a set of customized EEGLAB (Delorme & Makeig, 2004) and ERPLAB (Lopez-Calderon & Luck, 2014) functions.

First, the data was re-referenced to the average reference and epoched into 5.8 second chunks around the presentation of the target memory set. The data was then visually inspected for large artifacts. Both epochs containing large artifacts and corrupted channels were removed from the signal. AMICA (Palmer, Kreutz-Delgado & Makeig, 2012), a subtype of independent component analysis, was used to isolate and remove eye-blinks after which the missing channels were back-interpolated. The epochs were additionally cleaned of line noise using the CleanLine algorithm (Mullen, 2012), and clamped using the

beginning and end data points of an epoch in order to remove slow trends.

Stimuli

The task and the stimuli were programmed with PsychoPy v1.83.04 (Peirce, 2007).

The sets of stimuli comprised red [RGB: 255,0,0] and blue [RGB: 0,0, 255] rectangles (width 20 p, height 60 p) of 4 orientations (0º, 45 º, 90 º, 135 º), similar to those used by Vogel et al. (2005).

Task design

The design of Experiment 1 is outlined in Figure 3.

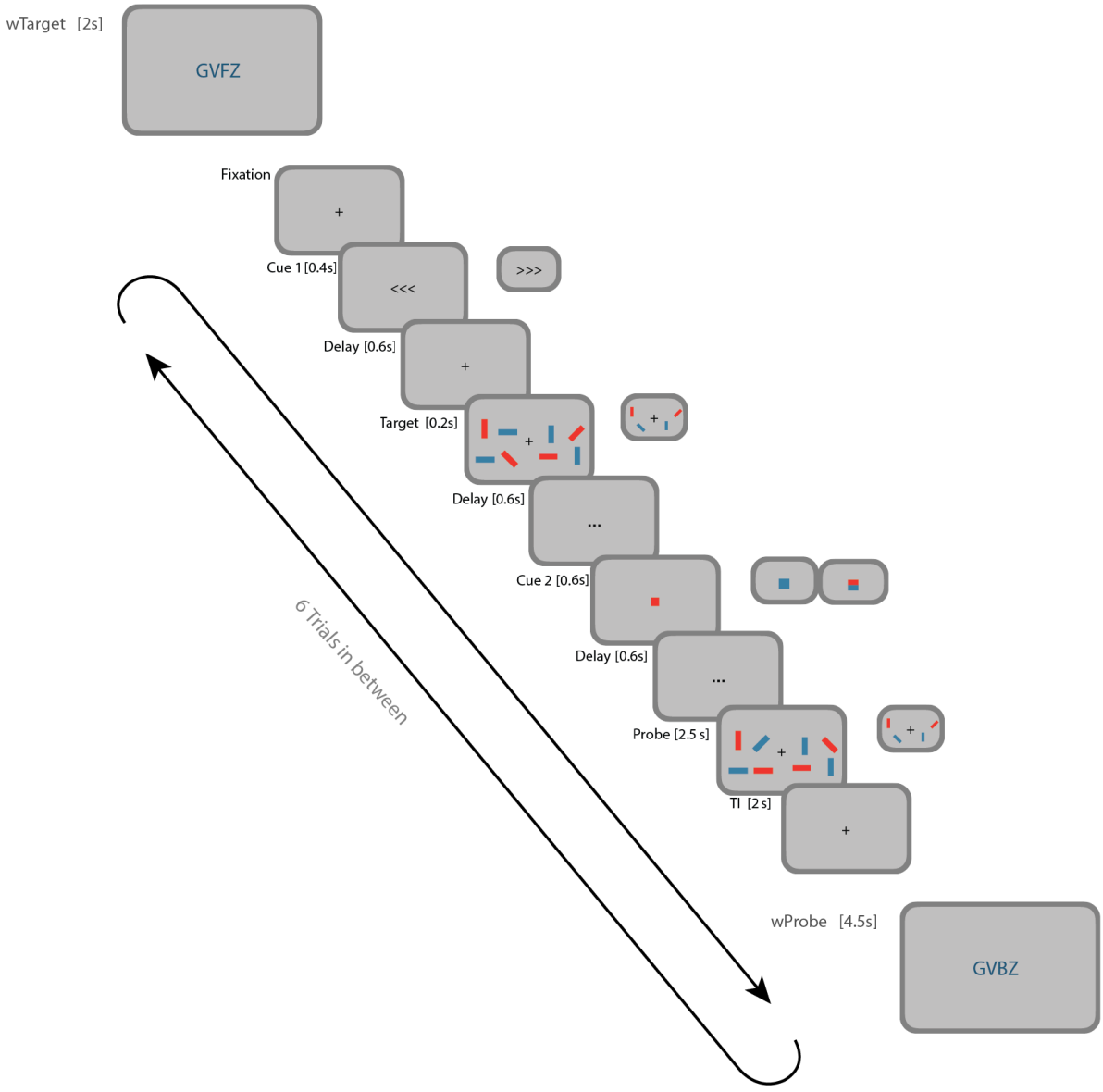

Figure 3. The task design of Experiment 1.

The Experiment 1 comprised a verbal suppression task and a vWM change-detection task.

The verbal suppression task was used to control and eliminate the possible influence of verbal working memory on visual WM performance. The task consisted of 4 to-be-remembered letters displayed for 2 seconds at the beginning of the block. It was then followed by 6 trials of vWM change-detection task. At the end of the block, participants were again shown 4 letters for 4.5 seconds and had to indicate whether they were the same or different.

The vWM change-detection task started with a fixation cross which was followed by the directional cue, a black arrow pointing left or right, for 0.4 seconds. This cue indicated on which side of the screen participants should focus while keeping the eyes on the center of the screen. After a short delay period, participants were presented with a target memory set for 0.2 seconds. The target stimuli comprised 2 or 4 red and blue rectangles on the cued side of the screen whose orientations participants were asked to remember. After the delay period, participants were shown a directed-remembering retro-cue for 0.6 s. The cue was a square of red, blue or half-red-half-blue color. The retro-cue indicated which initially memorized rectangles the participants should keep in memory: only the red ones, only the blue ones, or both the red and the blue ones (the whole initial memory set). After a delay, a probe of the same size as the initial memory set was shown. Participants had to make a binary decision by a button-press on whether the rectangles on the cued side and of the cued color have changed their orientation. The detailed timeline of the task is present in Figure 4.

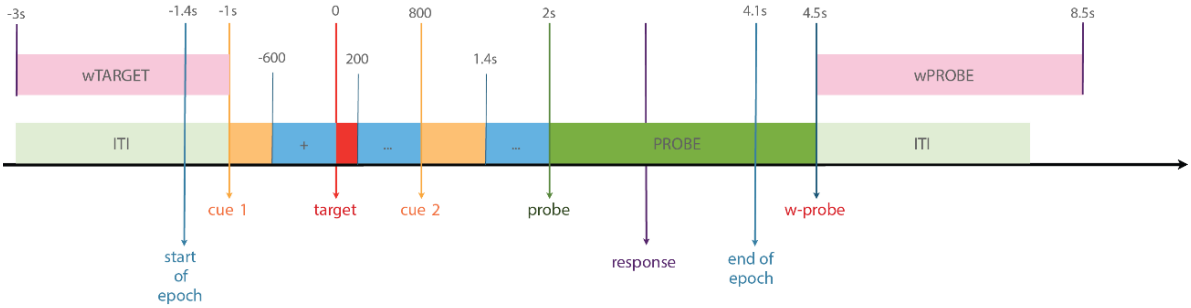

Figure 4. The detailed timeline of Experiment 1.

The four different aforementioned conditions (section 1.8. *Hypotheses*) were used in Experiment 1:

Keep 2: Participants were asked to remember orientations of 1 red and 1 blue rectangle on the cued side of the screen. The retro-cue was a half-red-half-blue square and indicated that participants should keep remembering both rectangles for the probe.

Keep 4: Participants were asked to remember orientations of 2 red and 2 blue rectangles on

the cued side of the screen. The retro-cue was a half-red-half-blue square and indicated that participants should keep remembering all four rectangles for the probe.

Drop 2: Participants were asked to remember orientations of 1 red and 1 blue rectangle on the cued side of the screen. The retro-cue was a red or a blue square and indicated that participants should keep remembering the orientation of only one rectangle of the cued color (red or blue).

Drop 4: Participants were asked to remember orientations of 2 red and 2 blue rectangles on the cued side of the screen. The retro-cue was a red or a blue square and indicated that participants should keep remembering the orientations of two rectangles of the cued color (red or blue).

The experiment 1 comprised 15 blocks of 48 trials (8 verbal suppression sub-blocks in each block), 720 trials in total. Before the actual task, participants performed 2 training blocks of 7 trials. The task took approximately 1.5 hours (around 2.5 for the whole experiment procedure).

Computation of the index K and CDA

Behavioral data was extracted from the log files using a customized Python script. Memory capacity index K was calculated using the Pashler's variant of the formula for the whole-display change-detection task (Rouder et al., 2011):

$$K = N * (\frac{(HitRate - FalseAlarm)}{(1 - FalseAlarm)})$$

where *N* corresponds to the number of items in the initial memory set (2 or 4).

For the ERP analysis, the CDA was computed as the average difference between the contralateral and ipsilateral (in regard to the memorized stimuli) EEG activity for each pair of channels and 4 conditions separately. The signal was baseline corrected and low-pass filtered at 60 Hz. A region of interest (ROI) for the analysis was defined by the topological map of the CDA in the Keep 4 condition, and comprised the average waveform of PO7/8, P5/6, O1/2 and P7/8 channels.

Two Times of Interest (TOIs) were chosen for the analysis. The first TOI corresponded to

the classic vWM storage-related CDA peak activity (Perez & Vogel, 2012) and was between 400 and 800 ms, while the second TOI corresponded to the CDA activity after the retro-cue and was between 1000 and 1400 ms.

Mean amplitudes of the average channel between the two latencies of each TOI were extracted for each participant and used in further statistical analysis.

Statistical analysis

Statistical analysis and visualization of the results was performed in R (© Free Software Foundation, Inc) and RStudio (© RStudio, Inc).

Analysis of Variance (ANOVA) was used to compare the 4 conditions in terms of their average capacity index K and mean CDA amplitude, while the differences in accuracy were estimated using binomial logistic regression.

In addition, Pearson's product correlation was used to estimate the relationship between the CDA amplitude difference between load 4 and load 2, and the memory capacity index K at Keep 4 condition.

Finally, the Mass-Univariate-Toolbox (Groppe et al. 2011) was used to detect reliable CDA differences from the baseline in each condition, as well as the differences between all pairs of conditions. Analysis was performed for all time-points of two TOIs and all left side electrodes, as well as the average electrode (ROI). Right side and midline electrodes were excluded due to their redundant information and in order to increase the power of the analysis.

2.2. Experiment 2

Participants

Thirty-three participants (29 females; 32 right-handed) with an average age of 21.6 years (*SD* = 3.70) were recruited between October and December, 2016. The participants either received academic credits for their participation, when applicable, or participated on a voluntary basis. The experiment was approved by the Faculty of Arts Ethics Committee at Faculty of Arts, University of Ljubljana, all participants were informed about the purpose and procedure of the experiment, and signed an informed consent form prior to participation.

EEG recordings and preprocessing

EEG recordings were performed with the same equipment, software and parameters as in Experiment 1. The preprocessing pipeline was the same with the sole difference of a shorter epoch length of 4.2 seconds.

During the preprocessing stage, three participants were identified and excluded from further statistical analysis due to the large amount of muscle artifacts.

Eye-tracker

Experiment 2 was aided by a mobile eye-tracking system Eye Tribe (before 2016 © Eye Tribe Co; after 2016 © Oculus), which was placed under the stimulus presentation screen in front of the participant. The eye-tracking system was used to detect eye-movements and blinks at critical moments during the task (e.g. presentation of the cue or target). However, the system could not be used in about half of the recordings due to calibration difficulties. In these cases, the experiment was run without the eye-tracker, but participants received additional reminders to keep their gaze at the center of the screen. Moreover, a video camera was used during the training blocks to monitor and provide feedback to the participants on their eye-movements.

Stimuli

Experiment 2 used stimuli of the same colors, size and orientations as Experiment 1, with the addition of black [RGB: 0,0,0] color.

Task design

The design of Experiment 2 is outlined in Figure 5.

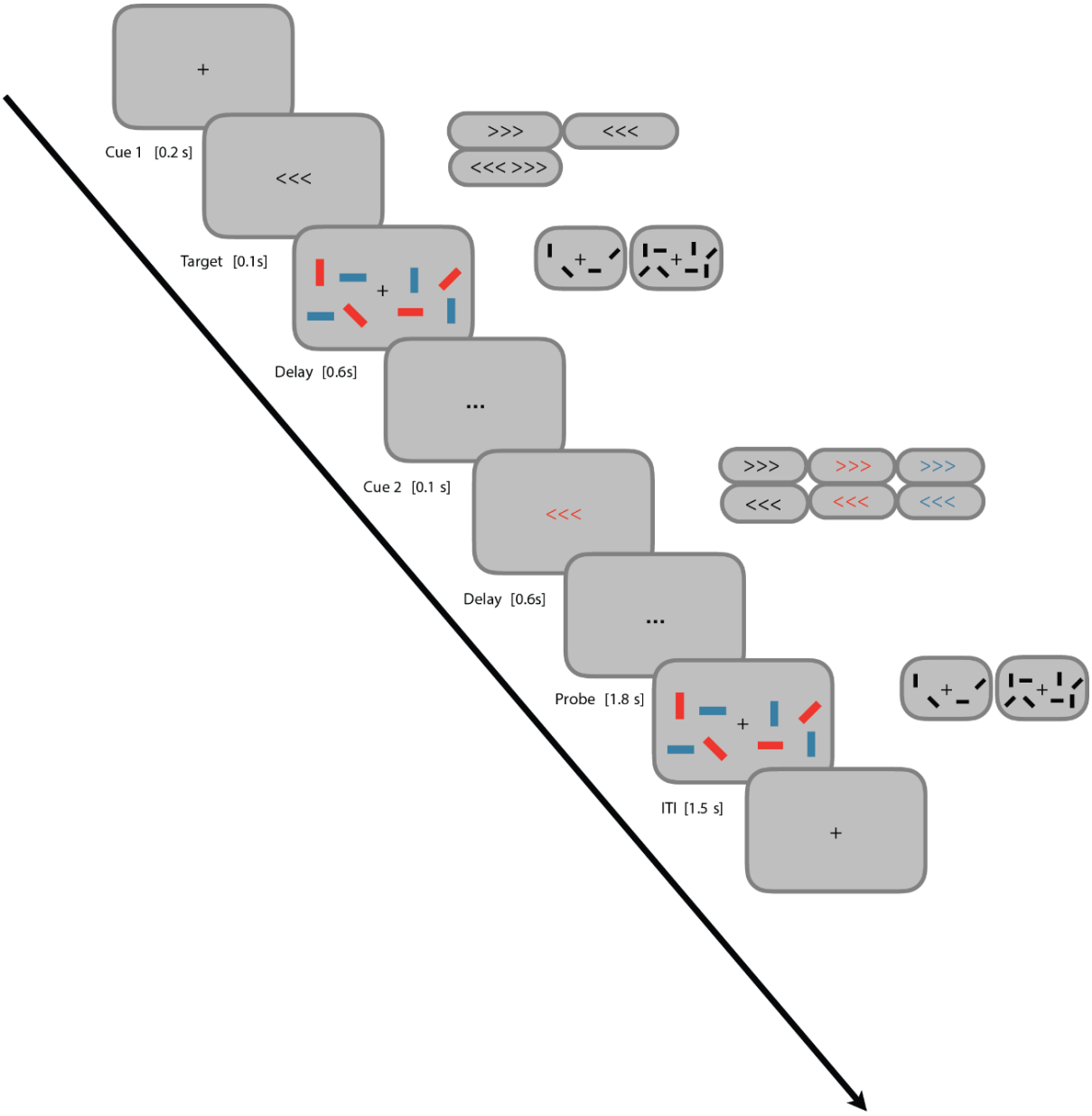

Figure 5. The task design of Experiment 2.

The Experiment 2 comprised only a visual WM change-detection task. The verbal suppression task was omitted as verbal WM has been shown to be independent from the performance of visual WM tasks (Luck & Vogel, 1997; Todd & Marois, 2004).

The task started with a fixation cross followed by the directional cue, a black arrow pointing left, right or to both sides, for 0.2 seconds. The arrow indicated to the participants on which side of the screen they should focus while keeping the eyes on the center of the screen. In case of an arrow pointing both to the left and right, participants were asked to focus on both sides of the screen. Immediately after the directional cue, participants were presented with a target memory set for 100 milliseconds. The target stimuli comprised 2 or 4 rectangles on the cued side of the screen. In case of bi-directional cue, the target memory set comprised 2

rectangles on each side of the screen (4 in total). Participants were asked to remember orientations of the rectangles on the cued side of the screen. After a delay period of 0.6 s the participants were shown a directed-remembering retro-cue for 0.1 s. The cue employed either spatial cueing (a black arrow pointing left or right) or color cueing (a red or blue arrow). After another delay period of 0.6 seconds, a probe of the same size as the initial memory set was shown. Participants had to make a binary decision by button-press on whether any of the rectangles on the cued side and/or color have changed. The detailed timeline of the task in Experiment 2 is outlined in Figure 6.

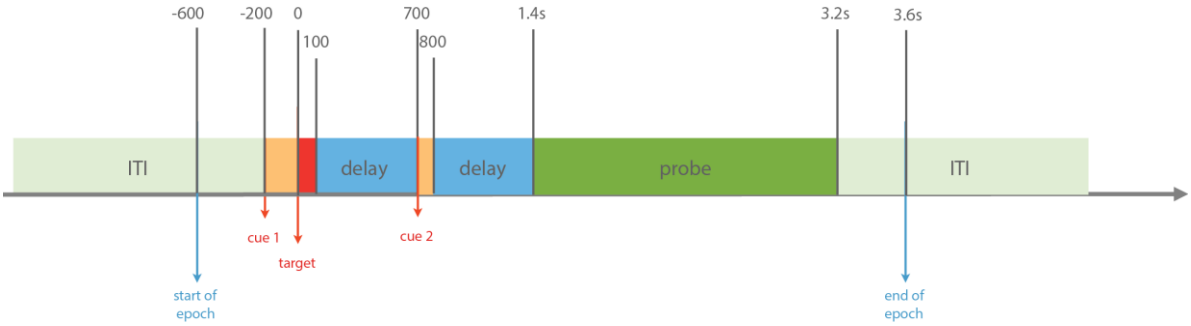

Figure 6. The detailed timeline of a trial in Experiment 2.

The four different aforementioned conditions (section 1.8. *Hypotheses*) were used in Experiment 2:

Keep 2: Participants were asked to remember orientations of 2 black rectangles on the cued side of the screen. The retro-cue was a black arrow pointing to the same side of the screen as the initial cue, indicating that participants should keep remembering the same 2 rectangles for the probe.

Keep 4: Participants were asked to remember orientations of 4 black rectangles on the cued side of the screen. The retro-cue was a black arrow pointing to the same side of the screen as the initial cue, indicating that participants should keep remembering the same 4 rectangles for the probe.

Cue-after-target: Participants were first asked to remember orientations of 2 black rectangles on each side of the screen (4 in total). The retro-cue was a black arrow pointing left or right and indicating that participants should only keep remembering the two rectangles on the left or right for the probe.

Drop 4: Participants were asked to remember orientations of 2 red and 2 blue rectangles on the cued side of the screen. The retro-cue was a red or blue arrow pointing to the same side of the screen as the initial cue. It indicated that participants should keep remembering the orientation of only two rectangles of the cued color (red or blue).

The experiment consisted of 19 blocks with 32 trials in each block (608 trials in total). Trials terminated by the eye-tracker due to blinks or eye-movements were appended at the end of the block so as to ensure the same number of trials for all participants. Before the actual task, participants performed at least 2 training blocks of 16 trials. The task took approximately 1 hour to complete (around 2 hours for the whole experimental procedure).

Computation of the index K and CDA

Behavioral index K and the CDA were computed using the same procedures and formulas as in Experiment 1.

The ROI and the second TOI for the CDA were the same as in Experiment 1, however, the first TOI was between 300 and 700 ms due to the different timeline (faster target presentation).

Statistical analysis

Experiment 2 employed the same statistical analysis as Experiment 1. In addition, one-sample t-test was used to evaluate mean CDA amplitude changes from the baseline in Cue-after-target condition.

3. Results

3.1. Experiment 1

Behavioral results

2x2 ANOVA with a within-subject factor of load (2 levels: 2 and 4) and a within-subject factor of task type (2 levels: Keep and Drop) on average vWM capacity index K revealed a statistically significant main effect of load, $F(1, 23) = 38.7$, $p < .001$, $\eta^2 = .287$, with higher K values for load 4, and a main effect of task type, $F(1, 23) = 90.5$, $p < .001$, $\eta^2 = .296$, with lower K values for the Drop task, as well as their interaction, $F(23, 1) = 11.1$, $p = .003$, $\eta^2 = .043$ (Figure 7, B).

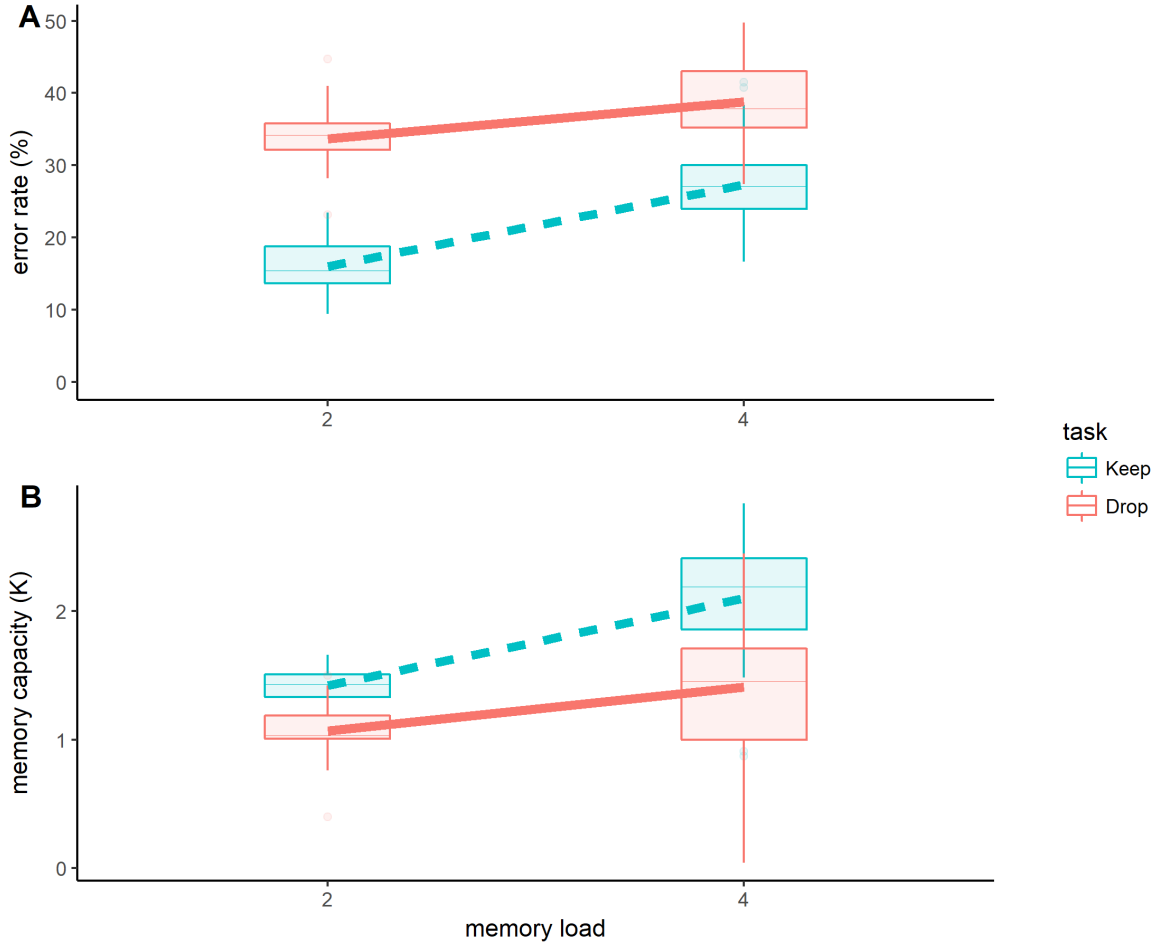

*Figure 7. Behavioral results of Experiment 1. **A**. Average error rate for two different loads (2 and 4) and task types (Keep and Drop). **B**. Average vWM capacity index K scores for 2 different loads (2 and 4) and task types (Keep and Drop).*

Similarly, binomial logistic regression on accuracy scores (error rate) revealed a significant main effect of Load, $z = -4.91$, $p < .001$, Task, $z = 18.7$, $p < .001$, and their interaction, $z = -6.60$ $p < .001$, where higher load was weighting towards wrong answers ($OR = 0.802$), while

task type *Keep* was reflected in lower error rate (*OR* = 2.67). The combination of higher load and *Keep* type of task weighted towards wrong answers (*OR* = 0.629) (Figure 7, A).

ERP results

2×2 ANOVA with a within-subject factor of Load (2 levels: 2 and 4) and a within-subject factor of Task type (2 levels: Keep and Drop) on the mean CDA amplitude in the 400–800 ms time window revealed a significant main effect of load, $F(23, 1) = 7.73$, $p = .011$, $\eta^2 = .024$, with load 4 resulting in more negative CDA amplitude. As expected, the factor of Task, $F(23, 1) = 0.514$, $p = .481$, $\eta^2 < .001$, or their interaction, $F(23, 1) = 0.543$, $p = .469$, $\eta^2 = .001$, did not show a significant effect. For the 1000–1400 ms time-window, there was no significant effect of Load, $F(23, 1) = 0.145$, $p = .707$, $\eta^2 < .001$, Task, $F(23, 1) = 0.339$, $p = .566$, $\eta^2 = .001$, or their interaction, $F(23, 1) = 0.038$, $p = .847$, $\eta^2 < .001$ (Figure 8, B, C).

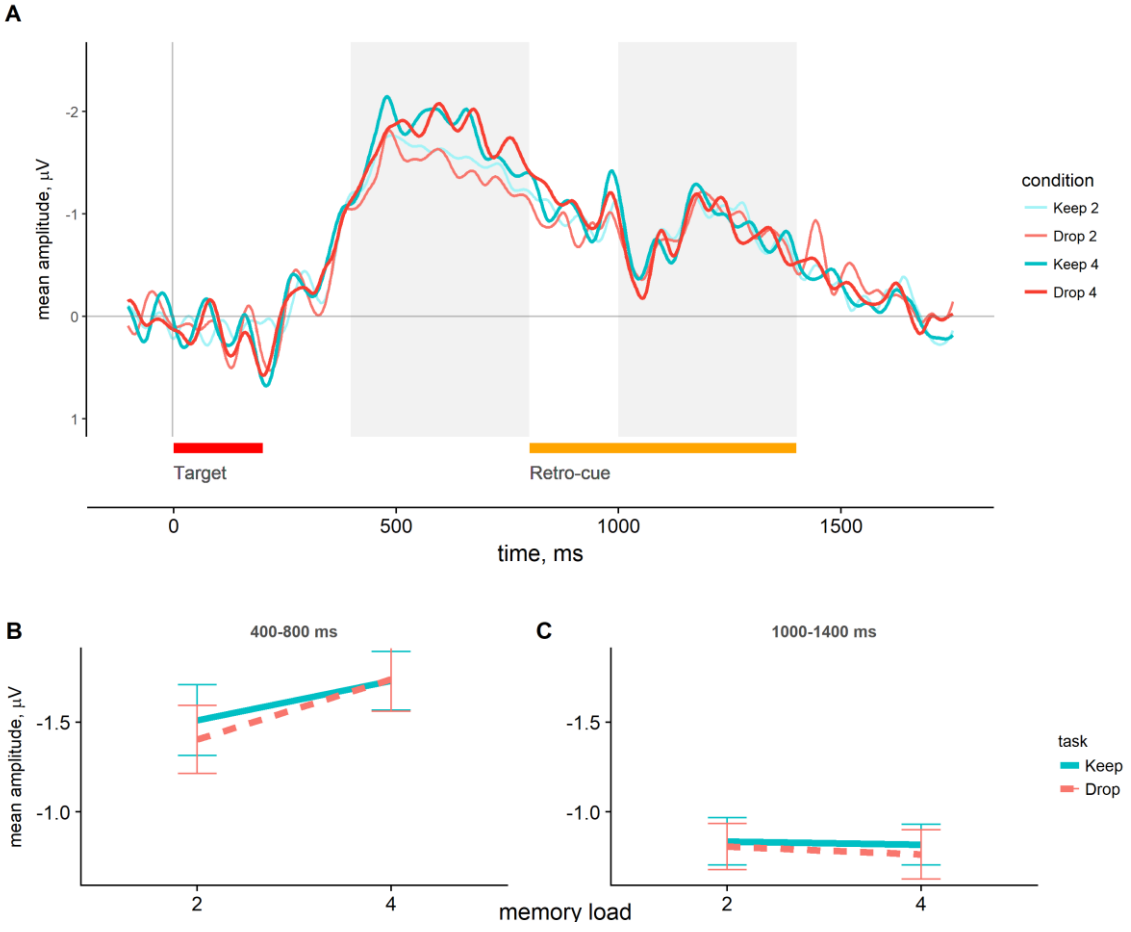

Figure 8. ***A****. The grand average CDA waveform in the average channel (ROI). Grayed areas represent two TOIs used for the analysis (400–800 ms, 1000–1400 ms), horizontal lines indicate the onset and duration of the target and the retro-cue.* ***B****. The mean CDA amplitude for 2 different loads (2 and 4) and task types (Keep and Drop) at 400–800 ms TOI.* ***C****. Mean CDA amplitude for 2 different loads and task types at 1000–1400 ms TOI.*

Pearson's Product Correlation analysis was used to estimate the relationship between mean amplitude change from load 4 to load 2 and the memory capacity index K in Keep 4 condition. At the first TOI (400–800 ms), this relationship was significant for the task type Keep, Pearson's $r(24) = -.41$, $p = .045$, indicating that a larger decrease between the amplitudes is related to a larger memory capacity index K. However, the relationship was not significant for the task type Drop, Pearson's $r(24) = -.05$, $p = .833$. During the second TOI (1000–1400 ms), the relationship was not significant for the Keep task type, Pearson's $r(24) = -.08$, $p = .727$, yet it was significant and positive for the Drop task type, Pearson's $r(24) = .47$, $p = .022$. (Figure 9)

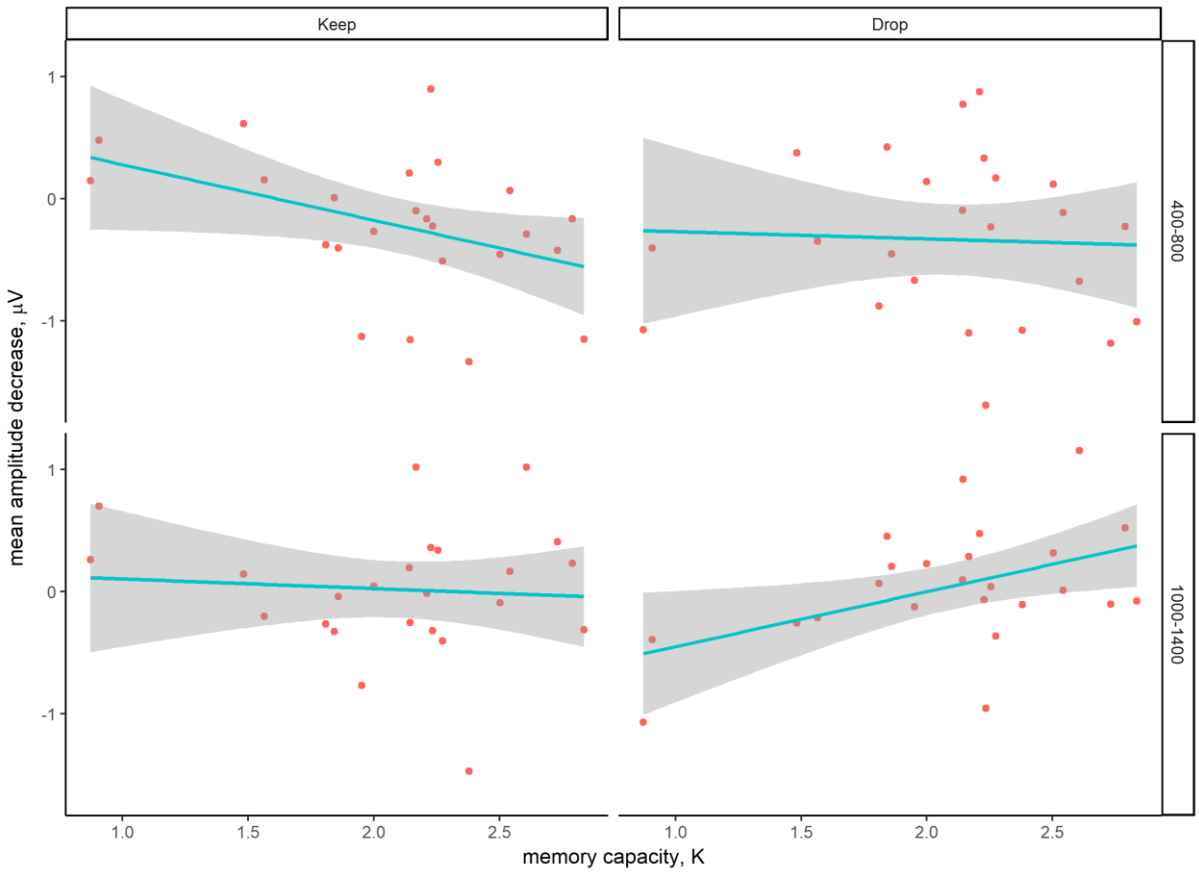

Figure 9. Relationship between average CDA amplitude decrease from load 2 to load 4 and the memory capacity index K at Keep 4 condition at two different TOIs (represnted by 2 rows) and for 2 different task types (represented by 2 columns).

Mass-univariate analysis results

Mass-univariate analysis (MUA) employed repeated measures two-tailed permutation based test on tmax statistic (Blair & Karniski, 1993) and a family-wise alpha level of .05.

Five thousand random within-participant permutations of the data were used to estimate the distribution of the null hypothesis (H_0: no difference). Based on this estimate, a critical t-score (t_c) was derived for each randomization test.

MUA revealed that all four conditions significantly differed from the baseline in both TOIs with the differences mostly situated in temporal-posterior regions, $t_c(23) = \pm 5.05$, $t_c(23) = \pm 5.08$, $t_c(23) = \pm 5.05$, $t_c(23) = \pm 4.81$, for Drop 2, Keep 2, Drop 4 and Keep 4 conditions, respectively. During the first TOI, the differences were larger (both in temporal and spatial dimension) in conditions of greater memory load (Keep 4 and Drop 4). However, during the second TOI, the differences in condition Drop 4 appear to be the smallest both in temporal and spatial dimensions (Figure 10). There were, however, no significant differences between any of the 4 conditions (Appendix).

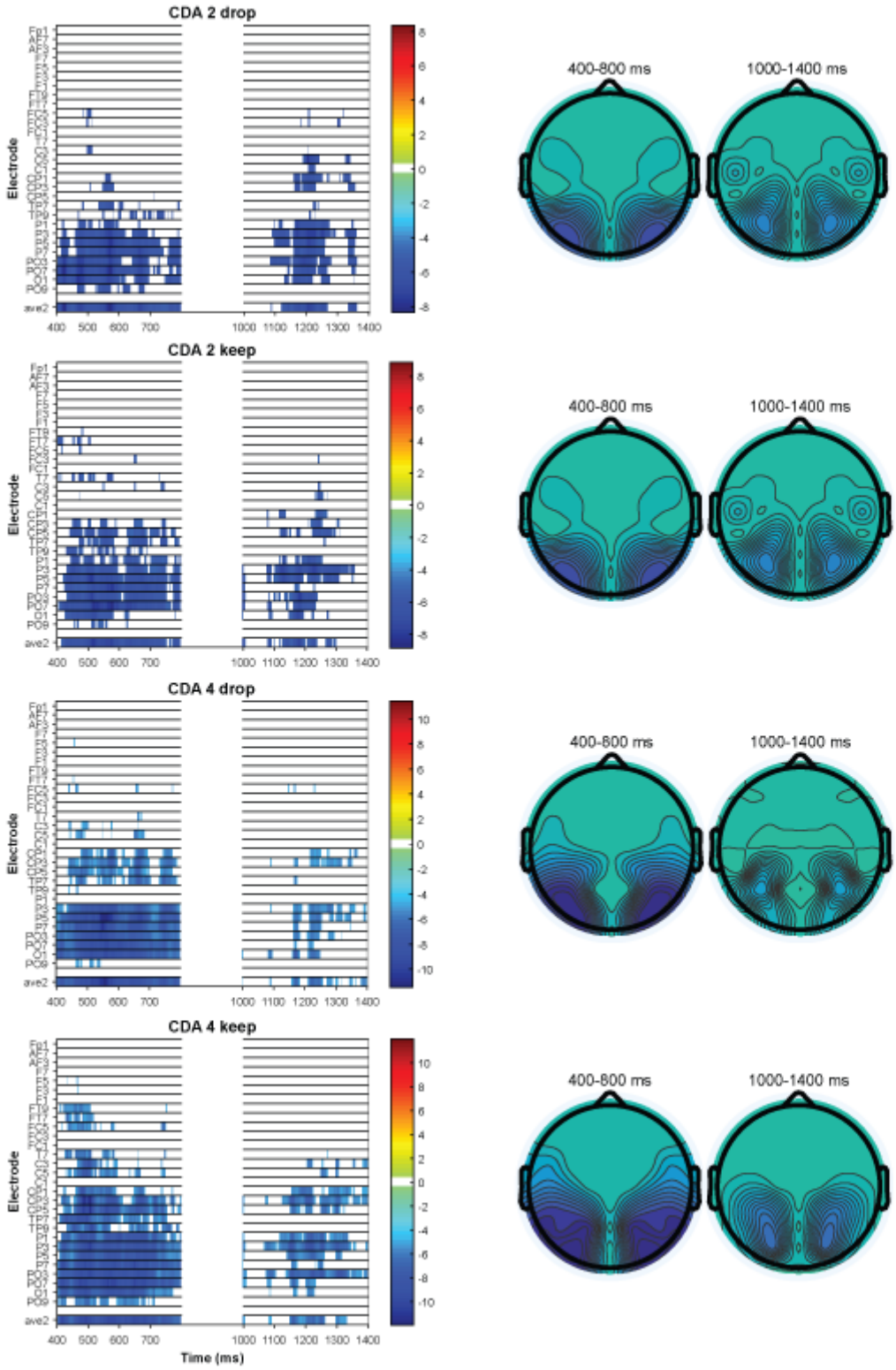

Figure 10. Significant differences, as estimated by MUA, of 4 conditions (represented by rows) from the baseline. The differences are ilustrated by t-value raster (left column) and topological images (right column), with all non-significant t-values masked.

3.2. Experiment 2

Behavioral results

Repeated measures ANOVA on average memory capacity index K in three conditions of load 4 (CAT, K4, D4) revealed that the conditions were statistically significantly different, $F(64, 2) = 123$, $p < .001$, $\eta^2 = .501$. Paired sample t-test with Bonferroni correction clarified that all three conditions were different from each other, $p < .001$, with Cue-after-target condition characterized by the largest average memory capacity index K, whereas Drop 4 by the lowest (Figure 11).

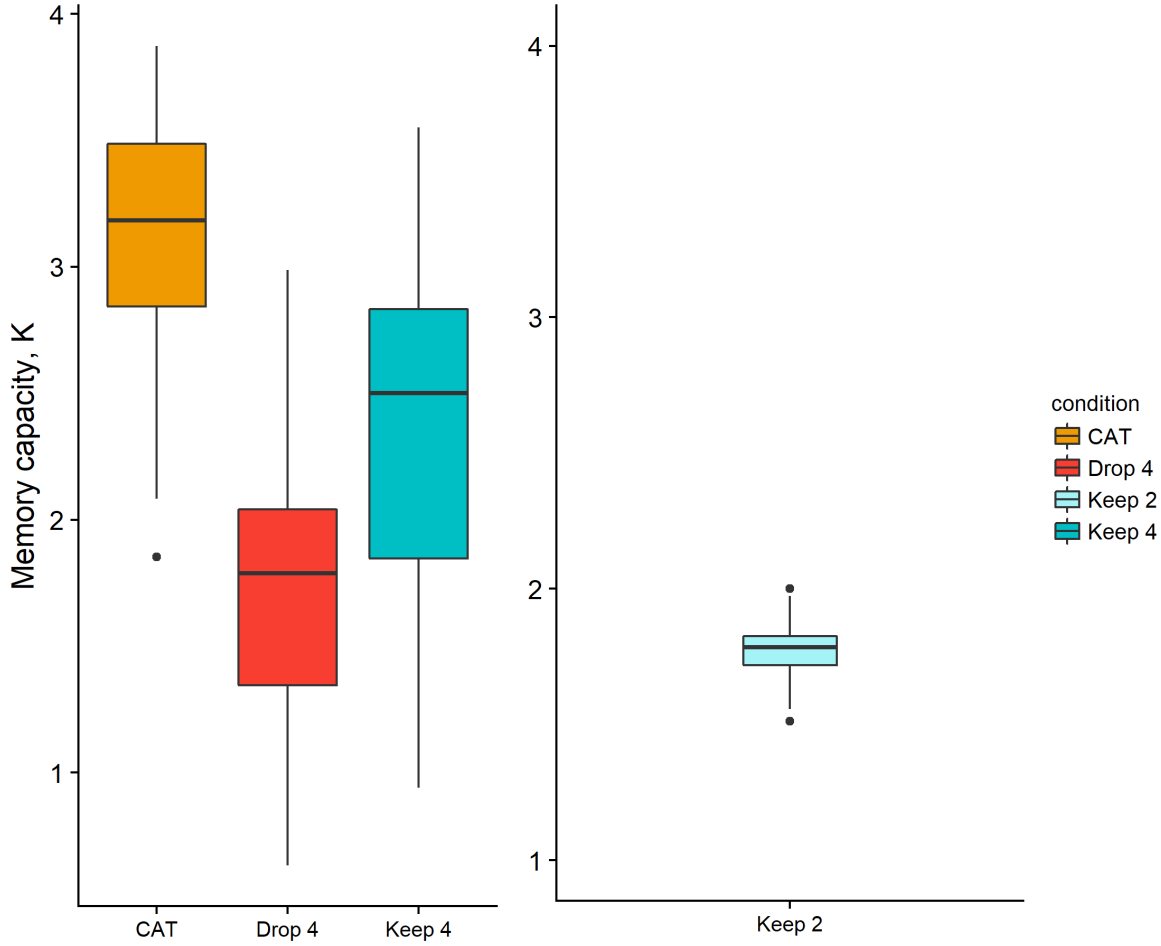

Figure 11. Average memory capacity index K in three conditions of load 4, plot on the left, and average memory capacity index K in Keep 2 condition, presented for comparative purpose, plot on the right.

Binomial logistic regression model on accuracy scores (error rate) revealed a significant main effect of Load, $z = -20.5$, $p < .001$, reflecting a higher error rate for a higher memory load (OR=0.309) (Figure 12). There was, however, no significant main effect of task type, $z = -1.51$, $p = .131$.

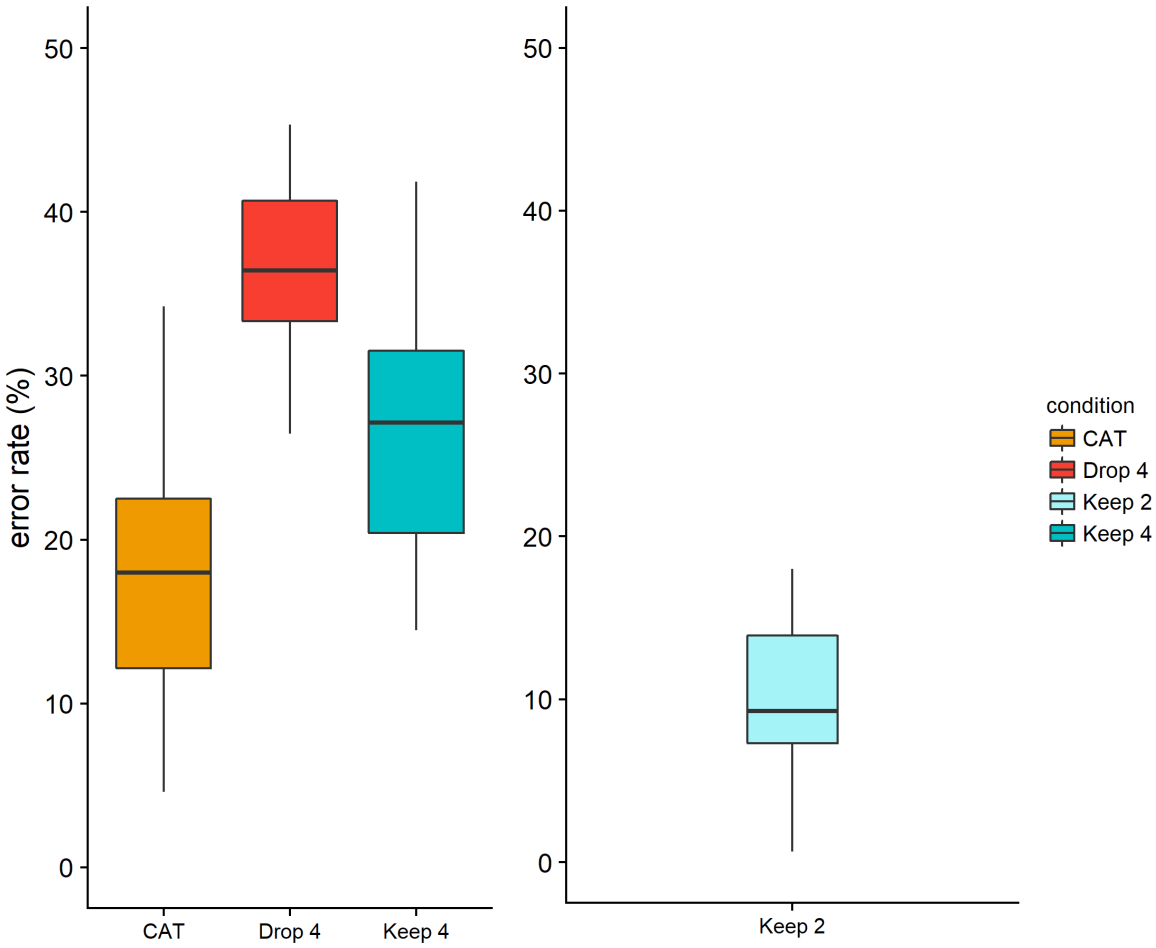

Figure 12. Average error rate in three conditions of load 4 (plot on the left), and load 2 (plot on the right).

EEG results

Repeated measures ANOVA on the average CDA amplitude revealed a significant main effect of condition for the first TOI (300–700 ms), $F(87, 3) = 46.9$, $p < .001$, $\eta^2 = .409$. Pairwise t-test analysis with Bonferroni correction showed that the average amplitude in Cue-after-target condition was significantly larger than in all other conditions, $p < .001$. However, there was no significant main effect of condition in mean CDA amplitude during the second TOI (1000–1400 ms), $F(87, 3) = 1.88$, $p = .139$, $\eta^2 = .034$ (Figure 13, B, C).

One sample t-test showed that the mean amplitude of the CDA in Cue-after-target condition was not significantly different from the baseline at the 300–700 ms time-window, $t(29) = 1.84$, $p = .076$, however, it significantly decreased from the baseline at the 1000–1400 ms time-window, $t(29) = -3.51$, $p = .0015$ (Figure 14).

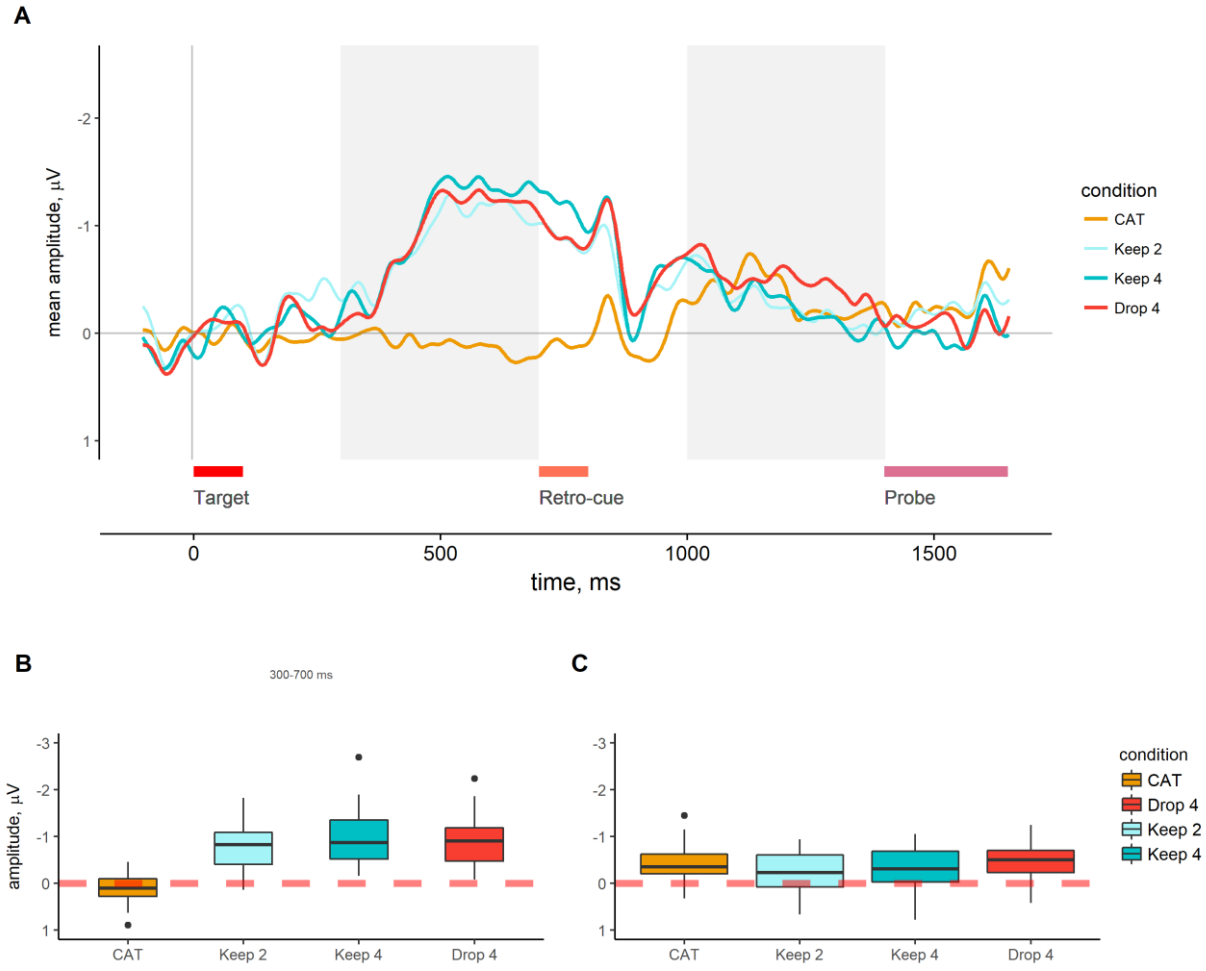

Figure 13. ***A****. The grand average CDA waveform in the average channel (ROI). Grayed areas represent two TOIs used for the analysis (300–700 ms, 1000–1400 ms), horizontal lines indicate the onset and duration of the target, retro-cue and probe.* ***B****. Mean CDA amplitude in four experimental conditions at 300–700 ms TOI, dashed horizontal line highlights the baseline.* ***C****. Mean CDA amplitude in 4 different conditions at 1000–1400 ms TOI, dashed horizontal line highlights the baseline.*

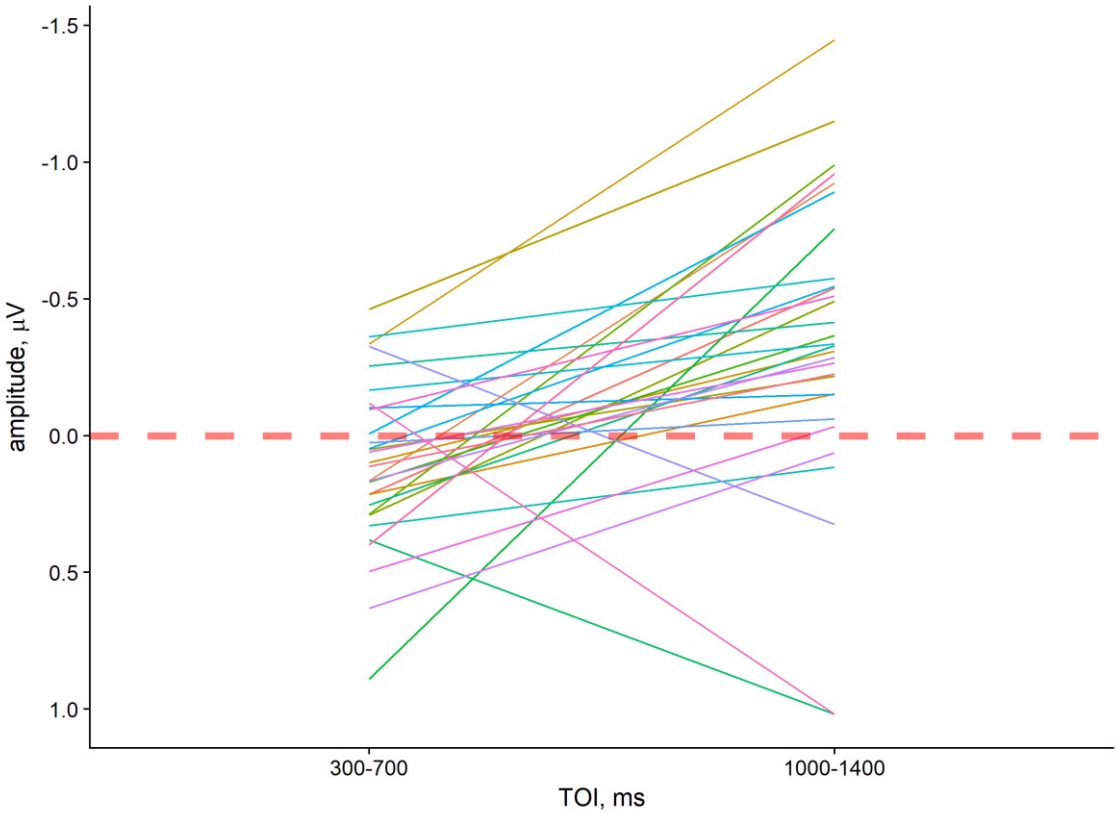

Figure 14. Average CDA amplitude decrease from the 1st TOI to the 2nd TOI in each participant (represented by different color lines), red dashed line highlights the baseline.

Pearson's product correlation analysis showed no statistically significant relationship between the mean CDA amplitude decrease from load 2 to load 4 and memory capacity index K in Keep 4 condition for either of the TOIs: 300–700 ms, Pearson's $r(30) = .03$, $p = .891$; 1000–1400 ms, Pearson's $r(30) = -.24$, $p = .193$ (Figure 15).

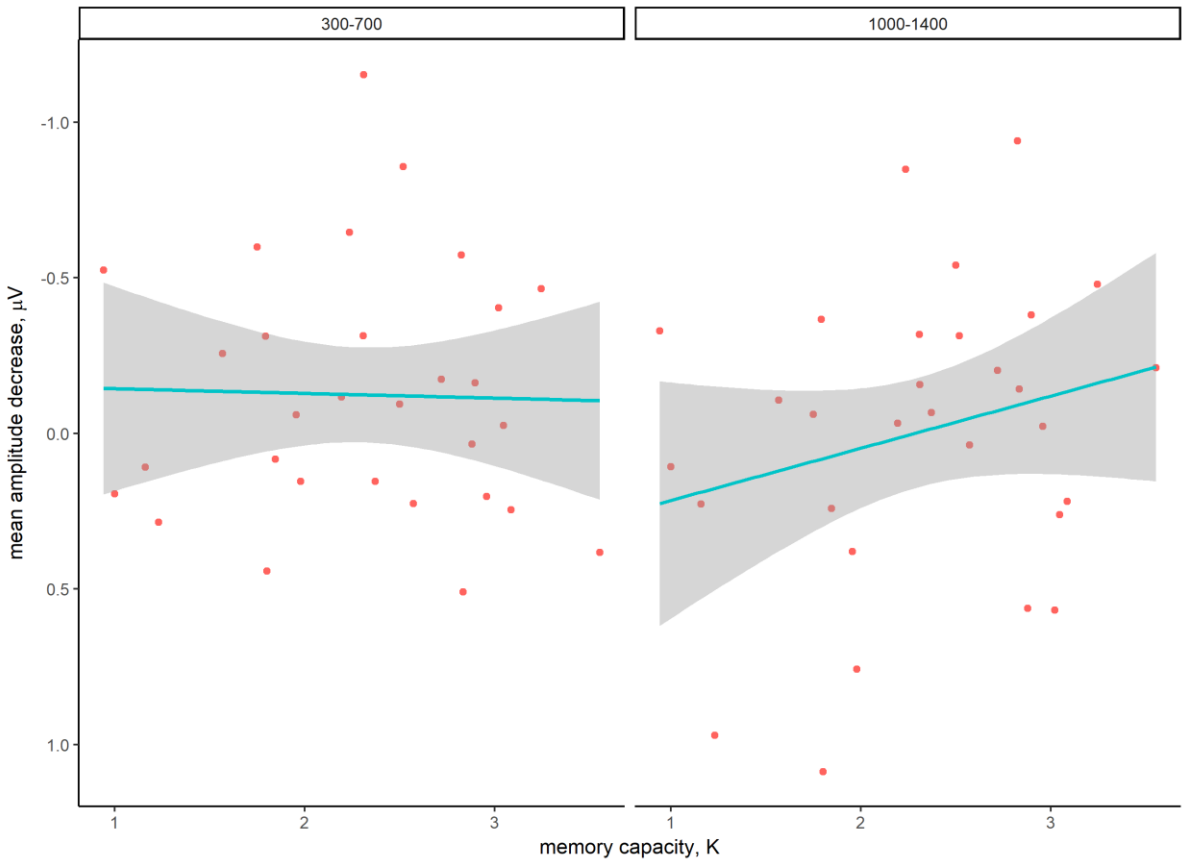

Figure 15. Relationship between the average CDA amplitude decrease from load 2 to load 4 and memory capacity index K at Keep 4 condition at two different TOIs.

Mass-univariate analysis results

Mass-univariate analysis (MUA) employed repeated measures two-tailed permutation based test on tmax statistic (Blair & Karniski, 1993) and a family-wise alpha level of .05. Five thousand random within-participant permutations of the data were used to estimate the distribution of the null hypothesis (H_0: no difference). Based on this estimate, a critical t-score (t_c) was derived for each randomization test.

MUA revealed that all initially lateralized conditions (Keep 2, Keep 4, Drop 4) were significantly different from the baseline during the first TOI (300–700 ms) at temporal-posterior scalp sites, however, Cue-After-Target condition, as expected, showed no difference from the baseline. During the second TOI (1000–1400 ms) all four conditions showed some significant differences from the baseline with more central-parietal distribution as compared to initial CDA, $t_c(29) = \pm 4.96$, $t_c(29) = \pm 4.65$, $t_c(29) = \pm 4.67$, $t_c(29) = \pm 4.71$, for CAT, Keep 2, Keep 4 and Drop 4 conditions respectively (Figure 16).

Moreover, MUA revealed that CAT condition was different from all 3 other conditions during the first TOI at temporal-posterior scalp sites, $t_c(29) = \pm 4.86$, $t_c(29) = \pm 4.89$, $t_c(29)$

= ± 4.88, for Keep 2, Keep 4 and Drop 4, respectively (Figure 17).

There were, however, no differences between the remaining 3 conditions in either of the TOIs or scalp locations (Appendix).

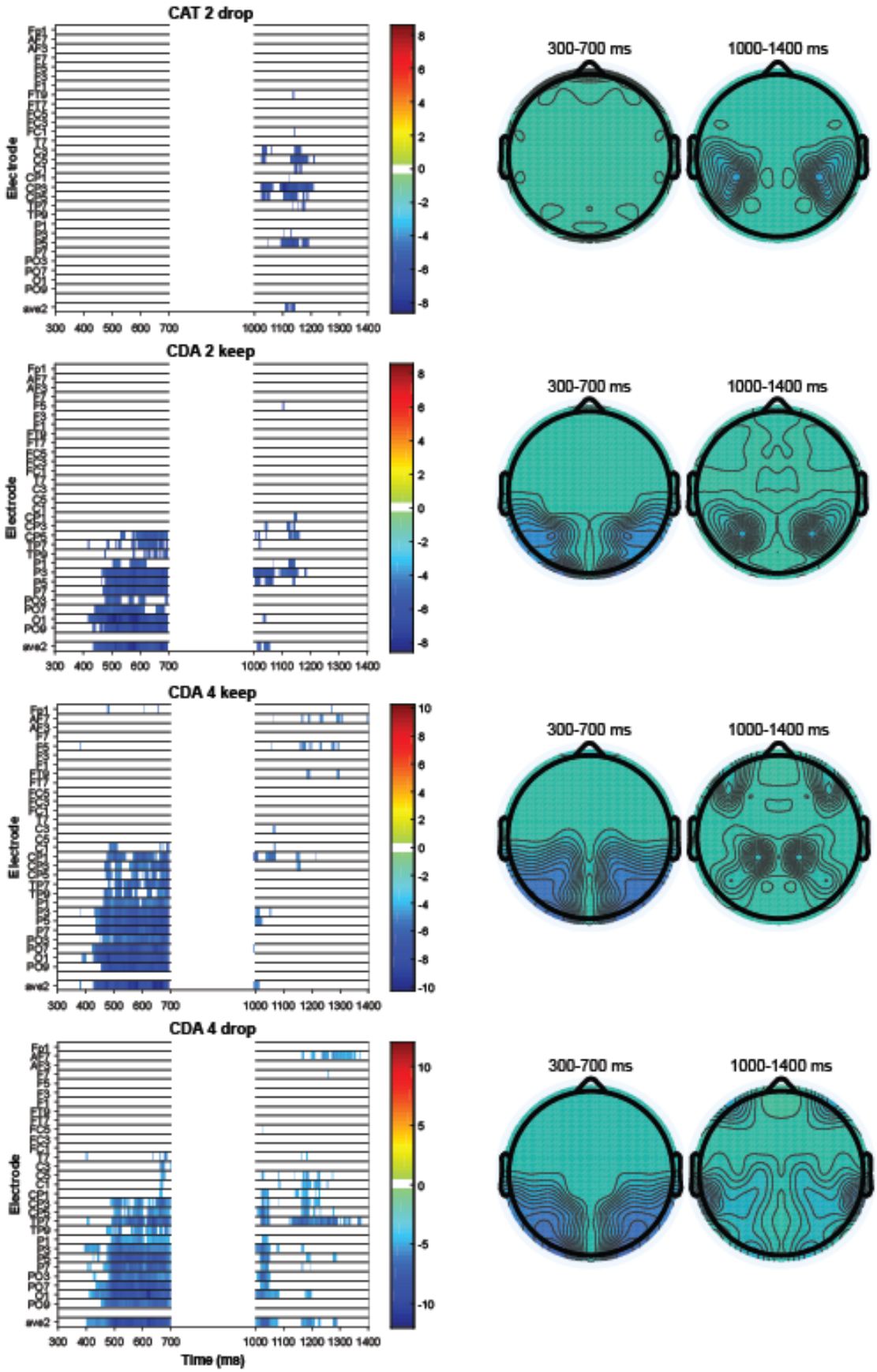

Figure 16. Significant differences, as estimated by MUA, of 4 conditions (represented by rows) from the baseline. The differences are ilustrated by t-value raster (left column) and topological images (right column), with all non-significant t-values masked.

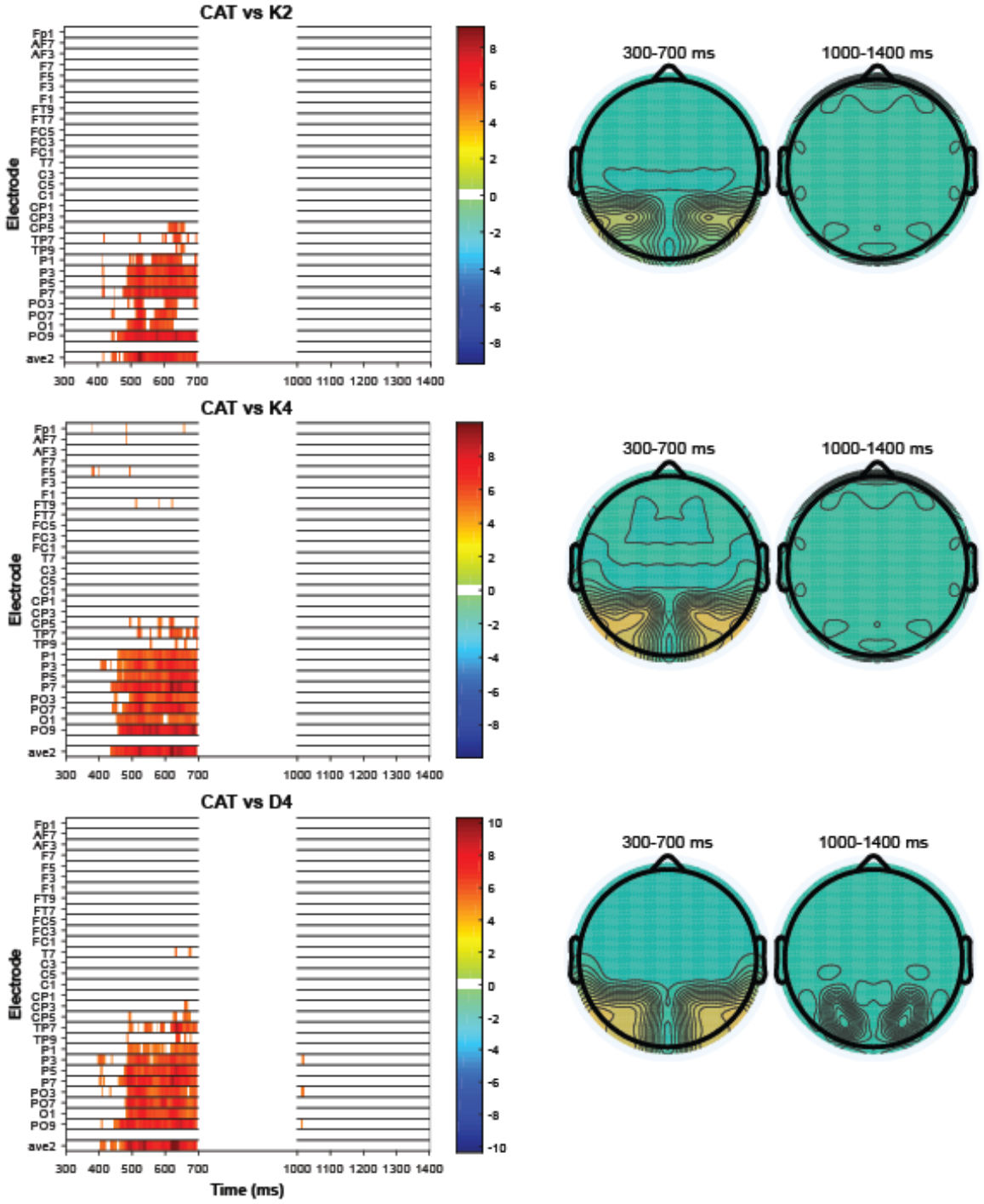

Figure 17. Significant differences, as estimated by MUA, between CAT and 3 other conditions (Keep 2, Keep 4, Drop 4, represented by rows). The differences are ilustrated by t-value raster (left column) and topological images (right column), with all non-significant t-values masked.

4. Discussion

In this study we have tested two hypotheses regarding dynamic memory representation elimination as a vWM capacity control mechanism. The first hypothesis was designed to probe the elimination of task-irrelevant representations within a single visual hemifield, while the second one tested "dropping" of an entire visual hemifield (i.e. elimination of all representations from one hemifield). As its main means of analysis, the study employed the behavioral capacity index K and the electrophysiological visual WM capacity marker CDA.

4.1. Experiment 1

The behavioral results of the first experiment indicate that both load (2 or 4) and task type (keep or drop) had a statistically significant effect on working memory performance, both in terms of accuracy and memory capacity index K. The decrease in accuracy with increasing set size is well established (Gao et al., 2009; McCollough, Machizawa & Vogel, 2007; Palva et al., 2011; Todd & Marois, 2004; Vogel & Machizawa, 2004). Similarly, the significant increase in the index K from load 2 to 4 was expected: Memory sets of 2 items are, normally, below an individual memory capacity limit and show very little interpersonal variability, whereas memory sets of 4 items normally are supra-threshold and better reflect actual capacity limits across individuals and are marked by higher interpersonal variability. The surprising discovery, however, was that the Drop type of the task was reflected by lower accuracy and capacity index K both with load 2 and load 4 (representing easy and difficult conditions respectively). In general, it is widely accepted that retro-cueing has a beneficial effect on accuracy and performance in a range of cognitive tasks, including working memory tasks (Maxcey & Woodman, 2014; Pertzov et al., 2013). This beneficial effect was established both for color (Pertzov et al., 2013) and directed-remembering retro-cues (Williams et al., 2013), as it was used in this experiment. It is, thus, surprising that in our experiment, participants showed very poor performance even in the easy condition, where they only had to remember two items and discard one of them. Indeed, the index K in the dropping condition with load 2 is, on average, around 1, meaning that participants were close to guessing and could only retain one item of the two-item set.

One possible explanation of such poor behavior could be based on the feature integration theory (Treisman, & Gelade, 1980). According to the theory, visual features are perceived automatically and in parallel, whereas their conjunctions, which are necessary for object integration, are processed by serial focus of attention. Our task required from participants a successful integration of spatial and orientation features in order to perform the task

correctly. However, the dropping task was based on an additional feature, color, which might have not been integrated into the originally perceived objects, and thus could have caused illusionary conjunctions. An alternative explanation, for at least the Drop 4 condition, could lie in an observation that retro-cues lose their beneficial effect when more than 1 spatial location is cued (Makovski & Jiang, 2007).

The ERP results of Experiment 1 show a clear and statistically significant separation between the average CDA amplitude at load 2 and load 4 after the onset of the memory set. This difference was expected, as CDA is known to reflect memory load differences by its amplitude (Vogel & Machizawa, 2004). Importantly, it also shows that participants had no trouble to initially encode the same number of representations both in Keep and Drop types of tasks. This suggest that the detrimental effect of Drop type of task might be associated with the processing of the retro-cue or inference from the probe, consistent with the aforementioned possible explanations based on feature integration theory or multiple cued objects. However, after the first TOI (400–800ms) the CDA waveforms of all 4 conditions converged and decreased in amplitude making it impossible to identify any differences in vWM sub-processes after the onset of the retro-cue.

Vogel and Machizawa (2004) have established that individual decrease in the CDA amplitude from load 2 to 4 is strongly correlated with the individual vWM capacity index K. Similarly, the individual decrease in the CDA amplitude has been shown to correlate with filtering efficiency, an important vWM capacity control mechanism at encoding stage (Vogel et al., 2005). Therefore, we used the same method to test if the relationship between the individual decrease in the CDA amplitude and memory capacity index K would hold for tasks requiring elimination of task-irrelevant items during the maintenance phase. We could replicate a statistically significant, though weaker, linear relation between the CDA amplitude decrease and individual K at the Keep condition for the first TOI, which is equivalent to the reported relationship in Vogel et al. (2005). However, we could not replicate this relationship for the Drop condition or second TOI (1000–1400 ms) after the retro-cue. This indicates that the individual memory capacity estimates in retro-cueing conditions were, at least in this study, independent from the amplitude changes in the CDA. Consequently, it may indicate that the poor performance in retro-cueing/dropping conditions was caused by processes other than vWM storage, possibly related to cue processing and attention.

Mass univariate analysis confirmed the observed CDA differences during the first TOI (400-800 ms), with expected temporal-parietal topography and established time-line

(McCollough et al., 2007; Perez & Vogel, 2012). The average CDA activity after the retro-cue (1000–1400 ms) remained significantly different from the baseline in all 4 conditions, however, the magnitude of the differences was smaller while the topography seemed to be more central, though, still posterior. As the topography shift is present both in the Keep and Drop conditions, it could be assumed that it reflects natural decay of the CDA waveform or general retro-cue processing, rather than "dropping" of the task-irrelevant representations. In addition, the lack of differences between the 4 conditions, as revealed by MUA, provides additional evidence that the average CDA activity could not provide relevant differentiation between Keep and Drop type of tasks.

To sum up, Experiment 1 revealed significant and unexpected decrease in behavioral performance when the participants were asked to drop the task-irrelevant memory representations within a single visual hemifield. However, these differences were not captured by the CDA activity.

4.2. Experiment 2

The behavioral results of the Experiment 2 pointed to two important findings. First, they confirmed the detrimental effect of the color retro-cue for elimination of task-irrelevant items within a single visual hemifield that we observed in Experiment 1: The performance in the Drop 4 condition was significantly worse than in other two conditions with the same load (Keep 4 and Cue-after-target). Second, the cue-after-target condition representing "dropping" of an entire visual hemifield, was significantly higher both in accuracy and capacity index K than in the Keep 4 condition, indicating a beneficial retro-cueing effect. However, both accuracy and index K were still lower than the baseline condition Keep 2. This indicates that whereas the retro-cue had a beneficial effect on performance, it did not pull the performance to the level of the simple task of keeping two items in memory. This observed effect is in line with theories that postulate a large degree of independence between the two visual hemifields and flexible resource allocation between them (Allon et al., 2014; Ma et al., 2011)

The ERP results were strongly in line with our second hypothesis. At the initial maintenance phase (300–700 ms), there was no significant lateralized activity in the cue-after-target condition as compared to the other 3 conditions which were showing great negative deflection. However, the 3 lateralized conditions did not significantly differ among themselves. This lack of a significant difference may be attributed either to the poor SNR

of the data or to the shifted time-line of the experiment, which could result in insufficient CDA differentiation during the first TOI.

After the directed-remembering retro-cue a slow negative wave resembling the CDA emerged in the cue-after-target condition confirming our hypothesis that the dropping of the memory items from one entire hemifield was successful and the task became lateralized in its nature. This finding was confirmed with a one-sample t-test indicating that the CDA amplitude significantly diverged from the baseline. The new emerged waveform in the CAT condition reached the same amplitude as that in the other 3 conditions. However, similarly as in the first experiment, the CDA waveforms in different conditions converged and decreased in their amplitude to an extent that made it impossible to reveal any significant differences among them.

The correlational analysis of the mean amplitude decrease between the waveforms of load 4 and load 2, and individual memory capacity index K, did not replicate our findings of Experiment 1. However, this could be attributed to the aforementioned delay in differentiation of the CDA waveform in conditions Keep 4 and Keep 2 during the first TOI, and to the large decrease in the CDA amplitude during the second TOI.

The MUA revealed a few interesting findings. First, as expected, it showed no significant differences from the baseline in the cue-after-target condition during the initial TOI. However, it also revealed that the chosen first TOI should have been adjusted, as the onset of the CDA seemed to happen only 400 ms after the onset of the target. In Experiment 2 we chose our first TOI to start at 300 ms rather than 400 ms (as in Experiment 1) in order to keep the time between the off-set of the target and the TOI constant (200 ms), thus providing sufficient and constant time for its visual processing. However, it seems that despite the faster presentation of the target (100 ms instead of 200 ms), the processing of the memory set took around 400 ms, similarly to Experiment 1. This finding was unexpected as, based on the literature, the CDA should have emerged at around 250 ms after the onset of the target (Drew et al., 2006; Drew & Vogel, 2009; Perez et al., 2012; Vogel & Machizawa, 2004). On the other hand, the topography of all lateralized conditions was compatible with the established temporal-posterior distribution of the CDA activity. During the second TOI (1000–1400 ms), all 4 conditions showed some differences from the baseline. In general, the differences were smaller than those observed in Experiment 1, but, similar to Experiment 1, the topography seemed to shift centrally. The cue-after-target condition showed this centrally shifted CDA activity as well, indicating that the change from bilateral to unilateral task did not affect the natural CDA dynamics. The mass-univariate-analysis of the

differences among the four conditions showed the expected differences between the CAT and the 3 other conditions during the first TOI, mirroring the observed differences between the 3 conditions and the baseline. No additional differences among the 3 conditions were identified.

To sum up, both behavioral and electrophysiological findings supported our second hypothesis regarding task-irrelevant item elimination from an entire visual hemifield. However, similarly as in the Experiment 1, we observed detrimental effect of retro-cueing for item elimination within a single visual hemifield.

4.3. Joint conclusions

The following conclusions can be drawn from the two experiments:

1. The first hypothesis regarding task-irrelevant memory item elimination within a single visual hemifield was not confirmed either by behavioral or electrophysiological markers. The directed-remembering color retro-cue had a detrimental effect on performance both at low and high memory load conditions. Moreover, the CDA did not reflect this effect, indicating that the possible mechanisms of poor performance might have been related to processes other than vWM storage.
2. The second hypothesis regarding task-irrelevant memory item elimination from an entire visual hemifield was confirmed both by behavioral and electrophysiological findings. The electrophysiological CDA marker of "dropping" an entire hemifield was confirmed both by conventional and mass-univariate statistical analysis.
3. The CDA waveform in our study showed some differences from those reported in literature: The observed onset of the waveform was about 400 ms after the onset of the target, which is later than expected. Moreover, the topography of the CDA seemed to shift more centrally at the later stages of maintenance. This shift in topography seems to be a general property of the CDA unrelated to the dynamic change in the vWM capacity load.

4.4. Limitations and future directions

Both Experiment 1 and Experiment 2 in this study suffered from a relatively low SNR of the CDA, causing the possible differences between the conditions to blur. In our effort to increase the SNR we paid a lot of attention both to the data preprocessing and study design, however, changes in data collection procedures, such as lower impedance, might be

necessary in the future. Moreover, in this study we used average reference of the EEG data, however, linked mastoid reference could yield slightly larger amplitude of the CDA activity.

The detrimental effect of color retro-cue for item elimination within a single visual hemifield poses a lot of questions and ideas for future studies. First, another experiment could be used to establish whether the observed effect is due to the retro-cueing of multiple objects. Second, it should be clarified whether the detrimental effect of the retro-cue could have occurred due to the larger number of relevant visual features in the Drop task than in the Keep task. Alternatively, we should test if the difficulty could be ameliorated by the successful integration of color into the initial memory set by using a blocked rather than random study design. Finally, it would be interesting to test whether some alternative electrophysiological marker, such as theta or gamma changes, could be used to probe dynamic item elimination in vWM.

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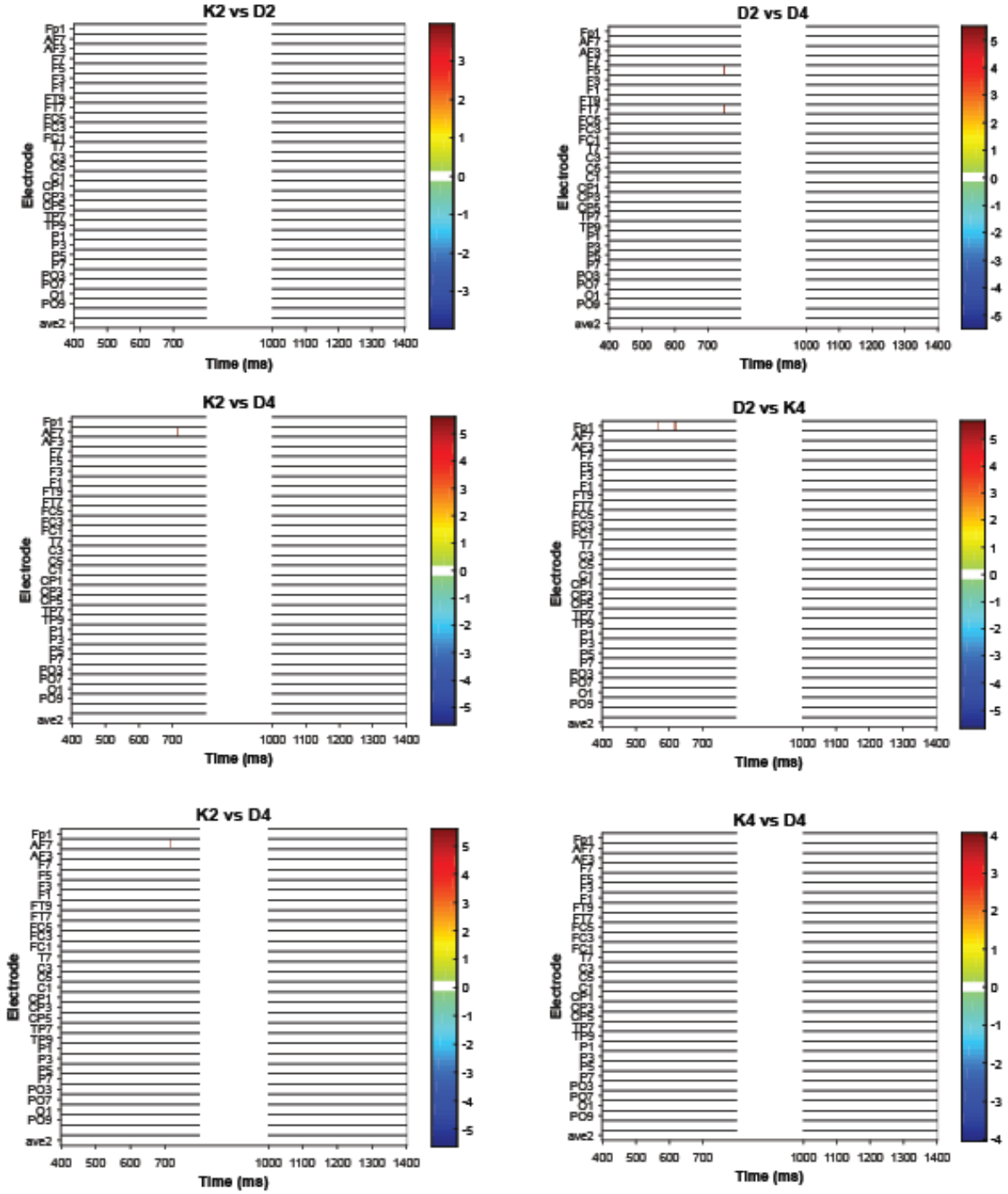
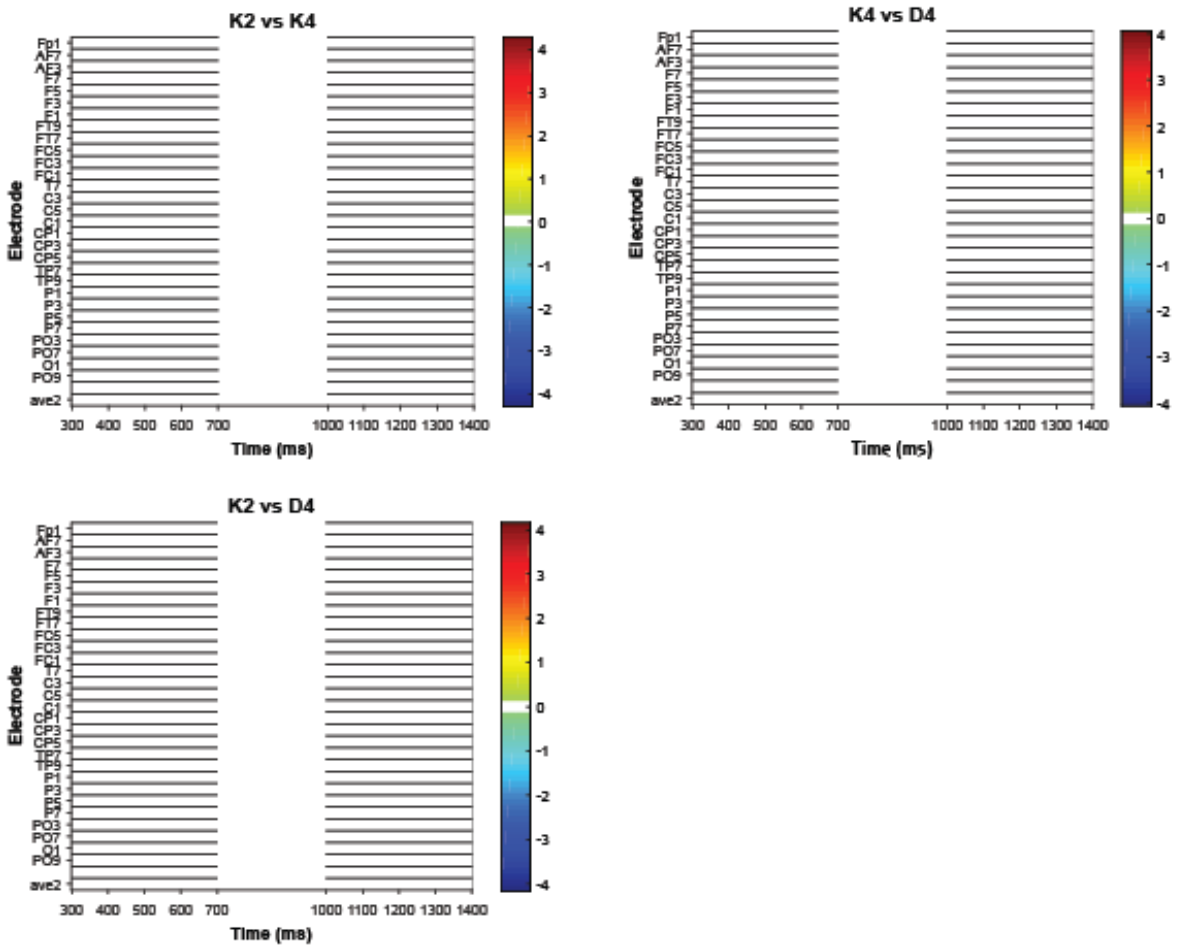
Appendix



Non-significant mass-univariate analysis results of Experiment 1, indicating lack of differences among 4 experimental conditions in either of two TOIs and scalp locations.



Non-significant mass-univariate analysis results of Experiment 2, indicating lack of differences among 3 initially lateralized experimental conditions in either of two TOIs and scalp locations.

Abstract

Einleitung

Das “Visuelle Arbeitsgedächtnis” (vAG) wird als die Fähigkeit, eine kleine Menge an Informationen kurzfristig zu speichern verstanden. Das vAG spielt in vielen kognitiven Prozessen eine zentrale Rolle: Unter anderem bildet es die Grundlage für höhere kognitive Fähigkeiten, wie etwa der fluiden Intelligenz, dem logischen Denken oder der Auffassungsgabe. Daher können individuelle Unterschiede der kognitiven Leistungsfähigkeiten zwischen Individuen, sowohl bei gesunden Menschen als auch in klinischen Populationen, durch unterschiedliche Kapazität des vAG zurückgeführt werden. Im Durschnitt kann ein gesunder Mensch nur zwischen 3-4 Details verlässlich im vAG behalten. Unklar ist daher, wie das vAG trotz dieser limitierten Kapazität derart effizient arbeiten kann.

Aus Studien ist bekannt, dass für eine gegebene Augabe irrelevante Informationen in der Kodierungsphase ausgeblendet werden können. Weniger gut verstanden sind allerdings die Prozesse zur dynamischen Adaptierung des bereits kodierten Inhalts des vAG bei veränderten Anforderungen. Hierzu müssten abgespeicherte nicht-mehr relevante Details dynamisches aus dem Gedächtnis gestrichen werden. Unsere Studie untersucht zwei Mechanismen eben jenes selektives Vergessens von irrelevanten Informationen - innerhalb eines einzelnen visuellen Hemifeldes und im ganzen Gesichtsfeldbereich.

Methoden

Es wurden zwei unabhängige Experimente mit insgesamt 5 Versuchsbedingungen durchgeführt: Alle 5 experimentelle Bedingungen basieren auf dem Erkennen von bilateralen Veränderungen des Stimulus (*bilateral change-detection-task*) mit Retrohinweisreizen (*retro-cueing*). Zur Bewertung der vAG-Kapazität im Verhaltensexperiments wurde der Index K verwendet. Zusätzlich wurde während des Experiments EEG der Teilnehmer aufgezeichnet, um die Resultate des Verhaltensindex mit einem neurophysiologischen Marker zu untermauern. Hierzu wurde die kontrolaterale zeitliche Verzögerung der induzierten Aktivität (Contralateral Delay Activity, short CDA) verwendet. Statistische Auswertung der CDA-Differenzen zwischen verschiednen Bedingungen wurde sowohl an Hand klassischer als auch univariater Massenstatistik (mass univariate analysis) – Ansätze durchgeführt.

Ergebnisse und Diskussion

Verhaltens und ERP - Ergebnisse bestätigen bisherige Ergebnisse, dass Aufgaben-irrelevante Informationen eines gesamten visuellen Hemifeld nach retro-cueing gelöscht werden können. Allerdings war es Probanden nicht möglich, erfolgreich selektiv einzelnen Items innerhalb eines Hemifeldes aus dem vAG zu entfernen. Diese Bedinung war im Allgemeinen problematisch für die Probanden, wie die Ergebnissen des Verhaltensexperiments zeigen. CDA-Ergebnisse weisen darauf hin, dass die Schwierigkeiten im Verarbeiten des Reizhinweises oder auch an Interferenzeffekten beim Abrufen der relevanten Information liegen könnte. Diese Resultate sind neu und überraschen, da in der Vergangenheit eine erfolgreiche Reduzierung der vAG-Auslastung für verschiedene Hinweisreize, wie z.B. Farb-Hinweise oder auch für sog. *Directed-remembering* Hinweise, gezeigt werden konnte. Der von uns beobachtete Effekt könnte im Rahmen der Merkmalsintegrationstheorie (*feature integration theory*) erklärt werden.