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Costs of storing colour and complex shape in visual working memory: Insights from pupil size and slow waves

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ABSTRACT

We investigated the impact of perceptual processing demands on visual working memory of coloured complex random polygons during change detection. Processing load was assessed by pupil size (Exp. 1) and additionally slow wave potentials (Exp. 2). Task difficulty was manipulated by presenting different set sizes (1, 2, 4 items) and by making different features (colour, shape, or both) task-relevant. Memory performance in the colour condition was better than in the shape and both condition which did not differ. Pupil dilation and the posterior N1 increased with set size independent of type of feature. In contrast, slow waves and a posterior P2 component showed set size effects but only if shape was task-relevant. In the colour condition slow waves did not vary with set size. We suggest that pupil size and N1 indicates different states of attentional effort corresponding to the number of presented items. In contrast, slow waves reflect processes related to encoding and maintenance strategies. The observation that their potentials vary with the type of feature (simple colour versus complex shape) indicates that perceptual complexity already influences encoding and storage and not only comparison of targets with memory entries at the moment of testing.

1. Introduction

Visual working memory (VWM) refers to temporary storage of visual information which is possible only for a few items. This capacity limit is often estimated by a change detection task introduced by Luck and Vogel (1997). Usually a small set of objects is briefly presented and after a short interval another set of objects appears accompanied by the task to decide whether they are the same or something has changed. In this simple task people can remember only up to four objects, which is why it is uncontroversial that the capacity of VWM is limited (Luck & Vogel, 1997). However, it is strongly debated whether the limit is defined by the number of objects or the number and type of features (cf. Luck & Vogel, 2013). Related to this is the question what amount of cognitive effort is necessary to store certain objects and features. Does storage of easy features (e.g. colours) cost more cognitive effort than storage of complex features (e.g. shapes) and how does the number of task-relevant objects or features influence cognitive effort?

1.1. Object based VWM

According to the object based view, VWM capacity is confined purely by the number of objects whereas it is unimportant which or how many features are represented (Fukuda, Awh, & Vogel, 2010; Luck & Vogel, 1997; Vogel, Woodman, & Luck, 2001; Xu, 2002). For instance Luck and Vogel (1997) demonstrated that performance in a change detection task was the same when participants had to focus on one (e.g., colour) compared to four different features (gap, size, orientation, colour) of the presented objects. Further evidence for the object based position is provided by the contralateral delay activity (CDA), an electrophysiological negativity which can be observed contralateral to the visual hemi-field in which the to-be-memorized items appear if the lateralized version of the change detection task is used. This component is sometimes also called sustained posterior contralateral negativity (Jolicoeur, Brisson, & Robitaille, 2008; Robitaille & Jolicoeur, 2006). The amplitude of the CDA increases with the number of memorized items and reaches its asymptote at the individual's maximal memory performance. The amplitude of the CDA is therefore considered as an estimate of the number of stored items (Vogel & Machizawa, 2004). In support of the object based view, it was shown that the CDA amplitude is a function of the number of maintained items not of the features until the individual capacity limit is achieved (Luria & Vogel, 2011; McCollough, Machizawa, & Vogel, 2007; Vogel & Machizawa, 2004; Wilson, Adamo, Barense, & Ferber, 2012). However, also inconsistent results were reported. When different features (e.g., orientation or colour) of the same objects were critical, the CDA varied with the type of feature even though the number of objects was constant (Gao, Ding, Yang, Liang, & Shui, 2013; Luria, Sessa, Gotler, Jolicoeur, & Dell'Acqua, 2010; Woodman & Vogel, 2008). This demonstrates that the CDA is

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not unambiguously an indicator of the number of objects. It may also reflect other aspects of processing. Independent of this ambivalence, proponents of the object based view postulate that the capacity limit is set by the individual number of "slots" available for storing integrated objects rather than individual features separately, suggesting that the number of features defining an object does not influence capacity.

1.2. Feature based VWM

In contrast to the object based and in accordance with a feature based position, other researchers reported that the amount of information held in VWM does not only depend on the number of perceived objects but also on the number of their features (Bays & Husain, 2008; Bays, Wu, & Husain, 2011; Oberauer & Eichenberger, 2013; Olson & Jiang, 2002). A corollary hereof is that it is task dependent which features are stored and that features may differ in their storage demands. Two types of results were stressed in support of this position: memory declines if more features have to be remembered and it declines if the critical features are perceptually more demanding, e.g., shapes of random polygons versus colours. Oberauer and Eichenberger (2013) found that performance decreased strongly when more features per object were relevant. Bays and Husain (2008) observed that locations of items were remembered less precisely with increasing set size. Wheeler and Treisman (2002) suggested that storage in VWM is feature specific with limited resources within dimensions, e.g., two colours versus one colour, and no competition for resources between dimensions, e.g., colour and orientation. This model is based on the finding that performance on conjunction of features from different dimensions is on the same level as in the single feature condition (Wheeler & Treisman, 2002). Strong conjunction costs were observed if the features belonged to the same dimension (e.g., colour–colour-conjunctions) (Delvenne, Cleeremans, & Laloyaux, 2010; Olson & Jiang, 2002). Costs of conjunctions were not always reported, though (Luck & Vogel, 1997; Luria & Vogel, 2011). Nevertheless, the majority of results, however, support the assumption that memory load is influenced by the number and quality of an objects' features and not only by the number of presented objects itself.

1.3. Object complexity

It has been observed that not only the number but also the type of feature to be maintained in VWM is a capacity limiting factor (Eng, Chen, & Jiang, 2005). Alvarez and Cavanagh (2004) showed that capacity varies from 1.6 items when shaded cubes to about 4.4 items when coloured squares were presented in a change detection task. Likewise, VWM capacity for random polygons as relevant feature was found to be lower than for a feature as colour (Song & Jiang, 2006) or basic shapes (Gao et al., 2009). A part of this effect may be caused by a more demanding comparison process between the probe item and the memory representation if features are complex (Awh, Barton, & Vogel, 2007; Scolari, Vogel, & Awh, 2008), but other results demonstrate that also storage demands vary with stimulus complexity. Gao and colleagues showed that the CDA during maintenance is influenced by the type of to-be-memorized feature (Gao et al., 2009; Gao et al., 2013). Similarly, Luria, Sessa, Gotler, Jolicoeur and Dell'Acqua reported that the CDA was higher for visually complex than for simple items and it was argued that neurons have to "work harder" to store more complex objects (2010).

1.4. Effort in VWM

This conclusion introduced a new aspect which was so far ignored in the ongoing discussion. Even when the same number of objects is stored independently of the number and kind of relevant features, the effort to store these items may be different. The object-based view might be right in the assumption that the number of objects sets a limit to memory capacity but nevertheless the effort invested per item may vary with the quality of features. This option is supported by results from brain imaging studies. For example, it has been shown that activity in the parietal cortex – a core region of the VWM network – increases with the number of to be memorized items (Xu, 2007; Xu & Chun, 2006). This increase of neural activity was less pronounced if the items were trained and therefore more easily memorized (Zimmer, Popp, Reith, & Krick, 2012) which suggests that brain activity of the VWM network during change detection reflects the amount of processing demands. Alike, Song and Jiang (2006) showed that performance was lower and neural activity was higher when the item's shape (a complex polygon) was relevant than when only its' colour was relevant. Interestingly, in a condition where both colour *and* shape were task-relevant, brain activity and performance were on the level of the shape only condition (Song & Jiang, 2006). The same result was observed in a behavioural study by Brockmole, Parra, Sala, and Logie (2008). Obviously colour is an easy feature which seems to be remembered together with demanding features like random polygons without additional costs. In one study, compared to shape only, in a colour–shape-conjunction condition the same memory performance was even reached with less neural activity (Sala & Courtney, 2007).

Taken together, it is controversial whether storage demands in VWM vary with the type of feature and if they do so which factors are responsible for the different demands. Some studies are compatible with an object-based view, whereas others demonstrate that also processing demands of task-relevant features influence memory load. The CDA was introduced as a pure and preferable measure of memory because processing effects are removed from the data by subtracting ipsilateral from contralateral potentials. However, not only task-irrelevant but also task-relevant differences in processing effort are cancelled out. The difference wave may therefore be a good measure for the number of objects that can be attended in WM but not how this memory is provided. Brady, Konkle, and Alvarez (2011) suggested that item representations are hierarchical with objects on the top and structural descriptions of object features on lower levels. With such a representation it is possible to obtain effects of the number of objects independent of the underlying networks representing the objects' features. We therefore searched for a further online measure that is not only sensitive to the number of objects but also to processing effort of the memory tasks in order to investigate complexity related effects in VWM during maintenance. We decided for pupillometry because in other contexts it was proven that pupil size is a useful indicator of mental and attentional effort. We measured pupil size while participants hold a varying number of items in working memory in order to get insights into task-related attentional effort.

1.5. Task-related pupil response

The pupil signal is related to memory load, attention, and perception. For a review see Beatty and Lucero-Wagoner (2000). More specific, pupil sizes were found to correlate with the number of items held in working memory and with task difficulty (Beatty, 1982; Kahneman & Beatty, 1966; Klingner, Tversky, & Hanrahan, 2011; Verney, Granholm, & Marshall, 2004). Pupil diameter increased with set size in digit span tasks (Beatty, 1982; Kahneman & Beatty, 1966), and with growing task difficulty in digit multiplication tasks (Ahern & Beatty, 1979; Hess & Polt, 1964; Klingner et al., 2011). Furthermore pupil diameter increased with the difficulty of a visual search task and the authors discussed this in the context of varying demands on memory (Porter, Troscianko, & Gilchrist, 2007). This task-related pupil signal is probably triggered via the noradrenergic system. Aston-Jones and Cohen (2005) could show that changes in pupil size and activity of the locus coeruleus strongly correlated during a signal detection task. This neural structure influences cognitive control via the norepinephrine system. It was shown that lesions of the locus coeruleus in monkeys lead to a decrease of alertness in general and of attention to novel stimuli in an oddball