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Review

The contralateral delay activity as a neural measure of visual working memory

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ABSTRACT

The contralateral delay activity (CDA) is a negative slow wave sensitive to the number of objects maintained in visual working memory (VWM). In recent years, a growing number of labs started to use the CDA in order to investigate VWM, leading to many fascinating discoveries. Here, we discuss the recent developments and contribution of the CDA in various research fields. Importantly, we report two meta-analyses that unequivocally validate the relationship between the set-size increase in the CDA amplitude and the individual VWM capacity, and between the CDA and filtering efficiency. We further discuss how the CDA was used to study the role of VWM in visual search, multiple object tracking, grouping, binding, and whether VWM capacity allocation is determined by the items' resolution or instead by the number of objects regardless of their complexity. In addition, we report how the CDA has been used to characterize specific VWM deficits in special populations.

Contents

1. Introduction

Visual working memory (VWM) is a limited workspace that can hold information online, ready to be accessed and manipulated by higher cognitive functions (Luck and Vogel, 2013). In recent years, there has been a growing use of electrophysiology to investigate VWM. Specifically, the contralateral delay activity (CDA), a negative slow wave whose amplitude corresponds to the number of objects maintained in VWM was extensively used, leading to many exciting and important results that have considerably advanced our understanding of how VWM processes information. The goals of this paper are to validate, unequivocally, the CDA as

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a measure of VWM capacity, and to review the recent developments and contributions of the CDA in investigating how VWM operates.

2. A brief history

The first demonstration of a sustained EEG activity during working-memory retention interval was reported by Ruchkin et al. (1990, 1992). However, this activity could be also attributed to several non-mnemonic processes occurring during the retention interval (such as preparation, arousal or other attentional processes). A few years later, Klaver et al. (1999) observed a negative activity over posterior electrodes for an item that was presented either on the left or on the right side of fixation. This result did not receive much attention, presumably because in another condition, the authors presented two items on both sides of the fixation, observing only baseline activation, and this pattern was interpreted as indicating limited resource processing.

In 2004, Vogel and Machizawa (2004) capitalized on advances in the VWM field and developed a bi-lateral version of the change-detection paradigm. The bi-lateral presentation allows observing a more specific mnemonic related activity because it relies on a difference between an attended and a non-attended side (see Fig. 1). They observed a slow negative wave that persisted throughout the retention interval, and was sensitive to the number of objects maintained in memory. Shortly afterwards, the CDA was used to provide compelling evidence that individual difference in VWM capacity are related to the ability to filter out irrelevant information from the VWM limited workspace (Vogel et al., 2005). This research demonstrates the powerful arguments that can be derived by using the CDA as a marker for VWM capacity, conclusions that are otherwise inaccessible by means of behavioral measures only.

The CDA was first measured in the change detection paradigm during the retention interval, so that ‘delay activity’ seemed an appropriate terminology. In the following years, similar activity was observed in several other tasks and paradigms, not necessarily during the retention period, reflecting that working memory is involved in other functions than just online storage. Notably, several studies referred to the VWM activity as CNSW (Contralateral Negative Slow Wave, Klaver et al., 1999), SPCN (Sustained Posterior Contralateral Negativity, Brisson and Jolicoeur, 2007; Perron et al., 2009) and CSA (Contralateral Search Activity, Emrich et al., 2009). All of these abbreviations indicate the same VWM processes and the use of multiple names is obviously confusing. We will continue to use CDA for the rest of the paper.

In the last decade, there has been a growing use of the CDA leading to many exciting and important results. This review will try to summarize the recent developments and contributions of the CDA in investigating VWM. We will review evidence demonstrating the sensitivity of the CDA to the number of items represented in VWM, and its correlation with the individual VWM capacity. We then move to describe several research fields in which the CDA successfully improved our understanding of VWM.

3. The CDA as an index of VWM capacity

The most important characteristic of the CDA is that its amplitude increases according to the number of objects maintained in VWM. This set-size related rise in amplitude is not due to overall task difficulty, because the CDA amplitude reaches an asymptote at about 3–4 items, which is the usual estimate of working-memory capacity (Cowan, 2001; Luck and Vogel, 2013). Importantly, the CDA asymptote (defined as the further increase in amplitude beyond one or two items) was found to correlate with the individual VWM capacity, such that high capacity individuals show a larger increase in the CDA amplitude when more items are encoded, corroborating the increased storage and improved processing abilities of high capacity individuals. In order to better quantify this relationship between the CDA and the individual VWM capacity, we tracked 11 studies (Diamantopoulou et al., 2011; Drew and Vogel, 2008; Jost et al., 2011; Kang and Woodman, 2014; Kundu et al., 2013; Kuo et al., 2012; Lefebvre et al., 2013; Leonard et al., 2013; Stormer et al., 2013; Tsubomi et al., 2013; Vogel and Machizawa, 2004) that calculated a correlation between these variables on 12 subject samples, and performed a meta-analysis (see Fig. 2 a). The combined correlation was $r = 0.596$, and the 95% confidence interval between 0.510 and 0.670. In order to falsify this relationship (the fail-safe N measure, Orwin, 1983), 350 studies with an averaged zero correlation are needed. This is very strong evidence indicating that the CDA is sensitive to the number of objects maintained in VWM, since the increase in CDA amplitude as more items are added happens to a lesser extent for individuals with lower capacity.

A recent latent-variable study with 164 participants (Unsworth et al., 2014) found a correlation of −0.49 between the CDA amplitude and fluid intelligence, which is similar in magnitude to the correlation observed between behavioral VWM estimates and intelligence (Fukuda et al., 2010). To the best of our knowledge, this is the only reported correlation between any ERP component and fluid intelligence calculated at the factor level. Moreover, structural equation modeling revealed that individual differences in the CDA reflected both the ability to maintain distinct number of items and attentional control ability (i.e., the ability to select and protect targets and to filter out irrelevant distractors, see below).

Other studies have provided additional evidence validating the CDA as an index of VWM capacity. Notably, the CDA amplitude was significantly reduced on incorrect trials relative to trials with a correct response (McCollough et al., 2007), which is in line with the assumption that errors occur due to the loss of relevant information from VWM. In addition, it was demonstrated that the CDA amplitude is insensitive to low level visual attributes such as the distance between the objects (McCollough et al., 2007), or micro-saccades (Kang and Woodman, 2014).

Another potential confound is that typically each object is presented in a unique position on the screen, raising the possibility that the CDA tracks the number of spatial positions instead of the number of objects. In order to resolve this confound, the CDA amplitude was recoded in a condition in which four colors were presented sequentially (two colors followed by another pair of colors). The second color pair was presented either at the same spatial positions as the first two colors, or at different spatial positions. The CDA amplitude was identical in both cases, supporting the argument that the CDA corresponds to the number of objects and not to the number of spatial positions in VWM (Ikkai et al., 2010). Further support comes from studies showing that superimposing two items does not necessarily lead to a CDA amplitude equal to just one item (Balaban and Luria, 2015a; Luria and Vogel, 2014).

Several studies reported that manipulating the stimulus contrast in the change detection paradigm, while resulting in an impaired behavioral performance, did not have any effect on the CDA (Gao et al., 2013; Ikkai et al., 2010; Luria et al., 2010; Ye et al., 2014). This result is significant because it reveals a dissociation between the low accuracy performance (usually taken as a marker of VWM capacity) and the intact CDA amplitude, and serves as additional evidence that the CDA does not simply reflect the task difficulty. Importantly, this result is in line with claims stating that when complex perceptual information is encoded, the low accuracy in the change detection is the result of an error prone comparison process, and does not reflect the actual VWM representations (Awh et al., 2007). This highlights the importance of the CDA as a reli-

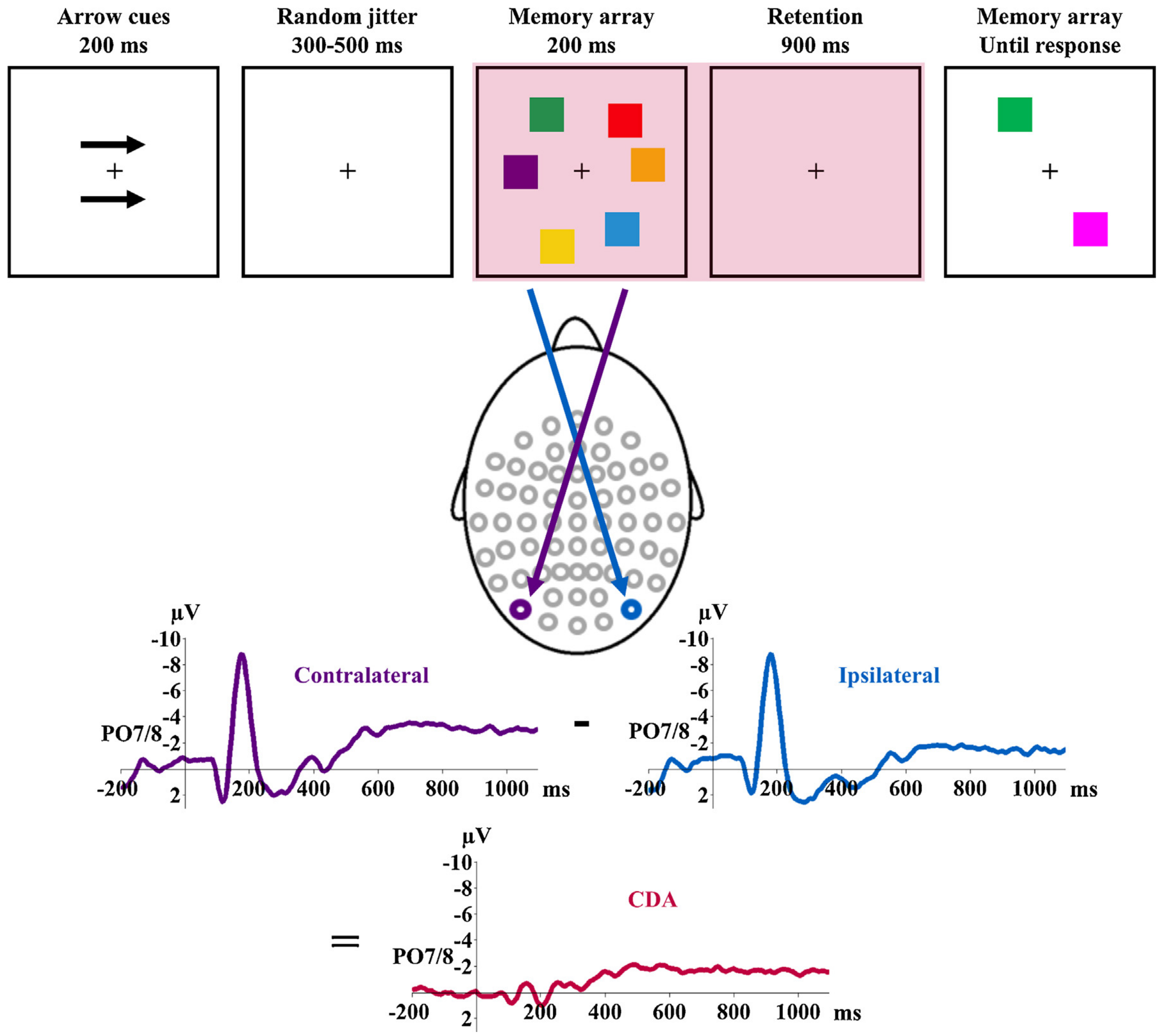

Fig. 1. An illustration of a typical change detection trial and the resulting CDA waveforms. This example (adapted from Allon et al., 2014) is a grand average of 20 participants, at the PO7/PO8 electrodes, where the CDA is usually most pronounced. Subjects were presented with 3 colors for 200 ms, and had to memorize them during the 900-ms retention interval. The CDA is time-locked to the onset of the memory array, and the activity is measured throughout the retention interval (resulting, in this example, in a 1100-ms long time-window), but before the onset of the test array. Note that the waveforms include both right and left trials, such that the contralateral activity is generated from *right* electrodes on *left* trials and *left* electrodes on *right* trials (this is an example of a right trial, and hence PO7 registered contralateral activity and PO8 registered ipsilateral activity). The CDA is the subtraction of ipsilateral activity from contralateral activity.

able marker of the contents of VWM in situations when behavioral measures are not indicative enough.

3.1. The CDA as a difference wave

Note that the CDA is calculated as the difference in amplitude between the contralateral side and the ipsilateral side of fixation (defined by an arrow that precedes the stimuli array or by a predefined color, see Fig. 1). The logic is that the amplitude on the ipsilateral side is assumed to reflect mostly low level and early perceptual processing, while the amplitude on the contralateral side reflects both low level processes and VWM related activity. Thus, the subtraction is intended to “clean” the wave from low level processes and local noise (the logic is similar to calculating the N2pc or the LRP). While the underlying assumptions behind the subtraction seem reasonable, it is still possible that there is merit in separately investigating the two raw waves. For example, it is not clear when the contralateral and the ipsilateral are negative or positive, since the CDA only indicates that the contralateral is more negative than the ipsilateral (but both could be positive). We are aware of only one study that separately manipulated the number of items on each side creating conditions with unequal items on the contralateral and ipsilateral side, in order to investigate whether the number of items on the ipsilateral side affected the CDA on the contralateral side and vice versa. It was found that the number of items on the ipsilateral side affected the contralateral wave only when one item was encoded on the contralateral side. Similarly, the ipsilateral wave amplitude increased in response to items in the contralateral side only when one item was presented on the ipsilateral side, but when more items were presented on the ipsilateral side, its amplitude was not affected by the number of items on the contralateral side (Arend and Zimmer, 2011). In addition, a recent paper successfully correlated the contralateral amplitude with measures of filtering in a change detection task (Liesefeld et al., 2014), but it was not clear whether the CDA difference wave showed better (or worse) correlations. We conclude that more research is needed in order to fully understand the differences between the ipsilateral and contralateral waves, and their underlying cognitive mechanisms.

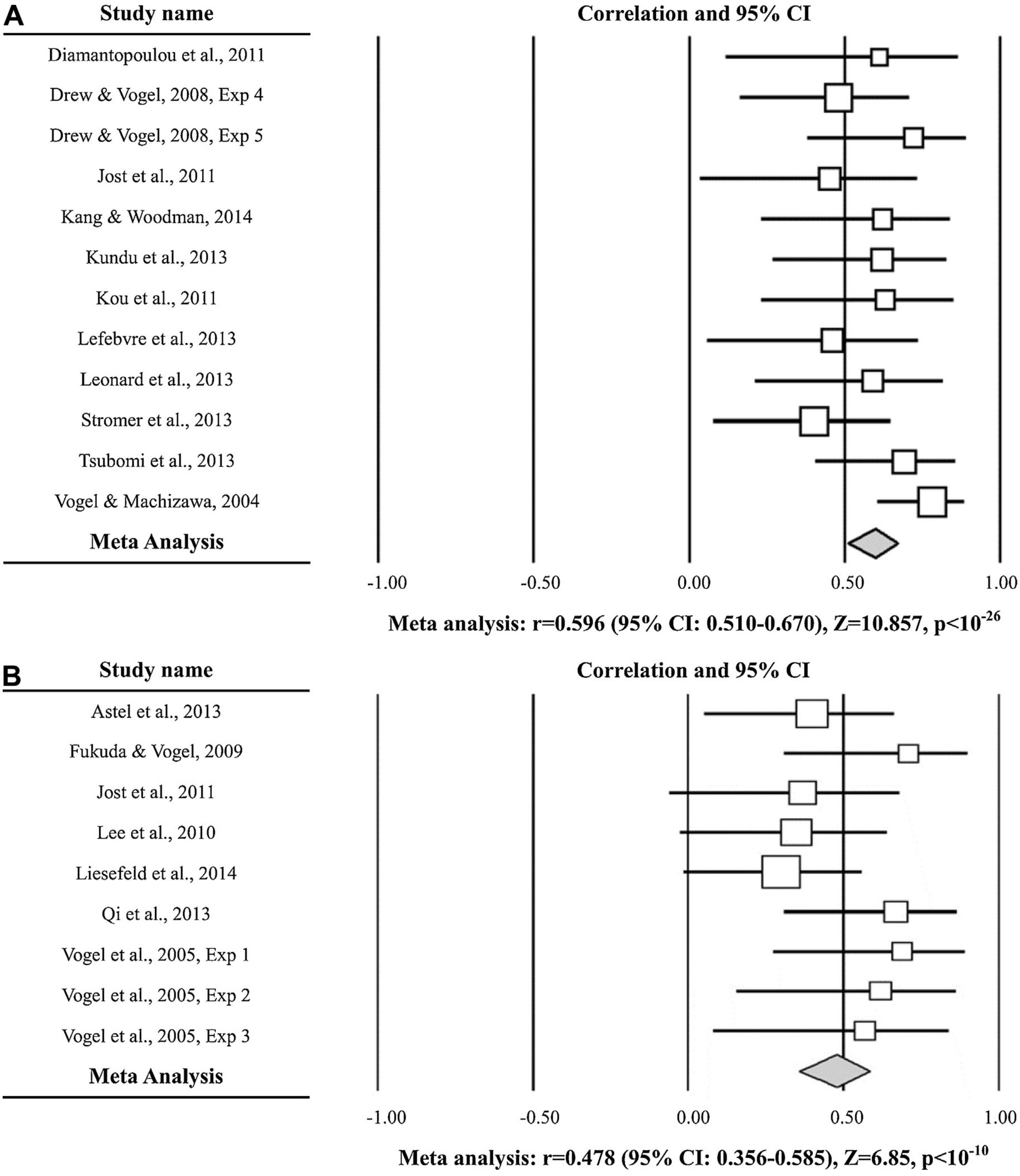

Fig. 2. Meta-analyses of the correlations involving individual CDA amplitude set-size effects. All analyses and computations were carried out using the Comprehensive Meta-Analysis software (Biostat, Inc.), and assumed random effects models (since these are more conservative). For both meta-analyses, each line of the plot represents a single experiment. In the plots, the squares represent each study's obtained correlation and the horizontal lines represent its 95% confidence interval (CI). Square size represents sample size (and the relative weight assigned to that study in the meta-analysis). The bottom line of each plot presents the combined results of all experiments. The gray diamond represents the weighted average correlation, and its width is the 95% CI of the combined effect.

(A) A meta-analysis of the correlation between VWM capacity and the CDA amplitude set-size effect (calculated as a difference between the CDA amplitude of 1 or 2 objects and the amplitude of 3 or 4 objects). Studies were selected through a search in the Google Scholar database using the following keywords: contralateral delay activity or sustained posterior contralateral negativity intersected with capacity and ERP. The inclusion criteria were: (1) publication in the English language; (2) the study measured the CDA for at least 2 different set-sizes, in displays containing only relevant distinctive visual items; (3) the study measured behavioral VWM capacity; (4) the study included a group of normal young adults; (5) the study reported or allowed a calculation of a correlation between the CDA set-size effect (i.e., the difference in amplitude between two set sizes) and behavioral capacity among young adults. The above criteria led to 12 samples from 11 studies, with 286 subjects in total.

The meta-analysis produced a correlation of $r = 0.596$ ($Z = 10.857$, $p < 10^{-26}$), with a 95% confidence interval of 0.510–0.670. We calculated a fail-safe number (i.e., the number of studies with an average correlation of $r = 0.00$ that are required to bring the combined effect down to a marginally-significant level) of 350, suggesting a very robust correlation. The effect was very homogeneous: $Q = 10.164$ ($p = 0.516$), Tau-squared = 0.000.

(B) A meta-analysis of the correlation between VWM capacity and the CDA filtering efficiency index, calculated as the difference in CDA amplitude between a distractor-present condition and a distractor-absent condition (e.g., the difference in amplitude between presenting 2 to-be-remembered items alone, and presenting them along with

3.2. Neural origin of the CDA

One important question in VWM research is to detect the brain areas that are responsible for encoding and maintaining online information. fMRI studies have identified the posterior parietal cortex as the main neural locus of VWM (Todd and Marois, 2004; Xu and Chun, 2006), and there have been several attempts to understand the neural origin of the CDA as well. Two MEG studies (Becke et al., 2015; Robitaille et al., 2009) identified parietal cortex regions (as well as regions in the ventral extrastriate cortex that presumably do not contribute to the ERP signal) as the origin of the CDA, which is in line with the fMRI findings. In addition, a study that measured ERP and intracranial activity in monkeys was able to observe the human CDA homolog in the monkeys' ERPs. Intracranial recordings revealed that frontal local field potentials from the frontal eye field and the supplementary eye field contribute to the generation of the CDA measured at parietal-occipital electrodes (although frontal electrodes do not show sustained ERP activity after the contralateral-ipsilateral subtraction). This suggests that multiple sources and regions are involved in maintaining online information.

In terms of the neural mechanisms that can produce a sustained delay activity, it was argued that asymmetric modulation of lateralized alpha activity could generate the CDA activity (Mazaheri and Jensen, 2008; van Dijk et al., 2010). However, a recent work provided convincing evidence that alpha activity and the CDA exhibit different temporal characteristics and when correlated with behavior explain unique variance in performance (Fukuda et al., 2016). Thus, the specific neural mechanism that could produce this slow wave activity is still unknown.

4. Using the CDA to study VWM

The advantages of measuring the CDA (and any other ERP component) is that it can reveal sub-processes underlying VWM that are otherwise impossible to investigate, because behavioral measures reflect only the end result of the processing or are contaminated by processes that are unrelated to VWM. Indeed, since 2004 there is a constant increase in studies tracking the CDA as their dependent measure in various tasks, such as visual search (Emrich et al., 2009; Luria and Vogel, 2011b; Woodman and Arita, 2011), mental rotation (Prime and Jolicoeur, 2010) and dual-tasks (Brisson and Jolicoeur, 2007). Another example that highlights the important advances in VWM made by the CDA is the recent findings demonstrating that similar CDA activity could be observed when the items remain within view (without any retention interval). Contrary to the traditional view that conceptualized working memory as a memory unit (Baddeley, 2003; Cowan, 2001; Jonides et al., 2008; Vogel et al., 2001), this finding demonstrates that VWM is about 'working' (i.e., online processes) rather than 'memory' (Tsubomi et al., 2013).

Broadly speaking, we have identified two methods of using the CDA. The first is to measure the CDA amplitude to investigate whether VWM representations are affected by a certain manipulation, and the second is to associate variability in the CDA to predefined individual characteristics (such as anxiety, age, or the individual VWM capacity).

Another general distinction within studies that tracked the CDA as their dependent variable is between using the "raw" CDA amplitude and using a CDA difference between two experimental conditions. Most of the reviewed studies fall into the second category, presumably because using a difference between experimental conditions allows controlling for various components that add general noise to the amplitude (so that the subtraction itself serve as an additional control). However, at least when simple stimuli are encoded, the raw CDA amplitude successfully correlated with the individual VWM capacity in some cases (Luria and Vogel, 2011b; Voytek and Knight, 2010; Wiegand et al., 2013) and with RT or accuracy in other cases (Carlisle et al., 2011; Gunseli et al., 2014a,b; Woodman and Arita, 2011). We now turn to review evidence from several fields in which the CDA was successfully used in order to increase our understanding of how VWM operates.

4.1. Filtering efficiency

Vogel et al. (2005) compared the CDA amplitude between conditions that included only task relevant items (two or four items), and a filtering condition that included two relevant items and two task irrelevant items. The results indicated that low VWM capacity individuals had difficulties filtering out irrelevant information. Namely, low capacity individuals represented also the task irrelevant information, as reflected by their CDA amplitude in the filtering condition that was similar to the CDA amplitude in the condition with four relevant items. Conversely, high capacity individuals successfully rejected the irrelevant items as was evident in their CDA amplitude in the filtering condition that was similar to the condition with only two relevant items.

Following Vogel et al. (2005), the relation between VWM capacity and filtering efficiency was extensively investigated using the CDA. The significance of such an argument is that it attributes individual differences in VWM capacity to the ability to reject irrelevant information from reaching the limited VWM storage, instead of assuming differences in the actual storage space. The observed correlation between the individual filtering efficiency and VWM capacity is a key finding for this account. We tracked 7 studies that measured the correlation between these variables (Astle et al., 2014; Fukuda and Vogel, 2009; Jost et al., 2011; Lee et al., 2010; Liesefeld et al., 2014; Qi et al., 2014; Vogel et al., 2005), and performed a meta-analysis (see Fig. 2b). The overall correlation was $r = 0.478$ (95% CI between 0.356 and 0.585), providing strong support that filtering efficiency plays an important role in determining the individual VWM capacity.

4.2. Visual search

Models of visual search attributed an integral role for VWM during the search process that included storing the target template, categorizing, and comparing between the target candidate and the desired template (Bundesen, 1990; Desimone and Duncan, 1995; Duncan and Humphreys, 1989). Despite these arguments, direct behavioral evidence was lacking (Woodman et al., 2001), and only recent research that used the CDA was able to better clarify the role of VWM in visual search.

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2 to-be-ignored items). Hence, when filtering is efficient, a condition containing 2 targets and 2 distractors should be more similar to 2 targets alone (since effectively ignoring the 2 distractors means that only 2 items were maintained in WM), and less similar to 4 targets alone, producing a larger filtering efficiency index.

Studies were selected through a search in the Google Scholar database using the following keywords: contralateral delay activity or sustained posterior contralateral negativity intersected with filtering and ERP. The inclusion criteria were: (1) publication in the English language; (2) the study measured the CDA for at least 2 conditions, one of which included only relevant items, and the other included also some to-be-ignored distractors; (3) the study measured behavioral WM capacity; (4) the study included a group of normal young adults; (5) the study reported or allowed a calculation of a correlation between the CDA filtering-efficiency and behavioral capacity among young adults. The above criteria led to 9 samples from 7 studies, with 200 subjects in total.

The meta-analysis produced a correlation of $r = 0.478$ ($Z = 6.850$, $p < 10^{-10}$), with a 95% confidence interval of 0.356–0.585. We calculated a fail-safe number of 114, suggesting a robust correlation. The effect was very homogeneous: $Q = 7.786$ ($p = 0.455$), Tau-squared = 0.000.

First, it was demonstrated that the CDA could be observed during the visual search task (Emrich et al., 2009). Following studies showed that high VWM capacity individuals search more efficiently, because they are better at locking on the target and avoid representing distractors, resulting in lower CDA amplitudes relative to low capacity individuals (Luria and Vogel, 2011b). A parallel line of investigation has refined the role of VWM in holding the target template. It was shown that when a new target is presented it is being held in VWM but then gradually moves to LTM. This hand-off between VWM and LTM leads to better search efficiency, so that as the CDA amplitude decreased (indicating less involvement of VWM) search RT improved (Carlisle et al., 2011; Schmidt et al., 2014; Woodman and Arita, 2011). The hand-off between VWM and LTM did not depend on the target complexity level, but when the target was associated with a high reward, VWM continued to represent the target, indicating a more controlled search in high reward conditions (Gunseli et al., 2014a,b; Reinhart and Woodman, 2014). Notably, this line of research supports the argument that the CDA tracks the involvement of the ongoing VWM processing involved in preforming visual search tasks.

4.3. *Multiple objects tracking*

In multiple object tracking (MOT), participants are required to constantly follow moving objects. The CDA amplitude was found to be an excellent predictor of the tracking performance, and was able to capture online changes in the number of tracked objects: when additional items were added during the trial, the CDA amplitude increased according to the actual number of tracked items. Furthermore, the real-time aspects of the CDA were exploited to dissociate different factors influencing task performance: while increasing the speed of the moving objects increased the chances of dropping a target item during the tracking period as was evident in a decrease in the CDA amplitude, increasing the number of distractors led to swapping of a target item with a distractor, affecting the behavioral performance (i.e., lower accuracy performance), leaving the CDA amplitude unchanged (Drew et al., 2013, 2012; Drew and Vogel, 2008).

4.4. *Complexity and resolution*

The CDA was used to investigate whether VWM representations are sensitive to the object's complexity and to the resolution with which objects are maintained or whether VWM is sensitive only to the number of encoded items. Behavioral evidence is mixed, with some studies indicating that complex objects consume more WM capacity (Alvarez and Cavanagh, 2004), but others providing evidence for intact representations for complex stimuli, attributing the previously reported decrement in performance to processes following VWM retention interval, such as the comparison process (Awh et al., 2007). Studies that measured the CDA amplitude for complex objects such as random polygons showed higher CDA amplitude relative to the same number of colors (Gao et al., 2009; Luria et al., 2010; Luria and Vogel, 2011a). This evidence was interpreted as supporting the resolution view of VWM capacity allocation (Ma et al., 2014), since the amount of VWM resources devoted to an item (as reflected by the CDA amplitude) was found to be a function of the object complexity. However, a recent study demonstrated that while the CDA amplitude for random polygons may increase following task related resolution demands, it could not be decreased to the level of simple items such as colors. In this study (Allon et al., 2014), lowering the resolution demands was manipulated by asking subjects to monitor for a category change (e.g., between a polygon and a color). Thus, there was no need for maintaining any fine detailed information. While this manipulation improved the accuracy performance, the CDA amplitude did not show any reduction relative to a condition in which the task required encoding the full polygon's resolution. Moreover, a recent study (Balaban and Luria, 2015b) found that one polygon had the same CDA amplitude relative to just half of that polygon, even though a polygon is evidently more complex than its half.

Studies that directly manipulated color resolution also found that it had no effect on the CDA (Ikkai et al., 2010; Luria et al., 2010; Ye et al., 2014) and studies that manipulated orientation resolution reported mixed results (Gao et al., 2011a,b; Machizawa et al., 2012). Note that increasing the number of relevant features within an object did not affect the CDA (Luria and Vogel, 2011a; Woodman and Vogel, 2008). Thus, we conclude that the CDA is not affected by the item's resolution per se.

One option is that VWM devotes more than one slot to items that do not have a LTM trace, in line with some sort of a slot + averaging model (Zhang and Luck, 2008). Thus, polygons show increased CDA activity because they do not have LTM traces, consuming multiple slots in order to be actively represented. Corroborating this argument, it was found the CDA for non-words is higher than the CDA for words (Predovan et al., 2009), so that "complexity" might arise due to the lack of semantic meaning. Another option is that resolution and capacity rely on separate mechanisms (Awh et al., 2007; Ye et al., 2014). The question of whether VWM capacity is allocated flexibly according to the items resolution or is allocated according to the number of objects is still an open question in VWM (Bays et al., 2009; Zhang and Luck, 2011), and the CDA is likely to play an important role in investigating this topic.

4.5. *Binding and grouping*

Most theories agree that working memory capacity is strictly limited (Bays and Husain, 2008; Cowan, 2001; Luck and Vogel, 2013). One way of bypassing this constraint is by uniting several features or objects to form a bound representation that can fit within working memory capacity limits. For the current purpose, we refer to the ability to integrate several features such as color and orientation into a bound object representation as the binding ability (Hommel, 2004; Treisman, 1996), and to the process of integrating several objects into one group, as the grouping ability (Peterson et al., 2015; Woodman et al., 2003). The CDA is ideally suited for investigating binding and grouping because any decrease in the number of maintained objects (for example by grouping 2 items into just one VWM representation) should be followed by a similar decrease in the CDA amplitude.

The question of how we solve the binding problem and integrate several features to perceive a bound object representation has a long history in cognitive research (Treisman, 1996). In the context of VWM, studies using the CDA confirmed that simple features such as color and orientation were easily integrated into one representation. For example, the CDA amplitude of just an orientation was equivalent to the CDA amplitude of a colored orientation, and smaller than an orientation and a color patch presented as separate items, even though this last condition contained the exact information as in the integrated object (Luria and Vogel, 2011a; Woodman and Vogel, 2008). Interestingly, the same trend was observed for random polygons, such that adding a color to a polygon (so that the task required monitoring both color and shape change, instead of just monitoring a shape change) did not further increase the CDA amplitude.

While most evidence suggest that binding a small set of different features is a fast and cost-free process, CDA evidence also suggests that VWM is rather flexible in terms of which object's features are encoded and maintained, indicating that binding may not be an obligatory process (at least under some conditions). For example, when colored random polygons were presented, participants could selectively encode only one of the objects' features but ignoring the other, such that the CDA amplitude was lower when the task required monitoring only the color (the polygon's shape could not change) relative to a condition in which only the shape was the task relevant feature (Luria et al., 2010). Thus, VWM representations as indicating by the CDA amplitude were modulated depending on the relevant task feature, even though identical stimuli were presented across conditions. This reveals the flexible nature of VWM when determining which objects' features to encode in its limited workspace.

The ability to group separate objects into one representation was traditionally studied using Gestalt principles such as similarity, connectedness and common fate. Indeed, several studies investigated how these cues affect working memory representations by measuring the CDA. In the case of similarity, it was found that identical colors were integrated in VWM such that the CDA amplitude for 4 identical colors was comparable to the amplitude of just one color, and both were lower than a condition with four different colors (Gao et al., 2011a,b; Peterson et al., 2015). Recent research that studied the common fate grouping cue, revealed a more complicated picture. While common fate was successful in integrating colors once they moved together (Luria and Vogel, 2014), a distinct color and an orientation were not integrated even when moving together, one on top of another (Balaban and Luria, 2015a). This is evidence that the stimulus type plays a major role in the ability of VWM to group objects.

Moreover, it was shown that other non-perceptual factors affected grouping processes in VMW. One example is that the items' history as moving separately or together affected the grouping ability, such that after an independent movement period, when colored patches shared the same spatial position forming color-color conjunction (which can be seen as a strong proximity cue), these color-color conjunctions were not fully integrated, as indicated by the CDA amplitude that was higher than a condition with the same number of simple colors (Luria and Vogel, 2014). The CDA also revealed that object grouping might take time to establish, so that in the case of stationary colors sharing the same position (and also when the colors were connected by a line), the CDA amplitude gradually decreased during the retention interval (Luria and Vogel, 2011a; Peterson et al., 2015). Remarkably, these studies reveal that although Gestalt cues affect VWM representations, they do not cause grouping in a reflexive and 'automatic' manner. Rather, there are several factors such as the stimuli categories and the items recent history (as being separated or grouped) that certainly influence, and could sometimes even override strong Gestalt cues such as common fate. To summarize, the CDA research regarding binding and grouping reveals a more complex and flexible mechanism than just following bottom-up salient objecthood cues.

5. CDA as an index of WMC in special populations

It has been claimed that VWM is impaired in several clinical and sub-clinical populations. Following these arguments, the CDA has been used to characterize the specific deficit in VWM in these special populations. It was demonstrated that the filtering efficiency was impaired in Parkinson patients (Lee et al., 2010), in dysphoriatic individuals (Owens et al., 2012, 2013), in old age (at early stages of processing, Jost et al., 2011) and in anxious individuals (Meconi et al., 2014; Qi et al., 2014; Stout et al., 2013). The filtering deficit for anxious individuals was found when encoding threatening and untrustworthy faces, but also when encoding neutral distractors, which might suggest a general filtering deficit in this case. More general VWM impairments, as evident in a general amplitude difference relative to a control group, were found in Parkinson disease (Lee et al., 2010), schizophrenia (Leonard et al., 2013) and in ALS patients (Zaehle et al., 2013), even when the ALS patients did not show any impaired behavioral performance. Interestingly, the CDA set-size was reduced for older adults at a risk for developing mild cognitive impairments (before exhibiting any severe symptoms) compared to a matched age group (Newsome et al., 2013). Thus, the CDA may be a reliable and potent tool in these special circumstances.

6. Summary

We have reviewed evidence supporting that the CDA tracks the online VWM processes related to the task at hand. The CDA amplitude is highly sensitive to the number of represented items, strongly correlates with the individual VWM capacity, and is able to predict performance in a variety of tasks and populations. Findings from numerous CDA studies indicate that VWM capacity is tightly related to filtering ability, explain how VWM is involved when searching targets among distractors and enable observing how the target information is transferred from working memory to LTM. Other results support that VWM capacity allocation follows the number of represented objects rather than the item's complexity, and highlight VWM flexibility when grouping and binding several objects or features. Overall, these results support the idea that the CDA is a valuable tool in any task that involves online processing of visual information. Rather than just following the number of items maintained in VWM, the CDA is a marker for the involvement of working memory online processing and is likely to play a an important role in future investigations of how VWM operates and how it guides behavior.

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