



The capacity and resolution of spatial working memory and its role in the storage of non-spatial features

Cody W. McCants, Tobias Katus, Martin Eimer*

Department of Psychological Sciences, Birkbeck, University of London, Malet Street, London WC1E 7HX, UK

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ABSTRACT

The question whether the storage of spatial locations and other non-spatial features in visual working memory (WM) is based on shared or separate processes remains unresolved. We recorded contralateral delay activity (CDA) components as on-line electrophysiological markers of WM maintenance in two tasks where observers had to retain either the colors or locations of sample stimuli. CDA components were elicited both in the Color and in the Location task, and increasing WM load had identical effects on CDA amplitudes, suggesting shared underlying mechanisms. However, CDA amplitudes were generally larger in the Location Task. Experiment 2 demonstrated that the CDA is sensitive to the resolution demands of spatial WM tasks. CDA amplitudes elicited during the storage of object locations in WM were larger when these locations had to be retained with higher precision. These findings support the hypothesis that spatial and non-spatial features of visual objects are represented in an integrated fashion in WM. The activation of these representations is controlled by space-based attentional control processes, and their spatial resolution can be regulated in line with current task demands.

1. Introduction

Working memory (WM) is responsible for the active short-term maintenance of information that is no longer perceptually available, and for making this information accessible to ongoing cognitive activities. The classic multiple-component model of WM (e.g., [Baddeley & Hitch, 1974](#)) postulates the existence of separate storage systems for verbal and visual information (the phonological loop and the visuospatial scratchpad), and a central executive that allocates attention and controls the activation states of representations in these storage systems. More recent extensions of this model (e.g., [Baddeley, 2003](#)) include the addition of a third independent storage system (the episodic buffer), as well as an important distinction within the visuospatial scratchpad between the storage of spatial locations and the maintenance of other types of non-spatial visual information (e.g., [Logie & Pearson, 1997](#); [Zimmer, 2008](#)).

The question whether and how visual WM for locations differs from WM for other visual attributes such as color or shape is important for our understanding of how WM is organised, and of how WM storage is implemented in the brain. Early neural models of WM assumed that memorized objects are maintained in a modality-unspecific fashion in prefrontal cortex (e.g., [Goldman-Rakic, 1990](#)). In contrast, more recent sensory recruitment accounts of WM (e.g., [Postle, 2006](#)) postulate that

WM storage is primarily implemented by the modality-specific sensory brain areas that are also involved in the on-line perceptual analysis of incoming information. Evidence for such sensory recruitment mechanisms was provided by studies who found sustained activations during the delay period of visual WM tasks within extrastriate visual-perceptual areas (e.g., [Emrich, Riggall, LaRocque, & Postle, 2013](#); [Ranganath, Cohen, Dam, & D'Esposito, 2004](#)). In these areas, visual information is represented in a spatiotopic fashion in two-dimensional maps (e.g., [Franconeri, Alvarez, & Cavanagh, 2013](#)), and the active maintenance of this information is assumed to be controlled by the selective allocation of attention to particular locations within in these maps. Evidence for such links between spatial attention and visual WM storage comes from studies investigating memory for spatial locations (e.g., [Awh, Anillo-Vento, & Hillyard, 2000](#)), but it is plausible that attention is also involved in the maintenance of non-spatial visual attributes (see [Awh, Vogel, & Oh, 2006](#), for discussion). If WM maintenance is based on the allocation of attention to features or objects that are represented at particular locations within extrastriate visual maps, location information may always be explicitly represented, regardless of whether observers have to remember object positions or other non-spatial attributes of these objects (e.g., [Foster, Bsaies, Jaffe, & Awh, 2017](#)). More generally, this would also be in line with the suggestion that visual WM contains object-based representations where all features

* Corresponding author.

E-mail address: m.eimer@bbk.ac.uk (M. Eimer).

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of a memorized object (including its spatial location) are stored in a fully integrated fashion (e.g., Luck & Vogel, 1997).

The idea that visual WM representations integrate the location and other non-spatial attributes of visual objects is not universally accepted. An alternative possibility is that spatial locations and other non-spatial object features can also be represented in functionally and anatomically independent WM stores. This was suggested by Wheeler and Treisman (2002) on the basis of behavioral experiments that used variations of the change detection task introduced by Luck and Vogel (1997). A set of colored squares was presented in memory sample displays, and participants had to report whether or not there was a change in the memory test display that was presented after a delay period. In the color task, only the square colors could change, while only location changes were present in the location task. In another condition (either task), both color changes and location changes were possible and were randomly intermixed, so that participants had to independently memorize both dimensions of the sample stimuli on each trial. Performance was better in the location task than in the color task, but, critically, performance in the either task was identical to the color task. Wheeler and Treisman (2002) interpreted the absence of any costs in this task relative to the color task as evidence that colors and spatial locations can be held independently in parallel systems with separate storage capacities. In a fourth task where observers had to remember color/location conjunctions, performance costs were observed when memory test displays contained multiple objects. This suggests that colors and locations can also be represented in an integrated fashion, but that this type of storage requires additional attentional resources.

It is difficult to dissociate the integrated versus separate maintenance of spatial locations and non-spatial object features in visual WM exclusively on the basis of behavioral measures. For example, the performance costs found by Wheeler and Treisman (2002) in their color/location conjunction tasks are likely to be associated not with WM storage, but with subsequent sample-test comparison processes. An alternative approach is to measure brain activity elicited during visual WM task as a marker of WM maintenance processes. Previous event-related potential (ERP) studies (e.g., Vogel & Machizawa, 2004; McCollough, Machizawa, & Vogel, 2007) have employed a lateralized change detection task where bilateral memory sample displays contained colored objects in the left and right visual hemifield, and observers had to maintain the colors of sample stimuli on one side in order to compare them to a subsequent test display. ERPs recorded during the delay period between the memory and test displays revealed an enhanced negativity at posterior electrodes contralateral to the to-be-remembered display side (contralateral delay activity, CDA). This activity started around 300 ms after the onset of the memory sample display, persisted throughout the retention interval, increased in amplitude when memory load was increased, and was sensitive to individual differences in WM capacity (e.g., Vogel & Machizawa, 2004). These observations support the view that the CDA is an on-line neural marker of the storage of objects or object features in visual WM.

To address the question whether non-spatial features (color and orientation) can be represented separately in WM even when they belong to the same object, Woodman and Vogel (2008) measured CDA components to memory sample displays containing oriented colored rectangles in tasks where observers had to memorize either color, orientation, or the conjunction of both features. CDA amplitudes were larger when orientation as compared to color was task-relevant, in spite of the fact that sample displays were identical. Because no such CDA amplitude difference should have been present if color and orientation were always stored in an integrated fashion in WM, Woodman and Vogel (2008) interpreted this result as evidence that color and orientation information can be represented independently, even when the other feature is present in the same object. Here, we employed CDA measures to investigate whether spatial and non-spatial features are stored in WM in an integrated or independent fashion.

In line with the sensory recruitment model of WM, CDA components

observed during the retention of visual stimuli show a modality-specific topography CDA over contralateral posterior visual areas, suggesting that they reflect the activation of visual-perceptual brain regions during the maintenance of visual information. During the retention of tactile stimuli presented to the left versus right hand, a similar sustained contralateral component is elicited (tactile CDA; e.g., Katus, Grubert, & Eimer, 2015; Katus & Eimer, 2016), with a modality-specific topography over central somatosensory cortex. Given their likely origin in spatiotopic visual and somatosensory cortex, it is plausible to assume that the visual and tactile CDA components reflect the attentional activation of particular locations within the cortical maps in these areas (e.g., Berggren & Eimer, 2016; Katus & Eimer, 2015). If this was the case, load-related CDA amplitude differences should primarily reflect how many different locations are currently attended, rather than the number of features that are currently maintained in WM. In line with this hypothesis, visual CDA amplitudes were found to be similar when one feature (orientation) or two features (orientation and color) of the same object had to be memorized, and larger when the memorized orientation and color were presented at different locations (Luria & Vogel, 2011). However, results from another CDA study (Ikkai, McCollough, & Vogel, 2010, Exp. 2) suggest that this component does not directly reflect the number of attended spatial positions. In this experiment, two sample displays that each contained two task-relevant colored stimuli were presented sequentially, and the relevant stimuli either appeared at the same locations or at different locations in these two displays. CDA amplitudes increased in the interval following the second sample display, and this was the case not only on different-location trials, but also, critically, on same-location trials. This suggests that the CDA reflects how many objects are represented in WM, rather than the number of object locations.

Overall, current evidence about the link between CDA components and the storage of object features versus spatial locations in visual WM is inconclusive. Until now, visual CDA components have been exclusively measured under conditions where participants had to maintain non-spatial attributes of visual objects such as their color or shape, but not in purely spatial WM tasks. In order to understand whether the retention of spatial locations and non-spatial object attributes operates in an integrated or separable fashion, it is important to directly compare CDA components in both types of tasks. This was done in the present study. In Experiment 1, we measured CDAs in a standard color change detection task, and compared them to lateralized ERP components measured during the delay period of an exclusively location-based WM task where only spatial positions had to be retained. In both tasks, physically identical memory sample displays were shown, which contained one, two, three, or four colored items on the left and right side (see Fig. 1). The items on both sides differed in their shape (circles versus squares), and participants had to encode and maintain items in the pre-defined target shape in order to compare them to the subsequent bilateral test display that contained a single item on either side. The side on which the relevant sample and test stimuli appeared varied randomly across trials. In the Color Task, participants memorized the colors of the task-relevant sample items, and reported whether the test item on the same side matched or did not match one of the sample items. The locations where the sample stimuli appeared were irrelevant, as the test items were always presented at a different location as any of the samples. In the Location Task, participants were instructed to maintain the locations of the task-relevant samples, and match them to the location of the subsequent test item on the same side. The colors of the samples were now task-irrelevant, as the test items were always white. WM load was manipulated in the same way for both tasks, by presenting sample displays with 1, 2, 3, or 4 task-relevant items.

CDA components were measured during the retention interval between the memory sample and test displays, separately for the Color and Location tasks, and for each level of WM load. For the Color Task, results were expected to be similar to previous ERP studies using analogous color change detection procedures (e.g., Vogel & Machizawa,

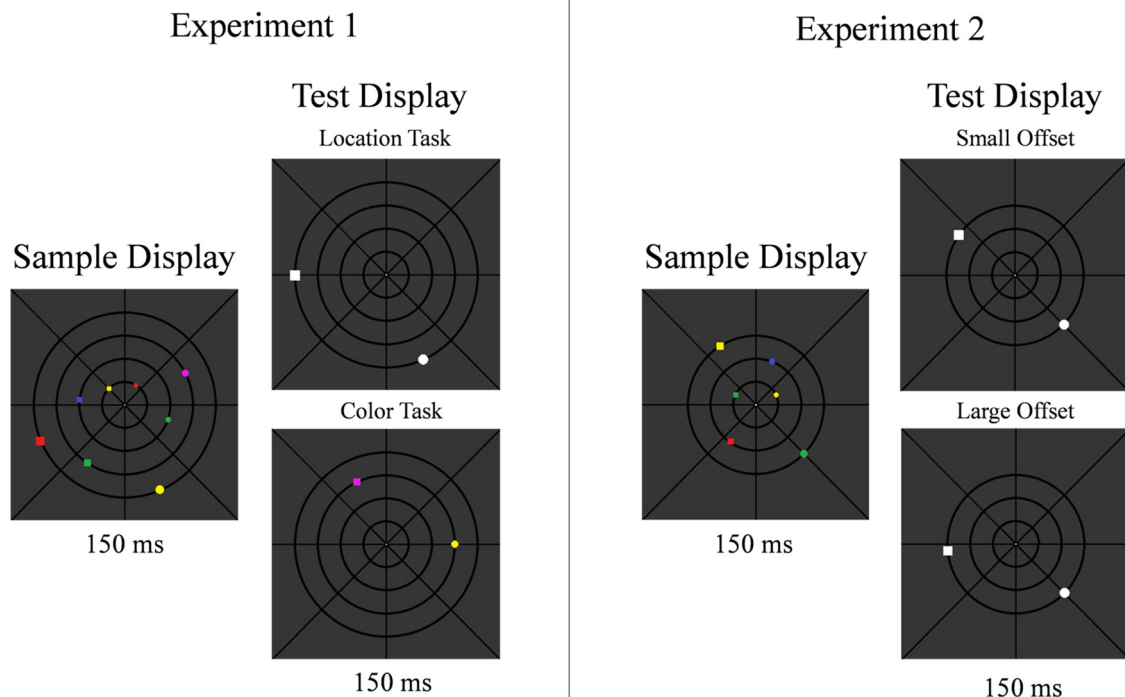


Fig. 1. Examples of memory sample and test displays in Experiment 1 (left panel) and Experiment 2 (right panel). In these examples, participants had to encode the locations or colors of the squares on the left side of the memory displays, in order to match the location/color of the square in the test display to one of the sample items. In Experiment 2, only stimulus locations had to be memorized. On mismatch trials, the spatial distance between the relevant item in the test display and the nearest item in the sample display was either small (Small Offset Task) or large (Large Offset Task). Only mismatch trials are shown in Fig. 1. See online article for a color version of this Figure.

2004; McCollough et al., 2007; Ikkai et al., 2010). CDA amplitudes should increase with increasing WM load, and reach asymptote at the typical WM capacity limit of 3 items. The critical new question was which pattern of CDA components would be observed in the Location Task. One possibility is that CDAs elicited during the retention of spatial locations are not sensitive to how many locations have to be maintained. This would suggest that in contrast to the storage of object colors, where the CDA reflects the number of individual objects that are currently maintained in WM, objects are not represented in an individuated fashion when only their locations have to be memorized. For example, they might be grouped and stored as single spatial pattern, irrespective of how many individual locations contribute to this pattern. The presence of load effects for CDA components in the Color Task and the absence of such effects in the Location Task would be indicative of fundamental qualitative differences between the storage of features and spatial locations in WM. Another possibility is that CDA components show load-dependent amplitude increases not only in the Color Task but also in the Location Task, but that these load effects differ systematically between the two tasks. For example, CDA amplitudes might reach asymptote earlier in the Color Task relative to the Location Task. This would point towards quantitative differences between WM storage mechanisms for colors and locations, in line with the suggestion by Wheeler and Treisman (2002) that these attributes are maintained independently in parallel stores with separate capacities. A third possible outcome is that the effects of WM load on CDA components are identical in both tasks, but that CDA amplitudes are generally larger in the Color Task. Such a result could indicate that locations are always represented explicitly even when they are irrelevant (e.g., Foster et al., 2017) whereas object colors are only maintained when WM for color is subsequently tested. In this context, a larger CDA in the Color Task would reflect stronger activations during the retention of two attributes for each memorized object (color and location) than when just the spatial locations of objects are maintained. This would be problematic

for the hypothesis that visual WM always represents spatial and non-spatial features in a fully integrated fashion, irrespective of which attribute has to be memorized (see Woodman & Luck, 2008, for the same logic applied to the storage of color and orientation). A final possibility is that there are no CDA differences at all between the Color and Location tasks. This would be consistent with the hypothesis that the maintenance of spatial locations and non-spatial features of objects are equally based on the allocation of spatial attention to specific locations in visual cortical maps. CDA amplitudes directly reflect the number of currently attended objects at particular locations within these maps. Because all features of these objects, including their spatial locations, are represented in an integrated fashion, WM maintenance processes will remain unaffected by whether object colors or locations are currently task-relevant.

2. Experiment 1

2.1. Method

2.1.1. Participants

Sixteen participants were tested for Experiment 1 (mean age 28 years, 6 female, 14 right-handed). All participants were neurologically unimpaired and gave informed written consent prior to testing. The experiment was conducted in accordance with the Declaration of Helsinki, and was approved by the Psychology Ethics Committee, Birkbeck, University of London.

2.1.2. Stimuli and procedure

The task was based on the visual task used in a previous multi-sensory WM experiment (Katus & Eimer, 2018). Visual stimuli were presented at a viewing distance of 100 cm against a dark grey background on a 22 inch monitor (Samsung SyncMaster 2233; 100 Hz refresh rate, 16 ms response time). Throughout the experiments, the

monitor showed black crosshairs (three lines at 0°, 45° and 90° polar angle; horizontal/vertical eccentricity: 9° of visual angle) and four black rings centred on the fixation dot (see Fig. 1, left panel). The eccentricity of the four rings was 2.18°, 4.24°, 6.41°, and 8.46°; respectively. Visual sample and test stimuli (circles and squares) were presented on top of these rings, and their size was scaled for eccentricity (circles: 0.34°, 0.40°, 0.52°, and 0.57°; squares: 0.30°, 0.36°, 0.46°, and 0.51°, from the innermost to outermost ring). On each trial, a memory sample display was followed by a retention period and then by a memory test display. Sample and test displays were each presented for 150 ms, and were separated by a period of 850 ms where only the rings/crosshair display was visible. Thus, the stimulus onset asynchrony (SOA) between memory sample and test displays was 1000 ms. Memory displays contained a set of colored circles and squares. Stimulus colors of the stimuli were drawn from a set of five equiluminant colors (~11.8 cd/m²; CIE color coordinates, red: .627/.336; green: .263/.568; blue: .189/.193; yellow: .422/.468; magenta: .289/.168).

There were two tasks (Color Task and Location Task). Participants had to memorize the sample stimuli in a predefined task-relevant shape (circles or squares), and to judge whether the test stimulus with the task-relevant shape matched the color or the location of one of the task-relevant items in the sample display (match trials) or not (mismatch trials). They responded by pressing one of two vertically aligned response buttons (top for match, bottom for mismatch) with the index finger of the left or right hand during a 1500 ms response period starting at the onset of each test display. In each memory sample display, squares and circles were always presented on opposite sides, to ensure that participants would always encode and maintain stimuli in one hemifield only. Sample displays with squares on the left and circles on the right, and vice versa, were randomly intermixed in each block. For eight participants, squares were task-relevant and circles had to be ignored, and this assignment was reversed for the other eight participants.

The number of to-be-memorized items in the sample display (WM load: one, two, three, or four items) was varied randomly across trials. Task-relevant sample stimuli were always accompanied by the same number of stimuli with the task-irrelevant shape on the opposite side. Memory sample displays for a given WM load (N) were generated by randomly selecting N colors and N locations on each trial, independently for the samples on the left and right side. Locations were sampled from 240 angular positions (in polar coordinates, left side: 120° to 240°, right side: 300° to 60°), with the constraint that any two sampled positions were at least 20° apart. Pairs of positions on the left and right side were assigned to the same concentric ring. N rings were selected without replacement to ensure that no ring contained more than one item on each side.

Test displays contained one circle and one square on the same side where circles and squares had appeared in the preceding memory sample display. In the Color task, participants judged whether the color of the test stimulus in the task-relevant shape matched the color of one of the task-relevant sample stimuli (50% match/mismatch). Sample stimulus locations were irrelevant, as this test stimulus appeared on the same side as the relevant sample stimuli, but at a randomly selected position. In the Location task, test displays always contained a white circle and a white square on opposite sides. Participants had to judge whether the location of the task-relevant test item matched the location of one of the relevant items in the preceding sample display, which was the case on match trials (50% of all trials). On mismatch trials, the location of this test item was shifted to a different location on the same ring that was previously occupied by a task-relevant sample item (25° angular offset relative to the original sample location; with upwards or downwards shifts equiprobable and randomly mixed across trials).

The experiment contained 20 blocks with 40 trials per block, resulting in a total of 100 trials for each WM load condition in either task. Task order was randomly determined for each participant, and varied in an ABBA fashion (i.e., the task changed after block five and after block

15). One training block was run prior to the start of the first experimental block. Feedback about the proportion of correct responses was given after each experimental block.

2.1.3. EEG recording and analysis

EEG data, sampled at 500 Hz using a BrainVision amplifier, were DC-recorded from 32 electrodes at standard locations of the extended 10–20 system. Two electrodes at the eyes' outer canthi monitored horizontal eye movements (horizontal electrooculogram, HEOG). Continuous EEG data were referenced to the left earlobe during recording, and re-referenced to the arithmetic mean of both earlobes for data pre-processing. Data were offline submitted to a 20 Hz low-pass filter (Blackman window, filter order 2000). To confirm that this specific filter setting did not affect the pattern of CDA effects, additional analyses were conducted on EEG data sets that were low-pass filtered at 40 Hz. Statistical results were virtually identical for both filter settings. Epochs were computed for the 1000 ms interval following the onset of a memory sample display, relative to a 200 ms pre-stimulus baseline.

Trials with saccades were rejected using a step function that ran on the bipolarized HEOG (step width 200 ms, threshold 25 μ V). Independent Component Analysis (ICA) (Delorme, Sejnowski, & Makeig, 2007) was used to correct for frontal artefacts such as eye blinks, and residual traces of horizontal eye movements that had not been detected by the step function. Trials were rejected when EEG amplitudes at any electrode exceeded a 100 μ V threshold, and when amplitudes in the time window of interest (i.e., between 300 and 1000 ms following sample display onset) exceeded a 20 μ V threshold in difference waveforms for lateral electrode pairs (such as O1 vs. O2). Trials with incorrect behavioral responses were also excluded from EEG analysis. Following trial rejection, an average of 75.6% of all trials were retained.

EEG was averaged separately for all four WM load conditions in the Color and Location tasks, for trials where the task-relevant memory samples appeared on the left or right side. CDA components were computed on the basis of mean amplitudes measured during the 300–1000 ms interval after sample display onset. The CDA was measured at lateral occipital electrodes PO7 and PO8 where this component is usually maximal. This was confirmed by quantifying mean CDA amplitudes across all task conditions separately for all four lateral posterior electrode pairs (mean CDA amplitudes at PO7/8: −1.18 μ V, P7/8: −1.05 μ V, PO9/10: −1.0 μ V, P9/10: −0.94 μ V). CDA mean amplitude differences between tasks and WM load conditions were assessed in a repeated measures ANOVA. To test whether the effects of manipulating WM load on WM accuracy and CDA amplitudes were identical or differed between the Color and Location tasks, we used Bayesian analyses (Rouder, Speckman, Sun, Morey, & Iverson, 2009) and the software Jasp (JASP Team, 2018) to calculate Bayes factors for interactions between the factors Task and WM Load. Bayes factors denote the relative evidence for the null hypothesis as compared to the alternative hypothesis, and thus allow for statistical inferences regarding the absence of differential effects. The Bayes factor for the null hypothesis (BF_{01}) corresponds to the inverse of the Bayes factor for the alternative hypothesis (BF_{10}), and indexes the relative evidence in the data that an effect is absent rather than present. Reliable evidence for the null hypothesis is provided by a $BF_{01} > 3$ (Jeffreys, 1961), suggesting that the empirical data is at least 3 times more likely under this hypothesis as compared to the alternative hypothesis.

3. Results

3.1. Behavioral performance

Memory accuracy was assessed in an ANOVA with the factors Task (Color versus Location) and WM Load (1, 2, 3, or 4 items). As can be seen in Fig. 2 (top left panel), accuracy was generally higher in the Color Task than in the Location Task (87.1% versus 80.6% correct

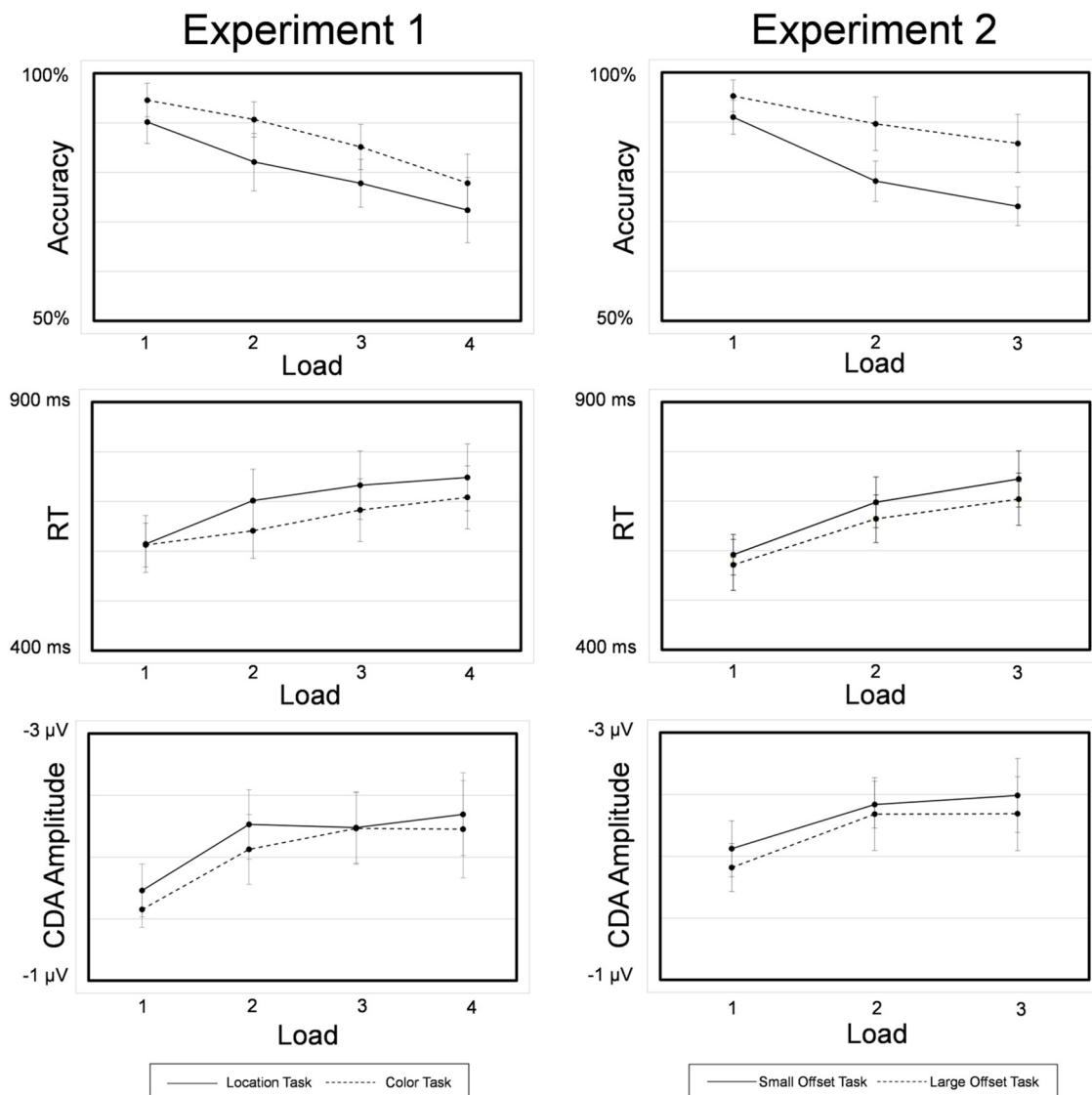


Fig. 2. Accuracy of WM performance (top panels), RTs to memory test displays (middle panels), and CDA amplitudes (bottom panel), shown separately for the two tasks and all WM load conditions in Experiment 1 (left) and Experiment 2 (right). Error bars in graphs indicate 95% confidence intervals (CIs) for the true population mean.

responses), as reflected by a main effect of Task ($F(1, 15) = 6.201, p = 0.025, \eta_p^2 = .292$). Unsurprisingly, accuracy dropped when WM load increased (main effect of WM Load: $F(1.55, 23.27) = 41.58, p < .001, \eta_p^2 = .735$). This effect of WM load on accuracy was similar in the Color and Location tasks, as reflected by the absence of an interaction between WM Load and Task ($F(3, 45) = 1.32, p = 0.279, \eta_p^2 = .081$). This hypothesis that the manipulation of WM load affected the accuracy of WM for colors and for locations in an essentially identical fashion was confirmed by the corresponding Bayesian analysis ($BF_{01} = 7.25$).

Reaction times (RTs) to memory test displays were slower in the Location Task than in the Color Task (699 ms vs. 661 ms), but this difference only approached significance ($F(1, 15) = 4.413, p = 0.053, \eta_p^2 = .227$). A main effect of Load ($F(1.37, 21.24) = 36.73, p < .001, \eta_p^2 = .710$) confirmed that RTs increased with increasing WM load. There was also an interaction between WM Load and Task ($F(1.42, 21.24) = 6.008, p = 0.002, \eta_p^2 = .286$). This was due to the fact that increasing WM load from one to two items had a stronger effect on RTs in the Location Task relative to the Color Task (87 ms versus 29 ms; $t(15) = 4.72, p < .001$).

3.2. CDA components

Fig. 3 shows CDA components elicited in the 1000 ms interval after memory sample display onset for displays containing one, two, three, or four lateralized task-relevant items, separately for the Location and Color Tasks. ERPs elicited at electrodes PO7/8 contralateral and ipsilateral to the task-relevant sample items are shown together with the corresponding contralateral-ipsilateral difference waveforms. CDA components were elicited in both tasks, and CDA amplitudes increased with increasing WM load. This is further illustrated by the topographical scalp distribution maps of lateralized ERP activity during the 300–1000 ms interval after sample display onset shown in Fig. 3. These spline-interpolated voltage maps were obtained by subtracting ERPs ipsilateral to the task-relevant target stimuli from contralateral ERPs, and flipping electrode coordinates over the midline for sample displays with task-relevant items on the left side. As a result, CDA components are reflected by negative potentials over the left hemisphere in these maps.

The analysis of CDA mean amplitudes with the factors Task, WM Load, and Laterality (electrode contralateral versus ipsilateral to the task-relevant samples) obtained a main effect of Laterality (F

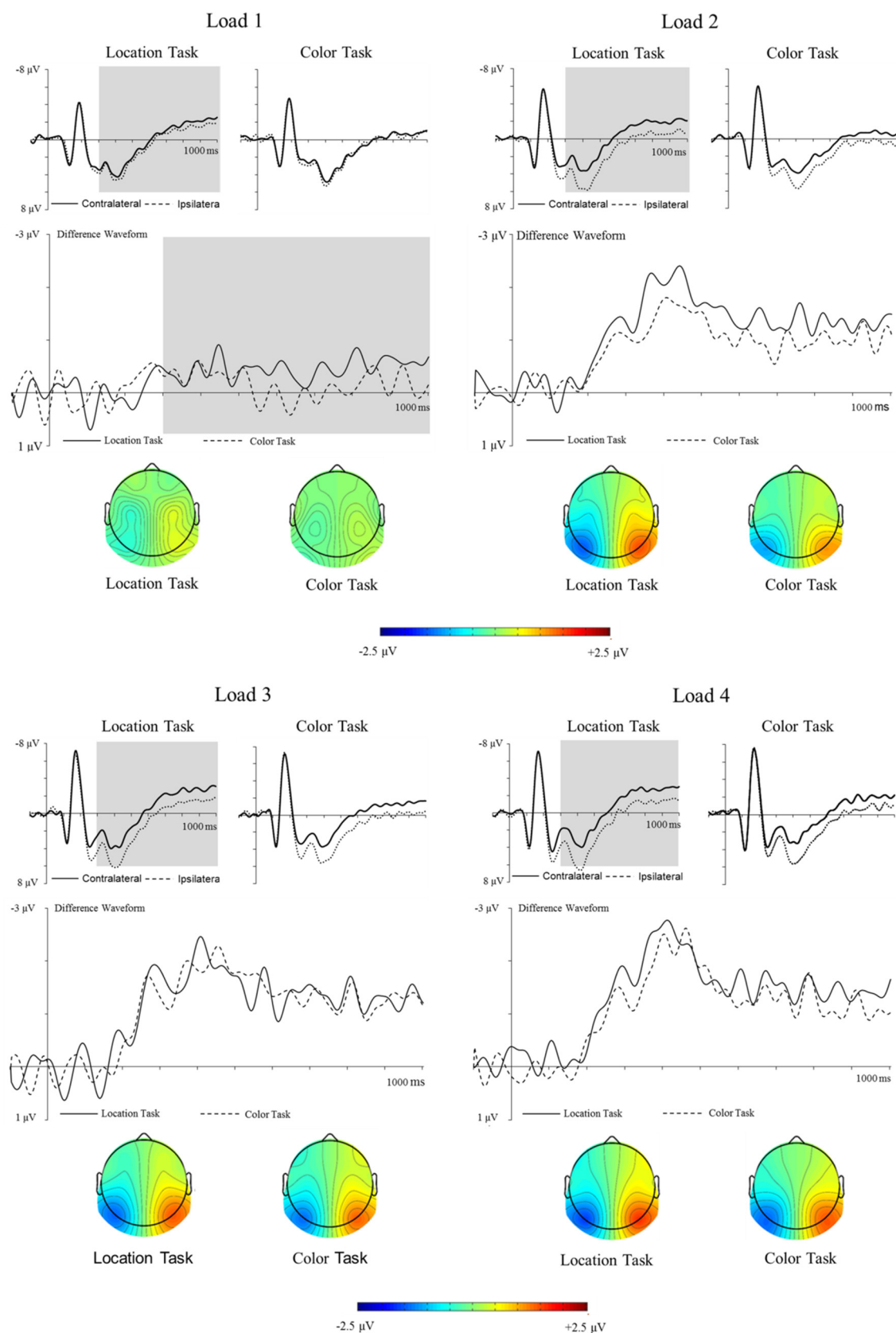


Fig. 3. Grand-averaged ERPs elicited in Experiment 1 in response to memory sample displays at electrodes PO7/8 contralateral and ipsilateral to the task-relevant sample display items. ERPs are shown separately for the Location and Color Tasks, together with difference waveforms obtained by subtracting ipsilateral from contralateral ERPs. Topographic maps show the scalp distribution of CDA components during the 300–1000 ms interval after memory display onset for both tasks. Data are shown separately for WM loads of 1, 2, 3, or 4 items. See online article for a color version of this Figure.

(1,15) = 28.32, $p < .001$, $\eta_p^2 = .654$), confirming the presence of reliable CDA components in Experiment 1. As expected, there was also an interaction between Laterality and WM Load ($F(3, 45) = 18.718$, $p < .001$, $\eta_p^2 = .555$), reflecting the increase of CDA amplitudes when WM load was increased. Importantly, there was also an interaction between Task and Laterality ($F(1, 15) = 8.66$, $p = 0.010$, $\eta_p^2 = .366$), as there was a small but systematic tendency for CDA amplitudes to be larger in the Location Task than in the Color Task. This difference remained reliable when CDA components were measured across all four lateral posterior electrode pairs (PO7/8, P7/8, PO9/10, P9/10; $F(1, 15) = 7.30$, $p = 0.016$, $\eta_p^2 = 0.327$), as larger CDA amplitudes in the Location task were present at all four pairs. This CDA enhancement in the Location Task is also illustrated in Fig. 2 (bottom left panel), which shows mean CDA amplitudes for each WM Load condition in both tasks. Finally, there was no three-way interaction between Laterality, Task, and WM ($F(3, 45) = 0.594$, $p = 0.622$, $\eta_p^2 = .038$), suggesting that the impact of increasing WM load on CDA amplitudes did not differ between the Color and Location tasks. The hypothesis that the manipulation of WM load had identical effects on CDA components in both tasks was confirmed by the corresponding Bayesian analysis ($BF_{01} = 7.545$).

4. Discussion of Experiment 1

Experiment 1 demonstrated that CDA components are not only triggered during the maintenance of non-spatial features of visual objects, but also when only the locations of these objects have to be retained in WM. Moreover, and importantly, the effects of increasing WM load on CDA amplitudes were identical in both tasks. These findings are in line with the hypothesis that the storage of colors and locations in visual WM is mediated by shared mechanisms. Object colors and spatial locations may both be maintained by allocating spatial attention selectively to those locations within visual cortical maps that represent the currently task-relevant objects in a memory sample display. In this scenario, WM capacity limitations would reflect limitations in the ability to maintain multiple independent foci of spatial attention that are independent of which attributes are currently task-relevant (e.g., Franconeri et al., 2013). The observation that WM load had identical effects on WM accuracy and CDA amplitudes the Color and Location Tasks of Experiment 1 does indeed show that, at least for the task parameters of this experiment, WM for colors and locations did not differ in their capacities. The fact that increasing WM load from one to multiple items affected RTs to test displays more strongly in the Location Task than in the Color Task is unlikely to be linked to differences in storage capacity. Instead, it could reflect differences in WM retrieval and sample-test comparison processes between the two tasks.

These findings of Experiment 1 did not provide support for the hypothesis that colors and locations are stored in parallel in separate stores with independent capacities (Wheeler & Treisman, 2002). However, another aspect of the CDA results suggests that WM maintenance processes did not operate in an identical fashion in the two tasks. If locations are always maintained in an obligatory fashion even when colors have to be memorized, while colors are only retained if they are task-relevant, CDA amplitudes might have been generally larger in the Color Task relative to the Location Task, reflecting the maintenance of two versus just a single attribute for each stored sample object. This was clearly not the case. In fact, the opposite pattern was obtained, as CDA amplitudes were generally larger in the Location Task. Even though this effect was small, it was reliably present, and was independent of WM load. If the CDA reflects visual processing biases for task-relevant objects at currently attended locations that are elicited in the same way when colors or locations have to be memorized, no such CDA amplitude difference should have been observed. One possibility is that the storage of spatial and non-spatial information is based on partially separate mechanisms, with spatial WM associated with larger activation levels during the retention period. Alternatively, the presence of larger

CDAs in the Location Task could be due to the fact that this task was generally harder than the Color Task. This was reflected by reduced WM accuracy in the Location Task and a tendency towards slower RTs to test displays. As this task was apparently more demanding than the Color Task, it may have required participants to retain more precise WM representations, and this could have resulted in larger CDA amplitudes (see Reinhard et al., 2012, for links between CDA amplitudes and the spatial precision of memory-based behavior in humans and non-human primates). In this case, this CDA amplitude difference would not reflect qualitative differences between the WM storage of colors versus spatial locations, but rather a quantitative difference in the difficulty of these two WM tasks. This possibility was further investigated in Experiment 2.

5. Experiment 2

CDA components may have been larger in the Location Task than in the Color Task of Experiment 1 because the former task was harder, thus suggesting that maintaining sufficiently precise WM representations of spatial locations was more demanding than retaining object colors. The possibility that CDA amplitudes reflect task difficulty and/or the resolution with which objects are stored in WM has been investigated in several studies, which have generally obtained negative results (see Luria, Balaban, Awh, & Vogel, 2016, for review). Although the CDA increases in size when the complexity of memorized visual objects increases (Luria & Vogel, 2011), studies that manipulated the difficulty of color change detection tasks found no differential effects on CDA components (e.g., Ikkai et al., 2010; Ye, Zhang, Liu, Li, & Liu, 2014). One notable exception is a study by Machizawa, Goh, and Driver, (2012), who investigated how the difficulty of WM tasks involving line orientations affected CDA amplitudes. Participants had to memorize the orientations of two or four sample lines and to report whether a line in a subsequent test display was shifted in a clockwise or counter-clockwise directions. CDA amplitudes were larger in blocks where the line rotations in the test display were small, relative to blocks where this rotation was larger. This CDA amplitude increase was only found when WM load was small (2 sample items) but not when four line orientations had to be memorized. This suggests that voluntary adjustments of WM activation processes in line with the anticipated difficulty of subsequent memory-test comparison processes only take place under conditions where WM load remains below capacity. To confirm that the CDA amplitude increase in blocks with small line rotations was associated with more precise WM representation of line orientations, Machizawa et al. (2012) conducted another behavioral experiment where line colors in sample displays indicated whether the subsequent line orientation discrimination would be difficult or easy on most trials. On a minority of trials, test displays contained a line with an intermediate orientation shift. Performance on these critical trials was better when observers expected a difficult discrimination, demonstrating that they were able to vary the precision of WM representations in line with anticipated task demands.

The goal of Experiment 2 was to test whether the anticipated difficulty of location discriminations between memory and test displays would also affect CDA amplitudes, using a similar logic as Machizawa et al. (2012). Procedures were similar to the Location Task of Experiment 1, except that on mismatch trials, the spatial separation between the task-relevant item in the test displays and one of the relevant items in the sample displays was manipulated. In different blocks, this distance was either 40° (Large Offset Task) or 15° (Small Offset Task). The critical question was whether this difference in the difficulty of comparing spatial locations between sample and test displays would affect CDA components, with larger CDA amplitudes in the more difficult Small Offset Task. WM load (1, 2, or 3 relevant sample items) was also manipulated. Because Machizawa et al. (2012) found that task difficulty only modulated CDA amplitudes when WM load was low, WM load was blocked in Experiment 2. Foreknowledge about how many

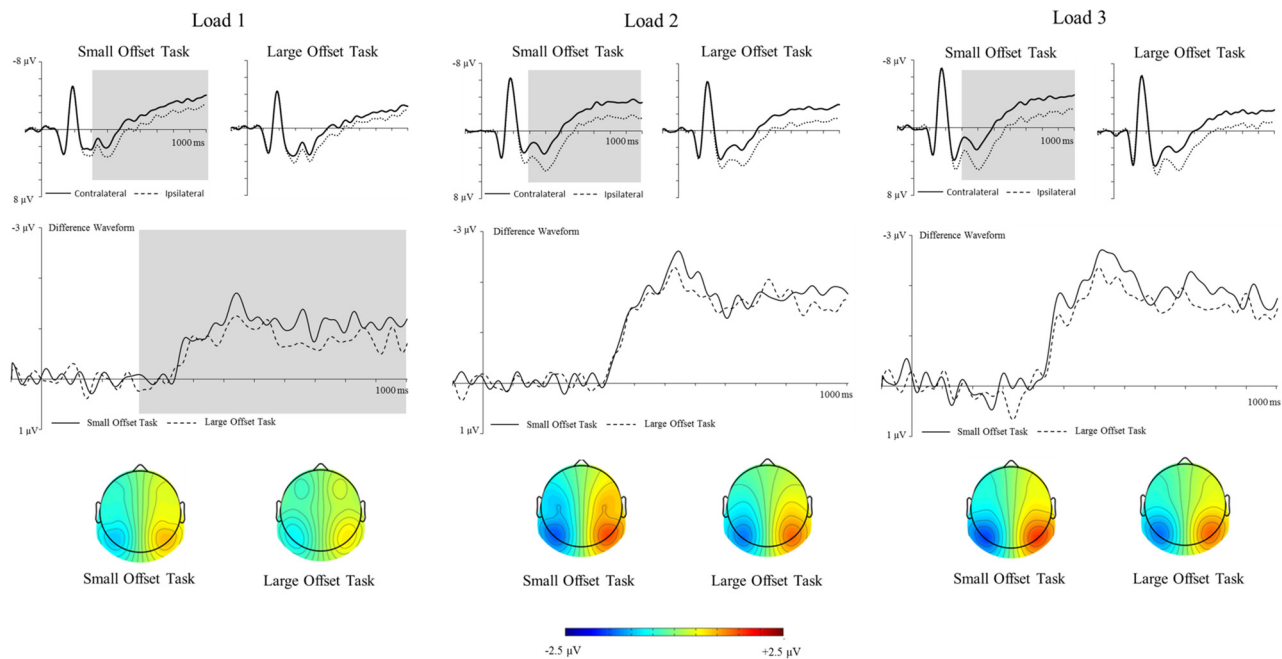


Fig. 4. Grand-averaged ERPs elicited in Experiment 2 in response to memory sample displays at electrodes PO7/8 contralateral and ipsilateral to the task-relevant sample display items. ERPs are shown separately for the Small Offset and Large Offset Tasks, and for WM loads of 1, 2, or 3 items, together with difference waveforms obtained by subtracting ipsilateral from contralateral ERPs. Topographic maps show the scalp distribution of CDA components during the 300–1000 ms interval after memory display onset for both tasks and each WM load condition. See online article for a color version of this Figure.

locations would have to be memorized for each sample display should maximize the chances to find load-related differences in the effects of task difficulty on CDA components in the Small versus Large Offset Task.

6. Method

6.1. Participants

Sixteen volunteers participated in Experiment 2 (mean age 29 years, 8 female, all right-handed). All participants were neurologically unimpaired and gave informed written consent prior to testing.

6.2. Stimuli, procedure, and analyses

These were the same as in the Location Task of Experiment 1, with the following exceptions. First, sample and test items now only appeared at one of three possible eccentricities (2.81°, 5.67°, 8.46°; stimulus size for circles: 0.40°, 0.52°, 0.57°; for squares: 0.35°, 0.46°, 0.54°, for the innermost to outermost eccentricity). The constant rings/crosshair display used in Experiment 1 was adjusted accordingly (see Fig. 1, right panel). Two versions of the Location Task were run, which only differed with respect to the size of spatial offset between a task-relevant sample and test location on mismatch trials. In the difficult Small Offset Task, this angular offset was 15°. In the easier Large Offset Task, it was 40°. Even though the color of memory sample stimuli was entirely irrelevant, we retained the same stimulus colors for these displays that were used in Experiment 1. There were three WM load conditions (one, two, or three). Load now remained constant within each block, and changed every two blocks, with the sequence of WM load conditions randomized for each participant. The task-relevant shape (circle versus square) in the memory sample and test displays was randomly determined for each participant before the first block, and changed after every 6 blocks (i.e., after block 6, 12, and 18). 24 blocks with 32 trials per block were run, resulting in a total of 128 trials for each WM load condition in the Small and Large Offset tasks. Eight participants first completed 12 Small Offset blocks prior to 12 blocks for

the Large Offset task, and this order was reversed for the other eight participants.

EEG processing and analysis procedures were the same as in Experiment 1. Following trial rejection, an average of 80.4% of all trials were retained for EEG analyses. The CDA was measured at electrodes PO7 and PO8 where CDA amplitudes were again maximal (PO7/8: $-1.52 \mu\text{V}$, P7/8: $-1.38 \mu\text{V}$, PO9/10: $-1.06 \mu\text{V}$, P9/10: $-0.91 \mu\text{V}$). Analogous to Experiment 1, Bayes factors were computed for interactions between the factors Task and WM Load to assess whether increasing the number of memorized locations had identical or different effects on WM accuracy and CDA amplitudes when the demands on spatial precision were either high (Small Offset Task) or low (Large Offset Task).

6.3. Results

6.3.1. Behavioral performance

As predicted, accuracy was impaired in the Small Offset Task relative to the Large Offset Task (80.7% vs. 90.2% correct responses; main effect of Task: $F(1, 15) = 28.550, p = .001, \eta_p^2 = .656$; see Fig. 2, top right panel). There was also a main effect of WM Load ($F(2, 30) = 70.35, p < .001, \eta_p^2 = .824$), as accuracy decreased when the number of locations that had to be memorized increased. Finally, there was an interaction between Task and WM Load ($F(2, 30) = 13.48, p = .001, \eta_p^2 = .473$). This is due to the fact that the reduction in WM accuracy in the Small Offset Task relative to the Large Offset task was much larger when two or three locations had to be memorized (12.7% and 11.5%, respectively) than when just one location had to be maintained (4.3%; both $p < .01$).

RTs to memory test displays (shown in Fig. 2, middle right panel) increased when WM load was increased ($F(1.46, 28.63) = 78.71, p < .001, \eta_p^2 = .840$). There was also a tendency for RTs to be slower in the Small Offset Task (678 ms vs. 647 ms in the Large Offset Task), but the main effect of Task only approached significance ($F(1, 15) = 3.90, p = 0.067, \eta_p^2 = .206$). There was no interaction between Task and WM Load for RTs ($F(2, 30) = 0.735, p = 0.488, \eta_p^2 = .047$).

6.3.2. CDA components

Fig. 4 shows CDA components elicited in response to memory sample displays containing one, two, or three lateralized task-relevant items in the Small and Large Offset Task at electrodes PO7/8 contralateral and ipsilateral to these items. The corresponding contralateral-ipsilateral difference waveforms and topographical maps are also shown. As expected, CDA amplitudes increased with the number of locations that had to be memorized. More importantly, CDA components also appear to be generally larger in the more difficult Small Offset Task. These observations were confirmed by an ANOVA with the factors Task (Small Offset, Large Offset), WM Load, and Laterality. There was a main effect of Laterality ($F(1,15) = 60.50$, $p < .001$, $\eta_p^2 = .654$), confirming the presence of reliable CDA components in Experiment 2. A significant interaction between WM Load and Laterality ($F(2, 30) = 16.14$, $p < .001$, $\eta_p^2 = .518$) reflected the increase of CDA amplitudes with increasing WM load. Critically, there was also an interaction between Task and Laterality ($F(1, 15) = 5.26$, $p = 0.037$, $\eta_p^2 = .260$), confirming that CDA components were larger in the Small Offset Task. This is also illustrated in Fig. 2 (bottom right panel), which shows mean CDA amplitudes for each WM Load condition in both tasks, and suggests that CDAs were larger in the Small Offset Task relative to the Large Offset Task irrespective of whether one, two, or three locations had to be memorized. Accordingly, there was no three-way interaction between Task, Load and Laterality ($F(2, 30) = 0.18$, $p = .83$, $\eta_p^2 = .012$). This observation that the increase of CDA amplitudes in the more difficult Small Offset Task was independent of WM load was confirmed by the corresponding Bayesian analysis ($BF_{01} = 5.705$).

7. Discussion of Experiment 2

Experiment 2 demonstrated that CDA amplitudes measured in spatial WM tasks are sensitive to the difficulty of these tasks. When the spatial separation between sample and test items on mismatch trials was small (Small Offset blocks), WM performance was impaired relative to Large Offset blocks. This impairment was particularly pronounced when two or three locations had to be memorized, showing that reducing the spatial offsets of sample and test stimulus locations on mismatch trials had the desired effect of increasing task difficulty. Critically, CDA components were generally larger in the Small Offset Task as compared to the Large Offset Task. This is in line with earlier observations by Machizawa et al. (2012), who found an analogous CDA amplitude increase when the difficulty of a WM task for line orientations was increased, as reflected by decrements of WM performance. Interestingly, and in contrast to Machizawa et al. (2012), Experiment 2 found no evidence for an effect of WM load on CDA amplitude differences between the two tasks, in spite of the fact that WM load was blocked, so that participants always knew how many locations they had to retain. CDAs were consistently larger in the Small Offset Task, regardless of whether one, two, or three spatial locations had to be memorized (see Fig. 2, bottom right panel). This will be further discussed below. More generally, the central finding of Experiment 2 is that CDA amplitude differences reflect differences in the anticipated difficulty of spatial comparisons between sample and test display locations. Based on an analogous pattern of CDA results, Machizawa et al. (2012) concluded that task difficulty affects the precision with which visual attributes (in their case, line orientations) are represented in WM, and provided additional support for this conclusion with their additional behavioral experiment (as described above). It is likely that this also applies to the results of Experiment 2, with larger CDA amplitudes in the Small Offset Task reflecting an increase in the spatial precision with which locations are represented in WM. As was also the case in Machizawa et al. (2012), any such improvement in the precision of WM representations was not sufficient to fully counteract the effects of increasing task difficulty on WM performance, which was worse in the more difficult Small Offset Task.

The fact that CDA amplitudes in Experiment 2 were sensitive to task

difficulty also has implications for the interpretation of the fact that CDA amplitudes were larger in the Location Task of Experiment 1. This difference is likely due to the fact that spatial task demands were higher in this task than in the Color Task where the locations of sample items were irrelevant and thus could be ignored.

8. General Discussion

The goal of the present study was to use CDA components as electrophysiological markers of WM maintenance processes to investigate the mechanisms involved in the storage of spatial locations, and compare them to the maintenance of non-spatial features (colors) of visual objects. In Experiment 1, we measured CDA components to physically identical sample displays that contained colored shapes under conditions where participant memorized either the locations of task-relevant sample items and ignored their colors, or vice versa. Clear CDA components that were sensitive to WM load were found in both tasks, and load-dependent CDA amplitude modulations were identical. This suggests that similar if not identical mechanisms are responsible for the storage of object locations and object colors in WM. However, CDA amplitudes were generally larger in the Location Task. To account for this unexpected result, we investigated in Experiment 2 whether CDA components are sensitive to the precision of WM representations for spatial locations. Participants memorized one, two, or three locations in blocks where the spatial offset between memorized and tested locations on mismatch trials was either small or large. Relative to Large Offset blocks, CDA amplitudes were larger in Small Offset blocks where the precision of represented sample locations in WM had to be higher. Thus, the CDA amplitude differences observed in Experiment 1 between the Location and Color Tasks are unlikely to reflect qualitative differences in the storage of spatial and non-spatial visual information. They are likely to be due to higher demands on spatial resolution in the former task.

The current results have implications both for our understanding of spatial WM, and of links between the maintenance of spatial and non-spatial attributes of visual stimuli. With respect to the mechanisms involved in the representation of spatial locations in WM, Experiment 2 showed that activation states of these representations can be adjusted in line with task demands, as reflected by corresponding CDA amplitude modulations. This is in line with previous findings by Machizawa et al. (2012) in a task that required WM for line orientation. In contrast to this earlier study, Experiment 2 found no evidence that such strategic adjustments are restricted to conditions where WM load is low. This could either be due to differences in the mechanisms involved in maintaining spatial locations and stimulus orientations, or to the fact that we only manipulated WM load up to a maximum of three locations in Experiment 2. It is possible that CDA components will no longer be sensitive to differential task demands when the number of sample locations clearly exceeds WM capacity, and this should be studied in future research. It is important to note that previous attempts to demonstrate analogous associations between task difficulty and CDA amplitude modulations in non-spatial WM tasks involving colored objects have generally been unsuccessful (e.g., Ye et al., 2014; see Luria et al., 2016, for review). This suggests that in contrast to spatial WM, the activation and/or precision of WM for non-spatial features such as colors can either not be regulated at all, or, if it can, that such adjustments are not reflected by the CDA. It is possible that voluntary control over the activation of visual WM representations is only available for WM tasks that have a strong spatial component. This was obviously the case in the Location tasks employed in the present experiments, but also in the study by Machizawa et al. (2012) where observers had to memorize line orientations. WM for orientations can be regarded as a variant of spatial WM, as observers might represent the orientation of lines in terms of the locations of cardinal points, such as line endings. The presence of task difficulty effects on CDA amplitudes in such spatial WM tasks, and their apparent absence in color change detection tasks

that lack a spatial component could point to a special role for space-based executive control processes in the regulation of visual WM.

This would be entirely consistent with the suggestion that spatial attention is responsible for the activation and maintenance of visual WM representations (e.g., Awh et al., 2006) that are held in two-dimensional maps in visual cortex (Franconeri et al., 2013). In such maps, representations of visual objects are addressed by their spatial location, irrespective of whether spatial positions or other non-spatial features are currently task-relevant. If top-down attentional control processes operate on the basis of spatial coordinates, it should be relatively straightforward to regulate their sensitivity in response to changing demands on the spatial precision of WM storage. The sensitivity of CDA amplitudes to task difficulty and thus to the required precision of spatial WM observed in Experiment 2 could reflect stronger attentional processing biases at object locations that have to be retained with high resolution. However, it is much more difficult to envisage how such space-based attentional control mechanisms might adjust the resolution with which non-spatial features such as object colors are stored in WM.

With respect to links between the storage of spatial and non-spatial information in WM, the current findings are in line with the hypothesis that memorized spatial and non-spatial features of visual objects are represented in an integrated fashion in visual cortical maps where these representations are maintained through the allocation of focal attention. There is however a possible alternative interpretation of the CDA pattern observed in Experiment 1. Previous research has shown that location information is encoded into WM even when it is entirely task-irrelevant (Foster et al., 2017), and it is possible that CDA components primarily or perhaps even exclusively reflect the maintenance of visual object locations in WM. If this was the case, the presence of CDA components in the Color Task could be interpreted as the result of an obligatory encoding of object locations. These spatial WM representations may be more strongly activated when the location of objects has to be actively maintained, and this could account for the fact that CDA amplitudes were larger in the Location Task than in the Color Task. While this interpretation is consistent with the pattern of CDA results observed in Experiment 1, findings from previous CDA experiments do not support the hypothesis that this component only reflects the representation of the spatial properties of objects in WM. For example, several studies (Woodman & Luck, 2008; Luria, Sessa, Gotler, Joliceur, & Dell'Acqua, 2010) have found systematic CDA amplitude differences in response to physically identical sample stimulus displays containing orientated colored rectangles or colored polygons between blocks where either color or orientation/shape was task-relevant. These results demonstrate not only that specific non-spatial features can be selectively prioritized in WM, but also that the CDA component is sensitive to this feature selectivity of WM storage processes. If the CDA exclusively reflected the representation of object locations in WM, it should not be affected by instructions to attend to different non-spatial feature of identical sample display objects.

In summary, the current study has provided new electrophysiological evidence that the maintenance of spatial locations and non-spatial features in visual WM is based on overlapping neural mechanisms. This conclusion was supported by the similarity of CDA components elicited during the storage of object colors and object locations, and by the fact that increasing WM load in both tasks had equivalent effects on CDA amplitudes. These observations are in line with the suggestion that different features of visual objects, including their spatial location, are represented in an integrated fashion in WM, and that the maintenance of these features is facilitated by the allocation of spatial attention to specific locations within spatiotopic maps in visual cortex. In spite of these similarities between the storage of spatial and non-spatial attributes, spatial WM may be special in one important aspect. In apparent contrast to non-spatial features, the resolution with which spatial locations are represented can be strategically adjusted in line with current demands on the precision of spatial WM.

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