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Research report

# Object representations in visual working memory change according to the task context

Halely Balaban [a,b,*] and Roy Luria [a,b]

[a] Sagol School of Neuroscience, Tel Aviv University, Tel Aviv, Israel
[b] The School of Psychological Sciences, Tel Aviv University, Tel Aviv, Israel

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ABSTRACT

This study investigated whether an item's representation in visual working memory (VWM) can be updated according to changes in the global task context. We used a modified change detection paradigm, in which the items moved before the retention interval. In all of the experiments, we presented *identical* color–color conjunction items that were arranged to provide a common fate Gestalt grouping cue during their movement. Task context was manipulated by adding a condition highlighting either the integrated interpretation of the conjunction items or their individuated interpretation. We monitored the contralateral delay activity (CDA) as an online marker of VWM. Experiment 1 employed only a minimal global context; the conjunction items were integrated during their movement, but then were partially individuated, at a late stage of the retention interval. The same conjunction items were perfectly integrated in an integration context (Experiment 2). An individuation context successfully produced strong individuation, already during the movement, overriding Gestalt grouping cues (Experiment 3). In Experiment 4, a short priming of the individuation context managed to individuate the conjunction items immediately after the Gestalt cue was no longer available. Thus, the representations of identical items changed according to the task context, suggesting that VWM interprets incoming input according to global factors which can override perceptual cues.



## 1. Introduction

Visual working memory (VWM) is the workspace in which we hold a limited amount of visual information in an active state, making it accessible to higher cognitive functions (for a recent review, see Luck & Vogel, 2013). It has robust connections to factors such as attentional control and fluid intelligence (e.g., Cowan et al., 2005), as well as to Alzheimer's disease and schizophrenia (e.g., Gold, Wilk, McMahon, Buchanan, & Luck, 2003; Parra, Della Sala, Abrahams, Logie, Mendez, & Lopera, 2011), corroborating the importance VWM representations play in guiding behavior.

One of the defining characteristics of VWM representations is their dynamic status. It is well established that VWM representations can be updated online according to

* *Corresponding author*. Sagol School of Neuroscience and The School of Psychological Sciences, Tel Aviv University, 6997801, Israel.
E-mail address: halelyba@mail.tau.ac.il (H. Balaban).

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changes in the stimulus-driven properties of the items. For example, VWM is able to track the constantly changing positions of several moving objects (Drew, Horowitz, Wolfe, & Vogel, 2011; Drew, Horowitz, Wolfe, & Vogel, 2012; Drew & Vogel, 2008). Additionally, when a stationary item changes its features, VWM can be updated accordingly. For example, Blaser, Pylyshyn, and Holcombe, (2000) asked subjects to monitor one of two superimposed objects, while both objects changed constantly in terms of color, spatial frequency, and orientation. Remarkably, subjects could successfully discriminate the target from the distractor, suggesting that VWM could track changes in the three dimensions simultaneously. Additionally, it was recently demonstrated that VWM can be updated according to the objecthood-history of the items (Luria & Vogel, 2014).

Apart from stimulus-driven factors, it has been shown that VWM representations can also change according to task-dependent properties. It was recently found that the interaction of probing method and task instructions influences VWM representations: color and shape were integrated only when both the stimulus-driven cues and the instructions encouraged a bound VWM representation (Vergauwe & Cowan, 2015; see also Wheeler & Treisman, 2002). Similarly, we recently found that integration versus individuation can be influenced by an interaction of task difficulty and the types of stimuli used (Balaban & Luria, 2015a).

These studies focused on factors which directly affect the represented items, whether in terms of their appearance, or in terms of the task performed on them. However, items in the real world are tightly connected to their environment, and therefore changing the environment, while leaving the item itself intact, might change the item's interpretation, and subsequently its representation. Importantly, we consider this as a more "global" manipulation, since the visual input of the represented item itself remains the same, and only the environment in which the item appears is modified. Whether VWM is flexible enough to integrate such global factors is an issue that was not yet examined.

The goal of the present work is to show that VWM representations can indeed be updated according to global factors, even when the stimulus-driven properties of the represented objects and the task performed on them remain unchanged. We will argue that an item's environment, manifested in the experimental design by the specific mixture of conditions in the experiment, creates a global context that greatly affects how VWM interprets incoming input. To this end, we examined the representations of *identical* stimuli in a VWM task, and manipulated the task context, by changing only the other conditions in the experiment. Thus, we could test whether an identical item is represented in different ways, according to the global context in which it appears, even with no "local" (i.e., stimulus-driven, or task-driven) demand for a change.

The stimuli whose representations we tested in all experiments were color–color conjunctions, i.e., a small colored square presented on top of a larger colored square. Previously, these stimuli were shown to be somewhat ambiguous, meaning they can be perceived either as an integrated bi-colored object (Luck & Vogel, 1997; Luria & Vogel, 2011, 2014; Vogel, Woodman, & Luck, 2001), or as two superimposed single-colored objects that are largely independent (Delvenne & Bruyer, 2004; Olson & Jiang, 2002; Parra, Abrahams, Logie, & Della Sala, 2009; Wheeler & Treisman, 2002). To further highlight the "objecthood" of the colors in the conjunction, in our task the colors moved together for a full second. Although this "common fate" is a strong Gestalt grouping cue, the movement itself was task-irrelevant, since subjects only had to encode the colors for a change detection task. Moreover, the change detection task is likely to encourage maintaining the colors separately in VWM, since a change can only happen to one color in the conjunction and not to both simultaneously, underlining their independence.

To determine VWM representations, we relied on an electrophysiological marker, namely the contralateral delay activity (CDA; McCollough, Machizawa, & Vogel, 2007; Vogel & Machizawa, 2004; for a review see Luria, Balaban, Awh, & Vogel, 2016). This event-related potential (ERP) component is a posterior negative sustained potential that is indicative of the number of individuated items in VWM. The amplitude of the CDA rises (i.e., becomes more negative) as more items are maintained in VWM. This rise is specifically related to the contents of VWM, and not to the difficulty of the task per-se, since the amplitude reaches a stable plateau at around 3 items (Vogel & Machizawa, 2004), which corresponds to the capacity limit of VWM. Furthermore, this plateau is correlated with the individual VWM capacity (e.g., Drew & Vogel, 2008; Tsubomi, Fukuda, Watanabe, & Vogel, 2013; Vogel & Machizawa, 2004; see Luria et al., 2016). Thus, for subjects that can maintain more items in VWM, the CDA will continue to rise further, suggesting this rise is indicative of adding more VWM-units. In order to minimize contamination from lower-level visual processing, the CDA is calculated using a bi-lateral version of the change detection task: the same number and types of stimuli are presented in the left and right sides of the screen, and subjects are directed, before the beginning of the trial, to allocate their attention to only one side. The sustained activity is more pronounced on the contralateral side, and the CDA is computed as a difference wave, controlling for perceptual processes (which should be present in both hemispheres equally).

The CDA has two important advantages over behavioral measures of VWM, such as change detection accuracy. First, it is specifically sensitive to VWM maintenance, while behavioral performance indicates the sum of all cognitive processes involved. For example, it has been shown that change detection accuracy is strongly influenced by the difficulty of the comparison between the memory and test arrays, a stage that follows VWM maintenance (Awh, Barton, & Vogel, 2007). In contrast, the CDA is measured before the test phase, and is thus insensitive to the comparison process itself. Similarly, as mentioned above, perceptual process, which precede VWM encoding and maintenance, also do not influence the CDA (e.g., Ikkai, McCollough, & Vogel, 2010). The second main benefit of the CDA is that, due to the excellent temporal precision of the ERP technique, it allows one to examine the development of VWM representations over time, and not just their final stage, as is measured by behavioral performance.

Importantly for the current study, the CDA amplitude reflects the number of integrated units in VWM, and not the number of features comprising the items (Luria & Vogel, 2011; Woodman & Vogel, 2008), or the number of locations

(Balaban & Luria, 2015a; Ikkai et al., 2010; Luria & Vogel, 2014). Therefore, the CDA can be used as a marker of integration, as indeed has been done in several studies (Balaban & Luria, 2015a, 2015b; Luria & Vogel, 2011; 2014; Peterson, Gözenman, Arciniega, & Berryhill, 2015; Wilson, Adamo, Barense, & Ferber, 2012; Woodman & Vogel, 2008). Across four experiments, we compared the VWM representations of four colors in two color–color conjunctions moving together (giving a common fate grouping cue), i.e., the "4-in-2" condition, to two and four separately moving colors, i.e., the "2-separate" and "4-separate" conditions. If the colors in the 4-in-2 condition are integrated in VWM, and represented as two bi-colored objects, the CDA amplitude in this condition should resemble the amplitude in the 2-separate condition, since in both cases only two units are maintained in VWM. In contrast, if the 4-in-2 condition is individuated in VWM and represented as four independent single-colored objects, the CDA amplitude in this condition should resemble the amplitude in the 4-separate condition, since four units are retained in VWM.

Critically, the 4-in-2 conjunction condition (as well as the 2-separate and 4-separate control conditions) was *identical* in all experiments, controlling for stimulus-driven properties. The experiments only differed in the conditions accompanying the 4-in-2 condition, manipulating the global context through which this condition is interpreted. We hypothesized that the representation of the 4-in-2 conjunction condition (i.e., as integrated or as individuated) would depend on these circumstantial cues, even though all stimulus-driven properties were identical.

Previous studies revealed many aspects of the complex nature of VWM representations, by showing that they are affected by items' stimulus-driven properties (e.g., Drew & Vogel, 2008), history (Luria & Vogel, 2014), and the task performed on them (e.g., Vergauwe & Cowan, 2015). Importantly, our study took a different approach, in order to study the influence of context on VWM representation. The novelty of the current setup is that by manipulating only the other conditions in the task, we are able to isolate the influence of the global experimental context even when the stimuli and task remain identical. To the best of our knowledge, no study has previously shown the effect of global task context without changing the actual stimuli, the task instructions, or both. An influence of context when the manipulation is so indirect, and is not related to the represented items, would provide strong evidence that VWM is a highly flexible system that can pick up subtle environmental cues in determining the most appropriate representation for a given input, even contradicting Gestalt cues, which is an important step forward in the current understanding of how information is represented in VWM.

Experiment 1 examined the representation of the 4-in-2 condition in the most minimal context: the experiment included only the 4-in-2, and the 2-separate and 4-separate conditions, serving as control conditions. The other experiments contained these three conditions, and further included another condition aimed to change the context towards integration (Experiment 2) or individuation (Experiments 3 and 4). In each experiment, we tested how the identical 4-in-2 condition would be represented. If VWM is purely stimulus-driven, the results of all experiments should be the same, since they all included identical stimuli. However, if VWM is sensitive to the global context in which an item appears, it might be possible to change the representations of the identical 4-in-2 condition only by manipulating its experimental environment.

## 2. Experiment 1: minimal context

Experiment 1 examined the representations of the 4-in-2 condition in the most minimal context possible. That is, aside from the 4-in-2 condition, the experiment included only conditions of two or four separate colors, which were necessary to determine the VWM representations of the 4-in-2 condition (since an integration would result in a CDA amplitude similar to two separate items, and an individuation would result in a CDA amplitude similar to four separate items).

### 2.1. Materials and methods

#### 2.1.1. Participants

Participants were Tel Aviv University students who received partial course credit or 40 NIS (approximately $10) per hour for participation. All subjects had normal or corrected-to-normal visual acuity and normal color-vision. All participants gave informed consent following the procedures of a protocol approved by the Ethics Committee at Tel Aviv University. The experiment included 15 subjects in the final analysis (9 females, mean age 25.5). One subject was replaced because of a >25% rejection rate due to blinks or eye movements.

#### 2.1.2. Stimuli and procedure

The sequence of events in each trial of the change detection task is depicted in Fig. 1. Each trial started with the presentation of a white fixation cross ($.4^\circ \times .4^\circ$) in the center of the gray screen for 750 msec. Then, two white arrows ($1.9^\circ \times .4^\circ$) were presented for 200 msec above and below fixation, pointing either left or right (with an equal probability). Participants were instructed to attend and memorize only the items at the side indicated by the arrows, while holding fixation. The arrows were followed by another fixation display, lasting either 300, 400, or 500 msec (randomly determined with an equal probability). Then, a memory array, consisting of colored squares at both sides of the screen, was presented for 1000 msec. The two sides were always equated in terms of the number and type of items. Stimuli appeared at random locations inside an imaginary $4.5^\circ \times 3.5^\circ$ rectangle (one in each side of the screen), with the constraint that the distance between the centers of the stimuli would not be smaller than $2^\circ$, and that no more than two items would appear in each quadrant at the end of the memory array presentation. Seven highly discriminable colors were used (red, RGB values: 255, 0, 0; magenta: 255, 0, 255; blue: 0, 0, 255; cyan: 0, 255, 255; green: 0, 255, 0; yellow: 255, 255, 0; and white: 255, 255, 255). The exact colors were randomly selected with no replacement at the beginning of each trial, independently for each side. The squares were either large ($1.3^\circ \times 1.3^\circ$) or small ($.8^\circ \times .8^\circ$).

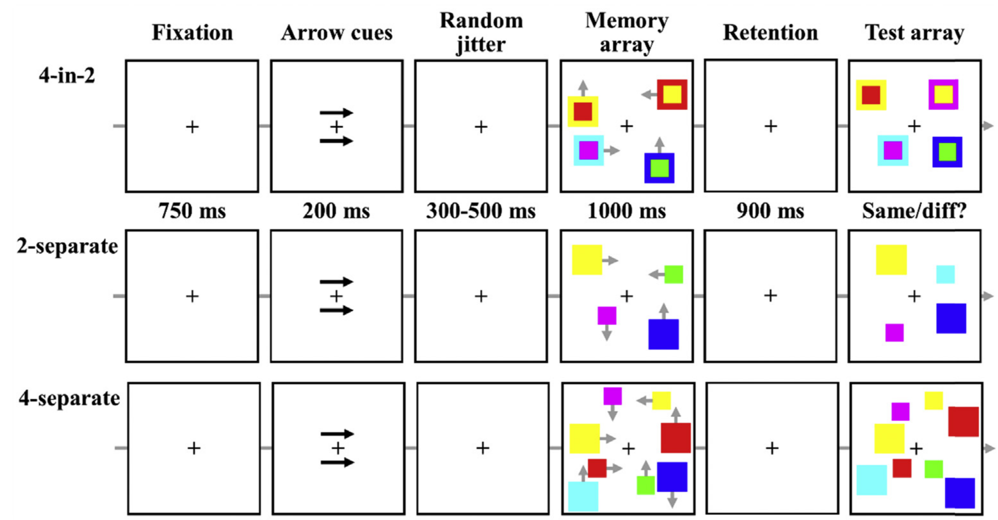


**Fig. 1 – An illustration of the task and different conditions in Experiment 1 (Experiments 2–4 additionally included another condition). The arrows in the memory array only indicate the movement directions and were not seen in the experiments. Note that only one side was relevant in each trial (to control for low-level processing when calculating the CDA), as indicated by the arrow cues, and hence only half of the items were to-be-remembered. When referring to the number of items, we consider only the relevant side. The different conditions, from top to bottom: the 4-in-2 condition, in which four colors formed two color–color conjunctions that moved together in "common fate", the 2-separate condition, and the 4-separate condition, both of which included independently moving colors. The VWM representation of the 4-in-2 condition was tested in all four experiments.**

The colored squares in the memory array moved for 1000 msec before disappearing, covering a distance of about 1.5° (allowing the movement to stay within a certain quadrant). Their trajectories were straight, and the movement was restricted to a single side of the screen, i.e., the items never crossed the center of the screen. The allowed directions (randomly determined with an equal probability) were up, down, or horizontally towards the fixation. The task was to memorize the colors, and the movement was completely task-irrelevant (which the subjects were informed of), and was used only to manipulate objecthood. After the presentation of the dynamic memory array, a retention interval of 900 msec was displayed, during which only the fixation cross was visible. Then the test array appeared, including the items presented in the memory array, at their final locations. On half of the trials, one of the colors at the relevant side changed to a new color (i.e., a color not included in the memory array of this side). The irrelevant side was always identical to the memory array. The test array remained visible until a response was emitted. Subjects were asked to indicate via button press whether the test array included only old colors or one new color (using the "Z" and "/" keys on a computer keyboard, indicating "same" and "different", respectively). Accuracy was stressed over speed.

The experiment included 3 conditions that were randomly intermixed with equal probabilities. In the 2-separate condition, each side contained two colored squares, one in the upper quadrant and one in the lower quadrant. Each square was equally likely to be small or large. In the 4-separate condition, each side contained four colored squares, with one large square and one small square in each quadrant. In these conditions, each color was presented at a unique location, and its movement direction was determined independently of the other colors. The 4-in-2 conjunction condition included four colors that were arranged in two groups. That is, each quadrant included a set of a small square and a large square, presented at the same location. The items in each group moved together throughout the duration of memory array presentation (i.e., a common fate objecthood cue). Participants started with a practice block of 16 trials, followed by 12 blocks of 60 trials each.

### 2.1.3. *EEG recording*

The electroencephalography (EEG) was recorded inside a shielded Faraday cage, using a Biosemi ActiveTwo system (Biosemi B. V., The Netherlands). Data was recorded from 32 scalp electrodes at a subset of locations out of the extended 10–20 system, including mostly occipital and parietal sites (in which the CDA is most pronounced): Fp1, Fp2, AF3, AF4, F3, F4, F7, F8, Fz, FCz, C3, C4, Cz, T7, T8, P1, P2, P3, P4, P5, P6, P7, P8, Pz, PO3, PO4, PO7, PO8, POz, O1, O2, and Oz. additionally, two electrodes were placed on the left and right mastoids. The horizontal electrooculogram (EOG) was recorded from two electrodes placed 1 cm to the left and right of the external canthi, in order to detect horizontal eye movements. The vertical EOG was recorded from an electrode placed beneath the left eye, in order to detect eye blinks and vertical eye movements. The single-ended voltage was recorded between each electrode site and the common mode sense/driven right leg (CMS/DRL) electrodes. Data was digitized at 256 Hz.

Offline signal processing and analysis was performed using EEGLAB Toolbox (Delorme & Makeig, 2004), ERPLAB Toolbox

(Lopez-Calderon & Luck, 2014), and custom Matlab (The Mathworks, Inc.) scripts. All electrodes were referenced to the average of the left and right mastoids.

The continuous data was segmented into epochs from −200 to +1900 msec relative to the onset of the memory array (i.e., including the full lengths of the memory array and retention interval). Artifact detection was performed using a peak-to-peak analysis, with a sliding window 200-msec wide in 100-msec steps. Trials containing differences of over 80 μV at the EOG electrodes, or over 100 μV at the analyzed electrodes (P7, P8, PO3, PO4, PO7, and PO8) were excluded from the averaged ERP waveforms. This procedure resulted in a mean rejection rate of 7.09%. Following the rejection procedure, the average number of trials (per condition per subject) was 202. The epoched data were low-pass filtered using a noncausal Butterworth filter (12 dB/oct) with a half-amplitude cutoff point at 30 Hz. Only trials with a correct response were included in the analysis.

#### 2.1.4. *CDA analysis*

The epoched data were averaged separately for each condition. We calculated a difference wave by subtracting the average activity recorded at the electrodes that were ipsilateral to the memorized side from the average activity recorded at the electrodes that were contralateral to the memorized side. We used the mean amplitude of this difference wave as the dependent measure. There were two major time windows: the *Tracking CDA* was measured from 500 to 1000 msec after memory array onset (i.e., during the tracking of the items while they were visible on the screen), and the *Retention CDA* was measured from 1100 to 1900 msec after memory array onset (i.e., during the retention interval). The *Retention CDA* was further divided to the *Early* (1100–1500) and *Late* (1500–1900) *Retention CDA*, allowing for a more fine-grained analysis. Note that the CDA can be measured irrespective of whether the items are retained in memory or are visible on the screen (e.g., Drew et al., 2011; Drew et al., 2012; Drew & Vogel, 2008; Tsubomi et al., 2013).

For the ease of description, we will only present the results from the PO7/8 electrodes, since that is where the CDA is most pronounced. However, we analyzed the results over neighboring electrodes (P7/8, and PO3/4) and found the same patterns of activity.

#### 2.1.5. *Statistical analysis*

We conducted a one-way analysis of variance (ANOVA), with condition as a within-subject variable on the CDA mean amplitudes (in the *Tracking* and *Retention* time windows, see above) and accuracy as dependent variables. All of these tests revealed a significant effect of condition, all $F$'s $> 7$, all Ps $< .001$. We do not further report them, focusing instead on the results of the planned comparisons (contrasts) between the different conditions.

### 2.2. **Results**

#### 2.2.1. *Electrophysiological results*

The common fate cue led to a perfect integration of the 4-in-2 conjunction condition during the tracking phase, but during the later stages of their memory retention, the items were partially individuated, beginning at around 1300 msec, see Fig. 2a. The statistical analysis revealed that the *Tracking CDA* amplitude (between 500 and 1000 msec from memory array onset, i.e., during the items' tracking while they were visible) in the 4-in-2 condition (−1.28 μV, SD: 1.08) was lower than the amplitude of the 4-separate condition (−2.04 μV, SD: 1.19), $F$ (1, 14) = 34.82, $p < .00005$, and was not significantly different from the amplitude of the 2-separate condition (−1.24 μV, SD: .99), $F < 1$, suggesting a perfect integration of the colors when the common fate cue was available.

During the retention of the items in VWM (i.e., when the items were no longer visible), the representations were partially individuated, as was evident from the *Retention CDA* (between 1100 and 1900 msec after memory array onset): the amplitude in the 4-in-2 conjunction condition (−1.16 μV, SD: .90) was lower than the amplitude of the 4-separate condition (−1.80 μV, SD: 1.10), $F$ (1, 14) = 19.78, $p < .001$, but higher than the 2-separate condition (−.87 μV, SD: .87), $F$ (1, 14) = 5.19, $p < .05$. A visual inspection of the waveforms suggested that the representations changed during the course of the retention interval. We thus divided the memory retention period to *Early* and *Late Retention CDA* (1100–1500 and 1500–1900 msec after memory array onset, respectively), as have been previously done (Drew et al., 2011, 2012; Luria & Vogel, 2011; Peterson et al., 2015). The following experiments relied on the same time windows.

Comparing the early and late stages of the memory retention, we found that the individuation of the representations developed gradually during the retention interval (starting at around 1300 msec, see Fig. 2a). While the *Early Retention CDA* amplitude in the 4-in-2 condition (−1.40 μV, SD: 1.13) was not different from the 2-separate condition (−1.19 μV, SD: .96), $F$ (1, 14) = 2.05, $p = .17$, the *Late Retention CDA* (−.92 μV, SD: .78) was higher than the 2-separate condition (−.53 μV, SD: .89), $F$ (1, 14) = 8.66, $p < .02$, but still lower than the 4-separate condition (−1.41 μV, SD: 1.01), $F$ (1, 14) = 7.71, $p < .02$. Thus, over the course of the memory retention (i.e., after the grouping cue was no longer visible), the VWM representations of the 4-in-2 conjunction condition gradually changed from being integrated to being partially individuated.

#### 2.2.2. *Behavioral results*

Mirroring the CDA results, the common fate cue in the 4-in-2 conjunction condition led to better behavioral performance compared with the same number of separate colors (i.e., the 4-separate condition), but a worse performance compared with the same number of moving groups (i.e., the 2-separate condition). Accuracy was higher for the 4-in-2 condition (.89, SD: .05) than for the 4-separate condition (.85, SD: .06), $F$ (1, 14) = 15.49, $p < .005$, even though both conditions included four colors. However, accuracy for the 4-in-2 condition was still lower than for the 2-separate condition (.98, SD: .02), $F$ (1, 14) = 58.97, $p < .000005$.

### 2.3. **Discussion**

In the minimal context of Experiment 1, the colors in the 4-in-2 conjunction condition were perfectly integrated during their visible movement, suggesting that common fate is indeed a potent grouping cue. However, towards the end of the

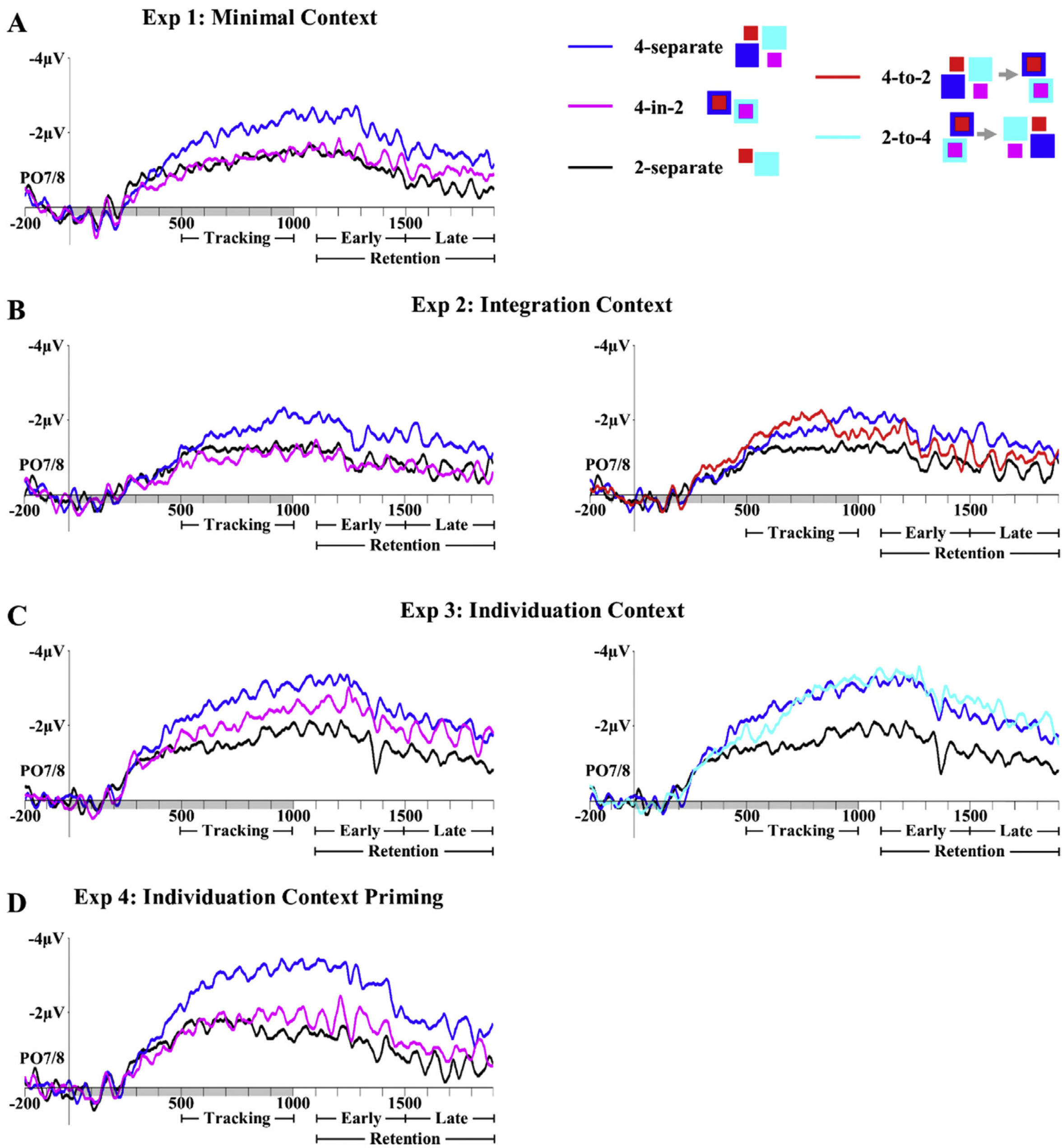


**Fig. 2 – CDA results in all four experiments at the PO7/8 electrodes. Gray bars denote the time span of the memory array, and the analyzed time-windows are indicated below each figure. (A) In Experiment 1, including only the 4-in-2, 2-separate, and 4-separate conditions, the representations of the 4-in-2 condition partially individuated towards the end of their memory maintenance. (B) In Experiment 2, which included also a 4-to-2 condition, the representations of the 4-in-2 condition were perfectly integrated (left panel). The right panel presents the results of the 4-to-2 condition, which was gradually integrated. (C) In Experiment 3, which included instead a 2-to-4 condition, the representations of the 4-in-2 condition began to be individuated already during their presentation, and eventually they were represented individually (left panel). The right panel presents the results of the 2-to-4 condition, which was gradually individuated. (D) In Experiment 4, which was identical to Experiment 1 except for a short "priming phase" including the 2-separate, 4-separate, and 2-to-4 conditions (without the 4-in-2 condition), the representations of the 4-in-2 condition were partially individuated, already at the start of their memory maintenance.**

retention interval, the representation became partially individuated. Note that previous studies that presented static color–color conjunctions, or moving color-shape conjunctions, found that integration developed throughout the trial (Balaban & Luria, 2015a; Luria & Vogel, 2011), while here we found the opposite pattern, such that the individuation of the objects gradually developed. We return to this issue in the General Discussion.

These results are not compatible with the perfect integration that was recently found for color–color conjunctions grouped by common fate (see Luria & Vogel, 2014). We argue that the reason for this discrepancy is the global task context, and specifically the mixture of conditions included in the experiment, and in Experiment 2 we directly tested this suggestion.

## 3. Experiment 2: integration context

The goal of Experiment 2 was to demonstrate that the colors in the 4-in-2 conjunction condition could be perfectly integrated within a context that supports such integration. Importantly, this pattern of results would provide evidence for the influence of global context on VWM when comparing identical stimuli.

The experiment was essentially identical to Experiment 1, with the only difference being the inclusion of a 4-to-2 meeting colors condition. In this condition, four colors started to move separately but then met to form two color–color conjunctions that moved together (see Fig. 3). We reasoned that this condition highlights the integration of the 4-in-2 conjunction condition, since here even separate colors join to create conjunctions, indirectly indicating that the colors indeed belong to one VWM unit. This experiment was a replication of a recent experiment that found a perfect integration of color–color conjunctions using a common fate cue (Experiment 3 from Luria & Vogel, 2014).

If, as we suggest, VWM representations are influenced by the context, we expect the 4-in-2 condition to be perfectly integrated (as in Luria & Vogel, 2014). In contrast, if a given stimulus is represented in VWM in the same manner regardless of its context, the results should be identical to Experiment 1, namely a partial individuation of the 4-in-2 conjunction condition at a relatively late stage of the memory retention period.

### 3.1. *Materials and methods*

The experiment was identical to Experiment 1, except as noted below.

#### 3.1.1. *Participants*

15 fresh participants (9 females, mean age 26.2) were used. None of them reached the exclusion criterion of 25%.

#### 3.1.2. *Stimuli and procedure*

The experiment included 4 conditions that were randomly intermixed with equal probabilities. The 2-separate, 4-separate, and 4-in-2 conditions were identical to Experiment 1. The additional condition was the 4-to-2 meeting colors condition. This condition started similarly to the 4-separate condition: each quadrant included one large and one small square. However, rather than an independent movement, the two colors in each quadrant moved towards each other for 600 msec, met to create a color–color conjunction, and then moved together for the remaining 400 msec of the memory array (as in Experiment 3 from Luria & Vogel, 2014). Thus, while the colors initially moved separately, in the final 400 msec of the movement phase this condition was identical to the 4-in-2 condition (see Fig. 3). Participants started with a practice block of 16 trials, followed by 15 blocks of 60 trials each (here, as well as in Experiments 3 and 4, we used 15 instead of 16 blocks, in order to keep the overall experimental procedure no longer than 2.5 h).

#### 3.1.3. *EEG recording*

The rejection procedure resulted in a mean rejection rate of 7.8%, and following it, the average number of trials (per condition per subject) was 180.

### 3.2. *Results*

#### 3.2.1. *Electrophysiological results*

In an integration context, the 4-in-2 conjunction condition was perfectly integrated, and remained so throughout the memory retention (see Fig. 2b, left panel). Both the *Tracking CDA* and the *Retention CDA* amplitudes in the 4-in-2 condition (*Tracking CDA*: −1.02 μV, SD: .65, *Retention CDA*: −.75 μV, SD: .62) were lower than for the 4-separate condition (*Tracking CDA*: −1.70 μV, SD: .92, *Retention CDA*: −1.54 μV, SD: .91), $F$ (1, 14) = 22.26, $p < .0005$, and $F$ (1, 14) = 20.91, $p < .0005$, respectively, and not significantly different from the 2-separate condition (*Tracking CDA*: −1.21 μV, SD: .72, *Retention CDA*: −.83 μV, SD: .60), $F$ (1, 14) = 1.15, $p = .30$, and $F < 1$, respectively.

The meeting and subsequent joint movement of the 4-to-2 meeting colors condition led to their integration in VWM, as can be seen from the decrease in CDA amplitude (starting at around 900 msec, see Fig. 2b, right panel). During the tracking period, while the colors moved separately towards each other, the colors were represented individually, so that the *Tracking CDA* amplitude (−1.80 μV, SD: 1.02) was not different from the 4-separate condition, $F < 1$, and higher than the 2-separate condition, $F$ (1, 14) = 10.89, $p < .01$. Following the meeting and joint movement, the colors were initially still represented individually in memory, resulting in an *Early Retention CDA* amplitude (−1.34 μV, SD: 1.08) not different from the 4-separate condition (−1.70 μV, SD: .94), $F$ (1, 14) = 2.84, $p = .11$, and marginally higher than the 2-separate condition (−.97 μV,

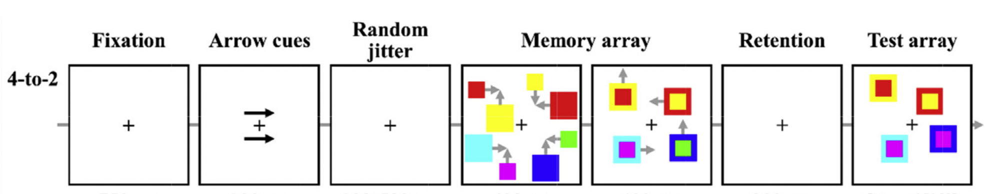


**Fig. 3 – The 4-to-2 condition, which was used in Experiment 2 to create an integration context. In this condition four independently moving colors met and started to move in two groups.**

SD: .64), $F$ (1, 14) = 4.09, $p$ = .06, but were eventually integrated, as can be seen from the *Late Retention CDA* amplitude (−.97 μV, SD: .93) that was lower than the 4-separate condition (−1.38 μV, SD: .94), $F$ (1, 14) = 5.53, $p$ < .05, and not significantly different from the 2-separate condition (−.68 μV, SD: .71), $F$ (1, 14) = 2.18, $p$ = .16.

#### 3.2.2. Behavioral results

Replicating the behavioral results of Experiment 1, we found that the common fate organization in the 4-in-2 conjunction condition led to a benefit compared with four separate colors, and a cost compared with two separate colors. Accuracy was higher for the 4-in-2 condition (.84, SD: .06) than for the 4-separate condition (.80, SD: .07), $F$ (1, 14) = 9.61, $p$ < .01, but still lower than for the 2-separate condition (.95, SD: .03), $F$ (1, 14) = 84.23, $p$ < .000001. A similar pattern was found for the 4-to-2 meeting colors condition (.83, SD: .06): accuracy in this condition was better than for the 4-separate condition, $F$ (1, 14) = 8.70, $p$ < .02, but lower than for the 2-separate condition, $F$ (1, 14) = 80.66, $p$ < .000001.

Notably, despite a perfectly integrated VWM representation, as indicated by the CDA, our accuracy results suggest that there was still a cost for the 4-in-2 condition compared with the 2-separate condition. This pattern replicates previous findings (e.g., Balaban & Luria, 2015b; Luria & Vogel, 2014). Importantly, accuracy indicates the end result of all processing stages, and therefore does not reflect solely the VWM representations themselves. Hence, the behavioral cost might be due to the comparison process of the task (Awh et al., 2007), in which each color changes independently. Namely, since the 4-in-2 conjunction condition had twice as many comparisons as the 2-separate condition, it is more prone to errors.

### 3.3. Discussion

In Experiment 2, the same 4-in-2 conjunction condition that was partially individuated in Experiment 1 was now perfectly integrated (cf., Luria & Vogel, 2014), once it was presented within an integration context. Since the 4-in-2 condition itself was identical in both experiments, the difference in how this condition was represented points to an influence of the global task context on VWM representations. Namely, we argue that the 4-to-2 meeting colors condition created a context that supported the integrated interpretation of the 4-in-2 condition over its individuated one.

To further test the influence of context on VWM representations, we next turned to demonstrate that the 4-in-2 conjunction condition could be individuated, when presented in an individuation context.

## 4. Experiment 3: individuation context

The goal of Experiment 3 was to show that the 4-in-2 conjunction condition could be individuated once the context strongly supports such interpretation. The current experiment was identical to Experiment 1, except for the inclusion of the 2-to-4 separating colors condition. This condition included colors that moved together for a short duration, and then separated and moved independently (see Fig. 4). Since the 2-to-4 and 4-in-2 conditions both start with similar color–color conjunctions, and the colors in the 2-to-4 separating colors condition then break apart, this condition emphasizes the individuated nature of the colors in the 4-in-2 conjunction condition as well. Thus, if the global context indeed shapes VWM representations, the colors in the 4-in-2 condition should be largely individuated, despite the strong Gestalt grouping cue.

### 4.1. Materials and methods

The experiment was identical to Experiment 1, except as noted below.

#### 4.1.1. Participants

15 fresh participants (11 females, mean age 24) were used. Three were replaced because of a >25% rejection rate (we decided to include one subject with a rejection rate of 25.75%).

#### 4.1.2. Stimuli and procedure

The experiment included 4 conditions that were randomly intermixed with equal probabilities. The 2-separate, 4-separate, and 4-in-2 conditions were identical to Experiment 1. The additional condition was the 2-to-4 separating colors condition. This condition started similarly to the 4-in-2 condition: each quadrant included a color–color conjunction, comprised of a small square on top of a large square. The colors in each group moved together for 170 msec. Then, one color changed trajectory and started to move to a different direction for the remaining 830 msec of the memory array, while the other color stayed on the same path (these timing details were chosen to allow the colors in each conjunction to reach sufficiently distant locations by the end of the memory array, thus maximizing their perceived independence). Thus, while this condition was identical to the 4-in-2 conjunction condition during the first 170 msec of the memory array, it was similar to the 4-separate condition in the final 830 msec of the movement phase (see Fig. 4). Participants started with a practice block of 16 trials, followed by 15 blocks of 60 trials each.

#### 4.1.3. EEG recording

The rejection procedure resulted in a mean rejection rate of 7.95%, and following it, the average number of trials (per condition per subject) was 205.

### 4.2. Results

#### 4.2.1. Electrophysiological results

When presented alongside the 2-to-4 condition, the 4-in-2 conjunction condition was represented in VWM as individuated colors, starting at around 500 msec, see Fig. 2c, left panel. Already during the tracking period, the *Tracking CDA* amplitude (−2.07 μV, SD: 1.24) was lower than the amplitude of the 4-separate condition (−2.69 μV, SD: 1.53), $F$ (1, 14) = 9.45, $p$ < .01, but higher than that of the 2-separate condition (−1.58 μV, SD: .89), $F$ (1, 14) = 6.68, $p$ < .05. Thus, even when the potent common fate grouping cue was available, VWM did not represent the 4-in-2 conjunction condition as perfectly integrated units, in sharp contrast to Experiment 2. The partial

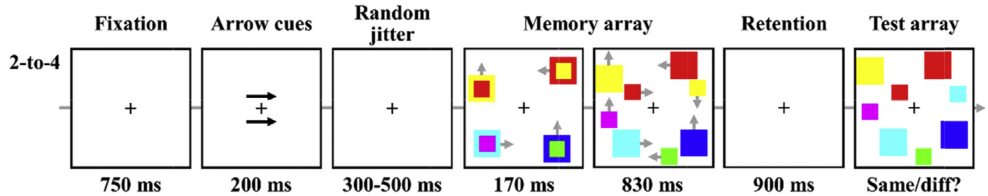


**Fig. 4 – The 2-to-4 condition, which was used in Experiment 3 and in the "priming phase" of Experiment 4 to create an individuation context. This condition included four colors that moved in two groups, and then separated and started to move independently.**

individuation persisted in the early stage of the memory retention: the *Early Retention CDA* of the 4-in-2 condition (−2.34 μV, SD: 1.27) was lower than the amplitude of the 4-separate condition (−2.83 μV, SD: 1.25), $F$ (1, 14) = 5.03, $p < .05$, but higher than that of the 2-separate condition (−1.60 μV, SD: .76), $F$ (1, 14) = 12.28, $p < .005$.

Throughout the memory retention, the individuation of the representations continued. The *Late Retention CDA* amplitude of the 4-in-2 condition (−1.75 μV, SD: .72) was not significantly different from the 4-separate condition (−1.99 μV, SD: .79), $F$ (1, 14) = 1.60, $p = .23$, and was higher than the amplitude of the 2-separate condition (−1.12 μV, SD: .36), $F$ (1, 14) = 17.32, $p < .001$. Thus, by the final stages of their memory retention, the colors in the 4-in-2 condition were held separately in VWM.

Following their separation, the items in the 2-to-4 separating colors condition were indeed represented individually in VWM, producing a representation that did not differ from four separate colors (starting at around 500 msec, see Fig. 2c, right panel). The *Tracking CDA* amplitude of the 2-to-4 condition (−2.58 μV, SD: 1.34) was not different from the 4-separate condition, $F < 1$, and was higher than the 2-separate condition, $F$ (1, 14) = 15.52, $p < .002$. This pattern continued to the retention interval, such that the *Retention CDA* amplitude in the 2-to-4 condition (−2.67 μV, SD: 1.02) was higher than the 2-separate condition (−1.36 μV, SD: .53), $F$ (1, 14) = 41.85, $p < .00002$, and even marginally higher than the 4-separate condition (−2.41 μV, SD: .96), $F$ (1, 14) = 4.38, $p = .06$.

#### 4.2.2. Behavioral results

Replicating the behavioral results of Experiments 1 and 2, the common fate cue in the 4-in-2 condition led to a benefit compared with four colors, but a cost compared with two colors. Accuracy was higher for the 4-in-2 conjunction condition (.91, SD: .06) than for the 4-separate condition (.89, SD: .06), $F$ (1, 14) = 5.75, $p < .05$, but still lower than for the 2-separate condition (.97, SD: .02), $F$ (1, 14) = 23.67, $p < .0005$. As can be expected, the 2-to-4 separating colors condition (.88, SD: .06) showed similar accuracy as the 4-separate condition, $F$ (1, 14) = 2.94, $p = .11$.

Interestingly, even though the CDA indicates an individuation of the 4-in-2 conjunction condition, we still found a benefit in accuracy for this condition compared with the 4-separate condition. Since the individuation of the 4-in-2 condition took time to develop, and during the tracking phase the representations were still partially integrated, the benefit might have originated from this earlier integration. This makes sense when considering the fact that accuracy reflects the end result of several processes, and the benefit could have originated in any one of them (not necessarily at the memory retention phase). Alternatively, the benefit might simply be due to an easier comparison process (Awh et al., 2007), since in the 4-in-2 conjunction condition the four colors appeared in only two locations, perhaps creating a stronger change signal.

### 4.3. Discussion

In Experiment 3, the same 4-in-2 conjunction condition that was perfectly integrated in Experiment 2, was represented individually in VWM. Furthermore, compared with the partial and late individuation of Experiment 1, in Experiment 3 the individuation of the 4-in-2 representations occurred both earlier (i.e., already during the movement of the items) and to a greater extent. Since the only difference between the three experiments was the context created by the other conditions (i.e., the minimal context of Experiment 1, the integration context of Experiment 2, and the individuation context of the present experiment), these results support the idea that VWM representations are flexibly adapted to the context in which an item appears, and that identical stimuli can produce very different VWM representations in different contexts.

Notably, in Experiment 3 we found that the 4-in-2 conjunction condition was already partially individuated during the tracking phase, even when the common fate grouping cue was still available. This suggests that the global context has a potent influence on VWM representations, since it could override a very strong Gestalt principle. We return to this point in the General Discussion.

In Experiment 4, we attempted to promote individuation by priming the subjects shortly before they first encounter the 4-in-2 conjunctions.

## 5. Experiment 4: individuation context priming

The goal of Experiment 4 was to examine whether a relevant context can be established even before subjects first encounter the 4-in-2 conjunction condition. Thus, in this experiment the individuation context was only seen during a preliminary "priming phase" that preceded the main experimental phase. The short priming phase (4 experimental blocks of 60 trials each) included the 2-to-4 separating colors condition, and also the 2-separate and 4-separate conditions.

Critically, it did not include the 4-in-2 conjunction condition. The main experimental phase was identical to Experiment 1, i.e., it included only the 4-in-2 conjunction condition, and the 2-separate and 4-separate conditions. Importantly, the 2-to-4 condition that includes a visual separation cue was only present during the priming phase and was never included alongside the 4-in-2 conjunction condition. Hence, Experiment 4 was identical to Experiment 1, except for the short priming phase aimed to establish an individuated interpretation of the experimental context. Note that this priming manipulation is very subtle, and therefore we did not expect to find a complete individuation in this experiment.

## 5.1. *Materials and methods*

The experiment was identical to Experiment 1, except as noted below.

### 5.1.1. *Participants*

15 fresh participants (12 females, mean age 24.1) were used. Two were replaced because of a >25% rejection rate.

### 5.1.2. *Stimuli and procedure*

The experiment included two parts. The first part (i.e., the "priming" phase), which consisted of 16 practice trials followed by 4 experimental blocks of 60 trials each, included the 2-separate, 4-separate, and 2-to-4 conditions (see Figs. 1 and 4). In the second part (i.e., the main experimental phase), the 2-to-4 condition was replaced by the 4-in-2 condition. Thus, this part was identical to Experiment 1, except that each participant performed 11 instead of 12 blocks.

### 5.1.3. *EEG recording*

The rejection procedure resulted in a mean rejection rate of 7.6%, and following it, the average number of trials (per condition per subject) was 186.

## 5.2. *Results*

### 5.2.1. *Electrophysiological results*

The 4-in-2 conjunction condition was partially individuated, and the individuation occurred already towards the end of the memory array presentation (at around 800 msec, see Fig. 2d). During the tracking phase, i.e., when the common fate cue was present, the 4-in-2 condition was perfectly integrated in VWM. The *Tracking CDA* amplitude (−1.78 μV, SD: 1.11) was lower than the 4-separate condition (−2.92 μV, SD: 2.01), $F$ (1, 14) = 12.60, $p < .005$, and was not different from the 2-separate condition (−1.60 μV, SD: 1.26), $F$ (1, 14) = 1.71, $p = .21$. However, when considering the memory retention of the items, we found that the colors in the 4-in-2 conjunction condition were partially individuated, as can be seen from the *Retention CDA* (−1.32 μV, SD: .93) which was higher than for the 2-separate condition (−.89 μV, SD: .82), $F$ (1, 14) = 5.38, $p < .05$, but lower than for the 4-separate condition (−2.25 μV, SD: 1.64), $F$ (1, 14) = 12.95, $p < .005$. Furthermore, here we found an individuation already in the earlier part, with an *Early Retention CDA* (−1.67 μV, SD: 1.05) that was lower than for the 4-separate condition (−2.86 μV, SD: 2.09), $F$ (1, 14) = 12.60, $p < .005$, and higher than for the 2-separate condition (−1.19 μV, SD: .87), $F$ (1, 14) = 7.98, $p < .02$.

### 5.2.2. *Behavioral results*

Replicating the behavioral results of the previous three experiments, and mirroring the CDA pattern, the common fate cue led to a benefit compared with four colors, but a cost compared with two colors. Accuracy was higher in the 4-in-2 conjunction condition (.91, SD: .07) than in the 4-separate condition (.89, SD: .08), $F$ (1, 14) = 5.96, $p < .05$, but still lower than in the 2-separate condition (.97, SD: .04), $F$ (1, 14) = 34.49, $p < .00005$.

## 5.3. *Discussion*

Despite the fact that Experiment 1 and 4 were identical, except for a short priming phase intended to establish an individuation context, the partial individuation of the representations of the colors in the 4-in-2 conjunction condition occurred at an earlier stage in Experiment 4 than in Experiment 1. Therefore, the results of Experiment 4 suggest that the individuation context that was primed before the main experimental phase could influence the interpretation of the 4-in-2 condition that first appeared during the main experimental phase. Notably, an effect on the representations was found even though the priming manipulation was very subtle (including only four blocks which differed from the main experimental phase in only one condition), again suggesting that the global context is an important factor in VWM.

# 6. Cross-experiment analyses

Our main analyses were restricted to each experiment, comparing the 4-in-2 condition to the same control conditions. We now turn to perform cross-experiment analyses on the CDA amplitude of the 4-in-2 condition, to shed more light on the contextual effects found in the present study. Specifically, for each time window, we performed an ANOVA on CDA amplitude, with Experiment as a between-subjects factor. All four tests were significant (all $F$'s > 3, all $p$'s < .05). We then compared specific pairs of experiments, to clarify the origins of these effects. For the sake of simplification and to avoid multiple comparisons, we focused on the patterns identified in the within-experiment analyses. We used a False Discovery Rate (FDR) procedure (Benjamini & Hochberg, 1995) to compensate for multiple comparisons. FDR yielded a corrected alpha of .034.

## 6.1. *Tracking CDA*

Already during the presentation of the common fate cue, we found an influence of context on the representations of the 4-in-2 condition. The cross-experiment analysis confirmed that the individuation context of Experiment 3 produced a more individuated representation of the 4-in-2 condition, compared with the minimal and integration contexts. Specifically, the 4-in-2 amplitude was marginally higher (compared to an FDR-corrected alpha) in Experiment 3 than in the minimal context of Experiment 1 [F (1, 56) = 4.28, $p = .043$] and higher than the integration context of Experiment 2 [F (1, 56) = 7.61, $p = .008$].

### 6.2. Retention CDA

When the items were held in memory, task context continued to influence the representations of the 4-in-2 condition. The cross-experiment analysis confirmed that the integration context of Experiment 2 produced a more integrated representation than the individuation context: the 4-in-2 amplitude was lower in Experiment 2 than in Experiment 3 [$F$ (1, 56) = 16.98, $p$ = .0001]. Contrary to the within-experiment analyses that found a more integrated representation in Experiment 2 than in the minimal context of Experiment 1 and the individuation priming of Experiment 4, the 4-in-2 amplitude did not significantly differ between these experiments [$F$ (1, 56) = 1.69, $p$ = .20, and $F$ (1, 56) = 3.24, $p$ = .08, respectively]. Additionally, the individuation context of Experiment 3 produced a more individuated representation (manifested by a higher CDA amplitude) than the minimal context of Experiment 1 or the individuation priming of Experiment 4 [$F$ (1, 56) = 7.96, $p$ = .007, and $F$ (1, 56) = 5.39, $p$ = .02, respectively], corroborating the within-experiment analysis.

Considering only the initial phase of the retention interval, we found that the individuation context of Experiment 3 produced a more individuated representation than the minimal context of Experiment 1 or the integration context of Experiment 2: the 4-in-2 amplitude was higher in Experiment 3 than in Experiment 1 [$F$ (1, 56) = 6.00, $p$ = .017] and Experiment 2 [$F$ (1, 56) = 14.46, $p$ = .0004]. Additionally, the individuation priming of Experiment 4 created a marginally (compared to an FDR-corrected alpha) more individuated representation (i.e., a higher CDA amplitude) than in the integration context of Experiment 2 [$F$ (1, 56) = 4.25, $p$ = .04]. However, we found no significant difference between the individuation priming of Experiment 4 and the minimal context of Experiment 1 ($F$ < 1).

Considering only the late part of the retention interval, we found that the individuation context of Experiment 3 created a more individuated representation compared with all other contexts: the 4-in-2 amplitude was higher than in Experiment 1 [F (1, 56) = 9.02, $p$ = .004, Experiment 2 (F (1, 56) = 16.60, $p$ = .0001], and Experiment 4 [F (1, 56) = 8.19, $p$ = .006]. The 4-in-2 condition in the integration context of Experiment 2 was not significantly different from the minimal context of Experiment 1 or the individuation priming of Experiment 4 [F (1, 56) = 1.15, $p$ = .29, and F (1, 56) = 1.47, $p$ = .23, respectively].

### 6.3. Discussion

The cross-experimental analyses generally supported the within-experiment analyses. Namely, the identical 4-in-2 condition was represented according to the context in which it appeared, such that the strongest integration was found in the integration context Experiment 2, the strongest individuation was found in the individuation context of Experiment 3, and intermediate patterns were found in the minimal context of Experiment 1 and in the individuation priming of Experiment 4. Most strikingly, these differences were evident already during the presentation of the potent Gestalt grouping cue, corroborating the important influence of global task context on VWM representations.

## 7. General discussion

The goal of this study was to test whether a given stimulus could be represented in VWM according to the context in which it appears. We examined the representations of four colors arranged in two common fate groups, i.e., the “4-in-2” conjunction condition. This condition was identical in all experiments, and we only changed the other conditions in the experiment, in order to manipulate the global context. Our measure of VWM representations was the CDA, an ERP component sensitive to the online deployment of VWM capacity (Vogel & Machizawa, 2004).

The CDA results indicated a clear influence of context on VWM representations. In a minimal context (Experiment 1), the colors in the 4-in-2 conjunction condition were integrated when the potent common fate cue was visible, but during the late stage of the retention interval, the representations were partially individuated. In an integration context, created by the 4-to-2 meeting colors condition (Experiment 2), the same 4-in-2 conjunction items were perfectly integrated. In contrast, when the context encouraged individuation by including the 2-to-4 separating colors condition (Experiment 3), the same 4-in-2 conjunction items were represented as individuated colors. When an individuation context was primed before the 4-in-2 conjunction condition was presented (Experiment 4), the individuation occurred at a relatively early stage. Since we used identical conjunction stimuli in all experiments, their different representations point to an influence of the context, created by the additional conditions, on VWM. Our results give strong support to the notion that VWM representations are not determined solely by stimulus-driven factors.

The present study might help shed new light on the ongoing debate in the field of VWM, regarding whether representations are feature-based or object-based. Specifically, a large number of studies used color–color conjunction stimuli to test whether the two colors in each conjunction consume the same VWM capacity as a single color or instead consume capacity that is similar to two separate colors that are not grouped together (Delvenne & Bruyer, 2004; Luck & Vogel, 1997; Luria & Vogel, 2011, 2014; Olson & Jiang, 2002; Parra et al., 2009; Vogel et al., 2001; Wheeler & Treisman, 2002). This condition is especially important since evidence showing that two features from different dimensions (e.g., the orientation and color of a tilted bar) consume as much capacity as a single-featured object was considered ambiguous: while they may reflect an object-based structure of VWM, they may instead reflect a domain-specific organization of VWM, such that each dimension has a separate capacity limitation. In contrast, an advantage for single-dimension conjunction stimuli can only reflect some sort of object-benefit mechanism. Interestingly, past studies found largely inconsistent results, from a perfect integration of the color–color conjunction (e.g., Vogel et al., 2001), to no benefit at all (e.g., Delvenne & Bruyer, 2004), which is puzzling since the stimuli and task used in the above mentioned studies were similar. Notably, our results show that even for identical items and within the same task, VWM representations depend on subtle global factors such as the mixture of conditions included in the experiment. Even if the conditions are identical, a short exposure to a certain context might still change the representations (see the priming manipulation of Experiment 4). Thus, there seems to be no single answer to the question of how stimuli are represented in VWM, since the representations are very flexible, and are affected by factors such as Gestalt cues, items' history, and global context (e.g., Vergauwe & Cowan, 2015).

Broadly speaking, our results are compatible with the long line of research, from fields other than VWM, demonstrating effects of context on human perception and cognition. The immediate environment (e.g., the surrounding objects or background) of an item, as well as the task instructions given to subjects, can influence a wide range of processes, such as identification and classification (for a review, see Bar, 2004), or the extent to which the item will compete with other items over limited resources (e.g., in the attentional blink paradigm, Dux & Coltheart, 2005). Importantly, the current findings suggest that even very subtle contextual cues can dramatically change the active representations in VWM.

First, unlike previous studies, we used identical stimuli and did not change the task or the instructions given to participants. Nevertheless, VWM responded to the inclusion of other conditions, suggesting that it can pick up on the context even when all other factors remain identical. Second, our context manipulation consisted of a very small change, namely, in each experiment we only added a single condition. Furthermore, this condition did not appear simultaneously with the 4-in-2 condition, but could still influence its representation. Third, we found that even a short priming phase can have an effect on VWM representations. This suggests that the current context shapes not only our active representations, but also our future interpretation of the visual input. Finally, the context was able to change VWM representations even when it contrasted with a strong local visual cue. Specifically, an individuation context managed to cause VWM to represent the colors in the 4-in-2 conjunction condition individually, even during the presentation of a potent Gestalt grouping cue, such as common fate (Experiment 3). Taken together, our findings suggest that context is a very important factor in determining VWM representations: as we constantly accumulate information on our dynamic environment, VWM flexibly adapts the active representations to best fit the global context.

Notably, our minimal context (Experiment 1) resulted in a partial individuation of the 4-in-2 conjunction condition, at a relatively late stage of the retention. While the specific cause for this pattern does not directly impact our findings, it is interesting to speculate about the reasons for the individuation, which is at odds with the strong grouping cue provided by the common fate movement. Additionally, it should be noted that previous studies using Gestalt cues have found either a perfect integration (e.g., Luria & Vogel, 2014), or a gradual integration (e.g., Luria & Vogel, 2011), while here (as well as in Experiments 3 and 4) we found a gradual *individuation*, suggesting that the common fate cue had a certain initial influence that then decreased. First, it is reasonable that the change detection task encourages individuation, due to the independence of the colors. Since a change could only occur in one color, performance could benefit from keeping the items represented individually (see also Balaban & Luria, 2015a). Second, it is possible that the representations of Experiment 1 were also influenced by the context created by the other two conditions, i.e., the 2-separate and 4-separate colors conditions. These conditions include the colors moving separately, which highlights the potential independence of the colors in the 4-in-2 conjunction condition. While it would be interesting to examine the "pure" representations of the 4-in-2 conjunction condition with no context at all, the CDA amplitude in this situation can be very difficult to interpret, since it has no baseline amplitudes to be compared with. Of course, these ideas are not mutually exclusive.

Finally, an open issue regarding our findings is the meaning of the "partial individuation" found. Namely, the CDA amplitude in the 4-in-2 conjunction condition of Experiments 1 and 4 was intermediate between the 2-separate and 4-separate colors conditions. A similar pattern has been reported previously both for the CDA (e.g., Balaban & Luria, 2015a; Luria & Vogel, 2011) and for functional imaging signals (e.g., Xu & Chun, 2007). A likely possibility is that this reflects the averaging of different types of trials, some of which included perfectly integrated representations and others consist of perfectly individuated representations. Since the CDA (as most ERP components) has to be measured using many trials, we cannot yet provide further support for this idea.

To conclude, the results were straight-forward: we demonstrated that identical stimuli could be represented according to the global context in which they appear. The influence of context determined the status of VWM representations even when the local information (e.g., grouping cues) contradicted it. The current findings suggest that VWM is a very flexible mechanism, which can adapt its representations not only to stimulus-driven cues, but also to the most appropriate interpretation implied by the global context.

## Conflict of interest

The authors declare no competing financial interests.

## Acknowledgments

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## REFERENCES

Awh, E., Barton, B., & Vogel, E. K. (2007). Visual working memory represents a fixed number of items regardless of complexity. *Psychological Science, 18*(7), 622–628. doi:PSCI1949.

Balaban, H., & Luria, R. (2015a). Integration of distinct objects in visual working memory depends on strong objecthood cues even for different-dimension conjunctions. *Cerebral Cortex*. http://dx.doi.org/10.1093/cercor/bhv038.

Balaban, H., & Luria, R. (2015b). The number of objects determines visual working memory capacity allocation for complex items. *NeuroImage, 119*, 54–62.
Bar, M. (2004). Visual objects in context. *Nature Reviews Neuroscience, 5*(8), 617–629.
Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, 289–300.
Blaser, E., Pylyshyn, Z. W., & Holcombe, A. O. (2000). Tracking an object through feature space. *Nature, 408*(6809), 196–199.
Cowan, N., Elliott, E. M., Scott Saults, J., Morey, C. C., Mattox, S., Hismjatullina, A., et al. (2005). On the capacity of attention: its estimation and its role in working memory and cognitive aptitudes. *Cognitive Psychology, 51*(1), 42–100. doi:S0010-0285(05)00002-2.
Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods, 134*(1), 9–21. http://dx.doi.org/10.1016/j.jneumeth.2003.10.009.
Delvenne, J. F., & Bruyer, R. (2004). Does visual short-term memory store bound features? *Visual Cognition, 11*(1), 1–27. http://dx.doi.org/10.1080/13506280344000167.
Drew, T., Horowitz, T. S., Wolfe, J. M., & Vogel, E. K. (2011). Delineating the neural signatures of tracking spatial position and working memory during attentive tracking. *The Journal of Neuroscience, 31*(2), 659–668. http://dx.doi.org/10.1523/JNEUROSCI.1339-10.2011.
Drew, T., Horowitz, T. S., Wolfe, J. M., & Vogel, E. K. (2012). Neural measures of dynamic changes in attentive tracking load. *Journal of Cognitive Neuroscience, 24*(2), 440–450. http://dx.doi.org/10.1162/jocn_a_00107.
Drew, T., & Vogel, E. K. (2008). Neural measures of individual differences in selecting and tracking multiple moving objects. *The Journal of Neuroscience, 28*(16), 4183–4191. http://dx.doi.org/10.1523/JNEUROSCI.0556-08.2008.
Dux, P. E., & Coltheart, V. (2005). The meaning of the mask matters evidence of conceptual interference in the attentional blink. *Psychological Science, 16*(10), 775–779.
Gold, J. M., Wilk, C. M., McMahon, R. P., Buchanan, R. W., & Luck, S. J. (2003). Working memory for visual features and conjunctions in schizophrenia. *Journal of Abnormal Psychology, 112*(1), 61–71.
Ikkai, A., McCollough, A. W., & Vogel, E. K. (2010). Contralateral delay activity provides a neural measure of the number of representations in visual working memory. *Journal of Neurophysiology, 103*(4), 1963–1968. http://dx.doi.org/10.1152/jn.00978.2009.
Lopez-Calderon, J., & Luck, S. J. (2014). ERPLAB: an open-source toolbox for the analysis of event-related potentials. *Frontiers in Human Neuroscience, 8*, 213. http://dx.doi.org/10.3389/fnhum.2014.00213.
Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature, 390*(6657), 279–281. http://dx.doi.org/10.1038/36846.
Luck, S. J., & Vogel, E. K. (2013). Visual working memory capacity: from psychophysics and neurobiology to individual differences. *Trends in Cognitive Sciences, 17*(8), 391–400. http://dx.doi.org/10.1016/j.tics.2013.06.006.
Luria, R., Balaban, H., Awh, E., & Vogel, E. K. (2016). The contralateral delay activity as a neural measure of visual working memory. *Neuroscience and Biobehavioral Reviews, 62*, 100–108.
Luria, R., & Vogel, E. K. (2011). Shape and color conjunction stimuli are represented as bound objects in visual working memory. *Neuropsychologia, 49*(6), 1632–1639. http://dx.doi.org/10.1016/j.neuropsychologia.2010.11.031.
Luria, R., & Vogel, E. K. (2014). Come together, right now: dynamic overwriting of an object's history through common fate. *Journal of Cognitive Neuroscience, 26*(8), 1819–1828. http://dx.doi.org/10.1162/jocn_a_00584.
McCollough, A. W., Machizawa, M. G., & Vogel, E. K. (2007). Electrophysiological measures of maintaining representations in visual working memory. *Cortex, 43*(1), 77–94.
Olson, I. R., & Jiang, Y. (2002). Is visual short-term memory object based? rejection of the "strong-object" hypothesis. *Perception & Psychophysics, 64*(7), 1055–1067.
Parra, M. A., Abrahams, S., Logie, R. H., & Della Sala, S. (2009). Age and binding within-dimension features in visual short-term memory. *Neuroscience Letters, 449*(1), 1–5. http://dx.doi.org/10.1016/j.neulet.2008.10.069.
Parra, M. A., Della Sala, S., Abrahams, S., Logie, R. H., Mendez, L. G., & Lopera, F. (2011). Specific deficit of colour-colour short-term memory binding in sporadic and familial alzheimer's disease. *Neuropsychologia, 49*(7), 1943–1952. http://dx.doi.org/10.1016/j.neuropsychologia.2011.03.022.
Peterson, D. J., Gözenman, F., Arciniega, H., & Berryhill, M. E. (2015). Contralateral delay activity tracks the influence of gestalt grouping principles on active visual working memory representations. *Attention, Perception, & Psychophysics*, 1–14.
Tsubomi, H., Fukuda, K., Watanabe, K., & Vogel, E. K. (2013). Neural limits to representing objects still within view. *The Journal of Neuroscience, 33*(19), 8257–8263. http://dx.doi.org/10.1523/JNEUROSCI.5348-12.2013.
Vergauwe, E., & Cowan, N. (2015). Working memory units are all in your head: factors that influence whether features or objects are the favored units. *Journal of Experimental Psychology: Learning, Memory, and Cognition*.
Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature, 428*(6984), 748–751. http://dx.doi.org/10.1038/nature02447.
Vogel, E. K., Woodman, G. F., & Luck, S. J. (2001). Storage of features, conjunctions and objects in visual working memory. *Journal of Experimental Psychology: Human Perception and Performance, 27*(1), 92–114.
Wheeler, M. E., & Treisman, A. M. (2002). Binding in short-term visual memory. *Journal of Experimental Psychology: General, 131*(1), 48–64.
Wilson, K. E., Adamo, M., Barense, M. D., & Ferber, S. (2012). To bind or not to bind: addressing the question of object representation in visual short-term memory. *Journal of Vision, 12*(8), 14. http://dx.doi.org/10.1167/12.8.14.
Woodman, G. F., & Vogel, E. K. (2008). Selective storage and maintenance of an object's features in visual working memory. *Psychonomic Bulletin & Review, 15*(1), 223–229.
Xu, Y., & Chun, M. M. (2007). Visual grouping in human parietal cortex. *Proceedings of the National Academy of Sciences of the United States of America, 104*(47), 18766–18771. doi:0705618104.