Binding in visual working memory is task-dependent

Ruoyi Cao[1] and Leon Y. Deouell [1,2*]

[1]Edmond and Lily Safra Center for brain sciences, The Hebrew University of Jerusalem, Jerusalem 9190401, Israel

[2]Department of Psychology，The Hebrew University of Jerusalem, Jerusalem 9190401, Israel

Author note :

Ruoyi Cao: https://orcid.org/0000-0003-3255-3112

Leon Y. Deouell : https://orcid.org/0000-0002-6147-5208

Leon Y. Deouell is a co-founder, shareholder and consultant of Innereye Ltd., a neurotech start-up company. However, the activities of Innereye Ltd. are not related to the research presented in this manuscript. Ruoyi Cao declares no conflicts of interest.

The datasets and analysis for this study are accessible on OSF (Open Science Framework) at the following link: osf.io/nd4rb

Abstract

Working memory is a neurocognitive system for maintaining and manipulating information online for a short period after the source of information disappeared. What information is held in working memory was shown to flexibly match current functional goal. Considering this, we revisited the question of whether information is held in WM as separate features or as bound objects. We conjectured that rather than having a fixed answer, the format in which information is maintained in working memory is also task-dependent. In two studies focusing on binding between two non-spatial features (color and orientation), or between a spatial and a non-spatial feature (location and color), we manipulated the relative relevance of conjunctions and separate features, in a delayed (Yes/No) recognition task. We found that memory for feature conjunctions was better when required by the task for both types of binding. Moreover, we found that the memory of the spatial feature was impaired when conjunction was not encoded or maintained, while memory for non-spatial features was found to be relatively independent of the task. We conclude that the representation format of objects in working memory is influenced by task requirements.

Keywords: Visual Working Memory, Binding problem, Object representation, Task-dependency

Introduction

Visual Working memory (VWM) refers to the function of preserving and manipulating visual information for a short duration when the physical stimuli are absent from direct perception (Baddeley, 1992; Esposito & Postle, 2015; Goldman-Rakic, 1995). Studies in both animals (Gilad et al., 2018; Rao, Rainer, & Miller, 1997) and humans (Myers, Stokes, & Nobre, 2017) regard VWM as a dynamic system that prioritizes task-relevant information, rather than as passive short-term storage. This was demonstrated for example by studies showing that VWM can flexibly maintain task-relevant locations (Griffin & Nobre, 2003) or non-spatial features while ignoring irrelevant ones that were simultaneously presented (Park, Sy, Hong, & Tong, 2017; Pertzov, Bays, Joseph, & Husain, 2013; Ye, Hu, Ristaniemi, Gendron, & Liu, 2016). In this study, we investigate the flexibility of another level, namely, whether separate features or bound objects are the units of storage, which we refer to as storage format below.

Studies investigating the storage format of objects in visual working memory that relied on the notion of limited VWM capacity yielded conflicting results. Specifically, some studies suggested that the number of objects (conjoined features), rather than the number of features, is the limiting factor (Luria & Vogel, 2011; Woodman, Vogel, & Luck, 2001aa), while others found that the number of features limit performance (An, Gong, McLoughlin, Yang, & Wang, 2014; Delvenne & Bruyer, 2004; Fougnie, Asplund, & Marois, 2010; Oberauer & Eichenberger, 2013; Olson & Jiang, 2002). One of the explored factors is whether the relevant features come from the same dimension or not. According to the multiple-resources view proposed by Wheeler and Treisman (2002), VWM maintains features from different feature dimensions (e.g. color and orientation) in parallel, with no additional cost, while features from the same feature dimension (e.g. two colors) compete for storage space (Wang, 2017; Wheeler & Treisman, 2002).

Another important factor is the specific factors involved. There is contradictory evidence regarding the VWM retention of orientation and color. Some studies found similar memory

performance for orientation and color conjunctions as for the memory of only one dimension, suggesting conjoined maintenance (Luck & Vogel, 1997; Olson & Jiang, 2002). Others found that when participants were asked to recall both the color and orientation of an object, errors in memory for one feature did not significantly affect memory for the other feature, suggesting separate storage (Fougnie & Alvarez, 2011). However, while the quantity of recalled objects was largely unaffected by increasing the number of features, the precision of these representations dramatically decreased (Fougnie et al., 2010).

Similar to binding between two non-spatial features, mixed results have been obtained for a non-spatial feature binding with location. Object-to-location binding is believed to mediate the binding of other features (Fougnie & Marois, 2009; Schneegans & Bays, 2017). Indeed, some studies suggested that objects are automatically bound to their locations. This claim is supported by the above-chance decoding accuracy of task-irrelevant location (Foster, Bsales, Jaffe, & Awh, 2017), impaired recognition performance when memoranda appear at a location different from where they were encoded (Hollingworth, 2007; Olson & Marshuetz, 2005), and the activation of retinotopic organization in visual regions during memory delay (Beeck & Vogels, 2000; Dicarlo & Maunsell, 2003). However, other studies provided evidence for separate representation of object identities and their locations, including dissociation in performance between location and identity memory from lesion studies (Darling & Logie, 2006), multiple objects tracking tasks (Kondo & Saiki, 2012) , and behavioral interference studies (Darling, Della, & Robert, 2007). These studies also showed that memory for bound objects could be impaired without impairment in memory for individual features or locations in normal participants (Pertzov, Dong, Peich, & Husain, 2012), patients with a variant of encephalitis (Pertzov, Miller, et al., 2013) and Alzheimer's disease (Liang et al., 2016).

There are a few hints in the literature to suggest the heterogeneity of tasks might at least partially explain some of the different results, as different tasks make conjunctions more or less

relevant. Regarding the conjunction of location with objects, one study (Ester, Serences, & Awh, 2009) found that visual details were held in VWM through spatially global recruitment of the early sensory cortex including not only contralateral but also ipsilateral to the visual input; the decoding of items from BOLD signals was similar from the two hemispheres. In contrast, making the location task relevant, Pratte and Tong (2014) found that decoding accuracy for remembered items was higher on the contralateral sides than ipsilaterally.

Thus, we conjectured that the storage format (separate features or conjunctions) is actually flexible, and it is the task which determines how information is maintained in VWM. We focus on features from separate dimensions, and investigate the effect of task requirements on feature binding with (color-location) and without (color-orientation) the involvement of spatial features. Different from studies that manipulated the relevance of locations or other features, we were interested in manipulating directly the relevance of conjunctions.

We are aware of only one study which directly manipulated the relevance of binding. In their study, Vergauwe and Cowan (2015) compared reaction times (RT) when the subjects were explicitly instructed to search for colors, shapes, or both. They found that retrieval of both features took no longer than retrieval of a single feature when the memory of bound objects was encouraged. Otherwise, RT increased with the number of features to be retrieved. They concluded that whether participants preserved bound objects or separate features in VWM is dependent on the testing situation.

Here, we extended the question to binding between color and location, and surmised that even without explicitly instructing subjects about the preferred mode of maintenance, the format of items in working memory will be flexibly adjusted to optimally perform the task. We thus conducted two experiments to investigate the adaptivity of maintenance formats in WM for binding between two non-spatial features (color, orientation) and between a non-spatial features (color) and location. We hypothesized that when conjunctions are tested more frequently, items in working memory will be

maintained as bound objects, improving conjunctions recognition, whereas when separate features are tested more frequently, items in working memory will be maintained as separate features, impairing conjunction recognition

Experiment 1

The aim of this experiment was to test whether task requirements could influence working memory retention of conjunctions of two non-spatial features, color and orientation. We presented memory arrays with two items to be remembered, and subjects had to indicate whether a probe, presented after a delay, had been shown in the array or not. There were two types of probes, Binding probes and Feature probes, with different proportions in two separate blocks: Binding-Dominant (BD) and Feature-Dominant (FD) blocks. Binding probes required information about the conjunction, whereas Feature probes did not. We predicted that if storage format depends on the task context, performance for both binding and feature probes will be better in the block where they are dominant than in the other block.

Materials and Method

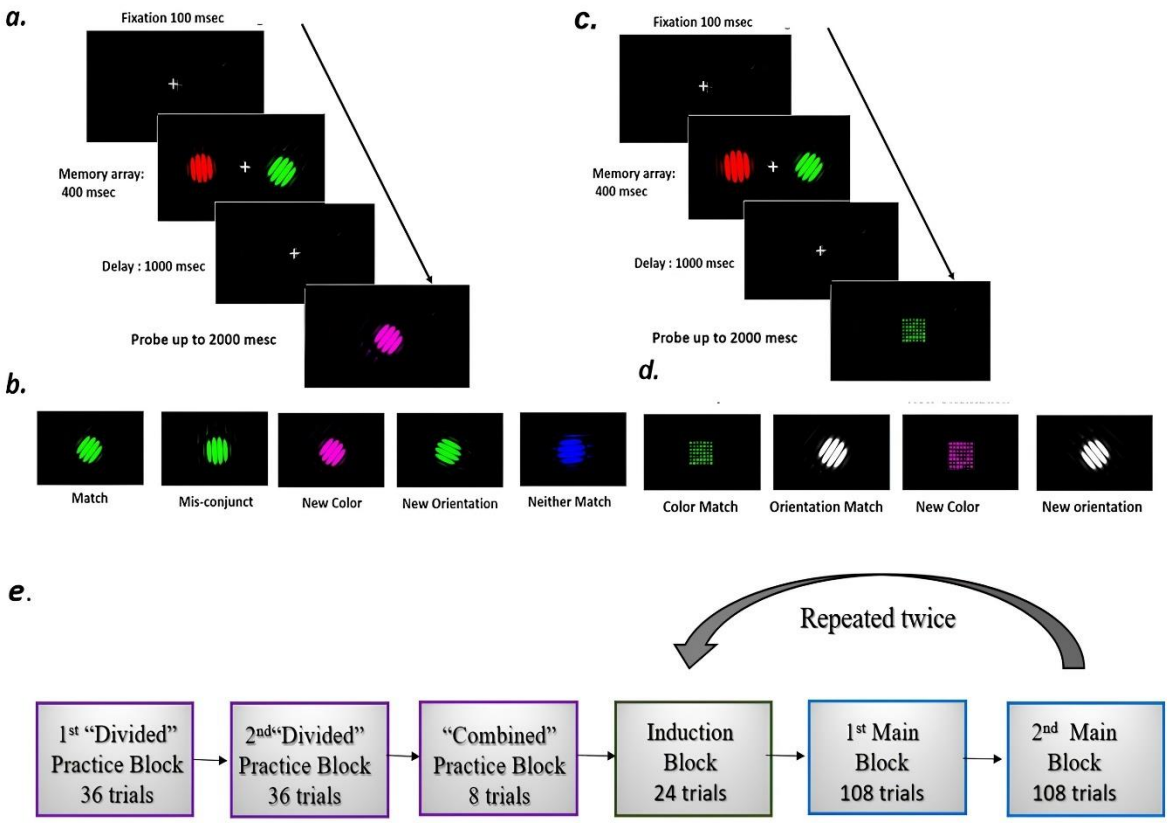
Participants

Thirty-one students were recruited through Hebrew University online study recruitment system (age range 21-36 years, mean± SD =24.79 ± 2.45, 80% females). Twenty-four of them passed the inclusion criteria described later. All participants reported no neurological ailments. The study was approved by the ethics committee of the Social Sciences Faculty at the Hebrew University of Jerusalem, Israel. Participants downloaded the computer program made with E-prime 3 online version (https://pstnet.com/eprime-go/) and performed the experiment on their own computers. Each participant conducted the two conditions of the experiment, each on different dates within a week. They received either two course credits or a monetary compensation of 60 NIS (~$15) for their participation.

Stimuli

Figure 1

Design of Experiment 1



Note. (a). Example of a binding trial with a "neither match" probe in the main blocks. (b). Examples of five Binding probes. The Match state label of the probe is relative to the memory array presented in panel a. (c). An example of a feature trial with a "New Color" probe. (d). Examples of four Feature Probes in the main blocks. The Match state label of the probe is relative to the array presented in panel c. (e). Experiment Procedure. Both conditions began with two "divided" practice blocks, one consisting of trials with Binding probes, and the other consisting of trials with Feature probes. This was followed by a "combined" practice block, where both types of probes were presented in a random order. Each participant then proceeded to complete two cycles, starting with an Induction block followed by two Main blocks. The Induction blocks consisted of Binding trials in the BD condition and Feature probes in the FD condition. The majority (72 out of 108) of probes in the Binding conditions were Binding trials, while the majority (72 out of 108) of probes in the Feature conditions were Feature trials.

The items were Gabor gratings (5 cycles, contrast 0.7; Figure 1). The exact visual angle and size of the stimulus varied as participants performed the tests on their own screens. Each memory array comprised two Gabor gratings, with each grating having a diameter of 300 pixels. One grating was positioned on the right side of the screen, while the other was located on the left side. The distance between the center of each Gabor grating and the screen center was 200 pixels. Each grating was assigned a color from a set of four distinct colors: red (255, 0, 0), green (0, 255, 0), magenta (255, 0, 255), and blue (0, 0, 255) with an orientation out of four possible angles (3, 49, 95, or 141 degrees) relative to the horizontal line. No two items within the same array had the same color or orientation, resulting in a total of 144 unique combinations. A subset of 108 of these combinations was randomly selected without repetition and used consistently across all subjects. The stimuli were created using Psychotoolbox-3, implemented in Matlab 2018 (The MathWorks, Inc., Natick, Massachusetts). Unlike the memory array, each probe contained only one grating. There were two types of probes: Binding probes (Figure 1b) and Feature probes (Figure 1d):

Binding probes

Binding probes could fall into one of five Match States: Matched, Mis-Conjunction, New-Color, New-Orientation, and Neither-Match (Figure 1b). A Matched probe shared both color and orientation with one of the items in the memory array. A Mis-Conjunction had the color of one of the items in the memory array (“old” color), with the orientation of the other item (“old” orientation). In a New-Color probe, the orientation of one of the items in the memory array was paired with a "New" color which was not present in the array, and vice versa for the New-Orientation probe. Finally, in the Neither-Match probe, both the color and orientation of the probe were “new”, that is, not present in the memory array.

Feature probes

Feature probes contained only one of the two relevant dimension: either color or orientation (Figure 1d). For a color probe, small, filled circles within a square of 300 pixels length in either old (Color match probe) or new (New Color probe) colors were presented at the center of the screen. For an orientation probe, a colorless gray Gabor grating was presented with an orientation either present in the memory array (Orientation Match probe) or not (New Orientation probe).

Thus, memory arrays were similar in binding and feature trials, and the appearance of the probe informed the subjects whether they needed to perform a color, orientation or color-orientation conjunction recognition.

Procedure

There were two conditions: Binding dominant (BD) and Feature dominant (FD), administered on separate days. In the BD condition, the majority of trials presented binding probes and in the FD condition the majority of trials presented feature probes. The order of conditions was counterbalanced between subjects and the order of trials was randomized within each subject.

Each condition consisted four block types: two Divided Practice Blocks, one Combined Practice Block, one Induction Block and two Main Blocks. The combination of one Induction Block with two Main Blocks was repeated twice (Figure 1e).

Divided Practice Blocks

The experiment began with two practice blocks with 36 trials each. One block included only trials with Binding probes, while the other consisted of only trials with Feature probes. The order of these two practice blocks was counterbalanced across subjects to minimize potential order effects. Each Practice trial began with a 100-millisecond fixation cross presented at the center of the screen. Next, the memory array appeared for 400 milliseconds, followed by a 1-second blank screen. After the delay period, a probe item was presented, and participants had to press a key to indicate whether the probe item was "old" (i.e. present in the memory array) or "new." The probe disappeared when the response

was made, or 3 seconds elapsed. Feedback was then given for 300 milliseconds, indicating whether the response was correct, incorrect, or too late (>3 sec).

Combined Practice Block

Following the divided practice blocks, participants proceeded to a combined practice block. The trial procedure in this block was the same as in the Divided Practice Blocks. However, this block presented both types of probes: Four Binding probe trials and four Feature probe trials, in random order. By exposing participants to the mix of probe types, the combined practice block familiarized subjects with switching between different types of probes.

Induction Block

After the practice phase, participants engaged in an Induction block with 24 trials. In the FD condition, the Induction block consisted of only feature probes with six trials for each probe type (color match, orientation match, new color, new orientation). In the BD session, the induction block consisted of only binding probes (12 Matched probe; 6 Mis-Conjunction probes; and 2 each of New-Color, New-Orientation, and Neither match probes). The aim of this block was to induce a specific maintenance format before the main testing blocks began.

Main Block

Upon completion of the Induction block, participants proceeded to two main testing blocks. Trials in these blocks had the same structure as in the practice blocks except that feedback was replaced by a 200-msec fixation cross, and that the maximum time for subjects to respond was reduced to 2 seconds (Figure 1a,b). Each testing block consisted of 108 trials. In the FD condition, there were 72 feature trials (18 trials for each of the color-match, orientation match, new color, new orientation probe) and 36 binding trials (18 matched probe trials, 9 mis-conjunction probe trials, and three trials for each of the other Match States). In the BD condition, there were 72 binding trials (36 matched probe

trials, 18 Mis-conjunct probe trials, and three trials for each of the other Match States) and 36 feature trials (nine trials for each Match State).

Analysis

Statistical analysis was conducted with JASP (Version 0.17.1; https://jasp-stats.org/) and figures were made by the python graphic library Seaborn (https://www.python-graph-gallery.com/seaborn/).

Proportion of correct responses and reaction times for correct trials were used as the dependent variables. The average response accuracy was calculated for each of four combinations made of two probe types (Binding probe vs Feature probe) and two probe frequency types (Frequent probe and Infrequent probe). Subjects with accuracy below chance level (50%) on two of these four combinations were excluded from further analysis under the premise that these subjects did not understand or pay attention to the task.

After verifying, using the Shapiro-Wilk test, that all RTs in this study were normally distributed (Shapiro and Wilk, 1965), we analyzed RTs with a Frequency (Frequent, Infrequent) × Type (Binding, Feature) 2×2 repeated-measures ANOVA. According to our flexible representation hypothesis, we expected performance to be better for more frequent probes (main effect of Frequency). When an interaction was found, simple effects were tested with Paired-Sample t-tests and Bayesian Paired-Sample t-tests. In this case, the prior distribution for Bayes analysis was assigned a Cauchy prior distribution (Ly, Verhagen, & Wagenmakers, 2016; Rouder, Speckman, Sun, Morey, & Iverson, 2009) with r= 1/√2(van Doorn et al., 2019).

Shapiro-Wilk test showed that the accuracy data was not normally distributed, therefore we used a data-driven permutation test to analyze accuracy data (Anderson and Ter Braak, 2003; Suckling and Bullmore, 2004). In this test, the F value of the data was compared against a distribution made of F values calculated from data in which the labels were randomly permuted iteratively. F values from the true data larger than 95% of the F values in the permuted distribution indicated a significant effect that

is unlikely due to chance. For the two-way repeated method ANOVA, each main effect and the interaction were tested separately. For example, to build up the null distribution of the main effect of Frequency, the label of Frequent or Infrequent was randomly permuted within each type and each subject 10000 times. Building up the null distribution of the interaction effect, on the other hand, involved random permutation of the label across both factors within each subject (Anderson & Ter Braak, 2003).

A main effect of Frequency in the analysis above might also be due to practice-related improvement for the frequent probe or surprise-related reduction for the infrequent probe. From all types of probes, only the Mis-conjunction probe required retention of conjunctions to allow accurate responses. Therefore, under the assumption that the task (induced by Frequency) affects the mode of retention beyond any practice\surprise effects, decrease in the performance for infrequent binding probes compared with frequent binding probe should be particularly large for Mis-Conjunction probes and not as much for other Match States. We thus predicted significant differences between the Frequent (BD) and the Infrequent (FD) condition for Mis-conjunction probes, while not on other Match States. To test this prediction, we compared performance of Frequent and Infrequent probe for each Match State of Binding trials with Paired-sample t-test (or Wilcoxon Signed-Rank Test when normality assumption was not satisfied) and Bayesian Paired-Sample t-tests with Cauchy distribution (Ly et al., 2016; Rouder et al., 2009) with $r= 1/\sqrt{2}$(van Doorn et al., 2019) as prior distribution (or Bayesian Wilcoxon Signed-Rank Test with 5000 permutations when normality assumption was not satisfied). Additionally, we compared differences in performance for Frequent and Infrequent probe on the Mis-conjunction probe against all the other four Match States (Match; New-Color; New-orientation; Neither -match probe) to test if the effect of Frequency on performance for the Mis-conjunction probes was larger than for other Match States.

The datasets and analysis for this study are accessible on OSF (Open Science Framework) at the following link: osf.io/nd4rb

Results and Discussion

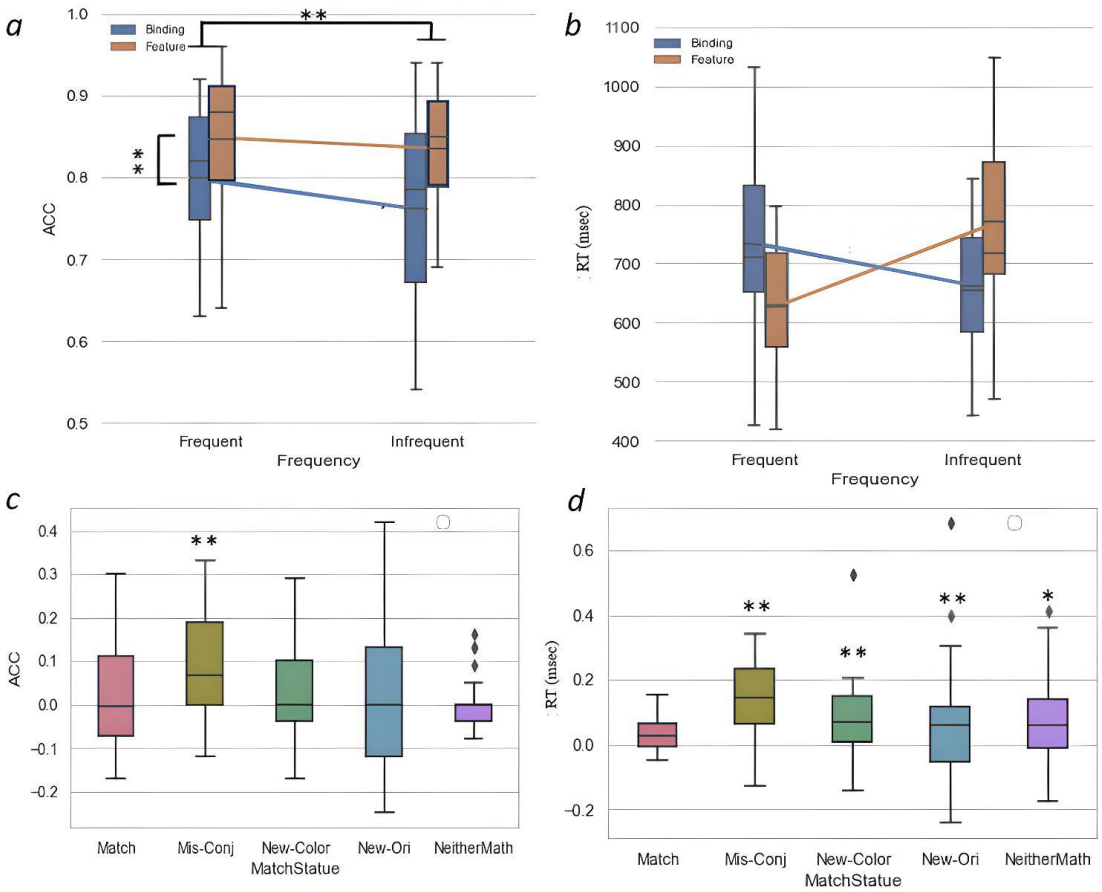
The effect of frequency for feature and binding probes.

A Frequency (Frequent, Infrequent) × Type (Binding, Feature) 2×2 repeated-measures permutation ANOVA was conducted on accuracy data. Accuracy was higher with Frequent probes than with Infrequent probes (Main effect of Frequency: $p = .005$), and accuracy for Feature probes was higher than for Binding probes (Main effect of Type $p < .001$, *Figure 2a*), with no interaction ($p = 0.23$).

For RTs, a Frequency (Frequent vs Infrequent) × Type (Binding vs Feature) 2 × 2 repeated-measures ANOVA revealed a significant interaction between Probe Type and Frequency (*Figure 3b*; $F(1,23) = 37.32$, $\eta 2 = 0.53$, $p < .001$). Simple effects for Frequency were therefore tested for binding probes and feature probes separately with paired sample t-test. The participants responded faster when the feature probe was frequent ($M = 629$ ms, $SE = 22.3$) than when it was infrequent ($M = 773$ ms, $SE = 31.29$), $t(23) = -7.16$, $p < .001$, Cohen'd $= -1.46$, $B10 = 59114.96$. However, for the binding probe, the subject response was slower when the probe was frequent ($M = 734$, $SE = 28.4$) than when it was infrequent. ($M = 664$ ms, $SE = 23.53$), $t(23) = 4.33$, $p < .001$, Cohen'd $= 0.88$, $B10 = 119.74$.

Figure 2.

Results of experiment 1



*Note.(***a)-(b)**. Average response accuracy **(a)** and reaction times **(b)** for frequent and infrequent binding and feature probes. Here and in other panels, boxes include values from the first quartile to the third quartile (the inter-quartile range [IRQ] including the central 50%) of the data. Horizontal lines across the boxes are at the median and mean .The means were connected with lines. The "whiskers" extend to points that lie 1.5 IQRs from the lower and upper quartile, and observations that fall outside this range are displayed independently as black markers. Significant main effects are marked with ** when p < .01 and * when p < .05; (**c)-(d)**: Response accuracy **(c)** and standardized reaction time **(d)** differences between the frequent probe and the infrequent probe for each Match State. Horizontal lines across the boxes are at the median. Significant differences from 0 are marked with ** when p < .01 and * when p < .05.

Table 1a

Wilcoxon Signed-rank Test on Effect of Frequency on each Match State of Binding Probe in ACC

F-IF	*W*	*z*	*p*	*Rank-Biserial Correlation*	BF_{10}
Match	151.50	0.41	.69	0.01	0.25
Mis-conjunct	233.50	2.91	.004	0.69	51.21
New-Color	114.00	1.24	.22	0.33	0.38
New-Orientation	120.00	0.16	.89	0.04	0.23
Neither	53.00	0.52	.62	0.17	0.23

Table 1b

Wilcoxon Signed-rank test on Effect of Trial Frequency on each Match State Binding Probe in Standardized RT

FI-F	*W*	*z*	*p*	*Rank-Biserial Correlation*	BF_{10}
Match	63.00	2.49	.01	0.58	12.90
Mis-conjunct	22.00	3.66	< .001	0.85	610.58
New-Color	52.00	2.80	.004	0.65	35.07
New-Orientation	95.00	1.57	.12	0.37	0.96
Neither	71.00	2.26	.02	0.53	5.29

It should be noted that the frequent feature probe (which elicited faster responses than the infrequent feature probe) and the infrequent binding probe (which elicited faster responses than the frequent binding probe) were both part of the FD block. Thus, a likely interpretation of the crossover interaction between the Frequency and the Probe type found is a block type (FD vs. BD) effect. To test this hypothesis, we reran the ANOVA arranging the data as Frequency (Frequent, Infrequent) × Block Type (FD, BD). RT was overall slower in the BD block than in the FD block, $F(1,23) = 37.32$, $p < .001$, $\eta 2 = 0.53$, with no interaction between the Block Type and Frequency of the probe, $F(1,23) = 0.11$, $p = .74$.

Thus, the interaction between Probe Frequency and the Probe Type in reaction time was due to the main effect of Block, where BD blocks were performed faster than FD block.

Importantly, a main effect of Frequency suggested that Frequent probes were performed faster than the Infrequent probe, $F(1,23) = 51.02, p< .001, \eta 2 =0.06.$ This is in line with our hypothesis that information is retained in a flexible, task-optimal way.

The effect of frequency on each type of binding probe.

Since the frequent probe was by design tested and practiced more than the infrequent probe, practice-related improvement for the frequent probe or surprise-related impairment for the infrequent probe could have contributed to the better performance in response to the frequent probes. We surmised that such practice/surprise effects should be similar for all Match states, but a true effect of the frequent task would be larger for the Mis-Conjunction probe compared to the other four Match States. This is because Mis-conjunction was the only Match state that requires binding information and therefore should be most sensitive to the induced task. Indeed, the planned contrast showed the frequency effect (Frequent-Infrequent) on accuracy was larger for the Mis-Conjunct probe than for the other probes combined, $t(92) = 2.63, p = .005$ *(Figure 2c).* That is, the Mis-Conjunction probes benefited from the binding probes being frequent more than other match states. Moreover, Wilcoxon Signed-Rank Test was applied to compare frequent and infrequent trials for each Match state. Only the Mis-conjunction probes elicited a significant effect of Frequency *(Table 1a).*

As reported above, RTs were overall faster in FD than BD blocks. Therefore, to examine the effect of frequency on different match states for RT, we first standardized RT for each Match state by dividing it by the mean RT of its respective block. That is, for frequent binding probes, each match state was divided by the mean reaction time of the BD blocks, and for infrequent binding probes, each match state was divided by the mean reaction time of FD blocks. The planned contrasts showed that the Frequency effect (Infrequent – Frequent RT) was larger for the Mis-Conjunction probe than for the other

match states*, t(92) = 2.61, p =.01 (Figure 2d).* This result suggests that the higher accuracy in the Frequent Mis- conjunction probe was not due to time-accuracy trade-off. Table 1b shows the Wilcoxon Signed-Rank Tests for each match state of RT separately.

To conclude, we found that memory was better for frequent probes than infrequent probes, supporting our hypothesis that maintaining color and orientation as separate features, or their conjunction, is task dependent. The Mis-conjunction probe showed the effect of Frequency more than other probes indicating that such task effect is not due to general practice. Additionally, we found that the trials in BD blocks were performed slower than FD block, suggesting that maintaining separate features might be easier than maintaining conjunctions.

Experiment 2

Experiment 1 revealed a flexibility of working memory maintenance for conjunctions of color and orientation, two non-spatial features. Experiment 2 aimed to examine the flexibility of maintaining conjunctions between color, and a spatial feature, location. The study manipulated the relevance of conjunctions and separate features, similar to Experiment 1 and predicted that the frequency of conjunction and features probes will affect the subjects' task set. Accordingly performance will be better, for both types of probes, when the task set biases the subject to use the relevant format of maintenance. Similar to Experiment 1, the study hypothesized that the effect of probe frequency would be observed mostly on Mis-Conjunction probes, which particularly required maintenance of conjunctions.

Materials and methods

Participants

Power analysis based on Experiment 1 suggested that fifteen participants were required to reach 80% of the power with an alpha of 0.05 for the critical contrast between frequent and infrequent

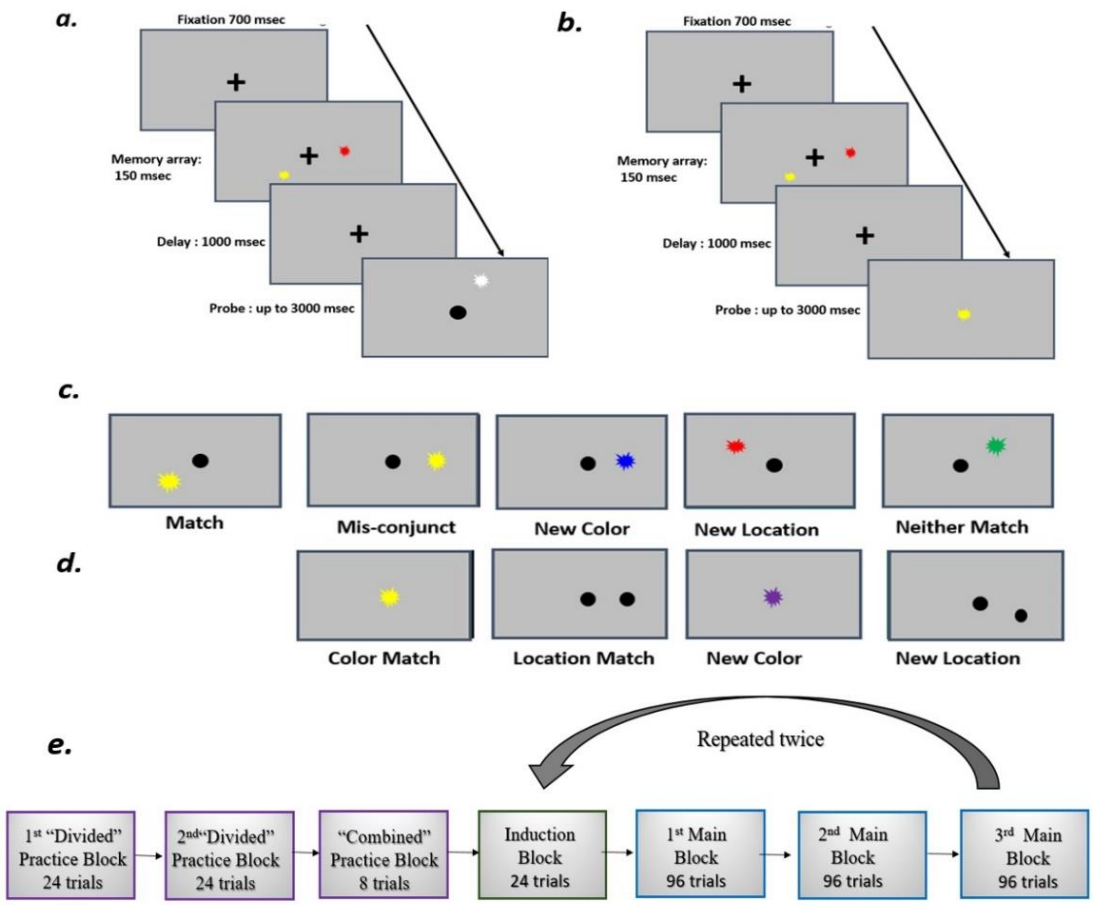
Mis-conjunction probes. Seventeen students, recruited through Hebrew University online study recruitment system, participated in the study (age range 21-35 years, mean± SD =25.02 ± 2.90, 77% females). Subjects with any two of four combinations (Frequent Binding Probe, Frequent Feature Probe, Infrequent Binding Probe and Infrequent Feature Probe) below response accuracy of 0.5 were excluded, resulting in the inclusion of fifteen participants. The study was approved by the ethics committee of the Social Sciences Faculty at the Hebrew University of Jerusalem, Israel. Subjects downloaded the computer program made with E-prime 3 online (https://pstnet.com/eprime-go/) to their own computers. Each participant conducted two conditions of the experiment on different dates within a week. They received either two course credits or a monetary compensation of 60 NIS (~$15)for their participation.

Stimuli

Stimuli consisted of spiky colored blobs, presented in memory arrays of two items. The color of each item was randomly selected out of six highly distinguished colors, including red (RGB: 255,0, 0), green (0, 255, 0), yellow (255,255, 0), blue (0, 0, 255), violet (255,255,0) and white (0,0,0). The same color never appeared twice in an array. The exact visual angle and size of the stimulus varied as participants performed the tests on their own screens. Each spiky colored blob was within a square of a diameter of 55 pixels. The locations of the two selected items were randomly selected out of six potential locations evenly distributed on an invisible circle with a diameter of 140 pixels centered on the fixation cross. The stimuli were created with Psychotoolbox-3, implemented in Matlab 2018. Unlike the memory array, each probe contained only one item of the same size as the items presented on the memory array. There were two types of probes: Binding probes (Figure 5c) and Feature probes (Figure 5d):

Figure 3

Design of Experiment 1



Note. (a): An example of a binding trial showing a Neither-Match binding probe. (b): An example of a feature trial showing a Color-Match probe. (c): Examples of five types of binding probe labeled in relation to the array shown in panel a. (d): Examples of four types of feature probes labeled in relation to the array shown in panel (e): Experiment Procedure. Both conditions began with two "divided" practice blocks, one consisting of trials with Binding probes, and the other consisting of trials with Feature probes. This was followed by a "combined" practice block, where both types of probes were presented in a random order. Each participant then completed two cycles, starting with an Induction block followed by three main blocks. The Induction blocks consisted of Binding trials in the BD condition and Feature probes in the FD condition. The majority (72 out of 96) of probes in the Binding conditions were Binding trials, while the majority (72 out of 96) of probes in the Feature conditions were Feature trials.

Binding probes

Binding probes (Figure 3c) included five Match States: (Match; Mis-Conjunction; New-color, New-location; Neither-match) according to their relation to the previous memory array with the same principle detailed in Experiment 1. The probes consisted of a single-colored item presented at one of the potential locations used in the memory arrays. To answer correctly, subjects had to maintain the conjunction information and answer whether the probe matched an item from the array in both color and location.

Feature probes

Feature probes (Figure 3d) Subjects were presented with either one black item at one of the possible locations (a location probe), or a colored item presented at the center of the screen (a color probe). Subjects were required to indicate if location probes appeared in the same location as one of the items as in the memory array (Location-match) or not (New-Location), whereas for color probes, subjects were required to indicate if the color of the item appeared in the memory array (Color-match) or not (New-color), regardless of its location. Thus, retention of separate features in working memory would allow a more effective response for feature probes than retention of conjunctions (which would entail a need to disconnect a stimulus from its bound location).

Procedure

The procedure was the same as in Experiment 1, with the exceptions of number of trials included in each block, the proportion of each probe type and the duration of the memory array presentation. For clarity, the full procedure is described as follows:

Divided Practice Blocks

The experiment began with two practice blocks of 24 trials. One block included only trials with Binding probes, while the other block consisted of only trials with Feature probes. The order of these two practice blocks was randomized across participants. Each Practice trial began with a 700-millisecond

fixation cross presented at the center of the screen. Next, the memory array appeared for 150 milliseconds, followed by a 1-second blank screen. After the delay period, a probe item was presented, and participants had to press a key to indicate whether the probe item was "old" (i.e. present in the memory array) or "new". The probe disappeared when the response was made, or 3 seconds elapsed. Feedback was then given for 300 milliseconds, indicating whether the response was correct, incorrect, or too late.

Combined Practice Block

Following the divided practice blocks, participants proceeded to a combined practice block. The trial procedure in this block was the same as that in Divided Practice Blocks. However, this block presented both types of probes: Four Binding probe trials and four Feature probe trials, in random order. By exposing participants to the mix of probe types, the combined practice block familiarized subjects with switching between different types of probes.

Induction Block

After the practice phase, participants engaged in an Induction block of 24 trials. The aim of the Induction block was to induce a specific maintenance format before the testing blocks began. Trials in induction blocks had the same structure as in the “divided” practice block. In the FD condition, the induction block consisted of only feature trials with six trials for each probe type (Location-Match probe, New-Location probe, Color-Match probe, New-Color probe). In the BD session, the induction blocks consisted of only binding probes (12 Matched probe; 6 Mis-Conjunct probes; 2 for New-Color, New-Location, and Neither match).

Main Block

Upon completion of the Induction blocks, participants proceeded to three main blocks. Trials in the main blocks had the same structure as in the practice blocks except that feedback was replaced by a 100-msec fixation cross, and the maximum time for subjects to respond was reduced to 2 seconds

(Figure 3a and b). Each testing block consisted of 96 trials. In the FD condition, there were 72 feature trials (18 trials for each of the color-match probe, color-mismatch probe, location-match probe, and location-mismatch probe) and 24 binding trials (12 Matched probe trials, 6 Mis-conjunct probe trials, and 2 trials for each of the other Match States). In the BD condition, there were 72 binding trials (36 matched probe trials, 18 Mis-conjunct probe trials, and three trials for each of the other Match States) and 24 feature trials (six trials for each Match State).

Analysis

The Analysis was the same as in Experiment 1. The datasets and analysis for this study are accessible on OSF (Open Science Framework) at the following link: osf.io/nd4rb

Results

The effect of frequency on binding and feature probes

Frequency (Frequent, Infrequent) ×Type (Binding, Feature) 2 × 2 repeated-measures permutation ANOVA was conducted on accuracy with 10000 permutations *(Figure 4a)*. Frequent probes were judged more accurately than infrequent probes (main effect of Frequency, $p < .001$), with neither a significant effect for the Probe Type ($p = .25$) nor a significant interaction between Frequency and the Type of the probe ($p = .34$)

A Frequency (Frequent, Infrequent) × Type (Binding, Feature) 2 × 2 repeated-measures ANOVA revealed a somewhat faster response to the frequent probes than infrequent probe (Main effect of Frequency, *Figure 4b*) , $F(1,14) = 17.03, p = .001, \eta 2 = 0.03$, and a somewhat faster responses to Binding probes than feature probes (Main effect of Type), $F(1,14) = 5.43, p = .04, \eta 2 = 0.01$. No significant interaction was found, $F(1,14) = 0.02, p = .88$.

Thus, for both Feature and Binding probes, frequent probes evoked faster and more accurate memory performance than the infrequent probes, which supported our hypothesis that the task demand could influence the retention formats of objects in working memory.

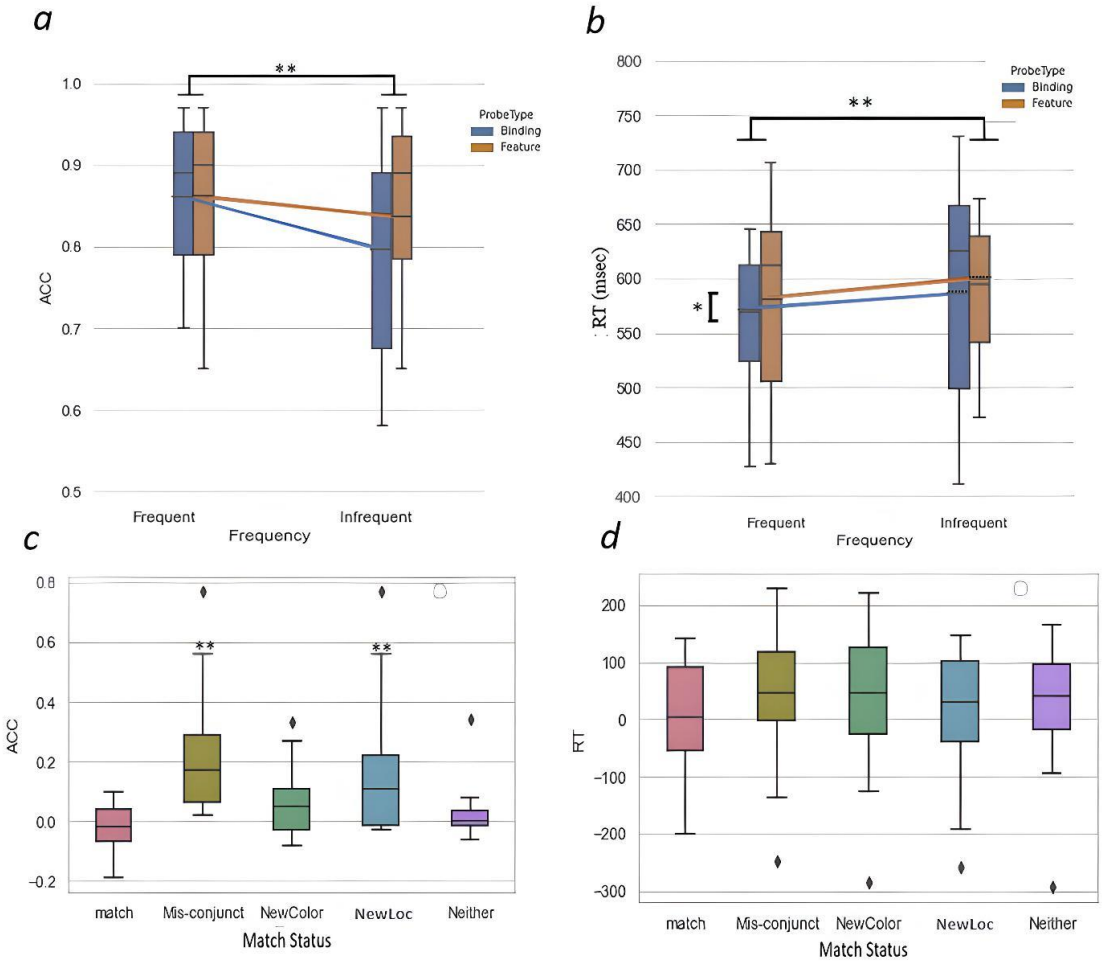
The effect of frequency on each type of binding probe.

We next split the Binding probe trials to examine the effect of frequency for each Match State of probe. As in Experiment 1, our flexible representation hypothesis predicted that larger differences between frequent and infrequent probes would be found in Mis-Conjunct probe trials than for other Match States. Consistently, the planned contrast between the Mis-Conjunction probe and all other Match States combined showed that the accuracy of the Mis-Conjunct probe was improved when binding probes were frequent compared to infrequent, more than other match states*, $t(56) = 3.38$, $p < .001$ (Figure 4c*). Wilcoxon Signed-Rank Test was further applied to compare the response accuracy for frequent and infrequent trials for each Match State. As expected, accuracy was higher for Mis-Conjunct probe when binding probes were tested frequently. In addition, the same effect was shown for the New-Location probe *(Table 2a),* but not for other Match States.

For all Match state, Frequent probes were nominally faster than Infrequent probes, but these differences were not significant, nor was the planned contrast between the Frequency effect for Mis-Conjunct probes and the other four Match States combined $t(56) = 1.08$ $p = .29$ *(Table 2b)*. This suggests that the difference in response accuracy between Match States is not due to speed-accuracy tradeoff.

Figure 4

Results of Experiment 2



Note. (a)-(b). Average response accuracy (a) and reaction times (b) for binding and feature probes, contrasting frequent and infrequent presentation; c-d: Response accuracy (c) and Reaction time (d) differences between the Frequent probe and the Infrequent probe for each Match State and Frequency. Box plot notations as in Figure 2.

Table 2a

Wilcoxon Signed-rank Test on Effect of Frequency on each Match State of Binding Probe in ACC

FI-F	*W*	*z*	*p*	*Rank-Biserial Correlation*	BF_{10}
Match	39.50	-0.82	.43	-0.25	4.79
Mis-conjunct	120.00	3.41	< .001	1.00	3165.12
New-Color	87.00	1.53	.13	0.45	1.09
New-Location	95.00	2.67	.008	0.81	15.71
Neither	29.00	0.77	.48	0.29	0.34

Table 2b

Student's t-test on Effect of Frequency on each Match State of Binding Probe in RT

FI-F	*t*	*df*	*P*	BF_{10}
Match	0.28	14	.78	0.27
Mis-conjunct	1.12	14	.28	0.45
New-Color	1.00	14	.33	0.40
New-Location	0.26	14	.80	0.27
Neither	0.74	14	.47	0.33

To summarize, this experiment showed that response accuracy was impaired when a Mis-Conjunction probe was presented in the context of infrequent binding probes. An unexpected finding was that response accuracy for new-location probes was also impacted when conjunction information was not task-relevant. In other words, when subjects were not required to report on the binding between color and location, location information tended to be lost. Maintaining features seemed to be

easier than maintaining conjunctions in Experiment 1, whereas in Experiment 2 this advantage was not seen, and in fact, the Binding probes elicited faster responses relative to the Feature probes, without compromising accuracy. To confirm this observation statistically, we compared the Feature advantage on ACC (*Frequent Binding probe -Frequent Feature probe*) and RTs (*Frequent Feature probe-Frequent Binding probe*) between Experiment 1 and Experiment 2. As expected, we found a significantly larger Feature advantage in trials with orientation and color (Experiment 1) compared with those with color and location (Experiment 2), both on ACC, $t(37) = 2.42, p=.021, Cohen'd = 0.36$, and RTs, $t(37) = 4.14\ p < .001, Cohen'd = 0.41$. This suggests that besides the task relevance, the involvement of specific stimulus dimensions may play a role in determining the representation formats.

General Discussion

In this study, we investigated whether the task determines the maintenance format in visual working memory - as separate features or as bound objects. In two studies using a delayed (Yes/No) recognition task we implicitly biased subjects to maintain features or conjunctions by manipulating the proportion of the probes which required conjunction information. Our results from the two studies show that both trials which required feature level information and those requiring conjunction information were performed better when being more frequent in a block of trials. Overall, this provides novel evidence for the flexibility of maintenance formats in VWM, based on task requirements.

Previous studies have demonstrated the flexibility of working memory by showing that task-relevant features could be selectively retained while discarding task-irrelevant features presented simultaneously (Park et al., 2017; Pertzov, Bays, et al., 2013; Ye et al., 2016). These observations emphasized the functional purpose of working memory and challenged the view that conceptualized working memory as a task-independent system (Nobre & Stokes , 2020). Our study investigated a different type of flexibility which received less attention in that respect: whether visual information is retained as separate features (e.g. color, orientation) or as bound objects. We presented probes that

required conjunction information and probes that did not, and by manipulating the relative dominance of these two probes within a block, we implicitly created a task set favoring one of the two maintenance formats. If the retention formats were independent of the task context, performance for both types of probes should have remained the same in the two dominance conditions. In contrast, we found that retention formats were shaped by the task requirement: performance with Binding probes was better when these probes were dominant (in the BD condition) than when Feature probes were dominant (in the FD condition), and vice versa for Feature probes. In accordance with what we expected, this effect manifested especially on trials in which Mis-conjunct probes were presented, a type of trial that required retention of conjunction information. These findings provide a new perspective to understand some seemly contradictory results and call for attention to task requirements when investigating formats of maintenance in VWM.

Whether conjunction memory is required in the task is a factor relevant to all experiments aiming to investigate the object representation formats. Some paradigms explicitly addressed this aspect. For example, to study whether the location is automatically bound with a non-spatial feature, studies usually make sure, and explicitly report, that the conjunction of spatial and non-spatial features itself is task-irrelevant (Foster et al., 2017). In other studies, the relevance of conjunction for completing the task is not reported but could be figured out from the paradigm. For example, a study by Fougnie and Alvarez (2011) found that errors in memory for one feature did not significantly affect memory for other features. They concluded that features were represented separately in visual working memory. However, in their design, participants were asked to recall either color or orientation of an object separately, rendering the conjunction information task-irrelevant. Whether their observation would hold had conjunction information been task-relevant is unknown. In some studies, the task-relevance information is subtler and cannot be directly figured out from the experimental paradigm without careful attention to the experimental details. For instance, in Wheeler and Treisman's (2002)

delay-match-to-sample task, features of different objects were not repeated within a memory array, and the probe either contained a new feature or matched one of the objects kept in working memory in both features, making it unnecessary to retain conjunctions. In contrast, in Luck and Vogel's study (1997; extended in Vogel, Woodman, & Luck, 2001), conjunctions were task-relevant as the memory array consisted of items with repeated features (e.g. two objects in an array could be red) and Mis-conjunction probes were presented occasionally. Consistent with this design difference, Wheeler and Treisman (2002) found that features were maintained separately, whereas Luck and Vogel concluded that features were conjoined in VWM. More investigation is required to test whether such subtle differences lead to different conclusions about retention format in VWM. Nevertheless, the flexibility of representation formats found in the current study, mandates that studies investigating retention formats will explicitly consider the task relevance of conjunctions in their design and investigate the effect of the task along with other variables of interest whenever possible.

Our study suggests that task relevance alone cannot completely determine the representation formats of objects in VWM. Rather, the degree of an object being kept in one format or the other varied depending on other factors. An exclusive task effect would have been reflected by better performance on Binding probes than Feature probes in the BD condition and better performance for Feature probes than Binding probes in the FD condition. However, this was not what we found. For two non-spatial features, performance for feature probes outperformed performance for binding probes (Experiment 1), regardless of whether conjunctions were task relevant. This finding is consistent with studies showing greater cognitive resources required for remembering the conjunction of two non-spatial features, including larger involvement of cortical regions (Parra, Della Sala, Logie, & Morcom, 2014) and increased impairment of conjunction memory due to a secondary task(He et al., 2020; Shen, Huang, & Gao, 2015). When location (spatial) and color (non-spatial) features were relevant (Experiment 2), we observed a different pattern, whereby subjects were faster for Binding probes than for Feature probes regardless of

task relevance of conjunctions. This finding is consistent with studies showing that location can be automatically encoded (Elsley & Parmentier, 2015; Foster et al., 2017; Olson & Marshuetz, 2005). Combining the results from both studies, the results confirm our hypothesis regarding the effect of task-relevance of conjunctions in determining the storage format in working memory and suggests a role also to the specific features to be encoded.

Specifically, participants had difficulty to identify new locations as such when the conjunctions were de-emphasized, which was not the case for new colors. That is, memory of color was not dependent on memory for its location, but the memory of location required it to be yoked with color. This observation might be surprising, as the spatial dimension has long been considered a primary dimension which allows us to bind other features, and to access our internal representations of objects, both visual (Kondo & Saiki, 2012; Rajsic & Wilson, 2012; Treisman & Zhang, 2006; Wheeler & Treisman, 2002), and auditory (Deouell, Bentin, & Soroker, 2000).

One of the causes of interdependence between location memory and conjunction memory observed in the current study might be difficulty in maintaining an empty location. There is some evidence showing that an empty location (i.e. one without other associated features) is especially difficult to remember. For example, when an object suddenly appeared in a previously empty location, infants at least 8 months old showed no surprise (Wynn & Chiang, 1998). In contrast, infants as young as 3 months old showed a surprise response when an item disappeared magically (Baillargeon & Devos, 2016). The above two phenomena could be explained by the lack of ability to encode and maintain an empty location. In this case no representation is formed in visual working memory before the object appears, and no conflict (or prediction error) occurs when it does. On the other hand, when an object is present at some locations, the memory system keeps the object bound with that location, and disappearance of the object conflicts with the previous representation in working memory. Difficulties in maintaining empty locations were also found in adults (Csink, Gliga, & Mareschal, 2022).

Our study has several limitations that should be addressed in future research. Since we only applied a single delay duration in our study, we could not investigate the temporal dynamics of the process. Specifically, research is necessary to discern whether the task manipulated the initial encoding into working memory or later retention processes. Second, the format of object representations in working memory were estimated indirectly, based on the assumption that the number of representation units (features or objects) correspondingly consumes a number of units of working memory resources. This assumption, however, was challenged by working memory models conceptualizing working memory capacity as continuous resources rather than discrete units (Ma, Husain, & Bays, 2014). To accumulate convergent evidence and generalize our results, the flexibility of the formats should be tested with a variety of paradigms without assuming the slot model of working memory (Fougnie et al., 2010).

In summary, our research offers new evidence that the way an object is represented in working memory, whether as distinct features or as integrated objects, varies depending on the specific task at hand. These findings highlight the adaptability of representation format beyond the task-relevance of any specific feature. It therefore emphasizes the role of experimental design, even implicit, in shaping the formats of objects in working memory.

References

An, X., Gong, H., McLoughlin, N., Yang, Y., & Wang, W. (2014). The mechanism for processing random-dot motion at various speeds in early visual cortices. *PLoS ONE*, *9*(3). https://doi.org/10.1371/journal.pone.0093115

Anderson, M. J., & Ter Braak, C. J. F. (2003). Permutation tests for multi-factorial analysis of variance. *Journal of Statistical Computation and Simulation*, *73*(2), 85–113. https://doi.org/10.1080/00949650215733

Baddeley, A. (1992). Working Memory Components of Working Memory Individual Differences in Working Memory The Slave Systems of Working Memory. *Science*, *255*(Mii).

Baillargeon, R., & Devos, J. (2016). Object Permanence in Young Infants : Further Evidence Author (s): Renée Baillargeon and Julie DeVos Published by : Wiley on behalf of the Society for Research in Child Development Stable URL : http://www.jstor.org/stable/1130803 Accessed : 16-04-2016 18, *62*(6), 1227–1246.

Beeck, H. O. P. D. E., & Vogels, R. (2000). Spatial Sensitivity of Macaque Inferior. *The Journal of Comparative Neurology*, *518*(June), 505–518.

Csink, V., Gliga, T., & Mareschal, D. (2022). Remembering nothing: Encoding and memory processes involved in representing empty locations. *Memory and Cognition*, *50*(1), 129–143. https://doi.org/10.3758/s13421-021-01205-x

Darling, S., Della, Æ. S., & Robert, S. Æ. (2007). Behavioural evidence for separating components within visuo-spatial working memory. *Cognitive Processing*, *8*(3), 175–181. https://doi.org/10.1007/s10339-007-0171-1

Darling, S., & Logie, R. H. (2006). Neuropsychological evidence for separating components of

visuo-spatial working memory. *Journal of Neurology*, *253(2)*, 176–180. https://doi.org/10.1007/s00415-005-0944-3

Delvenne, J. F., & Bruyer, R. (2004). Does visual short-term memory store bound features? *Visual Cognition*, *11*(1), 1–27. https://doi.org/10.1080/13506280344000167

Deouell, L. Y., Bentin, S., & Soroker, N. (2000). Electrophysiological evidence for an early (pre-attentive) information processing deficit in patients with right hemisphere damage and unilateral neglect. *Brain*, *123*(2), 353–365. https://doi.org/10.1093/brain/123.2.353

Dicarlo, J. J., & Maunsell, J. H. R. (2003). Anterior Inferotemporal Neurons of Monkeys Engaged in Object Recognition Can be Highly Sensitive to Object Retinal Position. *Journal of Neurophysiology, 89(6), 3264-3278.*, (Horel 1996), 3264–3278.

Elsley, J. V., & Parmentier, F. B. R. (2015). The asymmetry and temporal dynamics of incidental letter–location bindings in working memory. *Quarterly Journal of Experimental Psychology*, *68*(3), 433–441. https://doi.org/10.1080/17470218.2014.982137

Esposito, M. D., & Postle, B. R. (2015). The Cognitive Neuroscience of Working Memory. *Annual Review of Psychology*. https://doi.org/10.1146/annurev-psych-010814-015031

Ester, E. F., Serences, J. T., & Awh, E. (2009). Spatially global representations in human primary visual cortex during working memory maintenance. *Journal of Neuroscience*, *29*(48), 15258–15265. https://doi.org/10.1523/JNEUROSCI.4388-09.2009

Foster, J. J., Bsales, E. M., Jaffe, R. J., & Awh, E. (2017). Alpha-Band Activity Reveals Spontaneous Representations of Spatial Position in Visual Working Memory. *Current Biology*, *27*(20), 3216-3223.e6. https://doi.org/10.1016/j.cub.2017.09.031

Fougnie, D., & Alvarez, G. A. (2011). Object features fail independently in visual working memory: Evidence for a probabilistic feature-store model. *Journal of Vision*, *11*(12), 1–12.

https://doi.org/10.1167/11.12.1

Fougnie, D., Asplund, C. L., & Marois, R. (2010). What are the units of storage in visual working memory? *Journal of Vision*, *10*(12), 27. https://doi.org/10.1167/10.12.27

Fougnie, D., & Marois, R. (2009). Attentive tracking disrupts feature binding in visual working memory. *Visual Cognition*, *17*(1–2), 48–66. https://doi.org/10.1080/13506280802281337

Gilad, A., Gallero-salas, Y., Groos, D., Helmchen, F., Gilad, A., Gallero-salas, Y., … Helmchen, F. (2018). Behavioral Strategy Determines Frontal or Posterior Location of Short-Term Memory in Neocortex Article Behavioral Strategy Determines Frontal or Posterior Location of Short-Term Memory in Neocortex. *Neuron*, *99*(4), 814-828.e7. https://doi.org/10.1016/j.neuron.2018.07.029

Goldman-Rakic, P. S. . (1995). Cellular Basis of Working Memory Review. *Neuron*, *14*, 477–485.

Griffin, I. C., & Nobre, A. C. (2003). Orienting Attention to Locations in Internal Representations. *Journal of Cognitive Neuroscience*, (September), 1176–1194.

He, K., Li, J., Wu, F., Wan, X., Gao, Z., & Shen, M. (2020). Object-based attention in retaining binding in working memory: Influence of activation states of working memory. *Memory and Cognition*, *48*(6), 957–971. https://doi.org/10.3758/s13421-020-01038-0

Hollingworth, A. (2007). Object-Position Binding in Visual Memory for Natural Scenes and Object Arrays. *Journal of Experimental Psychology: Human Perception and Performance*, *33*(1), 31–47. https://doi.org/10.1037/0096-1523.33.1.31

Kondo, A., & Saiki, J. (2012). Feature-Specific Encoding Flexibility in Visual Working Memory. *PLoS ONE*, *7*(12). https://doi.org/10.1371/journal.pone.0050962

Liang, Y., Pertzov, Y., Nicholas, J. M., Henley, S. M. D., Crutch, S., Woodward, F., … Husain,

M. (2016). ScienceDirect Visual short-term memory binding deficit in familial Alzheimer ' s disease. *CORTEX*, *78*, 150–164. https://doi.org/10.1016/j.cortex.2016.01.015

Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature*, *390*(1996), 279–281.

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. https://doi.org/10.1016/j.neuropsychologia.2010.11.031

Ly, A., Verhagen, J., & Wagenmakers, E. J. (2016). Harold Jeffreys's default Bayes factor hypothesis tests: Explanation, extension, and application in psychology. *Journal of Mathematical Psychology*, *72*, 19–32. https://doi.org/10.1016/j.jmp.2015.06.004

Ma, W. J., Husain, M., & Bays, P. M. (2014). Changing concepts of working memory. *Nature Neuroscience*, *17*(3), 347–356. https://doi.org/10.1038/nn.3655

Myers, N. E., Stokes, M. G., & Nobre, A. C. (2017). Prioritizing Information during Working Memory: Beyond Sustained Internal Attention. *Trends in Cognitive Sciences*, *21*(6), 449–461. https://doi.org/10.1016/j.tics.2017.03.010

Oberauer, K., & Eichenberger, S. (2013). Visual working memory declines when more features must be remembered for each object. *Memory and Cognition*, *41*(8), 1212–1227. https://doi.org/10.3758/s13421-013-0333-6

Olson, I. R., & Jiang, Y. (2002). Is visual short-term memory object based? Rejection of the "strong-object" hypothesis. *Perception and Psychophysics*, *64*(7), 1055–1067. https://doi.org/10.3758/BF03194756

Olson, I. R., & Marshuetz, C. (2005). Remembering "what" brings along "where" in visual working memory. *Perception and Psychophysics*, *67*(2), 185–194.

https://doi.org/10.3758/BF03206483

Park, Y. E., Sy, J. L., Hong, S. W., & Tong, F. (2017). Reprioritization of Features of Multidimensional Objects Stored in Visual Working Memory. *Psychological Science*, *28*(12), 1773–1785. https://doi.org/10.1177/0956797617719949

Parra, M. A., Della Sala, S., Logie, R. H., & Morcom, A. M. (2014). Neural correlates of shape-color binding in visual working memory. *Neuropsychologia*, *52*(1), 27–36. https://doi.org/10.1016/j.neuropsychologia.2013.09.036

Pertzov, Y., Bays, P. M., Joseph, S., & Husain, M. (2013). Rapid Forgetting Prevented by Retrospective Attention Cues. *Journal of Experimental Psychology*, *39*(5), 1224–1231. https://doi.org/10.1037/a0030947

Pertzov, Y., Dong, M. Y., Peich, M. C., & Husain, M. (2012). Forgetting What Was Where: The Fragility of Object-Location Binding. *PLoS ONE*, *7*(10). https://doi.org/10.1371/journal.pone.0048214

Pertzov, Y., Miller, T. D., Gorgoraptis, N., Caine, D., Schott, J. M., Butler, C., & Husain, M. (2013). Binding deficits in memory following medial voltage-gated potassium channel complex antibody-associated limbic encephalitis, 2474–2485. https://doi.org/10.1093/brain/awt129

Rajsic, J., & Wilson, D. E. (2012). Remembering where: Estimated memory for visual objects is better when retrieving location with colour. *Visual Cognition*, *20*(9), 1036–1039. https://doi.org/10.1080/13506285.2012.726477

Rao, S. C., Rainer, G., & Miller, E. K. (1997). Integration of what and where in the primate prefrontal cortex. *Science*, *276*(5313), 821–824. https://doi.org/10.1126/science.276.5313.821

Rouder, J. N., Speckman, P. L., Sun, D., Morey, R. D., & Iverson, G. (2009). Bayesian t tests for accepting and rejecting the null hypothesis. *Psychonomic Bulletin and Review*, *16*(2), 225–237. https://doi.org/10.3758/PBR.16.2.225

Schneegans, S., & Bays, P. M. (2017). Neural architecture for feature binding in visual working memory. *Journal of Neuroscience*, *37*(14), 3913–3925. https://doi.org/10.1523/JNEUROSCI.3493-16.2017

Shen, M., Huang, X., & Gao, Z. (2015). Object-based attention underlies the rehearsal of feature binding in visual working memory. *Journal of Experimental Psychology: Human Perception and Performance*, *41*(2), 479–493. https://doi.org/10.1037/xhp0000018

Treisman, A., & Zhang, W. (2006). Location and binding in visual working memory. *Memory and Cognition*, *34*(8), 1704–1719. https://doi.org/10.3758/BF03195932

van Doorn, J., van den Bergh, D., Bohm, U., Dablander, F., Derks, K., Draws, T., … Wagenmakers, E.-J. (2019). The JASP Guidelines for Conducting and Reporting a Bayesian Analysis. https://doi.org/10.31234/osf.io/yqxfr

Wang, B. (2017). Separate Capacities for Storing Different Features in Visual Working Memory Journal of Experimental Psychology : Learning , Memory , and Cognition, *43*(July), 226–236. https://doi.org/10.1037/xlm0000295

Wheeler, M. E., & Treisman, A. M. (2002). Binding in short-term visual memory. *Journal of Experimental Psychology: General*, *131*(1), 48–64. https://doi.org/10.1037/0096-3445.131.1.48

Woodman, G. F., Vogel, E. K., & Luck, S. J. (2001). Visual search remains efficient when visual. *Psychological Science*, *12*(3), 219–224. https://doi.org/10.1111/1467-9280.00339

Wynn, K., & Chiang, W. C. (1998). Limits to infants' knowledge of objects: The Case of

Magical Appearance. *Psychological Science*, *9*(6), 448–455. https://doi.org/10.1111/1467-9280.00084

Ye, C., Hu, Z., Ristaniemi, T., Gendron, M., & Liu, Q. (2016). Retro-dimension-cue benefit in visual working memory. *Scientific Reports*, *6*(February), 1–13. https://doi.org/10.1038/srep35573

Knowlagent : Acknowledgments

We thank Yoni pertzov for inspiration on design and discussion of the present study. We thank Areej Mousa and Neta Licht for helping with running experiments.