

Location-based effects underlie feature conjunction benefits in visual working memory

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Studies of visual working memory (VWM) have reported that different features belonging to the same object (conjunctions) are better retained than the same features belonging to spatially separated objects (disjunctions). This conjunction benefit has been taken as evidence for the theory that VWM representations are object-based. However, compared to separate features, conjunctions also occupy fewer locations. Here we tested the alternative hypothesis that the conjunction benefit reflects a spatial-based rather than an object-based advantage. Experiment 1 shows a clear VWM conjunction benefit for spatially laid out displays of memory items. However, when the same items were presented sequentially at one location (i.e., location was noninformative), memory performance was equivalent for conjunction and disjunction conditions. Experiment 2 shows that only when the probe carries spatial information (i.e., it matches the location of the memory item) does a conjunction benefit occur. Taken together, these results put important boundaries on object-based theories of VWM.

Introduction

Visual working memory (VWM) allows the human cognitive system to temporarily retain visual information that is relevant for ongoing tasks. Ever since the hypothesized visuospatial sketchpad of Baddeley and Hitch (1974), spatial location has been thought to be a fundamental dimension of VWM, as it anchors visual features such as color and shape. Consistent with this, spatial location has proven to be a powerful retrieval cue for extracting other remembered visual information (Dell'Acqua, Sessa, Toffanin, Luria, & Joliceur, 2010; Richardson & Spivey, 2000; Spivey & Geng, 2001; Theeuwes, Kramer, & Irwin, 2011). In the current study we argue that this fundamental role of location may underlie what is known as the *object-based benefit* in VWM, which is the finding that the net memory performance for conjunctions of visual features is better than for those same features remembered separately.

The capacity of VWM has been investigated using change detection tasks (e.g., Luck & Vogel, 1997;

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Phillips, 1974; Vogel, Woodman, & Luck, 2001) and recall tasks (e.g., Fougnie & Alvarez, 2011; Prinzmetal, Amiri, Allen, & Edwards, 1998; Zhang & Luck, 2008). With these paradigms, previous studies have repeatedly demonstrated that the capacity of VWM is limited, which puts important constraints on human performance in various cognitively demanding tasks (for review, see Baddeley, 1992) and can predict individual differences in fluid intelligence (Fukuda, Vogel, Mayr, & Awh, 2010). Importantly, research has suggested that by binding individual features into integrated objects, the VWM capacity limit can effectively be increased, as the whole becomes less than the sum of its parts (Awh, Barton, & Vogel, 2007; Fougnie, Cormiea, & Alvarez, 2013; Luck & Vogel, 1997; Olson & Jiang, 2002; Vogel et al., 2001; Xu, 2002a, 2002b, 2006).

This idea of an object-based benefit in VWM is largely based on two types of experiments. In an earlier demonstration, Luck and Vogel (1997) found that memory performance was virtually the same when participants were required to remember all features of multiple-feature objects (e.g., color *and* orientation) versus only one of the features for each of those objects (e.g., color *or* orientation). However, several researchers have argued that this result might also have represented independent feature spaces, each with its own storage capacity (Magnussen, Greenlee, & Thomas, 1996; Wheeler & Treisman, 2002).¹ Consistent with the idea of independent feature stores theory, Fougnie and Alvarez (2011) found that the successful recall of an object-defining feature does not hinge on the successful recall of other object-defining features (see also Fougnie et al., 2013). Our recent work also indicates that there is little cross-dimensional interference in VWM, indicating that different visual features may tap into separate VWM capacities (Wang, Cao, Theeuwes, Olivers, & Wang, 2016; Wang & Wang, 2014).

A second line of studies (Olson & Jiang, 2002; Xu, 2002a, 2002b, 2006) has looked at memory performance for features when they belong to the same object (referred to as the “conjunction” condition by Xu, 2002a; see Figure 1A for an example), as compared to the exact same number of features when they belong to different objects (referred to as the disjunction condition by Xu, 2002a; see Figure 1B for an example). These studies have consistently found superior memory performance for conjunctions over disjunctions of features, a result that would not be predicted by completely independent feature stores. Arguably, the conjunction benefit is therefore providing the strongest evidence so far for the integration of features into object-based representations in VWM.

The conjunction versus disjunction comparison as a proxy for object-based representations is, however, not without problems. One potential confound is the fact

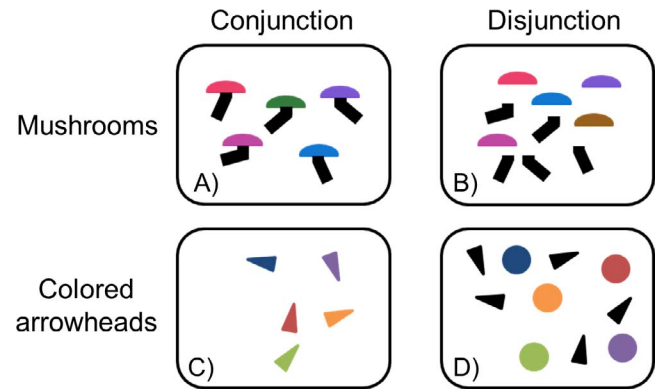


Figure 1. The stimuli used in the present experiments.

that separated features are spread across more locations than combined features. Of course, the spatial conglomeration of features is one of the characteristics of an object. Yet, the fact that separated features also occupy more locations is not trivial, especially when we take into account that locations are often used for binding, and subsequent retrieval of memories (as alluded to earlier in Dell’Acqua et al., 2010; Richardson & Spivey, 2000; Spivey & Geng, 2001; Theeuwes et al., 2011). Crucially, such binding of features to a location does not necessarily mean that the features themselves are also bound to each other into a single object. There may be separate feature stores, but within each store, the features are remembered in relation to a location. Compared to disjunction conditions, in conjunction conditions there are fewer associated locations to remember, and thus, the chances of overloading VWM is reduced, with higher performance as a consequence. That is, the conjunction benefit previously attributed to integrated object encoding may actually be a location-based benefit.

To test the hypothesis that any object-based benefit for conjunctions is a location-based benefit, Experiment 1 assessed memory performance for conjunctions and disjunctions where these were presented in either the standard spatial layout in which each was presented at its own location (and thus, the number of locations doubled from conjunction to disjunction conditions), or where conjunctions and disjunctions were all presented sequentially at the same location (and thus, location information did not differ across conjunction and disjunction conditions). The results show a clear conjunction benefit when location information is available, but no such benefit when location is non-informative. Experiment 2 replicated and extended this main finding by showing that the location-based benefits for conjunctions hold even when sequential presentations are used for all tasks, and by showing that these benefits occur only when location information is available at retrieval.

Experiment 1: Conjunction benefits disappear when location becomes irrelevant

To test the hypothesis that spatial location contributes to memory for feature conjunctions, Experiment 1 compared two different spatial layouts. In the *multiple-location* layout, all memoranda were presented simultaneously, each with its own location. The probe was also presented at one of these locations. In the *single-location* layout, all memoranda were presented sequentially at the same central location. The probe was then also presented at this central location. Thus, location provided a useful anchor for binding feature information only in the multiple-location layout. If the conjunction benefit is indeed location-based, then the prediction is that such benefits only occur in the multiple-location layout. To increase the generality of our findings, this was tested across two different stimulus types, both of which are illustrated in Figure 1. In Experiment 1A we used mushroom-like stimuli in which color and orientation were represented in different parts of the same object (Xu, 2002a). In Experiment 1B we used colored arrowhead stimuli in which color and orientation were contained in an object consisting of only one part (Fougnie et al., 2013).

Method

The research protocol reported for this study was approved by the Institutional Review Board of Center for Cognition and Brain Disorders at Hangzhou Normal University, and all participants gave written informed consent.

Participants

Participants in this and all subsequent experiments were recruited from the local community. They all reported normal color vision, and normal or corrected-to-normal visual acuity, and would gain monetary compensation (40 yuan/hour) for their participation. Eight adults (five women, three men; mean age: 21.4 years) took part in Experiment 1A and another group of eight adults (two women, six men; mean age: 24.9 years) took part in Experiment 1B.

Apparatus

Each experiment was conducted in a dimly lit laboratory. The stimuli were presented against a gray background (17.1 cd/m^2) on a 21-in. CRT monitor, at a viewing distance of 71 cm (maintained by using a

chinrest). Stimulus presentation and response registration were controlled by custom scripts written in Python.

Stimuli

Mushrooms and colored arrowheads were used as memory items in Experiments 1A and 1B, respectively. *Mushrooms*: In the conjunction condition, to-be-memorized items were five mushroom-like stimuli, with the cap subtended $1.5^\circ \times 0.5^\circ$ and the stem subtended $1^\circ \times 0.5^\circ$ (see Figure 1A). The cap colors were randomly selected from six near-equiluminant colors (range: $64.98\text{--}69.64 \text{ cd/m}^2$), evenly distributed along a circle in the CIE $L^*a^*b^*$ color space (centered at $L = 70$, $a = 5$, $b = 0$, with a radius of 60). The mushroom stems were black and were in one of seven orientations ($15^\circ\text{--}165^\circ$, in 25° steps). Mushroom caps and stems were detached in the disjunction condition, so the total number of feature values in the sample display was still 10 (see Figure 1B).

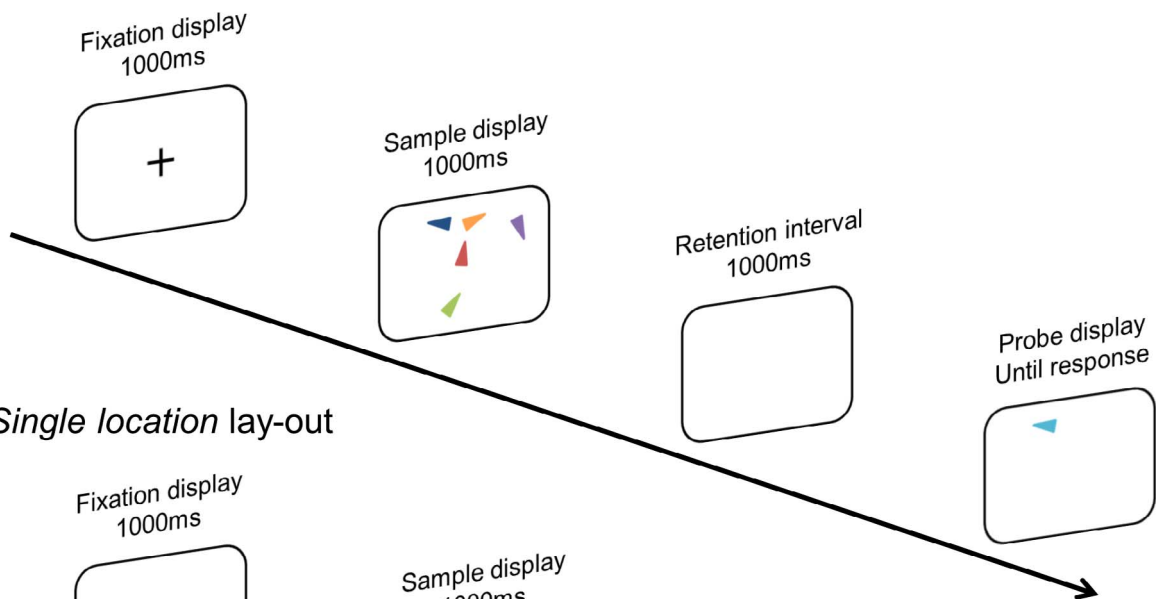
Colored arrowheads: In the conjunction condition, to-be-memorized items were five colored arrowheads, with sides measuring 1° , 1.92° , and 1.92° (see Figure 1C). Each arrowhead had a randomly chosen orientation ($10^\circ\text{--}325^\circ$, in 45° steps) and a randomly selected color (without replacement) from the same set of colors used for mushrooms. In the disjunction condition, half of the to-be-memorized items were filled color disks with a radius of 1° , and the other half were black arrowheads (see Figure 1D). The color of the disks and the orientation of arrowheads were randomly chosen from the same set of colors and orientations as in the conjunction condition.

Design

Both the multiple-location and single-location layouts were tested in Experiments 1A and 1B. Each had a conjunction condition and a disjunction condition. In the conjunction condition, to-be-memorized items were defined by both color and orientation, whereas in the disjunction condition to-be-memorized items were defined by either color or orientation. The total number of feature values was the same across these two conditions. If objects do benefit the memory of features, memory performance should be higher for the conjunction condition. If not, then memory performance should be the same for conjunction and disjunction conditions.

The present experiments adopted a 2 (spatial layout: multiple locations vs. single location) $\times 2$ (condition: conjunction vs. disjunction) within-subject design. All experimental cells were tested with a block of 160 trials and their sequence was counterbalanced across participants.

A) Multiple location lay-out



B) Single location lay-out

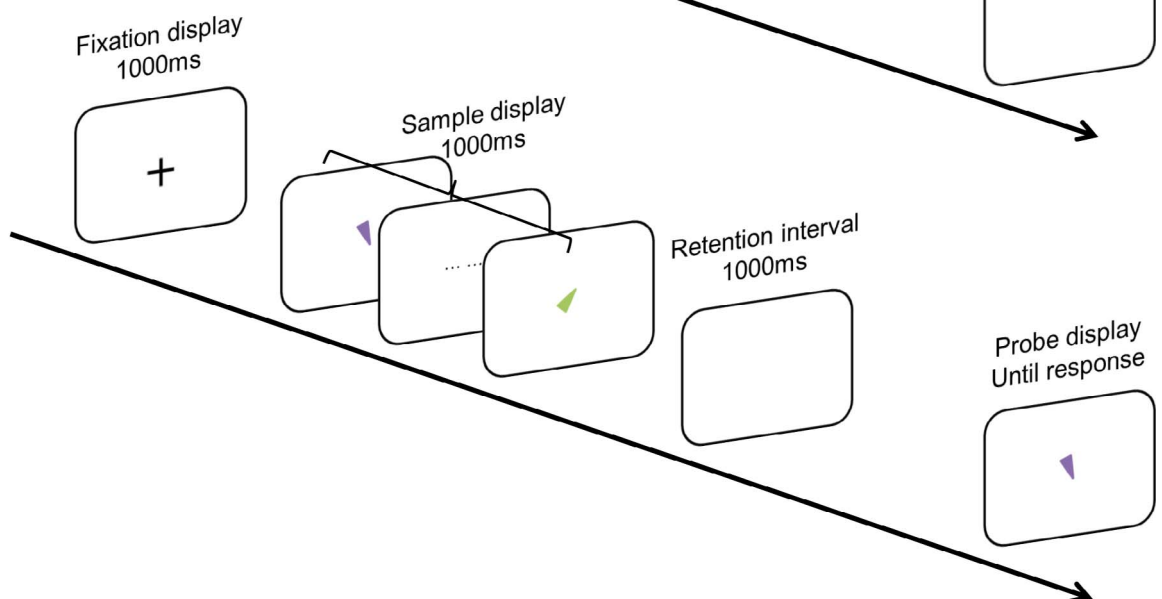


Figure 2. The procedures of the multiple-location layout (A) and the single-location layout (B). The total duration of the sample display was 1000 ms in both tasks.

Procedure

The sequence of events of a single trial in the multiple-location and the single-location layouts are illustrated in Figure 2A and B, respectively. Each trial began with the presentation of a fixation cross for 1000 ms. The sample display was then presented for 1000 ms, followed by a retention interval of 1000 ms and a probe display. After an intertrial interval (ITI) of 500 ms, the next trial started. Both layouts imposed no time pressure.

In the multiple-location layout, to-be-memorized items were presented on the sample display simultaneously for 1000 ms, with their locations randomly selected from an invisible 4×4 grids that measured $12^\circ \times 12^\circ$. To prevent adaptation, the stimuli were not

always presented at the center of the grids, but were randomly jittered by 0.4° in both horizontal and vertical directions on each trial. Only one item (probe) was presented in the probe display and participants were asked to indicate if it was the same as the item presented at the same location in the sample display, by pressing the “z” (same) or “/” (different) key on a standard QWERTY keyboard.

In the single-location layout, to-be-memorized items were presented sequentially at the center of the display. The total duration of the sample display was still 1000 ms. To equate the length of the sequences, each item was presented twice as long in the conjunction condition (200 ms) as in the disjunction condition (100 ms). If anything, this manipulation should contribute further to a conjunction benefit. Unlike the multiple-

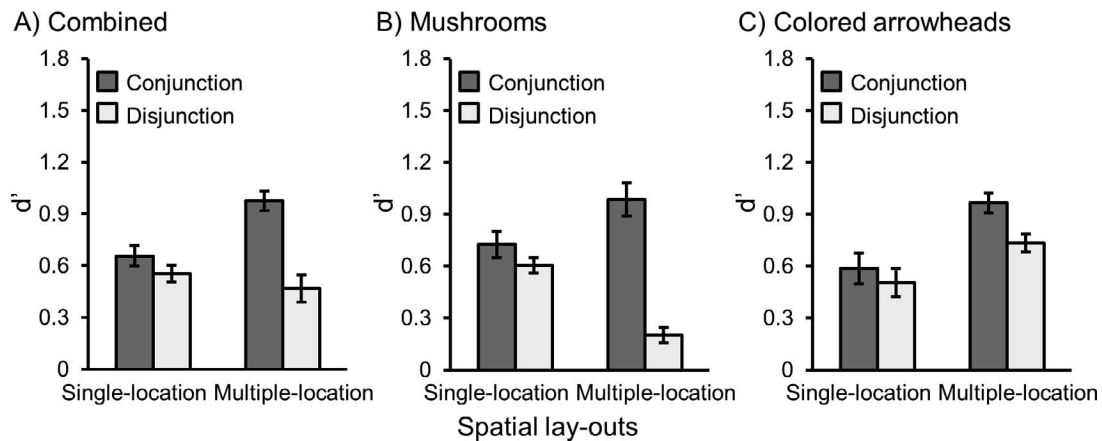


Figure 3. Mean memory performance (d') for the mushroom and colored arrowhead data combined (A), the mushroom data separately (B), and the colored arrowhead data separately (C) in Experiment 1. Error bars denote ± 1 SEM.

location layout, the probe was presented at the center of the display and participants indicated whether it had been presented in the sample display, by pressing the “z” (yes) or “/” (no) key.

The probe was presented as a conjunction in the conjunction condition, and as a disjunction in the disjunction condition. In both layouts, on 50% of the trials (change trials), the probe randomly assumed either a new color or a new orientation.

Analysis

The main dependent measure was change detection sensitivity, as computed through d' , expressed as $d' = z(H) - z(F)$, where H is the hit rate (the proportion of trials in which participants reported a change where indeed a change had occurred) and F is the false alarm rate (the proportion of trials in which participants reported a change where no change had happened). We note that the pattern of results also held when percentage correct was analyzed.

Results

Figure 3 shows the data of the mushrooms (Experiment 1A), colored arrowheads (Experiment 1B), as well as the combined results. Participants' change detection sensitivity (d') was entered in a repeated measures ANOVA, with variables Spatial Layout (multiple-location vs. single-location) and Condition (conjunction vs. disjunction) as within-subject factors, and Experiment (1A vs. 1B) as a between-subjects factor. A significant main effect was observed for condition, $F(1, 14) = 67.9$, $p < 0.001$, partial $\eta^2 = 0.83$, while there was a trend towards an effect of spatial layout, $F(1, 14) = 3.73$, $p = 0.074$, partial $\eta^2 = 0.21$. Here

sensitivity was higher in the conjunction condition and multiple-location layout.

Importantly, the two-way interaction between Spatial Layout and Condition was statistically reliable, $F(1, 14) = 22.6$, $p < 0.001$, partial $\eta^2 = 0.62$. Planned follow-up comparisons revealed that the d' was higher for conjunctions than for disjunctions in the multiple-location layout, $F(1, 14) = 125.41$, $p < 0.001$, partial $\eta^2 = 0.9$, but not in the single-location layout, $F(1, 14) = 2.43$, $p = 0.142$, partial $\eta^2 = 0.15$. These comparisons showed the same pattern of results when the experiments were analyzed separately. For mushrooms (Experiment 1A), d' was higher for conjunctions than for disjunctions in the multiple-location layout, $t(7) = 5.23$, $p = 0.001$, but not in the single-location layout, $t(7) = 0.72$, $p = 0.496$ (see Figure 3B). For colored arrowheads (Experiment 1B), d' was also higher for conjunctions than for disjunctions in the multiple-location layout, $t(7) = 9.91$, $p < 0.001$, but not in the single-location layout, $t(7) = 1.97$, $p = 0.09$ (see Figure 3C). That said, as can be seen from Figure 3B and C, the pattern of results was overall stronger for the mushrooms than for the arrowheads, especially in the multiple-location layout, which resulted in condition by experiment, spatial layout by experiment, and condition by spatial layout by experiment interactions, all $F_s > 9.17$, all $p_s < 0.009$.

Discussion

In the multiple-location layout, memory performance (d') was higher for conjunctions than that for separate features. This replicates the conjunction benefit reported in previous studies (Fougnie et al., 2013; Olson & Jiang, 2002; Xu, 2002a, 2002b). However, when the to-be-memorized items were all

presented at the same single location, and thus location was noninformative, memory performance was equivalent across the conjunction and disjunction conditions. These results suggest that what has previously been interpreted as an object-based benefit in VWM may actually be a location-based benefit for feature conglomerates relative to individual features presented at separate locations.

One might object that the multiple-location and single-location layouts differed in more ways than the spatial layout of the items. In the single-location layout the items were presented sequentially, which may have led to different encoding and retrieval strategies. One specific alternative explanation is that exactly because all conjunctions were presented at the same location in the single-location layout, observers had trouble encoding or maintaining the correct feature combinations in an integrated object representation, or such representations might be more easily overwritten by the next item. The fact that all features came from the same source (whether belonging to the same or to a different object), may have led to interference and misbinding within VWM. A further contributing factor here might be that on average conjunctions are more similar to each other (i.e., more likely to share at least one feature), and that this may have led to misbinding especially in the sequential condition. Finally, the sequential presentation in the single-location layout went with shorter exposure durations for each item, and it could be that the conjunction-based benefit disappeared because of this. Experiment 2 was designed to remedy this by comparing conditions in which all the items were presented sequentially.

Experiment 2: Location-based benefits for sequential presentations

In the newly added conditions of Experiment 2, all items were presented sequentially. Moreover, regardless whether features were presented in conjunctions or disjunctions, all items were given their own location. Importantly, the only thing we varied between conditions was the location of the probe item. In the *informative-location* layout, the probe was at the same location as the memorized item it was probing. In the *noninformative-location* layout, the probe was always presented at the center, a location never occupied by any memorized item. Thus, up to the probe phase all conditions were the same in terms of spatial information. The only difference was whether this location information was useful or not at probing. If observers store conjunctions as integrated object representations,

then a benefit should emerge for the conjunction condition relative to the disjunction condition regardless of the probe location. The location-based account, however, predicts something different: If spatial location aids in retrieving stored feature information—as has been suggested by many previous findings (Dell’Acqua et al., 2010; Richardson & Spivey, 2000; Spivey & Geng, 2001; Theeuwes et al., 2011)—then we should observe a benefit for conjunctions only in the condition where location is informative at probing. Furthermore, if the results of Experiment 1 were due to any confound derived from an unfair comparison between the multiple-location and single-location layouts, then we should observe no location-based benefits here, whether location was useful at probing or not. As in Experiment 1, we tested these hypotheses for two sets of stimuli, mushrooms (Experiment 2A) and arrowheads (Experiment 2B). Furthermore, Experiment 2 also included the exact same layouts and conditions as Experiment 1, to check if we could replicate our original results.

Method

Participants

Eight adults (five women, three men; mean age: 19.3 years) took part in Experiment 2A and another group of eight adults (seven women, one man; mean age: 19.9 years) took part in Experiment 2B.

Apparatus and stimuli

The apparatus and stimuli were the same as Experiment 1.

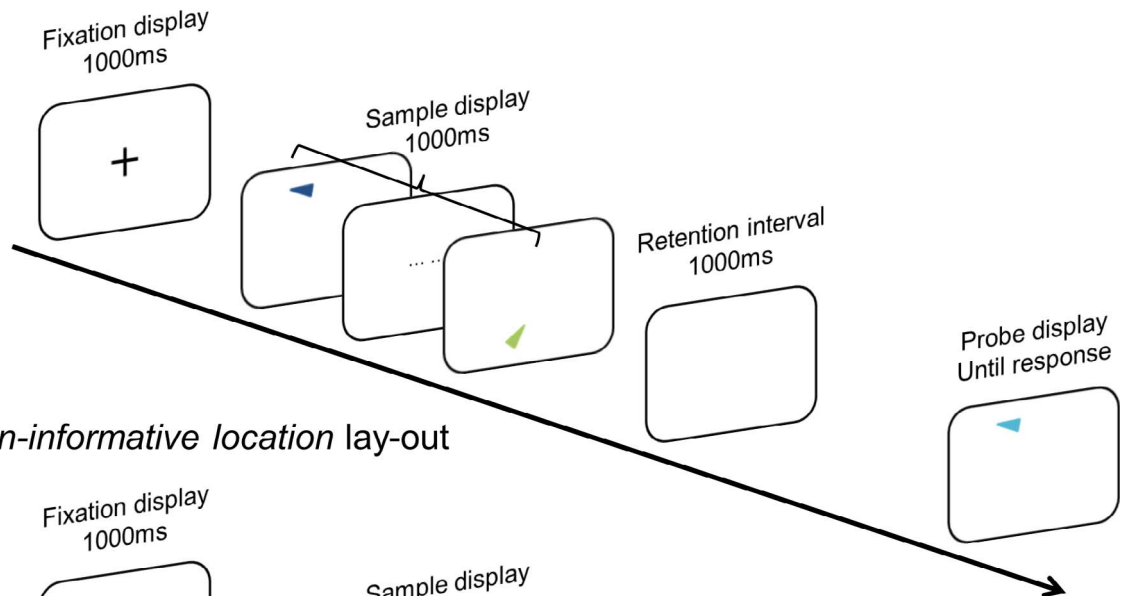
Design

All spatial layouts and conditions of Experiment 1 were replicated. Together with the newly added spatial layouts, each experiment tested a total of four spatial layouts: multiple-location, single-location, informative-location, and noninformative-location. Each layout had the conjunction and disjunction conditions in which each condition was tested with a block of 160 trials. The layouts and conditions were counterbalanced across participants. Mushrooms were used in Experiment 2A, and colored arrowheads were used in Experiment 2B.

Procedure

The procedures of the multiple-location and single-location layouts were the same as those in Experiment 1. For the newly added informative-location and noninformative-location layouts (see Figure 4, for an illustration), the to-be-memorized items were presented

A) Informative location lay-out



B) Non-informative location lay-out

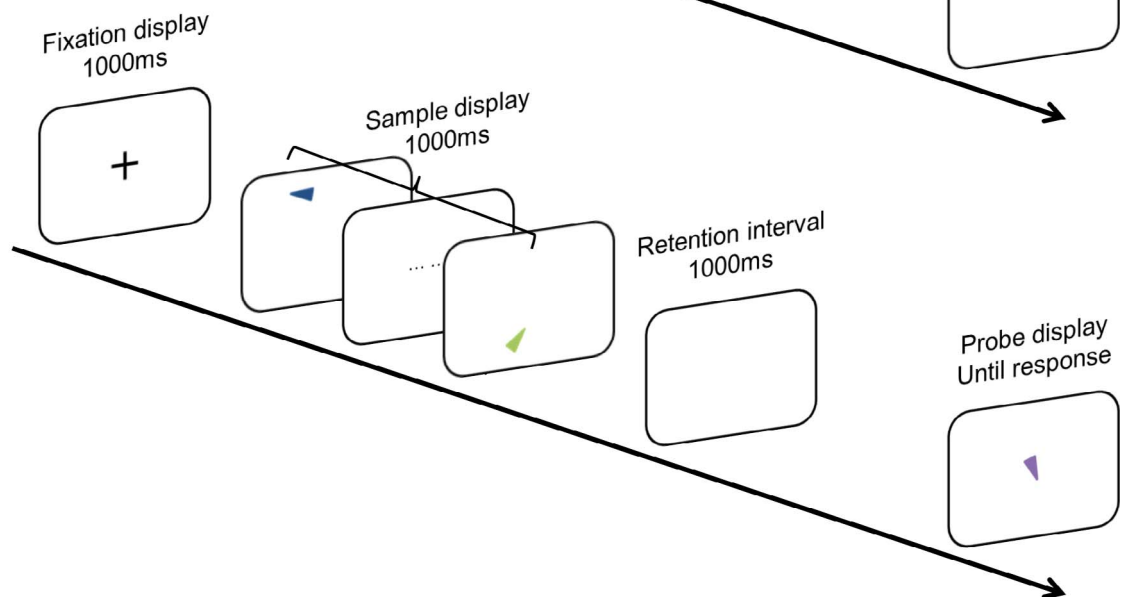


Figure 4. The procedures of the informative-location layout and the noninformative-location layout. Stimuli were presented in sequential in both tasks and, as in Experiment 1, the total duration of the sample display was 1000 ms.

sequentially for a total duration of 1000 ms, and each item was presented for 200 ms and 100 ms for the conjunction and disjunction conditions, respectively. In the informative-location layout, one probe was presented at the same location as the memorized item it was probing. Participants indicated if the probe was the same as this memorized item it was probing, by pressing the “z” (same) or “/” (different) key. In the noninformative-location layout, however, the probe was always presented at the center of the display, rendering the location of the to-be-memorized items irrelevant. Participants indicated if the probe had been presented, by pressing the “z” (yes) or “/” (no) key. On change trials, either the color or the orientation would be changed into a value that was not present in the display.

Results

The multiple-location and single-location layouts replicated the findings of Experiment 1. The results of these conditions are summarized in the Appendix. Here we focus on the results of the two newly added sequential presentation conditions (informative-location and noninformative-location).

Figure 5 shows the data of the mushrooms (Experiment 2A), colored arrowheads (Experiment 2B), as well as the combined results. As in Experiment 1, d' was entered in a repeated measures ANOVA, with variables Spatial Layout (informative location vs. noninformative location) and Condition (conjunction vs. disjunction) as within-subject factors, and Experiment (2A vs. 2B) as a between-subjects factor. A

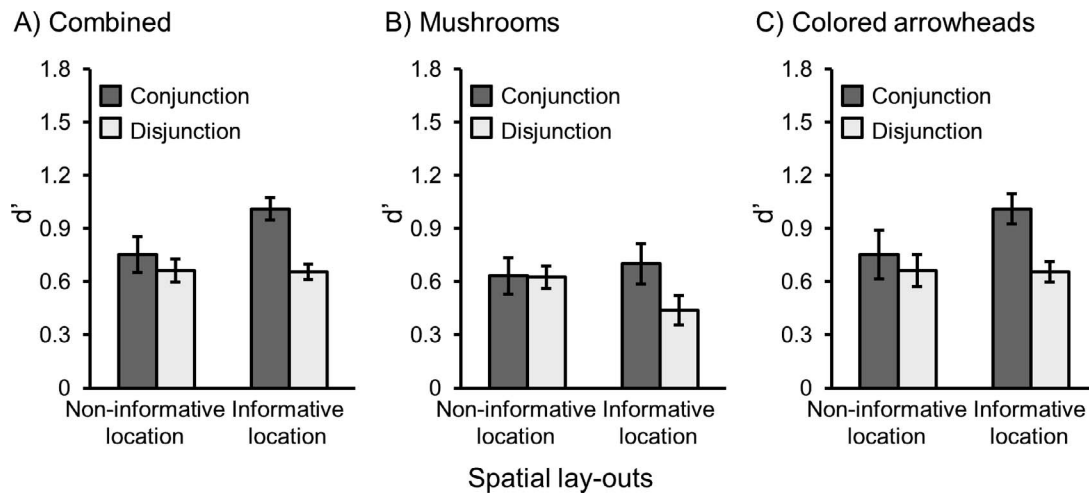


Figure 5. Mean memory performance (d') for the mushroom and the colored arrowhead data combined (A), the mushroom data separately (B), and the colored arrowhead data separately (C) in Experiment 2 were showed separately. Error bars denote ± 1 SEM.

significant main effect was observed for condition, $F(1, 14) = 16.96$, $p = 0.001$, partial $\eta^2 = 0.55$, with a higher d' observed in the conjunction condition. No interactions involving experiment were observed, all F s < 1.45 , all p s > 0.25 . Importantly, two-way interaction between Spatial Layout and Condition was very reliable, $F(1, 14) = 8.89$, $p = 0.01$, partial $\eta^2 = 0.39$. Planned follow-up comparisons revealed that the d' was higher for the conjunction condition relative to the disjunction condition in the informative-location layout, $F(1, 14) = 31.2$, $p < 0.001$, partial $\eta^2 = 0.69$, but not in the noninformative-location layout, $F(1, 14) = 0.53$, $p = 0.477$, partial $\eta^2 = 0.04$. These comparisons showed the same pattern of results when the experiments were analyzed separately. For mushrooms (Experiment 2A), d' was reliably higher for the conjunction condition relative to the disjunction condition in the informative-location layout, $t(7) = 3.26$, $p = 0.014$, but not so in the noninformative-location layout, $t(7) = 0.09$, $p = 0.93$ (see Figure 5B). For colored arrowheads (Experiment 2B), d' was higher for the conjunction condition relative to the disjunction condition in the informative-location layout, $t(7) = 4.68$, $p = 0.002$, but not in the noninformative-location layout, $t(7) = 0.86$, $p = 0.419$ (see Figure 5C).

Discussion

Experiment 2 replicated the main findings of Experiment 1: If location information is available at probing, a memory benefit emerges for conjunctions over disjunctions of features. If no such location information is available, performance for conjunctions drops down to the level of disjunctions. Importantly, this pattern emerges regardless of whether items are

presented simultaneously or sequentially. Moreover, Experiment 2 shows that only when the probe contains useful spatial information (i.e., it matches the location of the memory item) does a conjunction benefit occur.

General discussion

The present experiments successfully replicate earlier studies showing that memory performance is better for conjunctions of features than for the same number of features presented separately (Fougnie et al., 2013; Olson & Jiang, 2002; Xu, 2002a, 2002b, 2006). It is important to note, however, that our results also suggest that this conjunction benefit should not be taken as evidence that conjunctions are stored as integrated objects and are thus stored more efficiently than loose features (Xu, 2002a, 2002b). Instead, the conjunction benefit appears to stem from the fact that for conjunctions, the features are bound to fewer locations than for disjunctions. The evidence for this conclusion comes from Experiment 1, which showed that the conjunction benefit disappeared when all stimuli were presented sequentially at the same location (and thus, location becomes uninformative). Experiment 2 showed that this was not due to the sequential presentation of stimuli per se, since the conjunction benefit returned when location information was added to sequential presentations. All these effects were replicated for both multipart objects (mushrooms) and single-part objects (arrowheads). Taken together, these observations demonstrate that conjunction benefits per se do not provide evidence for object-based benefits. Rather, they appear to reflect location-based benefits.

This conclusion is further supported by the finding that conjunction-based benefits only occurred when location information was available at retrieval, as Experiment 2 demonstrated. Spatial separation during encoding and maintenance did not result in any conjunction benefits, unless participants could make use of this information during the probe. This means that whatever representation was instantiated during encoding and maintenance, it did not in itself benefit from the fact that its features belonged to the same object. This is not what is expected if object-based representations are more efficient, or suffer less from interference, as such benefits should occur regardless of the location of the probe object, and should play out most during encoding and maintenance. Instead, the fact that conjunction benefits occurred only when the location information was useful at retrieval is consistent with earlier evidence that locations is used as a cue to access stored feature information (Dell'Acqua et al., 2010; Theeuwes et al., 2011).

Multiple-part objects and disjunctions

Location-based benefits may also explain the finding that objects consisting of two separate (i.e., nonintegrated) parts that share the same location are better remembered than the same parts at different locations (Fougnie, Asplund, & Marois, 2010; Xu, 2002b). An exception is a study by Lee and Chun (2001), which involved an experiment in which the features of conjunctions could either overlap in space or not. They found that sharing a location did not benefit memory performance, and concluded that VWM capacity is determined by the number of conjunctions, rather than the number of locations. However, as pointed out by Xu (2002b), the conjunctions with overlapping features as used by Lee and Chun (2001) were visually more complex than the conjunctions with nonoverlapping features; this may have masked any location benefit for VWM. By eliminating this potential confound, Xu (2002b) found that memory performance was better for overlapping features compared to when they occupied separate locations.

Interestingly, Xu (2002b) also found an additional benefit for objects consisting of fully integrated features over objects consisting of two separate parts. For example, memory performance was better for colored bars (orientation and color integrated), than for black bars plotted on colored disks (orientation and color as different parts). This result could be interpreted as an integrated object benefit after all. We cannot exclude this possibility, but one could argue that the spatial representation of features also differs when they are integrated into one part relative to when they are represented across two parts. Integrated objects truly

occupy a single location. Separate parts could be argued to occupy separate locations in either two-dimensional or (when overlapping) three-dimensional space. The idea would then be that the closer together the features are in space (whether or not they belong to the same object), the easier they are to retrieve at test. Direct evidence for this comes from Xu (2006). In experiment 1 of her study, she systematically varied the distance between the parts of two-part objects (i.e., lollipop-like combinations of a colored disk and an oriented stem) and found that memory performance deteriorated with increasing distance.

A role for object representations and feature binding

We cannot completely exclude the possibility that memory storage and retrieval here is mediated by object representations. One might argue that the features of a conjunction are stored as an object *through* their common location—that is, location acts as the common representation or pointer to which the separate features are then bound. The features are not integrated as such (i.e., they are not bound to each other), but connect to a common location representation. The observed conjunction benefits in the multiple-location and informative-location layouts then occur through location-mediated retrieval of the associated features. One could still interpret such a location-mediated feature binding as an object representation. Add to this the fact that the probe was different across the conjunction and disjunction conditions (i.e., a conjunction in the conjunction condition and a disjunction in the disjunction condition),² which might have interacted differentially with location information. Specifically, one might argue that feature binding was required in the conjunction condition, but not in the disjunction condition. If such feature binding requires location information, as per the above argument, then the conjunction condition may favor the use of location information more than the disjunction condition. However, we argue that even if such location-mediated feature binding mechanisms play a role, they still imply a fundamental role for location information in producing conjunction benefits.

A role for object-based representations

Our claim is that the conjunction benefit in VWM is at least partly due to common location coding. This does not mean that object-based representations play no role in VWM. Using a redundancy gain paradigm (Miller, 1982), previous work has revealed perceptual benefits stemming from coactivation of features that

belong to the same object (Feintuch & Cohen, 2002), resulting in faster response times (RTs) if an object contains multiple target features. Saiki (2016) examined if this also holds for RTs to the probe in a VWM task. In his task, two color-shape conjunctions were first presented and participants then reported whether a probe contained any of the features shown in the sample display. The results revealed faster responses to the probe when it shared all the features with a shown color–shape conjunction than when it shared only one. Importantly, this redundancy gain was observed regardless of whether the probe appeared at the location of the probed color-shape conjunction or not. Saiki (2016) concluded that “a shared location is necessary in the formation of bound representations but unnecessary in their maintenance” (p. 178), implying integrated object-based representations that are independent of location. Saiki’s findings can also be explained in terms of a retrieval-induced code conflict in episodic memory, in the condition in which only one feature is shared (Keizer et al., 2008; van Dam & Hommel, 2010). When some, but not all, features of an object are repeated, they may trigger the retrieval of all features associated with the stored memory trace, which then conflicts with the presented feature(s). This code conflict brings up a performance cost in terms of RTs, which does not depend on the location of the maintained object (Keizer et al., 2008). This too represents some form of integration, but it remains to be seen whether such slower episodic retrieval (as expressed in slight increases in RTs) also explains proper memory errors when a feature cannot be retrieved at all. In any case, evidence for integrated representations per se, including Saiki’s (2016) findings does not undermine the present conclusion that location information benefits the maintenance and retrieval of object features.

Integrated representations may also play a strong role in representing familiar, everyday objects. For understandable reasons, studies on VWM tend to use artificial stimuli with ad hoc combinations of features, like colored bars, arrowheads or combination of disks and line segments. These features are then used again and again in different combinations from trial to trial. It may well be that such ad hoc combinations induce separate rather than integrated storage of features, if only to prevent proactive interference from previous combinations. We believe that this is likely to be different for everyday objects, as these are more likely to be stored as part of integrated conceptual units in long-term memory. In fact, for such objects it may sometimes be difficult to access the separate features they consist of (e.g., Melcher, 2001; Rensink, 2000). Both working memory capacity and working memory processing times appear to differ for everyday objects compared to more abstract ad hoc feature combinations (e.g., Alvarez & Cavanagh, 2004;

Brady, Konkle, Oliva, & Alvarez, 2009; Chun & Potter, 1995; Luck & Vogel, 1997; Melcher, 2001, 2006; Perez, Vogel, Luck, & Kappenman, 2012; Potter, 1976; Vogel et al., 2001; Vogel, Woodman, & Luck, 2006; Zhang & Luck, 2008), and may thus differ also in terms of how features are represented. It would therefore be interesting to see if for everyday objects, an object-based benefit occurs over and above a location-based benefit.

To conclude, we argue that conjunction benefits in VWM may in fact reflect location-based benefits, and as such do not provide evidence for object-based representations in VWM. Together with the evidence that other classic findings for object-based benefits (Luck & Vogel, 1997) can be explained through independent feature stores (Fougnie & Alvarez, 2011; Wheeler & Treisman, 2002), this means that very little evidence for object-based benefits in VWM is left, at least for the abstract stimuli frequently used to test VWM capacity.

Keywords: visual working memory, feature, conjunction, object-based benefit, location-based benefit

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Footnotes

¹ Luck and Vogel (1997, experiment 5) tried to control for this by showing that memory performance was constrained only by the number of visual items, even when they were constructed with feature values from the same dimension (color). However, this result has not been replicated, as others have found consistent degradation in performance when object features were drawn from the same dimension (Delvenne & Bruyer, 2004; Olson & Jiang, 2002; Wheeler & Treisman, 2002; Xu, 2002a).

² We thank a reviewer for pointing out these issues. We chose this design following Xu (2002a, 2002b),

which we wanted replicate, as this formed the basis of our study. The crucial finding was that indeed, when location was useful, we indeed replicated Xu's (2002a, 2002b) conjunction benefit, but when location information was no longer relevant, this conjunction benefit disappeared.

References

- Alvarez, G. A., & Cavanagh, P. (2004). The capacity of visual short-term memory is set both by visual information load and by number of objects. *Psychological Science, 15*, 106–111.
- Awh, E., Barton, B., & Vogel, E. K. (2007). Visual working memory represents a fixed number of items regardless of complexity. *Psychological Science, 18*, 622–628, doi:10.1111/j.1467-9280.2007.01949.x.
- Baddeley, A. (1992). Working memory. *Science, 255*, 556–559, doi:10.1126/science.1736359.
- Baddeley, A. D., & Hitch, G. (1974). Working memory. *Psychology of Learning and Motivation, 8*, 47–89.
- Brady, T. F., Konkle, T., Oliva, A., & Alvarez, G. A. (2009). Detecting changes in real-world objects. *Communicative & Integrative Biology, 2*(1), 1–3.
- Chun, M. M., & Potter, M. C. (1995). A two-stage model for multiple target detection in rapid serial visual presentation. *Journal of Experimental Psychology: Human Perception and Performance, 21*, 109–127.
- Dell'Acqua, R., Sessa, P., Toffanin, P., Luria, R., & Jolicœur, P. (2010). Orienting attention to objects in visual short-term memory. *Neuropsychologia, 48*, 419–428, doi:10.1016/j.neuropsychologia.2009.09.033.
- Delvenne, J., & Bruyer, R. (2004). Does visual short-term memory store bound features? *Visual Cognition, 11*, 1–27, doi:10.1080/13506280344000167.
- Feintuch, U., & Cohen, A. (2002). Visual attention and coactivation of response decisions for features from different dimensions. *Psychological Science, 13*, 361–369, doi:10.1111/1467-9280.00465.
- 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):3, 1–12, doi:10.1167/11.12.3. [PubMed] [Article]
- Fougnie, D., Asplund, C. L., & Marois, R. (2010). What are the units of storage in visual working memory? *Journal of Vision, 10*(12):27, 1–11, doi:10.1167/10.12.27. [PubMed] [Article]
- Fougnie, D., Cormiea, S. M., & Alvarez, G. A. (2013). Object-based benefits without object-based representations. *Journal of Experimental Psychology: General, 142*, 621–626, doi:10.1037/a0030300.
- Fukuda, K., Vogel, E., Mayr, U., & Awh, E. (2010). Quantity, not quality: The relationship between fluid intelligence and working memory capacity. *Psychonomic Bulletin & Review, 17*, 673–679.
- Keizer, A. W., Nieuwenhuis, S., Colzato, L. S., Teeuwisse, W., Rombouts, S. A., & Hommel, B. (2008). When moving faces activate the house area: An fMRI study of object-file retrieval. *Behavioral and Brain Functions, 4*, 50, doi:10.1186/1744-9081-4-50.
- Lee, D., & Chun, M. M. (2001). What are the units of visual short-term memory, objects or spatial locations? *Perception & Psychophysics, 63*, 253–257.
- Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature, 390*, 279–281, doi:10.1038/36846.
- Magnussen, S., Greenlee, M. W., & Thomas, J. P. (1996). Parallel processing in visual short-term memory. *Journal of Experimental Psychology: Human Perception and Performance, 22*, 202–212, doi:10.1037/0096-1523.22.1.202.
- Melcher, D. (2001). Persistence of visual memory for scenes. *Nature, 412*, 401–401, doi:10.1038/35086646.
- Melcher, D. (2006). Accumulation and persistence of memory for natural scenes. *Journal of Vision, 6*(1): 2, 8–17, doi:10.1167/6.1.2. [PubMed] [Article]
- Miller, J. (1982). Divided attention: Evidence for coactivation with redundant signals. *Cognitive Psychology, 14*, 247–279, doi:10.1016/0010-0285(82)90010-X.
- Olson, I. R., & Jiang, Y. (2002). Is visual short-term memory object based? Rejection of the “strong-object” hypothesis. *Perception & Psychophysics, 64*, 1055–1067.
- Perez, V. B., Vogel, E. K., Luck, S. J., & Kappenman, E. S. (2012). What ERPs can tell us about working memory. In E. S. Kappenman & S. J. Luck (Eds.), *The Oxford handbook of event-related potential components* (pp. 361–372), Oxford, UK: Oxford University Press.
- Phillips, W. A. (1974). On the distinction between sensory storage and short-term visual memory. *Perception & Psychophysics, 16*, 283–290.
- Potter, M. C. (1976). Short-term conceptual memory for pictures. *Journal of Experimental Psychology:*

- Human Learning and Memory*, 2, 509–522, doi:10.1037/0278-7393.2.5.509.
- Prinzmetal, W., Amiri, H., Allen, K., & Edwards, T. (1998). Phenomenology of attention: I. Color, location, orientation, and spatial frequency. *Journal of Experimental Psychology: Human Perception and Performance*, 24, 261–282.
- Rensink, R. A. (2000). The dynamic representation of scenes. *Visual Cognition*, 7(1–3), 17–42.
- Richardson, D. C., & Spivey, M. J. (2000). Representation, space and Hollywood Squares: Looking at things that aren't there anymore. *Cognition*, 76, 269–295, doi:10.1016/S0010-0277(00)00084-6.
- Saiki, J. (2016). Location-unbound color–shape binding representations in visual working memory. *Psychological Science*, 27, 178–190, <http://ps.sagepub.com/content/27/2/178.full>.
- Spivey, M. J., & Geng, J. J. (2001). Oculomotor mechanisms activated by imagery and memory: Eye movements to absent objects. *Psychological Research*, 65, 235–241.
- Theeuwes, J., Kramer, A. F., & Irwin, D. E. (2011). Attention on our mind: The role of spatial attention in visual working memory. *Acta Psychologica*, 137, 248–251, doi:10.1016/j.actpsy.2010.06.011.
- van Dam, W. O., & Hommel, B. (2010). How object-specific are object files? Evidence for integration by location. *Journal of Experimental Psychology: Human Perception and Performance*, 36, 1184–1192, doi:10.1037/a0019955.
- 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, 92–114, doi:10.1037/0096-1523.27.1.92.
- Vogel, E. K., Woodman, G. F., & Luck, S. J. (2006). The time course of consolidation in visual working memory. *Journal of Experimental Psychology: Human Perception and Performance*, 32, 1436–1451, doi:10.1037/0096-1523.32.6.1436.
- Wang, B., Cao, X., Theeuwes, J., Olivers, C. N., & Wang, Z. (2016). Separate capacities for storing different features in visual working memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, in press.
- Wang, B., & Wang, Z. (2014). Feature as the basic storage unit of visual working memory [Abstract]. *Journal of Vision*, 14(10), 38, doi:10.1167/14.10.38. [Abstract]
- Wheeler, M. E., & Treisman, A. M. (2002). Binding in short-term visual memory. *Journal of Experimental Psychology: General*, 131, 48–64, doi:10.1037//0096-3445.131.1.48.
- Xu, Y. (2002a). Limitations of object-based feature encoding in visual short-term memory. *Journal of Experimental Psychology: Human Perception and Performance*, 28, 458–468.
- Xu, Y. (2002b). Encoding color and shape from different parts of an object in visual short-term memory. *Perception & Psychophysics*, 64, 1260–1280, doi:10.3758/BF03194770.
- Xu, Y. (2006). Understanding the object benefit in visual short-term memory: The roles of feature proximity and connectedness. *Perception & Psychophysics*, 68, 815–828, doi:10.3758/BF03193704.
- Zhang, W., & Luck, S. J. (2008). Discrete fixed-resolution representations in visual working memory. *Nature*, 453, 233–235, doi:10.1038/nature06860.

Appendix

Results of the multiple-location and single-location layouts tested in Experiment 2

Figure A1 shows the data of the mushrooms (Experiment 2A), colored arrowheads (Experiment 2B), as well as the combined results. Participants' change detection sensitivity (d') was entered in a repeated-measures ANOVA, with variables Spatial Layout (multiple locations vs. single location) and Condition (conjunction vs. disjunction) as within-subject factors, and Experiment (2A vs. 2B) as a between-subjects factor. A significant main effect was observed for Spatial Layout, $F(1, 14) = 64.83$, $p < 0.001$, partial $\eta^2 = 0.82$, Condition, $F(1, 14) = 16.36$, $p = 0.001$, partial $\eta^2 = 0.54$, and Experiment, $F(1, 14) = 11.34$, $p = 0.005$, partial $\eta^2 = 0.45$. Sensitivity was higher in the conjunction condition and multiple-location layout, and mushrooms led to overall worse performance compared to colored arrowheads. No interactions involving Experiment were observed, all F s < 1.06 , all p s > 0.32 .

Importantly, the two-way interaction between Spatial Layout and Condition was again reliable, $F(1, 14) = 9.02$, $p = 0.009$, partial $\eta^2 = 0.39$. Planned follow-up comparisons revealed that the d' was higher for the conjunction condition relative to the disjunction condition in the multiple-location layout, $F(1, 14) = 18.29$, $p = 0.001$, partial $\eta^2 = 0.57$, but not in the single-location layout, $F(1, 14) = 1.91$, $p = 0.189$, partial $\eta^2 = 0.12$. As in Experiment 1, these comparisons showed the same pattern of results when the experiments were

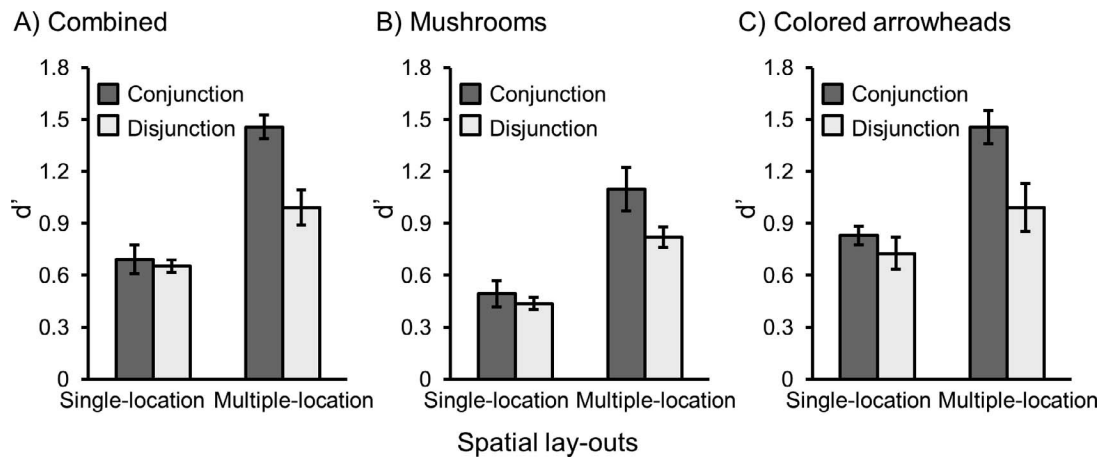


Figure A1. Mean memory performance (d') for the mushroom and colored arrowhead data combined (A), the mushroom data separately (B), and the colored arrowhead data separately (C) in Experiment 2 were shown separately. Error bars denote ± 1 SEM.

analyzed separately. For mushrooms (Experiment 2A), d' was reliably higher for the conjunction condition relative to the disjunction condition in the multiple-location layout, $t(7) = 3.54$, $p = 0.01$, but not so in the single-location layout, $t(7) = 0.81$, $p = 0.446$. For

colored arrowheads (Experiment 2B), d' was higher for the conjunction condition relative to the disjunction condition in the multiple-location layout, $t(7) = 3.0$, $p = 0.02$, but not in the single-location layout, $t(7) = 1.12$, $p = 0.299$.