What are the units of storage in visual working memory?

Daryl Fougnie Department of Psychology, Vanderbilt University, Nashville, TN, USA

Christopher L. Asplund Neuroscience Graduate Program, Vanderbilt Brain Institute, Nashville, TN, USA

René Marois Department of Psychology, Vanderbilt Brain Institute, Nashville, TN, USA

An influential theory suggests that integrated objects, rather than individual features, are the fundamental units that limit our capacity to temporarily store visual information (S. J. Luck & E. K. Vogel, 1997). Using a paradigm that independently estimates the number and precision of items stored in working memory (W. Zhang & S. J. Luck, 2008), here we show that the storage of features is not cost-free. The precision and number of objects held in working memory was estimated when observers had to remember either the color, the orientation, or both the color and orientation of simple objects. We found that while the quantity of stored objects was largely unaffected by increasing the number of features, the precision of these representations dramatically decreased. Moreover, this selective deterioration in object precision depended on the multiple features being contained within the same objects. Such fidelity costs were even observed with change detection paradigms when those paradigms placed demands on the precision of the stored visual representations. Taken together, these findings not only demonstrate that the maintenance of integrated features is costly; they also suggest that objects and features affect visual working memory capacity differently.

Keywords: memory, attention, visual cognition

Citation: 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, http://www.journalofvision.org/content/10/12/27, doi:10.1167/10.12.27.

Introduction

Objects, not features, are commonly viewed as the elementary building blocks of our visual representations, not only for perception (Blaser, Pylyshyn, & Holcombe, 2000; Duncan, 1984; Kahneman, Treisman, & Gibbs, 1992; Scholl, 2001) but for visual working memory (VWM) as well (Luck, 2008; Luck & Vogel, 1997; Rensink, 2002; Vogel, Woodman, & Luck, 2001). Experimental support for the view that VWM is object-based comes from change detection tasks in which participants memorize a sample display of objects in order to identify whether a subsequent probe object is the same as, or different from, one of the sample objects (Delvenne & Bruyer, 2004; Luck & Vogel, 1997; Olson & Jiang, 2002; Vogel et al., 2001; Wheeler & Treisman, 2002). Consider, for example, the change detection task shown in Figure 1A. On each trial of this task, three colored triangles are first briefly presented, followed by a blank retention interval, and then by a probe stimulus presented at the location of one of the three sample stimuli, with the observers instructed to remember the color, orientation, or both color and orientation of the sample stimuli in different blocks of trials. Performance on this type of task is the same regardless of whether participants have to maintain both color and orientation or either color or orientation alone (Delvenne & Bruyer, 2004; Luck & Vogel, 1997; Olson & Jiang, 2002; Vogel et al., 2001; Wheeler & Treisman, 2002). There are two specific circumstances under which costs for multi-feature objects have previously been found: when features form distinct object parts (Davis & Holmes, 2005; Delvenne & Bruyer, 2004, 2006; Xu, 2002; Xu & Chun, 2006) and when they come from the same feature dimension (e.g. multiple colors) (Delvenne & Bruyer, 2004; Olson & Jiang, 2002; Wheeler & Treisman, 2002). However, these findings have not dispelled the notion that objects are the sole units that constrain VWM capacity. Specifically, it has been suggested that complex, multi-part objects are stored in multiple object 'slots' (Luck, 2008; Vogel et al., 2001), and that costs for two features in the same dimension occur during perceptual processing rather than working memory storage (Luck, 2008). Moreover, studies that have added multiple distinct features to simple standard objects have replicated Luck and Vogel's (1997) initial finding (Delvenne & Bruyer, 2004; Olson & Jiang, 2002; Vogel et al., 2001; Wheeler & Treisman, 2002). Hence, the theory that VWM storage is constrained only by objects and not features continues to dominate the field (Huang, 2010; Kyllingsbaek & Bundesen, 2009; Raffone & Wolters, 2001; Wolters & Raffone, 2008), and has been recently reinforced (Zhang & Luck, 2008).

Although change detection studies indicate that the number of objects stored in VWM is independent of the

doi: 10.1167/10.12.27 Received April 27, 2010; published October 21, 2010 ISSN 1534-7362 © ARVO

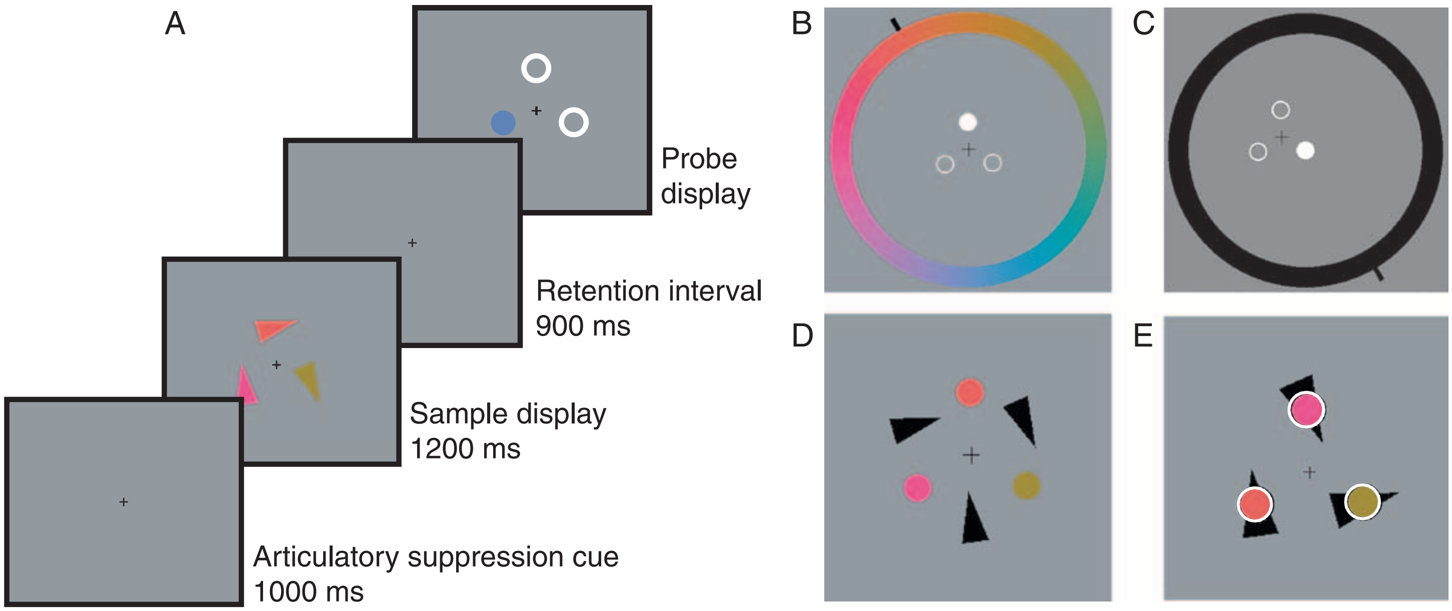

Figure 1. Experimental tasks. (A) Trial design for change detection experiments (Experiment 5). For feature report experiments (Experiments 1–4), the probe display was replaced with a feature response wheel for (B) color or (C) orientation. Note that the orientation wheel was presented around the probed location, and not fixation. (D–E) Example sample displays when the colors and orientations were in distinct objects in (D) separate locations or at the (E) same location.

number of distinct features they contain (Luck & Vogel, 1997), it is well established that VWM is not just limited by the number of object representations; there are also limits in the precision of these representations (Bays, Catalao, & Husain, 2009; Bays & Husain, 2008; Jiang, Shim, & Makovski, 2008; Magnussen & Greenlee, 1992, 1999; Wilken & Ma, 2004; Zhang & Luck, 2008). It is therefore conceivable that objects' featural complexity primarily affects the fidelity of object representations rather than the number of representations held in working memory. We tested this hypothesis in Experiment 1 using a recently developed mixture modeling method that provides independent measures of the quantity and resolution of VWM representations (Bays et al., 2009; Zhang & Luck, 2008, 2009).

Experiment 1

Methods

Participants

Fifteen young adults (6 males) participated for course credit or monetary reward. One participant's data were excluded from analysis because he/she showed a 100% guess rate for color probes in the conjunction condition.

Stimuli

The VWM sample consisted of three colored isosceles triangles presented in equally spaced positions along an imaginary ring 1.5° from fixation (Figure 1A). Each triangle had angles of 30°, 75°, and 75°, and sides subtending 0.6° × 1.4° × 1.4°. The orientation of the corner corresponding to the small angle was randomly determined for each triangle from one of 180 orientations (2°–360°, in 2° steps), with the restriction that no two triangles had orientation values within 30° to minimize the possibility that participants would encode two items as a single value. Each triangle was assigned to one of 180 equiluminant colors evenly distributed along a circle in the CIE L*a*b* color space (centered at $L = 54$, $a = 18$, $b = -8$, with a radius of 59), with any two triangles separated by at least 15 color steps.

Procedure

Depending on the block, participants were instructed to memorize the color, orientation, or both color and orientation of the triangles (conjunction blocks). During conjunction blocks, probe type was selected at random each trial. Each participant completed two color, two orientation, and four conjunction blocks of 76 trials per block. Instructions at the beginning of each block informed participants about the block type. Prior to the study, participants completed 12 practice trials of each condition.

A trial began with the presentation of a central cross that participants were instructed to fixate. Additionally, the central cross signaled participants to begin repeating the word '*the*' at a 3 Hz rate for the duration of the trial. This articulatory suppression was monitored remotely and required in all studies, and served to minimize verbal

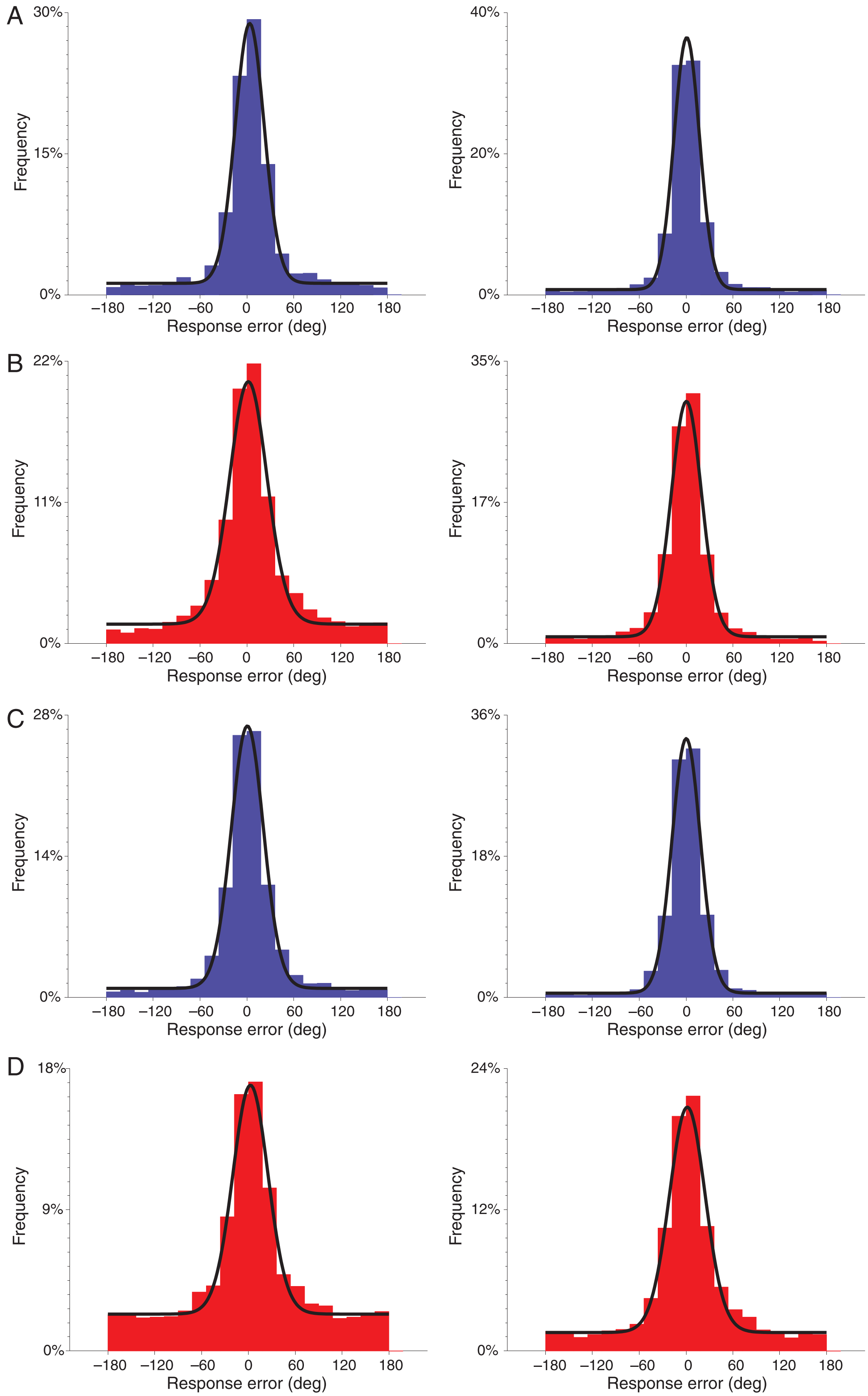

Figure 2. Histogram of all response errors (in degrees) for participants in (A–B) Experiment 1 and (C–D) Experiment 2 separated by condition: three (blue) or six (red) features and color (left) or orientation (right) probe. Note that the histogram has 20 equal bins, each 18° wide. The solid black line in each panel shows the best fitting mixture distribution for the data combined across participants. The continuous mixture distribution has been scaled to match the histogram's frequency values (*y*-axis).

	3 Features		6 Features	
	Color	Orientation	Color	Orientation
Experiment 1	18.79 (0.87)	16.83 (0.96)	25.28 (1.73)	19.73 (0.87)
Experiment 2	21.5 (1.14)	18.51 (0.91)	22.78 (1.81)	23.98 (1.44)
Experiment 3	20.04 (1.36)	16.53 (0.85)	25.06 (1.82)	16.59 (0.97)
Experiment 4	20.21 (0.94)	14.68 (0.63)	22.77 (0.93)	15.25 (0.63)

Table 1. The σ parameters of the mixture modeling analysis, before perceptual/response correction, for Experiments 1–4. Between-subject *SE* is shown in parentheses.

encoding and rehearsal of the visual stimuli. One second after the onset of fixation, the VWM sample appeared for 1200 ms. After a 900 ms retention interval, a solid white circle appeared at the location of the probed VWM stimulus (subtending 0.8° diameter), and hollow circles appeared at non-probed locations. A response wheel (subtending 0.7° wide, 6° radius) appeared around the probe display. For color probes the wheel was centered on fixation and consisted of 180 colored segments corresponding to the possible stimulus colors (Figure 1B). For orientation probes, a black wheel was centered on the probed item (Figure 1C). A black indicator line, with position determined by angular position of the cursor, appeared outside the color wheel to indicate the selected color or orientation. Participants selected one of 180 values by clicking the mouse when the indicator line matched the desired value. Responses were unspeeded. Feedback on response error (in degrees) was provided during the 1000 ms ITI. Mixture modeling analysis (Zhang & Luck, 2008) was conducted on the response error data (see Figure 2 for a histogram of response error data across all participants) in order to derive the guess rate and standard deviation of the error of non-guess responses for each experimental condition.

Mixture modeling analysis

A measure of response error for each participant and each experimental condition (single-feature color, single-feature orientation, dual-feature color, and dual-feature orientation) was calculated by subtracting the probed item's value (θ for color or orientation) from the response ($\hat{\theta}$). Note that response error was a mixture of two distributions, one corresponding to trials in which participants made a random guess and the other to trials in which participants made a non-guess response. Random guess responses came from a uniform distribution with a height parameter ($1 - P_m$). Target responses likely came from a von Mises (circular normal) distribution scaled by P_m with mean (μ) and standard deviation (σ) parameters (Zhang & Luck, 2008). To determine whether guessing rate or the precision of non-guesses changed across conditions, the response error distributions for each condition were fit using maximum likelihood estimation for the parameters P_m, σ, and μ in Equation 1. The probability in memory parameter (P_m) reflects the proportion of non-guesses and is thus the inverse of the height of the uniform distribution. The μ and σ parameters of the von Mises distribution detail the bias (either clockwise or counterclockwise on the response wheel) and precision of target responses, respectively. A higher σ for the von Mises distribution represents lower precision of stored representations. In all studies, we observed no significant biases, so these are not reported (Zhang & Luck, 2008).

$$(P_m)\phi_{\sigma,\mu}(\hat{\theta} - \theta) + (1 - P_m)/2\pi. \quad (1)$$

Importantly, each measured σ does not represent a pure measure of VWM imprecision: perceptual and/or response errors may also contribute. To specifically isolate the precision of VWM representations, we first estimated non-mnemonic contributions to σ from a perceptual task performed on a separate set of eleven participants. In this perceptual task, participants reported the color or orientation of a single colored triangle presented 3° to the bottom left of fixation (using the appropriate response wheel). Crucially, unlike the WM task, the colored triangle was presented throughout the duration of the feature report. Participants completed two color and two orientation response blocks of 76 trials in a random order. Predictably, mixture modeling on the resulting error distributions revealed that participants never guessed. More importantly, estimates of σ were significantly above zero: 10.91° for color responses and 7.42° for orientation responses. This demonstrates that the VWM task involves a surprisingly high amount of error not attributable to imprecision in memory. The σ of memory representations (σ) can be inferred by removing perceptual error (σ_{per}) from the observed σ (σ_{obs}) according to the following Equation 2:

$$\sigma = \sqrt{\sigma_{obs}^2 - \sigma_{per}^2}. \quad (2)$$

While corrected σ's are reported in all figures, a similar pattern of results was found for both corrected and non-corrected σ's. (See Table 1 for non-corrected σ's by condition.)

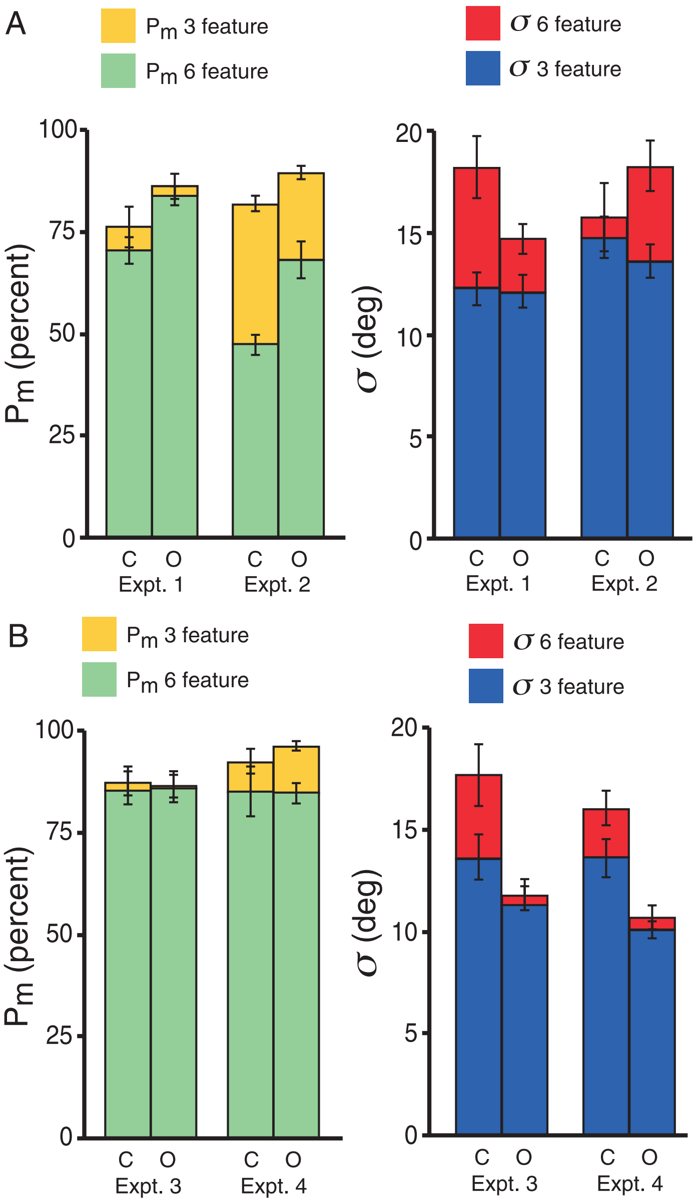

Figure 3. P_m (left) and σ (right) values for feature report experiments for both color (C) and orientation (O) probes. (A) Results for Experiments 1 and 2, in which the data was fit with a 3-parameter model (Zhang & Luck, 2008) with P_m, σ, and μ parameters (see Methods). (B) Results for Experiments 3 and 4, in which the data was fit with a 3-parameter model (Bays et al., 2009) with P_m, σ, and β parameters (see Methods). Yellow shows the cost in P_m (lower P_m) as the number of features increases from three to six. Red shows the cost in σ (increased σ) as the number of features increases from three to six. Error bars represent between-subject *SE*.

Results and discussion

The σ and P_m parameter values of the mixture modeling analysis are shown, by feature-load and feature-type, in Figure 3A. To determine how P_m and σ differed across experimental conditions we conducted a 2 (feature-load) × 2 (feature-type) ANOVA on each parameter. P_m did not significantly differ between three feature and six feature conditions, $F(1, 13) = 2.81$, $p > 0.1$. In contrast to the null for P_m, σ was increased for six features, $F(1, 13) = 36.37$, $p < 0.01$. The results also showed a main effect of feature-type such that P_m ($F(1, 13) = 20.94$, $p < 0.001$) was higher and σ ($F(1, 13) = 5.18$, $p = 0.04$) was lower for orientation than color probes (The feature-load × feature-type interaction was not significant for P_m, $F(1, 13) = 0.77$, $p = 0.4$, and was marginal for σ, $F(1, 13) = 3.63$, $p = 0.08$).

These parameter estimates were then combined across features and expressed on a common standardized scale to measure the percentage change in P_m and σ as feature load was increased. As shown in Figure 4A, the probability that an object was stored in VWM (P_m) was not affected by feature-load, $t(13) = 1.15$, $p = 0.27$. In contrast, the precision (σ) of the stored features decreased

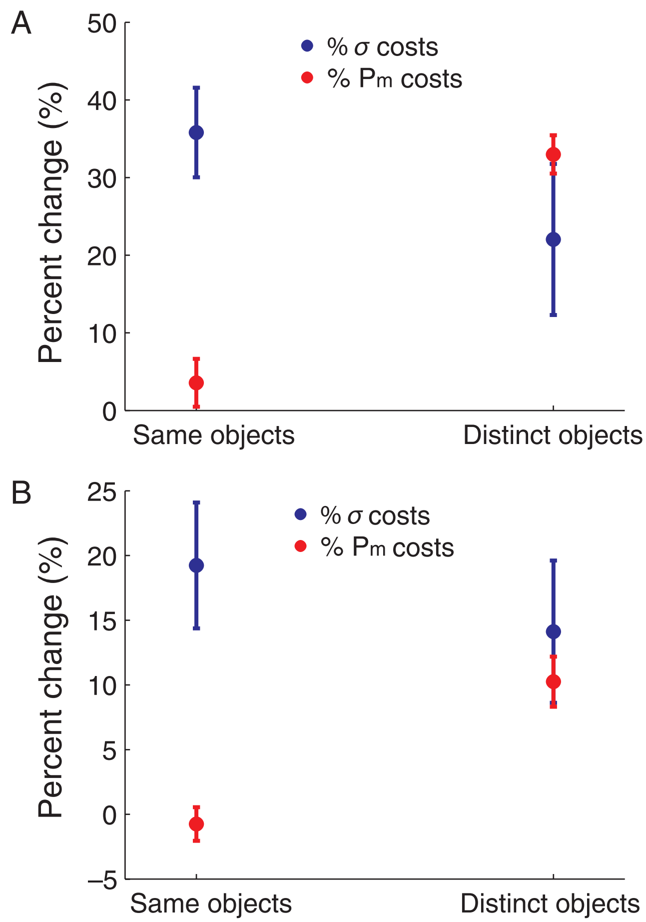

Figure 4. The percent costs in σ (blue) and P_m (red) for increased feature-load in feature report experiments. Feature-load was added either in the same (left) or distinct (right) objects. (A) Parameter estimates for Experiments 1 (left) and 2 (right) were derived using the standard mixture modeling method. (B) Parameter estimates for Experiments 3 (left) and 4 (right) were derived from the modified mixture modeling method that includes a non-target (β) response distribution. Error bars represent between-subject *SE*.

when the task required the maintenance of both color and orientation, $t(13) = 6.21$, $p < 0.001$. The markedly different effect of feature load on the probability that an object was stored in VWM, versus the precision at which it was stored, can be observed by comparing the P_m and σ costs (3.5% vs. 35.8%; $t(13) = 4.82$, $p < 0.001$). Thus, the results of Experiment 1 clearly indicate that increasing the feature load of VWM representations does not affect the likelihood that those representations are encoded (P_m), but does reduce their precision (σ).

Experiment 2

In Experiment 1, the distinct features were contained within the same objects. Does the selective cost in precision of VWM representations that feature load imposes depend on these features being added to the same objects? To test this possibility, orientation and color features were distributed across segregated objects in Experiment 2, such that doubling the number of features to be encoded also doubled the number of objects to be encoded.

Methods

Fifteen young adults (7 males) participated for course credit or monetary reward. The sample display was similar to Experiment 1 except that colors and orientations were presented as separate objects at distinct spatial locations (Figure 1D). Black isosceles triangles (0.9° × 0.9 × 0.3°) and colored circles (0.4° diameter) appeared in an interleaved fashion at six evenly spaced positions from fixation. Triangles appeared at positions corresponding to 60°, 180°, and 300°. Circles appeared at positions corresponding to 0°, 120°, and 240°. In all other respects, including data analysis, this study was the same as Experiment 1.

Results and discussion

P_m and σ values by feature-load and feature-type are shown in Figure 3A. P_m was significantly lower ($F(1, 14) = 212.36$, $p < 0.001$) and σ was significantly higher for six features ($F(1, 14) = 4.75$, $p < 0.05$). There was a main effect of feature-type for P_m, $F(1, 14) = 4.75$, $p < 0.05$, with better performance for orientation probes, but no main effect of feature-type on σ, $F(1, 14) = .47$, $p = 0.5$ (The feature-load × feature-type interaction was significant for P_m, $F(1, 14) = 6.13$, $p = 0.03$, but not σ, $F(1, 14) = 3.45$, $p = 0.09$).

These parameter estimates were then combined across features to measure the percentage change in P_m and σ as feature load was increased. This yielded both P_m (33.0%; $t(14) = -13.35$, $p < 0.001$) and σ costs (22%; $t(14) = 2.26$, $p = 0.04$; Figure 3A). Thus, unlike in Experiment 1, increasing the feature load across objects also increased P_m costs (see also Olson & Jiang, 2002; Xu, 2002). Indeed, the pattern of costs was different between Experiments 1 and 2 (interaction between Experiments and Parameters (P_m and σ) in a 2 × 2 ANOVA, $F(1, 27) = 11.38$, $p < 0.005$). We therefore conclude that the selective costs on the precision of VWM representations is dependent on features being added to the same objects, as distributing the features across objects also imposed costs on the number of objects encoded in VWM.

Experiments 3 and 4

It has recently been argued that the mixture modeling approach may overestimate costs in P_m because it assumes that all responses that don't originate from the target response distribution are the result of random guesses, ignoring the possibility that participants may report the value of a non-cued item (Bays et al., 2009). To determine whether this issue affects the pattern of costs obtained in Experiments 1 and 2, we replicated these two experiments in Experiments 3 and 4 using a modified mixture modeling analysis that included an additional parameter (β; corresponding to the percentage of trials in which participants report a non-cued item) to dissociate guess rate from misreports (Bays et al., 2009). These additional experiments were necessary because the non-random assignment of feature values in Experiments 1 and 2—no two stimuli could be within 30° of color or orientation space—prevented the use of this modified mixture modeling analysis. Moreover, to rule out the possibility that the P_m costs observed when features are spread across objects is due to an increase in the number of attended locations instead of in the number of objects, the orientation- and color-defined objects were spatially overlapped in Experiment 4 (Figure 1E) (Lee & Chun, 2001).

Methods

Experiment 3

Fifteen young adults (7 males) participated for course credit or monetary compensation. Stimulus presentation for Experiment 3 was the same as Experiment 1 except for the following change. In Experiments 1 and 2, the feature values for the stimuli were restricted such that no two objects had a value within 30° in the same feature. Because the β analysis requires that features be uncorrelated (Bays et al., 2009), in Experiment 3, the color and orientation values were assigned a random value independently for each object.

Experiment 4

Ten young adults (3 males) participated for course credit or monetary compensation. This experiment was identical to Experiment 3 except that colors and orientations of the sample display were presented as distinct but spatially overlapping objects (Figure 1E) by superimposing the colored circles on the black triangles (to increase object distinctiveness, a white outline was added to the circles).

Modified mixture modeling analysis

To examine the contribution of non-target responses, we adopted a modified mixture modeling analysis that includes an additional parameter (β) corresponding to the probability that participants reported the identity of a non-probed item (Equation 3). Specifically, the error distributions obtained from the VWM responses were fit as a mixture of three distributions: 1) a 'target-response' distribution that was a von Mises distribution with mean at 0 and a standard deviation of σ, 2) a 'mis-report' distribution that was an average of n − 1 von Mises distributions (where n = set size) with means at each non-target value and the same standard deviation as the 'target-response' distribution), and 3) a 'random guess' distribution that was a uniform distribution with height $(1 - P_m)$. This analysis could not be applied to Experiments 1 and 2 since it requires the feature values of stimuli to be assigned independently of one another.

$$(P_m - \beta)\phi_{\sigma,0}(\hat{\theta} - \theta) + (1 - P_m)/2\pi + \beta * \frac{1}{n-1}\sum_{i=1}^{n-1}\phi_{\sigma,0}(\hat{\theta} - \theta_i). \tag{3}$$

Results and discussion

P_m and σ values by feature-load and feature-type, for each experiment, are shown in Figure 3B, while the percent changes in P_m and σ as feature load was increased are shown in Figure 4B. β values are presented in the text below.

Experiment 3

The β values were 7.5%, 2.9%, 20.6%, and 8.2% for 3-feature color, 3-feature orientation 6-feature color, and 6-feature orientation conditions, respectively. β was significantly higher in six than three feature conditions ($F(1, 9) = 18.42$, $p < 0.005$), and higher for color than orientation probes ($F(1, 9) = 6.97$, $p < 0.05$). These results indicate that responses to non-cued items do affect feature-report responses, and that such responses occur more frequently with increased feature load.

Importantly, excluding responses to non-cued items from P_m estimation (by the inclusion of the β parameter to the mixture modeling analysis) did not eliminate the selective costs in precision with increased feature load. P_m still did not significantly differ between three feature and six feature conditions, $F(1, 9) = 0.15$, $p = 0.71$. In contrast, σ was significantly higher for six features, $F(1, 9) = 20.18$, $p < 0.005$. Correspondingly, measures of the percentage change in P_m and σ costs as feature-load increased (averaged across features) revealed costs in σ (19.3%, $t(9) = 3.6$, $p < 0.005$), but not in P_m (0%, $t(9) = -0.58$, $p = 0.58$).

Experiment 4

The β values were 4.5%, 2.8%, 10.3%, and 6.8% for 3-feature color, 3-feature orientation, 6-feature color, and 6-feature orientation conditions, respectively. β was higher in six than three feature conditions ($F(1, 9) = 5.64$, $p < 0.05$), but it was not different for color or orientation probes ($F(1, 9) = 0.6$, $p = 0.46$), Thus, as in Experiment 3, β increased with increased feature load.

As in Experiment 2, P_m was lower ($F(1, 9) = 30.77$, $p < 0.001$), and σ was higher ($F(1, 9) = 6.37$, $p < 0.05$), for six features. There was no main effect of feature-type for P_m ($F(1, 9) = 0.11$, $p = 0.75$), but σ was higher for color than orientation probes ($F(1, 9) = 23.01$, $p < 0.001$). Finally, measures of the percentage change in P_m and σ as feature-load increased (averaged across features) found costs in both P_m (10.3%, $t(9) = 5.29$, $p < 0.001$) and σ (14.1%, $t(9) = 2.57$, $p < 0.05$).

Thus, increasing the feature load within an object led to a selective decrease in VWM precision, and this pattern of costs is different from that obtained when features are distributed across objects (comparison of percentage costs in P_m and σ across Experiments 3 and 4 revealed an interaction between Experiments and Parameters (P_m and σ), $F(1, 18) = 4.27$, $p < 0.05$). Because these results replicate those of Experiments 1 and 2, we conclude that the influence of responses to non-target items cannot explain the distinct pattern of costs for increases in feature load within versus between objects. Thus, these studies provide further evidence that increasing the feature load within objects selectively impairs representational precision, and that such costs differ from those observed when feature load is increased by the addition of task-relevant objects. Of course, we cannot rule out that such results may be specific to the experimental design and analysis technique employed in the current studies, and future experiments will be required to determine whether these findings generalize to other WM paradigms. However, because Experiment 5 shows that costs in representational precision for increased feature load can be observed when the response probe is replaced with a typical change detection task, we can conclude that our results generalize to at least two distinct methods of probing visual working memory.

Experiment 5

If the storage of multiple features incurs costs in the precision of memory, then why haven't these costs been observed in previous change detection tasks? We considered the possibility that precision costs went unnoticed because change detection tasks used featural changes between sample and probe items that were too large for precision to affect response accuracy. Consistent with this possibility, the magnitude of the orientation change between sample and probe items in previous studies (Luck & Vogel, 1997; Vogel et al., 2001; Xu, 2002, 2006) (90°) were much larger than the estimated σ for six features in Experiments 1 and 2 (20.4° and 16.6°, respectively). While the ability to detect substantial feature changes depends primarily on whether the changed item is stored in memory (Awh, Barton, & Vogel, 2007; Barton, Ester, & Awh, 2009), detecting small-magnitude changes may also depend on whether items are maintained at sufficient fidelity to notice a difference. We tested this hypothesis in a change detection task with identical stimulus presentations to Experiment 1 except that the feature probe task was replaced with a change detection task in which participants indicated whether the single-item VWM probe matched the sample in the task-relevant feature(s). Participants were given separate blocks of large-magnitude (90°) and small-magnitude (20°) changes. We expected that increasing the featural load of VWM representations would affect performance when detecting small magnitude changes, but not when detecting large magnitude changes (Luck & Vogel, 1997; Vogel et al., 2001).

Methods

Thirteen young adults (5 males) participated in Experiment 5. One participant was excluded because change detection performance was not above chance, leaving 12 for analysis. Half of these participants completed the large-magnitude change detection task prior to the small-magnitude change detection task, and task order was reversed for the other participants.

The methods were as in Experiment 1 except that the VWM probe was either a colored circle (.4° diameter) or a black triangle at the position of one of the sample items with hollow circle placeholders at the non-probed locations (.4° diameter) (Figure 1A). For dual-feature blocks, probe type (color or orientation) was selected at random on each trial. On half of the trials the probe item was the same in color or orientation as the probed sample item. Otherwise, the stimuli differed by ±90° (large-magnitude blocks) or ±20° (small-magnitude blocks) in color or orientation space. Participants made one of two key presses to indicate whether the probe was 'same' or 'different'. Responses were unspeeded, and accuracy was stressed. Response accuracy feedback was provided after each response.

Results and discussion

Change detection accuracy for each condition is shown in Figure 5. Participants' ability to detect large-magnitude changes did not differ between three and six feature

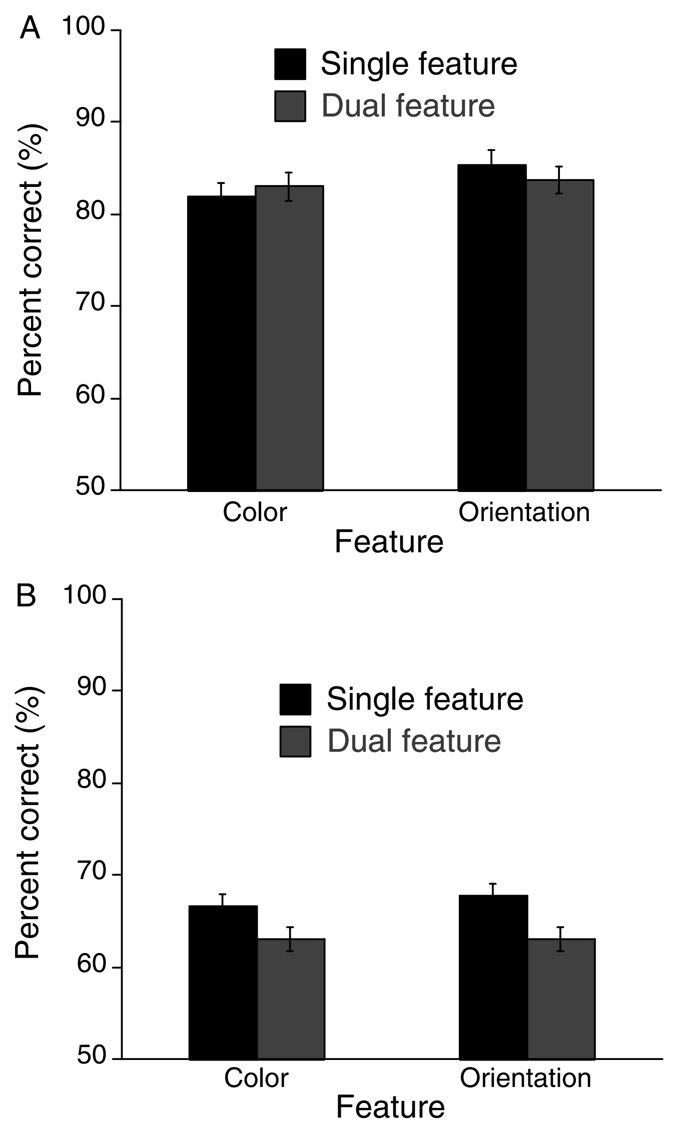

Figure 5. Percent correct in the change detection task of Experiment 5 (averaged across 'same' and 'different' trials). (A) Large-magnitude (90°) feature changes between sample and probes. (B) Small-magnitude (20°) feature changes between sample and probes. Error bars represent within-subject standard error (*SE*).

conditions ($F(1, 11) = 0.04$, $p = 0.85$), or between color and orientation probes ($F(1, 11) = 0.04$, $p = 0.85$), with no interaction between these factors, $F(1, 11) = .80$, $p = 0.4$. However, for small-magnitude changes, change detection performance was better for three than six features ($F(1, 11) = 9.43$, $p = 0.01$), with no difference between color and orientation probes ($F(1, 11) = 0.04$, $p = 0.85$), and no interaction between feature-load and feature-type ($F(1, 11) = 0.01$, $p = 0.77$). Moreover, the costs for encoding multiple features per object were greater in small-magnitude than large-magnitude blocks, $F(1, 11) = 5.23$, $p < 0.05$. Note that the large- and small-magnitude conditions also differed in terms of task difficulty. It is therefore possible that the differential multiple-feature costs for the small-magnitude condition occurred simply because that condition was more difficult. To rule out this possibility, ten naive participants were run in a control experiment consisting of the large-magnitude change detection condition with an increased set size (six items). To accommodate the increased display size, the display radius was doubled. Otherwise this experiment was the same as Experiment 5. Even though task performance (69%) was now comparable to the small-magnitude condition of Experiment 5 (independent-sample t-test, $p = 0.71$), we found no difference in detecting large magnitude changes between the six (70%) and twelve (68%) feature conditions ($p = 0.63$), suggesting that it was the requirement to detect small changes rather than differences in task difficulty that led to costs for the six feature condition of Experiment 5. We therefore conclude that VWM impairments from storing multi-feature objects can even be observed in change detection tasks if the task is rendered sensitive to the precision of stored items.

General discussion

It is commonly believed that VWM storage is sensitive to the number of objects, but not to the feature-load of objects (Luck & Vogel, 1997; Vogel et al., 2001; Wolters & Raffone, 2008; Zhang & Luck, 2008). However, in the current study we observed that increasing the feature-load of objects resulted in decreased precision of stored representations (Experiments 1 and 3). We propose that the failure of previous studies to find costs due to increased feature load is a result of those tasks being insensitive to representational precision. Indeed, increased feature load resulted in worse performance when the change detection task was rendered sensitive to representational precision (Experiment 5). The current results clearly indicate that the theory that VWM performance is limited by the number of objects but not features is untenable (Luck & Vogel, 1997; Vogel et al., 2001; Zhang & Luck, 2008): Maintenance of multiple features per object imbues strong costs in the precision of our VWM representations. However, the current results also demonstrate that VWM performance isn't entirely determined by feature load, as the manner in which features were distributed across objects determined whether there were costs in quantity and/or precision (Experiments 2 and 4).

The finding that storing features in VWM is costly is generally consistent with the suggestion that increasing object information complexity in a VWM task reduces change detection performance (Alvarez & Cavanagh, 2004; Eng, Chen, & Jiang, 2005). Worse change detection performance for complex stimuli has previously been attributed to the costs of comparing the probe and sample during retrieval (Awh et al., 2007; Barton et al., 2009) rather than limitations in working memory storage *per se*. This 'comparison error' account, however, cannot easily explain the present findings because the retrieval stage of our VWM task is equivalent across single and dual-feature conditions. We therefore conclude that at least a specific form of increased information complexity, i.e. feature load, can affect VWM storage. Moreover, this cost is manifested as a selective loss in the resolution of our mental representations and is therefore inconsistent with the proposal that VWM capacity is determined by representational slots of fixed precision (Zhang & Luck, 2008).

The present work also indicates that feature load and object load constrain WM differently. The impairment in VWM caused by the doubling of feature load was distinct when the features were in the same or in distinct objects, with only the latter showing costs in both P_m and σ. Evidently, adding more objects lowers both the probability that these objects will be encoded into VWM and the precision with which they are encoded, whereas adding additional features to the same objects primarily affects the resolution of these encoded objects. The fact that increased feature load didn't significantly raise guessing rate suggests that the probability of an object being stored in memory is independent of its information load, consistent with theories proposing a fixed upper limit on the quantity of representations in VWM (Cowan, 2006; Luck & Vogel, 1997; Zhang & Luck, 2008). However, representational precision decreased in the six-feature condition, which indicates that representational quality is inversely related to the amount of information that has to be stored in VWM, consistent with resource-based views of VWM (Alvarez & Cavanagh, 2004; Bays & Husain, 2008; Wilken & Ma, 2004). Thus, there may be distinct limits for representational quantity and representational precision, and these limits may have characteristics of slot-based and resource-based theories, respectively. Specifically, the quantity of stored representations may be governed, not by the information load of the to-be-stored information, but by the costs of keeping representations encapsulated such that information from multiple representations will not mutually interfere. In contrast, representational quality may rely on the division of WM storage resources to the information to be remembered. Increasing the information load of objects will inevitably spread resources thinner, leading to less precision in the stored representations. This proposed distinction is supported by functional neuroimaging evidence that distinct regions of the parietal cortex respond to the number of objects and the number of features (Xu, 2008; Xu & Chun, 2006, 2009).

In sum, our findings are inconsistent with the hypothesis that objects are the sole elementary units of our mental representations, but neither do they advocate that features are these basic building blocks. Rather, both hierarchical levels of perceptual organization appear to limit our mental representations of the visual world.

Acknowledgments

We thank Tristan J. Watkins and Janice Louie for help with data gathering. We are grateful to Michael N. Tombu for assistance with programming and discussion. This work was supported by NIMH grant (MH70776) to R.M. and NEI grant (P30-EY008126) to the Vanderbilt Vision Research Center.

Commercial relationships: none.
Corresponding author: Daryl Fougnie.
Email: darylfougnie@gmail.com.
Address: Department of Psychology, Harvard University, 33 Kirkland St., Cambridge, MA 02138, USA.

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. [PubMed]

Awh, E., Barton, B., & Vogel, E. K. (2007). Visual working memory represents a fixed number of items regardless of complexity. *Psychology Science, 18,* 622–628. [PubMed]

Barton, B., Ester, E. F., & Awh, E. (2009). Discrete resource allocation in visual working memory. *Journal of Experimental Psychology: Human Perception and Performance, 35,* 1359–1367. [PubMed]

Bays, P. M., Catalao, R. F., & Husain, M. (2009). The precision of visual working memory is set by allocation of a shared resource. *Journal of Vision, 9*(10):7, 1–11, http://www.journalofvision.org/content/9/10/7, doi:10.1167/9.10.7. [PubMed] [Article]

Bays, P. M., & Husain, M. (2008). Dynamic shifts of limited working memory resources in human vision. *Science, 321,* 851–854. [PubMed]

Blaser, E., Pylyshyn, Z. W., & Holcombe, A. O. (2000). Tracking an object through feature space. *Nature, 408,* 196–199. [PubMed]

Cowan, N. (2006). *Working memory Capacity*. New York: Psychology Press.

Davis, G., & Holmes, A. (2005). The capacity of visual short-term memory is not a fixed number of objects. *Memory Cognition, 33,* 185–195. [PubMed]

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

Delvenne, J. F., & Bruyer, R. (2006). A configural effect in visual short-term memory for features from different parts of an object. *Quarterly Journal of Experimental Psychology, 59,* 1567–1580. [PubMed]

Duncan, J. (1984). Selective attention and the organization of visual information. *Journal of Experimental Psychology: General, 113,* 501–517. [PubMed]

Eng, H. Y., Chen, D., & Jiang, Y. (2005). Visual working memory for simple and complex visual stimuli. *Psychonics Bulletin Reviews, 12,* 1127–1133. [PubMed]

Huang, L. (2010). What is the unit of visual attention? Object for selection, but Boolean map for access. *Journal of Experimental Psychology: General, 139,* 162–179. [PubMed]

Jiang, Y. V., Shim, W. M., & Makovski, T. (2008). Visual working memory for line orientations and face identities. *Perception & Psychophysics, 70,* 1581–1591. [PubMed]

Kahneman, D., Treisman, A., & Gibbs, B. J. (1992). The reviewing of object files: Object-specific integration of information. *Cognitive Psychology, 24,* 175–219.

Kyllingsbaek, S., & Bundesen, C. (2009). Changing change detection: Improving the reliability of measures of visual short-term memory capacity. *Psychonics Bulletin Reviews, 16,* 1000–1010. [PubMed]

Lee, D., & Chun, M. M. (2001). What are the units of visual short-term memory, objects or spatial locations? *Perception & Psychophysics, 63,* 253–257. [PubMed]

Luck, S. J. (2008). Visual short-term memory. In S. J. Luck & A. Hollingworth (Eds.), *Visual memory* (pp. 43–86). Oxford: Oxford University Press.

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

Magnussen, S., & Greenlee, M. W. (1992). Retention and disruption of motion information in visual short-term memory. *Journal of Experimental Psychology: Learning Memory and Cognition, 18,* 151–156. [PubMed]

Magnussen, S., & Greenlee, M. W. (1999). The psychophysics of perceptual memory. *Psychology Research, 62,* 81–92. [PubMed]

Olson, I. R., & Jiang, Y. (2002). Is visual short-term memory object based? Rejection of the “strong-object” hypothesis. *Perception & Psychophysics, 64,* 1055–1067. [PubMed]

Raffone, A., & Wolters, G. (2001). A cortical mechanism for binding in visual working memory. *Journal of Cognition and Neuroscience, 13,* 766–785. [PubMed]

Rensink, R. A. (2002). Change detection. *Annual Review of Psychology, 53,* 245–277. [PubMed]

Scholl, B. J. (2001). Objects and attention: The state of the art. *Cognition, 80,* 1–46. [PubMed]

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. [PubMed]

Wheeler, M. E., & Treisman, A. M. (2002). Binding in short-term visual memory. *Journal of Experimental Psychology: General, 131,* 48–64. [PubMed]

Wilken, P., & Ma, W. J. (2004). A detection theory account of change detection. *Journal of Vision, 4*(12):11, 1120–1135, http://www.journalofvision.org/content/4/12/11, doi:10.1167/4.12.11. [PubMed] [Article]

Wolters, G., & Raffone, A. (2008). Coherence and recurrency: Maintenance, control and integration in working memory. *Cognitive Process, 9,* 1–17. [PubMed]

Xu, Y. (2002). Encoding color and shape from different parts of an object in visual short-term memory. *Perception & Psychophysics, 64,* 1260–1280. [PubMed]

Xu, Y. (2006). Understanding the object benefit in visual short-term memory: The roles of feature proximity and connectedness. *Perception & Psychophysics, 68,* 815–828. [PubMed]

Xu, Y. (2008). Representing connected and disconnected shapes in human inferior intraparietal sulcus. *Neuroimage, 40,* 1849–1856. [PubMed]

Xu, Y., & Chun, M. M. (2006). Dissociable neural mechanisms supporting visual short-term memory for objects. *Nature, 440,* 91–95. [PubMed]

Xu, Y., & Chun, M. M. (2009). Selecting and perceiving multiple visual objects. *Trends in Cognitive Science, 13,* 167–174. [PubMed]

Zhang, W., & Luck, S. J. (2008). Discrete fixed-resolution representations in visual working memory. *Nature, 453,* 233–235. [PubMed]

Zhang, W., & Luck, S. J. (2009). Sudden death and gradual decay in visual working memory. *Psychology Science, 20,* 423–428. [PubMed]