Separating memoranda in depth increases visual working memory performance

Chaipat Chunharas[1,2], Rosanne L. Rademaker[1,3], Thomas C. Sprague[4], Timothy F. Brady[1], & John T. Serences[1,5,6]

[1]Psychology Department, University of California San Diego, La Jolla, California, USA

[2]King Chulalongkorn Memorial hospital, Chulalongkorn University, Bangkok, Thailand

[3]Donders Institute for Brain, Cognition and Behavior, Radboud University, Nijmegen, the Netherlands

[4]Department of Psychology, New York University, New York, New York, 1000, USA

[5]Neurosciences Graduate Program, University of California San Diego, La Jolla, California, USA

[6]Kavli Institute for Brain and Mind, University of California, San Diego, La Jolla, CA 92093

correspondence: cchunharas@gmail.com, chaipat.c@chula.ac.th

Pages: 28 pages

Figures: 7

Abstract: 255 words

Body: 6911 words

Conflict of interest: the authors declare no conflict of interest

Keywords: visual working memory; memory biases; depth perception

Acknowledgements

This work was supported by NEI R01-EY025872 and a James S McDonnell Foundation Scholar Award to JTS, by Thai Red Cross Society grant to CC, by the European Union's Horizon 2020 research and innovation program under the Marie Sklodowska-Curie Grant Agreement No 743941 to RLR, and by a NSF CAREER award (BCS-1653457) to TFB.

Abstract (255 words)

Visual working memory is the mechanism supporting the continued maintenance of information after sensory inputs are removed. Although the capacity of visual working memory is limited, memoranda that are spaced farther apart on a 2D display are easier to remember, potentially because neural representations are more distinct within retinotopically-organized areas of visual cortex during memory encoding, maintenance, and/or retrieval. The impact of spatial separability in depth on memory is less clear, even though depth information is essential to guide interactions with objects in the environment. On one account, separating memoranda in depth may facilitate performance if interference between items is reduced. However, depth information must be inferred indirectly from the 2D retinal image, and less is known about how visual cortex represents depth. Thus, an alternative possibility is that separation in depth does not attenuate between-item interference; separation in depth may even impair performance, as attention must be distributed across a larger volume of 3D space. We tested these alternatives using a stereo display while participants remembered the colors of stimuli presented either near or far in the 2D plane or in depth. Increasing separation in-plane and in depth both enhanced performance. Furthermore, participants who were better able to utilize stereo depth cues showed larger benefits when memoranda were separated in depth, particularly for large memory arrays. The observation that spatial separation in the inferred 3D structure of the environment improves memory performance, as is the case in 2D environments, suggests that separating memoranda in depth might reduce neural competition by utilizing cortically separable resources.

Introduction

Visual working memory (VWM) supports the integration of past and present sensory information via the short-term maintenance when such information is no longer directly accessible. Performance on VWM tasks is highly correlated with measures of general intelligence and other related outcome measures, and is therefore thought to reflect a core cognitive capacity (Baddeley, 1986; Conway, Cowan, Bunting, Therriault, & Minkoff, 2002; Engle, Tuholski, Laughlin, & Conway, 1999; Fukuda, Vogel, Mayr, & Awh, 2010). In most VWM studies, simple visual stimuli are presented on a 2D computer screen and participants remember specific features, such as color or orientation, that are presented at different spatial locations (Engle et al., 1999; Luck & Vogel, 1997; Simons & Levin, 1997; Zhang & Luck, 2008). Based on such work, VWM is known to be capacity limited (Bays, Catalao, & Husain, 2009; Bays & Husain, 2008; Ma, Husain, & Bays, 2014; Schurgin, Wixted, & Brady, 2018), such that increasing the number of to-be-remembered items or the delay duration leads to reductions in memory precision (Ma et al., 2014; Panichello, DePasquale, Pillow, & Buschman, 2018; Rademaker, Park, & Sack, 2018; Shin, Zou, & Ma, 2017; van den Berg, Shin, Chou, George, & Ma, 2012; Zhang & Luck, 2008), reductions in confidence (Rademaker, Tredway & Tong, 2012), the mis-binding or "swapping" of different visual features (Bays, 2016; Bays, Wu, & Husain, 2011; Bays, Gorgoraptis, Wee, Marshall, & Husain, 2011), and the tendency to chunk information into group-level ensemble representations (Brady & Alvarez, 2011).

One of the key factors that govern interactions between remembered items is the degree to which different memoranda can be bound to distinct spatial locations. For example, detecting a change in a remembered object is more challenging when the spatial configuration of the display is modified between encoding and test, highlighting the importance of spatial layout and spatial location in VWM (Hollingworth, 2007; Hollingworth & Rasmussen, 2010; Jiang, Olson, & Chun, 2000; Olson & Marshuetz, 2005; Phillips, 1974; Postle, Awh, Serences, Sutterer, & D'Esposito, 2013; Treisman & Zhang, 2006). Memory performance is improved when presenting multiple simultaneous memoranda far from each other, compared to close from each other, suggesting a role for spatial interference (Cohen, Rhee, & Alvarez, 2016; Emrich & Ferber, 2012). Furthermore, presenting memoranda sequentially in different spatial locations leads to better memory performance compared to sequentially presenting items in the same spatial location, even when location is task-irrelevant, (Pertzov & Husain, 2014).

The importance of 2D space in VWM is consistent with the clear map-like organization of 2D spatial position across the cortical surface, which should result in less neural competition and more distinct representations as items are spaced farther apart (Engel, Glover, & Wandell, 1997; Grill-Spector & Malach, 2004; Maunsell & Newsome, 1987; Sereno et al., 1995; Sereno, Pitzalis, & Martinez, 2001; Talbot & Marshall, 1941). This general idea is consistent with a sensory-recruitment account, which proposes that early sensory cortex supports the maintenance of sensory information in working memory (D'Esposito & Postle, 2015; Emrich, Riggall, Larocque, & Postle, 2013; Harrison & Tong, 2009; Pasternak & Greenlee, 2005; Rademaker, Chunharas, & Serences, 2018; Serences, 2016; Serences, Ester, Vogel, & Awh, 2009; Sreenivasan, Curtis, & D'Esposito, 2014). Thus, overlap or competition between representations in retinotopic maps may impose limits on how well visual information is encoded and remembered (Emrich et al., 2013, Sprague, Ester & Serences, 2014).

The impact of presenting memoranda in different depth planes is less clear. Given that the retina encodes a 2D projection of light coming from a complex 3D environment, depth information must be indirectly inferred based on binocular cues like retinal disparity, and on monocular cues from pictorial depth indicators. In addition to the second-order nature of depth computations, there is also far less evidence of map-like 3D spatial representations in visual cortex. However, a recent study suggests that there are topographic representations of depth encoded in some visual areas, so separation in 3D may operate much like separation in 2D (Finlayson, Zhang, & Golomb, 2017). In addition, studies of visual search suggest that 3D structure may generally facilitate information processing. For example, visual search performance is better when depth information is present, particularly when the 3D structure of the display is kept constant across trials (McCarley & He, 2001). Visual search performance is also substantially better when participants are searching for a combination of color and depth *or* motion and depth compared to searching for a combination of two visual features that are not separated in depth. This finding suggests that depth separation can facilitate the separate encoding of visual features (Nakayama & Silverman, 1986).

That said, the few previous studies that directly investigated the effect of depth on VWM task performance have reported conflicting evidence, with some finding performance improvements and some finding performance decrements (Qian, Li, Wang, Liu, & Lei, 2017; Reeves & Lei, 2014; Xu & Nakayama, 2007). In addition, studies that focus on different aspects of information processing such as selective attention suggest that separating visual stimuli in depth might lead to impaired performance because encoding across different depth planes increases the total volume of 3D space that participants must attentively monitor (Andersen, 1990; Andersen & Kramer, 1993; Atchley, Kramer, Andersen, & Theeuwes, 1997; Downing & Pinker, 1985; Enns & Rensink, 1990; Finlayson & Grove, 2015; Finlayson, Remington, Retell, & Grove, 2013; Theeuwes, Atchley, & Kramer, 1998). For instance, while attention tends to naturally spread across perceived 3D surfaces, it is not as easy to divide attention between two 3D surfaces (He & Nakayama, 1995). Similarly, separating memoranda in depth might hinder performance because of these limitations in attention. Thus, it remains unclear whether depth would be important in the same way as 2D space for improving the separability of representations in working memory.

To test these alternative accounts, we examined the effects of 2D in-plane and 3D depth separation on memory precision (Experiment 1), and interactions between separation in depth and the number of remembered items (i.e. the 'set-size' of the memory array, Experiment 2). In Experiment 1, we found that separating items in depth improves memory performance in a manner similar to separating items in the 2D plane. In Experiment 2, we found that the benefits of separating memoranda in depth were particularly evident in participants who were better able to perceive items in depth, and when participants had to remember a larger number of items. Together, these findings show that both 2D in-plane and 3D across-plane spatial separability improve VWM performance. Thus, performance benefits for items separated in the 2D plane may extend to structured representations of the inferred 3D layout of a visual scene, perhaps as a result of the recruitment of more retinotopically distinct neural resources.

Experiment 1

Methods

Participants. Thirty healthy volunteers (21 female, mean age of 20.87 ± 0.53 S.E.M.) from the University of California San Diego (UCSD) community participated in the experiment. All procedures were approved by the UCSD Institutional Research Board. All participants reported normal or corrected-to-normal vision without color-blindness, and provided written informed consent. To ensure that all participants had stereo-vision, we pre-screened for stereo-blindness by asking all participants to look at random-dot stereogram display through the binocular goggles and then to identify three different geometric shapes (a triangle, a square and a circle). These shapes can be seen only if participants successfully fuse the images from the left and right eyes. All participants in this study correctly identified all three shapes. Participants were naïve to the purpose of the study and received course credit for their time. Three participants were excluded from the analysis due to low performance (circular standard deviation of more than 45°).

Stimuli & Procedure. Stimuli were rendered using virtual reality goggles (Oculus® DK2, Microsoft, Redmond, WA) with a resolution of 1920 x 1080, at a 60 Hz refresh rate, and a screen size of 12.6 x 7.1 cm (subtending a visual angle of 90x60 degrees). Stimuli were generated on a PC running Ubuntu (v16.04) using MATLAB and the Psychophysics toolbox (Brainard, 1997; Pelli, 1997). Participants were instructed to maintain fixation on a white central fixation dot (0.25º diameter) presented on a mid-gray background of 6.54 cd/m2. To aid ocular fusion and to maintain stable and vivid depth perception, sixteen gray circular placeholders (each 0.8º in diameter) were presented at evenly spaced intervals along an imaginary circle with a radius of 2.5º. The location of the placeholders in depth was either –0.1° or 0.1° based on retinal disparity. Depth was varied such that alternating pairs of placeholders had either a positive or a negative disparity (i.e., two close, then two far, then two close, etc. see Figure 1). Memory item colors were selected from a circle in CIE La*b* color space (*L* = 70, *a* = 20, *b* = 38, radius = 60). The two target colors were always 90º ± 10º apart along the circular color space. We opted to maintain this separation in color space so that the separability of the memory items in color space would remain relatively stable, allowing us to manipulate only 2D and 3D spatial separability across experimental conditions. The two memory targets were always presented either close in two-dimensional space (adjacent, with their centers .98º apart) or farther away (their centers 2.78º apart) and the targets could be on the same or on different depth planes. This produced 4 levels of 3D (same vs. different) and 2D (close vs. far) separation: same-close, different-close, same-far, and different-far. Note that the two memory targets were always presented in the same hemifield to maximize inter-item competition (Alvarez & Cavanagh, 2005; Cohen et al., 2016; Störmer, Alvarez, & Cavanagh, 2014). No color calibration was done on the Oculus goggles. However, since the locations, sizes and colors of memory items are consistent across all conditions, we believe that any error from calibration will affect all conditions equally. In general, the error introduced by the memory task itself is very large relative to any display properties; reliable data in such paradigms can even be obtained in continuous color report tasks conducted in entirely uncontrolled settings (e.g., over the internet with all subjects using their own personal computer: Brady & Alvarez, 2015).

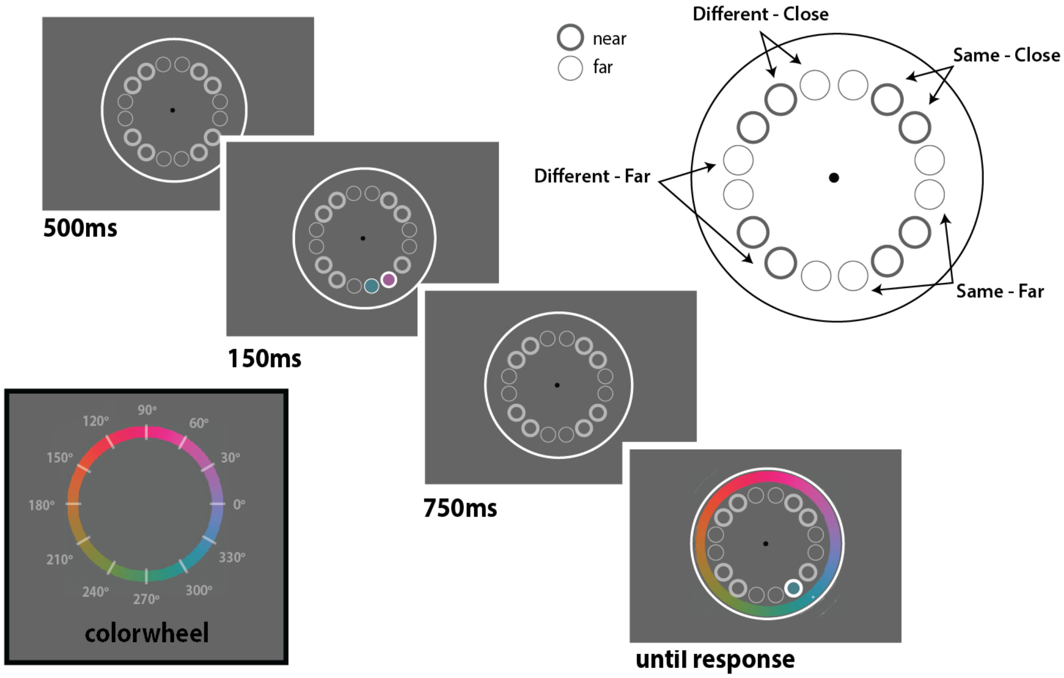

Figure 1. *Each trial started with a 500ms fixation period during which only the 16 placeholders were shown. Here, light and dark circles indicate placeholders on the far and near depth planes, respectively (this is only for visualization purposes – all placeholders were the same shade of grey in the actual experiment). Next, two memory targets were presented for 150ms, followed by a 750ms delay. After the delay, a color wheel was presented together with a cue outlining one of the previous target locations, and participants moved the cursor to report the hue previously shown at the cued location. The two target colors were presented either in the same or different depth planes in 3D coordinates (same vs. different) and either close or far in 2D space (see insert at top right). The lower left insert shows the color-wheel that we used in the experiment.*

On each trial, two colored stimuli were presented for 150ms and participants had to remember the color of both stimuli during a 750ms delay period. After the delay, one of the two colors was probed by increasing the thickness of one of the placeholders. Together with the location probe, a color-wheel (3° radius from the center, 0.5° wide, randomly rotated on each trial) and a crosshair appeared. Participants used the mouse to move the crosshair from its initially random location on the color-wheel, to the hue on the color-wheel that most closely resembled the color of the probed memory target (Wilken & Ma, 2004). The next trial started after participants clicked the mouse to record their response, and this procedure was repeated 96 times per experimental condition (384 trials in total, conditions randomly interleaved).

Analyses. We generated a distribution of errors for each participant by computing the difference between the cued target color and the reported color (reported° – target°) on each trial. To clearly visualize the shape of this error distribution, and its relationship to the non-target color, we flipped the sign of the error such that the non-target color was always 90º counter-clockwise to the cued target (Figure 2). A commonly used 'mixture model' (Bays et al., 2009; Zhang & Luck, 2008) was fit to the error distribution under the assumption that responses reflect a mixture of (1) responses to the target color, (2) responses to the non-target color, and (3) random guesses. This model had 4 free parameters – the bias (*b*, in degrees) of the responses, the standard deviation (*SD*) of the responses (both target and non-target), the probability of swapping errors (*s*, in %), and the guess rate (*g*, in %) - (Bays, 2015; Bays et al., 2009; Zhang & Luck, 2008). The model was fit separately to data from each condition for each participant using the Memtoolbox (Suchow, Brady, Fougnie, & Alvarez, 2013). A repeated-measures analysis of variance was then performed to evaluate the impact of 2D (near/far) and 3D (same/different depth plane) spatial separation on the estimated model parameters.

It is important to note that the mixture model may have limitations (Schurgin et al., 2018); in particular, precision and guess rate may not be truly separable parameters. However, we opted to use the mixture model in this particular experiment because it allowed us to account for systematic biases and for responses to non-targets (swap errors), which are difficult to account for without using a model of the response distribution. For example, without explicitly accounting for swap errors non-target responses would be treated as 90º errors even though they were actually accurate responses to the non-target color. However, to check that our results were not dependent on the details of the mixture model, we also performed a post-hoc analysis where we developed a non-parametric procedure to quantify memory precision while taking systematic biases and swap errors into account: First, we computed the error (in degrees) of all responses that were centered around the target and the non-target colors (i.e., including responses to non-target colors as precise responses). Then, in an effort to attenuate the effect of systematic biases, we computed the mean absolute error within +/- of 60º from the peak (mode) of each error response distribution (i.e. target and non-target distributions). This allowed us to non-parametrically examine errors without any strong assumptions about the separability of the guess rate and precision parameters of a mixture model.

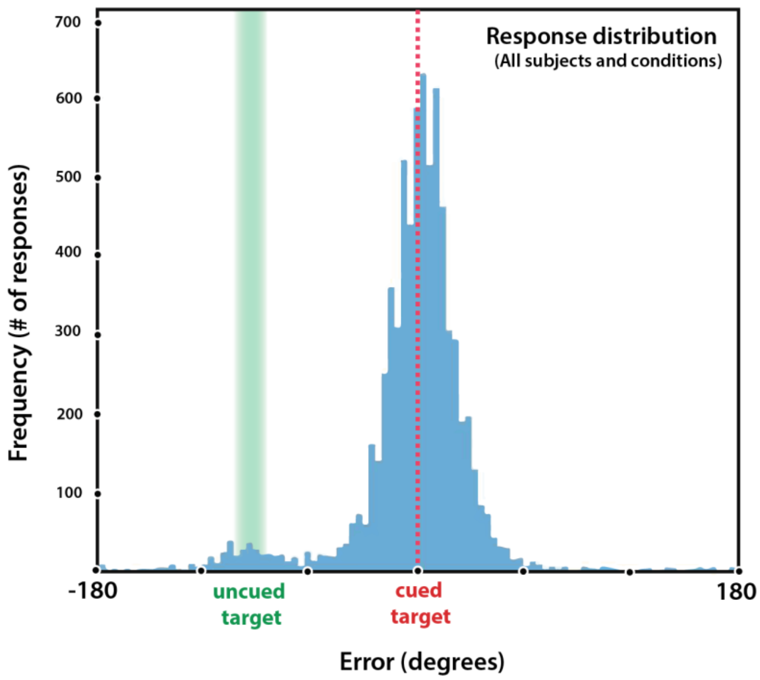

Figure 2. *Results of Experiment 1 as a histogram of the responses centered around the target color, shown collapsed across all participants and conditions. The non-target colors were aligned to approximately –90º (+/-10º) relative to the target color by flipping the sign of responses on trials where the non-target was +90º (+/-10º) relative to the target (note that width of the shaded green area reflects the +/-10º jitter in the uncued target color). Swap errors are apparent from the small bump centered on the non-target color.*

Results

Responses were more precise (lower mixture model *SD*) both when the two memoranda were separated by a greater distance in 2D spatial position (near/far: $F(1,26) = 4.921$, $p = 0.036$), and when the two memoranda were presented on different depth planes (same/different planes: $F(1,26) = 5.677$, $p = 0.025$) with no interaction between these factors ($F(1,26) = 0.06$, $p = 0.808$; Figure 3A). As shown in Figure 3B, there was a consistent bias such that responses were repelled slightly but consistently away from the non-target color ($t(1,26)=5.81$, 6.63, 6.47, and 7.77 for same-close, different-close, same-far, and different-far, respectively, with all $p<0.0001$). However, there was no difference in the magnitude of this bias as a function of separation in 2D or 3D, and no interaction between these factors ($F(1,26) = 0.002$, $p = 0.965$; $F(1,26) = 1.377$, $p = 0.251$; $F(1,26) = 0.983$, $p = 0.331$ respectively). The probability of swapping (i.e. non-target reports; Figure 3C) did not depend on whether the items were spatially close or far away from each other in 2D space ($F(1,26) = 1.633$, $p = 0.213$), and there was a non-significant trend towards more swap errors when targets were presented on different depth planes ($F(1,26) = 3.211$, $p = 0.085$). No interaction was observed ($F(1,26) = 1.889$, $p = 0.181$).

There were also no differences in guess rates estimated by the mixture model across conditions ($F(1,26) = 0.008$, $p = 0.93$, $F(1,26) = 1.481$, $p = 0.235$, and $F(1,26) = 0.366$, $p = 0.55$ for the main effects of separation in 2D, 3D, and their interaction, respectively. Figure 3D).

The quantitative results from this mixture modeling match with the qualitatively observable shapes of the kernel density plots for each condition (Figure 3A-D vs. 3E, computed using a Gaussian kernel with a standard deviation of 4°) and the non-parametric analysis of response precision yielded comparable results: The average absolute error around the target was higher when two items were separated both in 2D ($F(1,26) = 6.66$, $p = .016$) and 3D ($F(1,26) = 6.40$, $p = .018$), and there was no interaction ($F(1,26) = 0.46$, $p = .505$).

To evaluate statistical power in our study, we performed a post-hoc bootstrapping analysis in which we systematically varied the number of participants. We resampled with replacement data from different numbers of participants, ranging from 2 to 27, and on each resample we computed the mean differences between conditions – this process was then repeated 1000 times. On each iteration, we did the same analysis of both the parameters from the mixture model and the non-parametric mean absolute error, and found that both analyses reached stable statistical significance (two-sided p-value less than 0.05) with a minimum of 20 participants

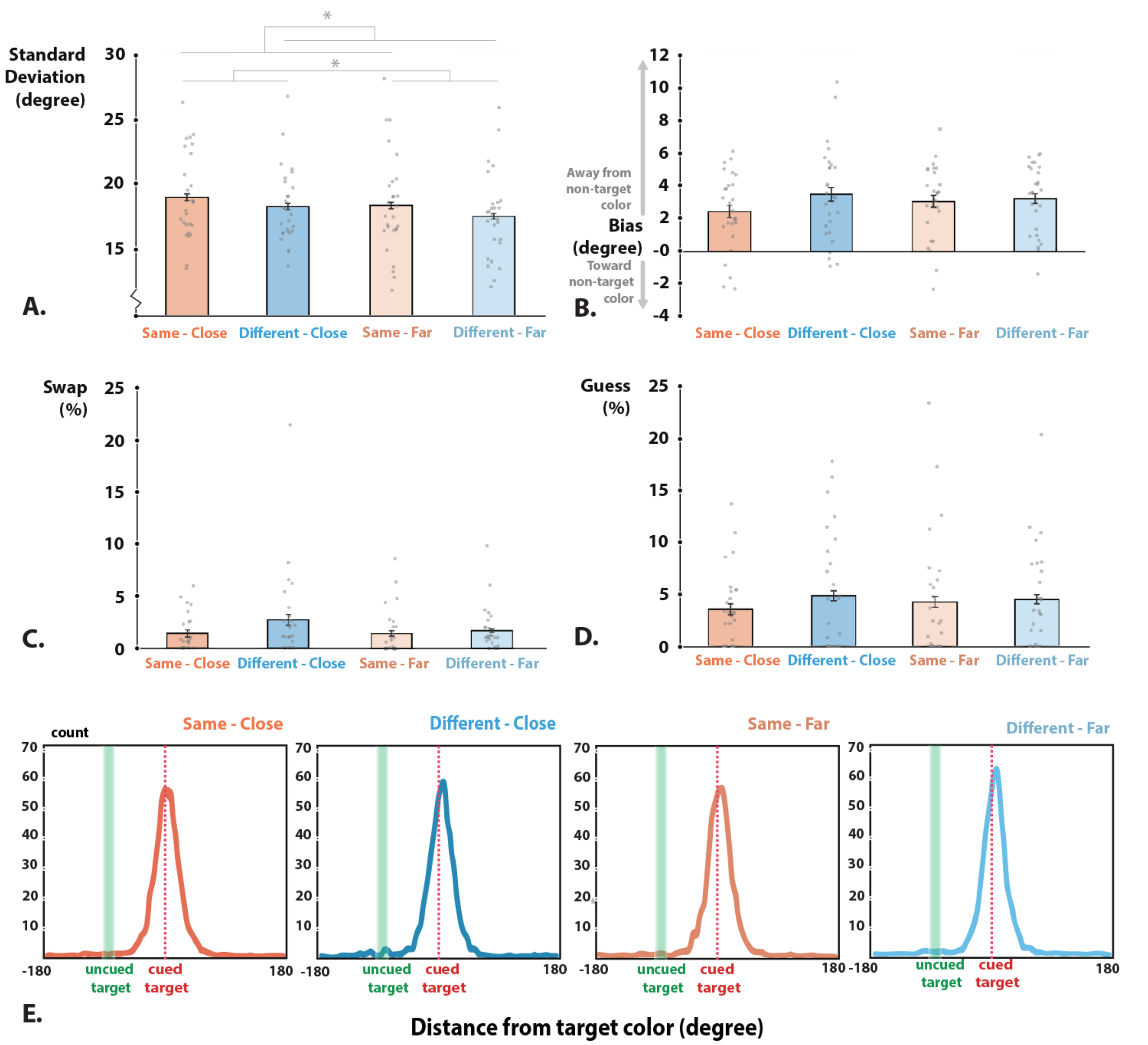

Figure 3. *Results of Experiment 1 in terms of the parameters from mixture modeling. A. The standard deviations are lower when two memory items are spatially far away or when they are on different depth plane (and lower standard deviation is associated with higher precision). * indicates p < 0.05. B. There are systematic biases away from the non-target color in all conditions but no significant differences in biases between conditions. C. There are no significant differences in swap error rate nor guess rate (shown in panel D). E. Four kernel density plots of group-level error responses of each condition centered around the target color (same-close, different-close, same-far and different-far from left to right). The shapes of the distributions qualitatively agree with the parameters from the model. Error bars (in A. B. and C.) represent ±1 S.E.M.*

Together these results suggest that spatial separability both within and between different depth planes is associated with higher precision memories in VWM. Importantly, no effects of spatial separability were found on any of the other parameters, suggesting that it is the memory strength that improved once items are separated either in 2D or 3D space.

Finally, note that the bias we observed in the target responses was always positive, or away from the non-target, which is consistent with previous studies showing repulsion biases away from other task-relevant items (Bae & Luck, 2017; Golomb, 2015; Marshak & Sekuler, 1979; Rademaker, Bloem, De Weerd, & Sack, 2015; Rauber & Treue, 1998; Scocchia, Cicchini, & Triesch, 2013). Interestingly, one study that examined repulsion bias as a function of color similarity between items showed repulsion biases only when items were close in feature space, specifically less than 60° apart in feature space (Golomb, 2015), while attraction biases were reported when memoranda were more than 60° apart in feature space. However, in the current study we observe repulsion biases even with colors separated by 90° in feature space. Numerous aspects of the current task differed from this previous work (e.g., number of memory items, encoding time, delay time), and many of these factors could affect whether repulsion or attraction is observed in the data, and account for the differences between these two sets of findings.

Experiment 2

The results from Experiment 1 suggest that separating memoranda within and between depth planes increases memory precision, presumably because interference between the items is reduced. Here we examine the effects of depth on VWM capacity, focusing on the ways depth might improve attentional filtering. Studies have shown that the number of items that people can hold in memory with high fidelity may decrease once the number of to-be-remembered items is large and difficult for participants to manage. For example, one person might be capable of remembering 4 items with a high degree of fidelity when there are only 4 items to be remembered. However, that same person might remember fewer than 4 items with a high degree of fidelity when there are 12 memoranda to retain (Cowan & Morey, 2006; Cowan, Morey, AuBuchon, Zwilling, & Gilchrist, 2010; Cusack, Lehmann, Veldsman, & Mitchell, 2009; Linke, Vicente-Grabovetsky, Mitchell, & Cusack, 2011; Vogel, McCollough, & Machizawa, 2005). This phenomenon has usually been attributed to a failure of attentional filtering, as trying to store everything in the display may have negative consequences. Previous work has shown that spatial location can aid attentional filtering (Vogel et al., 2005). Therefore, we hypothesized that separating items in depth might also aid attentional filtering. In particular, we predicted that once participants have a large number of items to remember and therefore must rely on attentional filtering to select a subset of items to represent with high fidelity, separation in depth should promote a higher memory capacity. Alternatively, it is possible that increasing the number of memory items in a 3D display might lead to poorer overall performance due to an increased demand to distribute spatial attention across a larger volume of space. To test these accounts, we manipulated memory set size across a range from 2-12 items. We also independently assessed each participant's ability to exploit stereo depth cues so that we could evaluate the relationship between the salience of depth information and its impact on VWM capacity across participants.

Methods

Participants A new set of 22 healthy volunteers (14 female, mean age of 19.67 years ± 0.45 S.E.M.) from the UCSD community participated in the experiment. All procedures were approved by the UCSD Institutional Research Board. All participants reported normal or corrected-to-normal vision without color-blindness, and provided written informed consent. Participants were naïve to the purpose of the study and received course credits or monetary compensation for their time ($10/hour). All participants passed the same stereo-vision test used in Experiment 1, and none were excluded.

Stimuli & Procedure. Unless otherwise mentioned, stimulus generation and presentation was identical to Experiment 1. The main visual working memory task in Experiment 2 (Figure 4A) employed a delayed-match-to-sample paradigm. At the beginning of each trial, twelve placeholders were presented (each 1º in diameter, presented at 2.5º from fixation) for 500ms. The depth separation of the placeholders was experimentally manipulated: Placeholder could all be presented on the same depth plane (all on the near plane on 25% of trials, or all on the far plane on another 25% of trials), i.e. the "same-depth" condition. On the remaining 50% of trials, half of the placeholders were on the near plane, while the other half were on the far plane, i.e. the "different-depth" condition. Next, 2, 4, 6, 8 or 12 colored memory targets were briefly presented (500ms) at a random subset of the 12 placeholders, with the restriction that in the "both-depths" conditions half of the items were assigned to near, and the other half to far placeholders (for set size 12 stimuli were shown in every placeholder). Colors were randomly chosen from a set of twelve unique colors. After a 900 ms delay, a single test color was presented at one of the memory target locations, and this test either matched or did not match the target color previously shown at that location. Participants indicated "match" or "non-match" by pressing the "x" or the "c" key, respectively, with matches occurring on 50% of trials, and non-matches created by placing one of the other remembered items from the initial display in the test location). For each participant, we collected 80 trials for each set-size (2, 4, 6, 8 and 12) and depth condition (same vs. different depth plane), leading to 800 total trials. Participants performed 10 blocks 80 trials each, with each block lasting ~5 minutes. Note that using a delayed-match-to-sample paradigm required less time per trial than continuous report and thus allowed us to quickly evaluate memory performance across 5 set-sizes for items on same and different depth planes.

To evaluate how well participants could perceive memoranda presented on the two different depth planes, participants also completed a 48-trial depth discrimination task (Figure 4B) prior to participating in the main task. During this independent depth discrimination task, two placeholders were presented for 500ms, with one of the placeholders on the near plane and the other on the far plane (with respect to fixation). The location of the two placeholders was chosen at random from the 12 possible locations used in the main task. Participants had to indicate whether a target (specified by a green circle outline) was on the near or far plane. The ability of each participant to accurately identify the correct depth plane in this task was used to predict the benefits of the depth information during the visual working memory task.

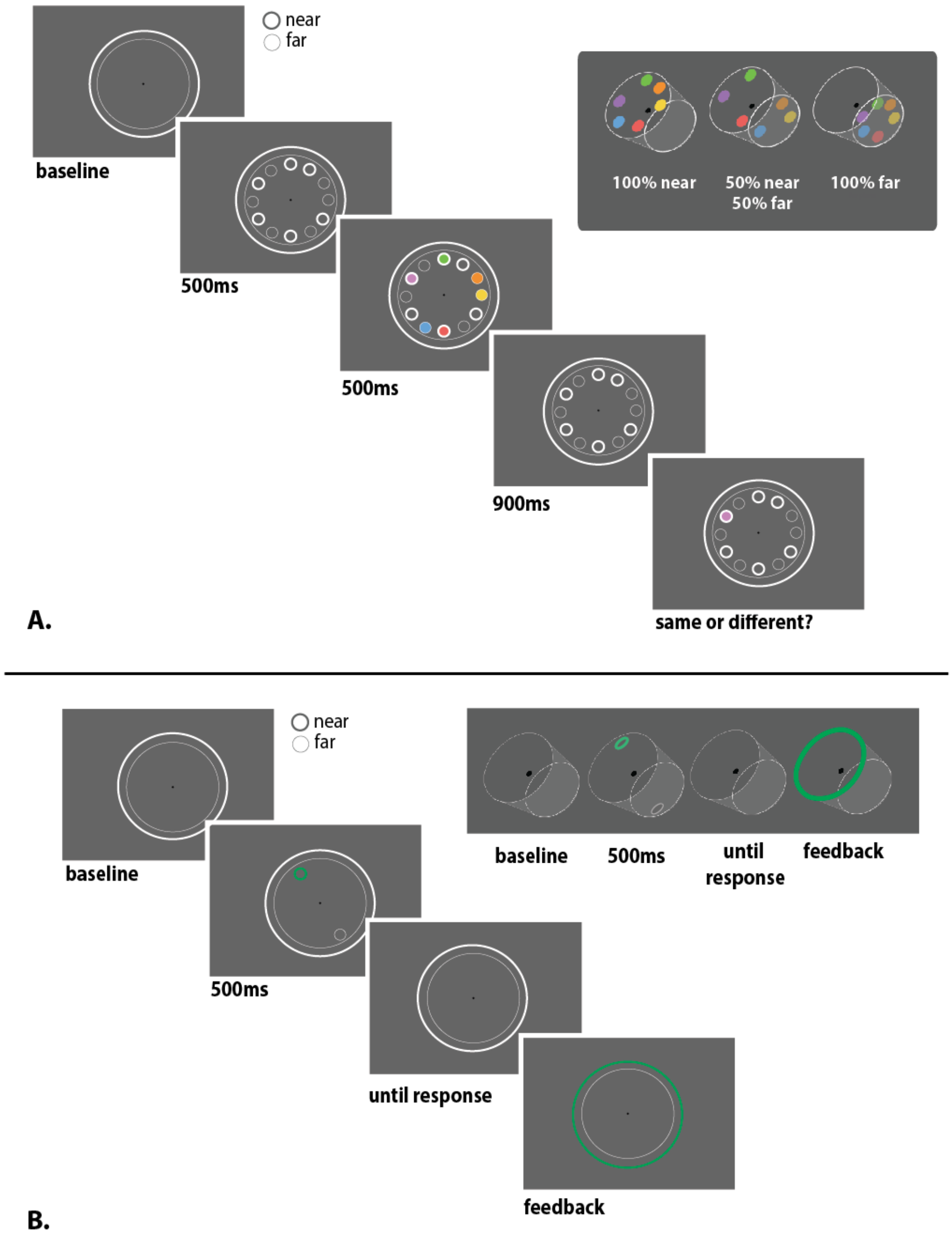

Figure 4. Experimental procedure for Experiment 2 *(A) In this single-probe change detection paradigm, each trial started with the presentation of 12 placeholders. Placeholders could have one of three possible depth relationships – all were on the near depth plane, all were on the far depth plane, or half were on the near and the other half were on the far depth plane. After 500 ms 2, 4, 6, 8 or 12 colored memory items were presented for 500ms, followed by a 900ms delay period. Next, a single test item was presented at a location previously occupied by one of the memory items, and participants indicated whether the color of the test was the same or different*

from the color of the memory target previously shown at that location. (B) The independent depth discrimination task. On each trial, two placeholders briefly appeared, each on a different depth plane. Participants indicated whether the target (in green) was on the near or far plane. Performance on this task used as an indicator of how well participants could perceive depth using our stereo-display setup.

Analyses. We estimated each participant's VWM capacity using a standard measure appropriate for single-probe change detection, Cowan's *k* (Cowan, 2010; Pashler, 1988), as follows:

$$k = (\text{hit rate - false alarm}) * \text{set-size}$$

As in Experiment 1, repeated-measures ANOVA's were used for the main analyses. Additionally, the impact of participant's ability to perceive the stimuli in depth (measured with the independent depth discrimination task) on performance during the working memory task was assessed using correlational analyses.

Results

There was a significant main effect of set size on observed *k* values ($F(4,84) = 5.26$, $p<0.001$; Figure 5A), such that estimates of capacity were lower for very small and for very large set sizes (a linear fit failed to capture a significant amount of variance (F1,215) = 0.59, p = 0.44, while adding a quadratic significantly improved the fit, $F(3,215) = 3.81$, $p= 0.011$). However, there was no effect of depth condition ($F(1,21) = 0.018$, $p = 0.895$) and no interaction between set size and depth condition ($F(4,84) = 0.107$, $p = 0.98$). While this may suggest that presenting memory items on the same vs. different depth planes did not impact memory capacity, we found a positive correlation between depth discrimination ability (as indexed during the independent depth discrimination task) and the impact of separation in depth (as manipulated in the main working memory task). Specifically, participants with better stereo depth perception showed a larger performance benefit when items were presented on different depth planes (Pearson's $r = 0.58$, $p = 0.004$; Figure 5B), and this correlation was still significant when participants with negative k-value were excluded from the analysis (Pearson's $r = 0.55$, $p = 0.012$). This effect was systematically related to set-size, such that correlations grew stronger as set-size increased (Figure 6, bottom row; rho = <0.0001, -0.05, 0.38, 0.42, 0.54 with p-values = 0.99, 0.81, 0.08, 0.05, 0.008 for set sizes 2, 4, 6, 8 and 12, respectively).

Importantly, the correlations between depth discrimination task and the VWM performance were found selectively in the 3D condition, but were not found in the 2D condition (Pearson's r = 0.49 and 0.05, p = .05 and .80 respectively). The correlation analyses after excluding two subjects with negative average k-values and found similar results (Pearson's $r = 0.49$, $p = 0.028$ in the 3D condition and Pearson's $r = -0.008$, $p = 0.97$ in the 2D condition). We ran a dependent correlation test and found a significant difference between the 2D and 3D correlations ($t=3.08$, $p=0.01$), showing that the 3D correlations were reliably higher than in the 2D condition. This indicates that the correlation was not related to differences in general arousal or motivation (Figure 6). We believe that the effect is robust given that these correlations grow monotonically stronger as set sizes increase. To ensure that this analysis had enough power, we did a bootstrapping analysis in which we resampled data from a different number of participants (between 5 and 22) with replacement 1,000 times (just as we did in Experiment 1). We found stable positive correlations (more than 97.5% of the simulations had positive correlations; equal to two-sided p-value of less than 0.05) when there were at least 10 participants included.

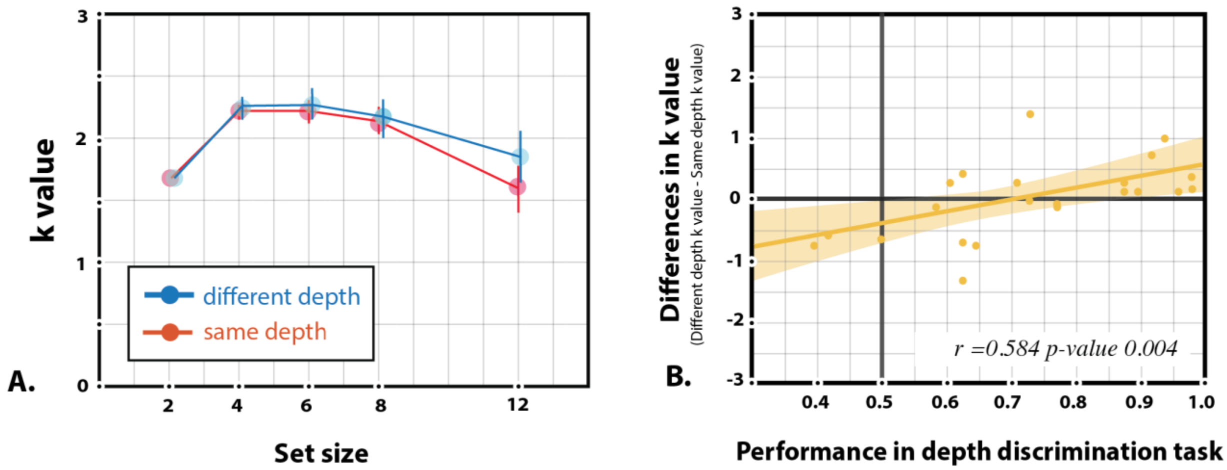

Figure 5**. **Main results Experiment 2. *(A) Visual working memory capacity (Cowan's k) as a function of set-size. There were no differences in VWM capacity when memory items were displayed on the same (red) or different (blue) depth planes. Observed changes in k as a function of set size are consistent with previous studies (Cowan & Morey, 2006). (B) The impact of depth separation (on the y-axis) was calculated by taking the capacity k for items presented on different depth planes, minus the k for items presented on the same depth plane. Thus, larger numbers indicate a larger benefit of presenting items separated in depth. The ability of participants to discriminate the two depth planes in our experimental setup (on the x-axis) was positively correlated with the benefits participants gained from items presented on different depth planes. Shaded regions indicate ± 1 S.E.M.*

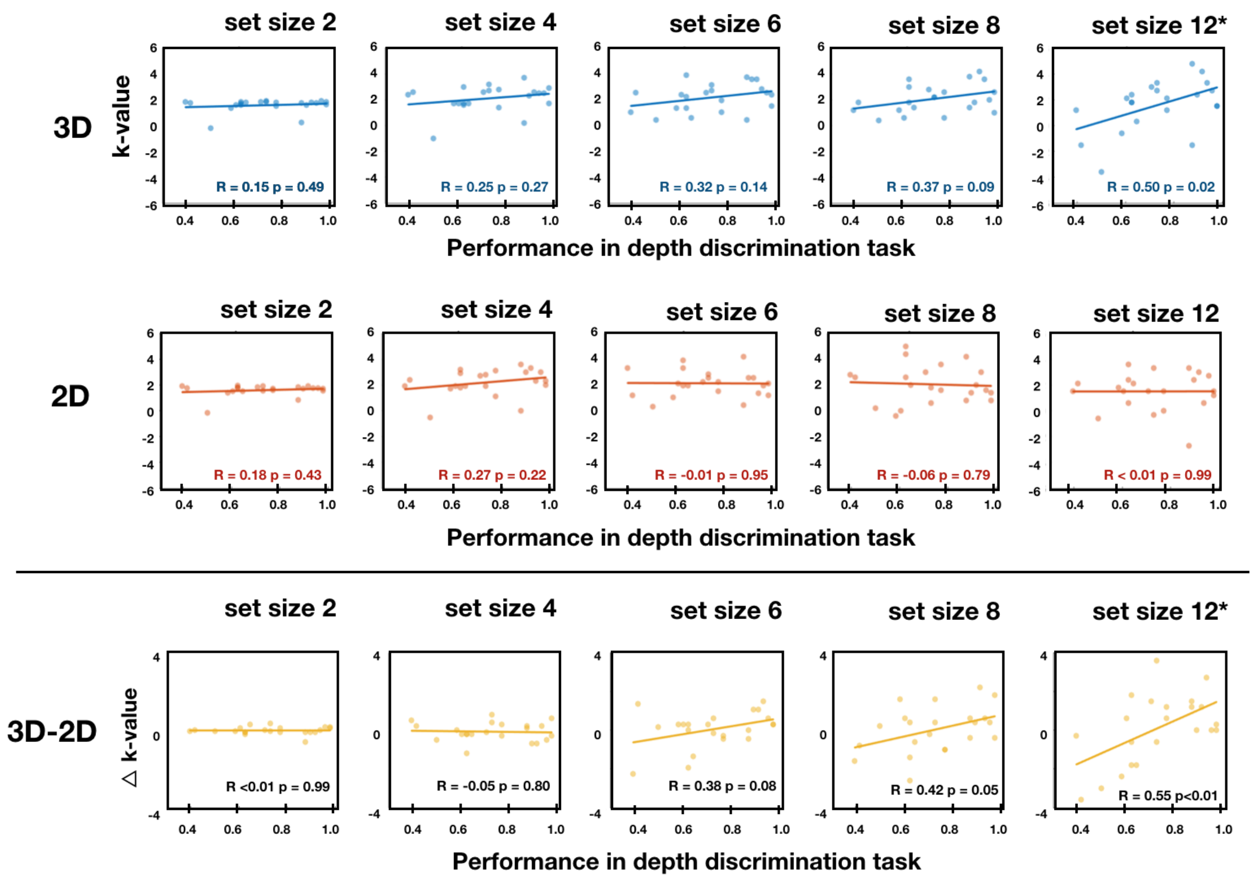

Figure 6. *The degree of positive correlation between depth discrimination ability (on the x-axis) and performance on the visual working memory task (on the y-axis). Participants who performed better on the depth discrimination task also performed better on the visual working memory task at larger set sizes, but only when the memoranda were on different depth planes (upper row). There was no correlation between performance on the depth discrimination task and the visual working memory task when the memoranda were in the same depth plane (middle row). The benefit associated with having the memoranda separated into different depth planes (difference in k-value on the y-axis) grew stronger as set-size increased (bottom row in panels).*

As an alternate means of assessing the data, we sorted participants into two groups based on a median-split of their depth discrimination ability as assessed using the independent task (Figure 7). We found a main effect of set-size ($F(4,80) = 5.22$, $p<0.001$) but not a main effect of depth plane ($F(1,20) = 0.03$, $p = 0.87$). There was also a significant two-way interaction such that separation in depth led to improved performance only for those subjects who performed well on the independent depth discrimination task ($F(1,20) = 10.95$, $p = 0.004$). Performance on the depth perception task was not associated with an overall change in WM performance levels collapsed across set size and condition, suggesting that the two groups of subjects were equally motivated to perform the task ($F(1,20) = 0.79$, $p = 0.39$). Nevertheless, there was a three-way interaction such that participants who performed well on the independent depth task showed the benefit of depth at larger set size ($F(4,80) = 3.622$, $p = 0.009$).

To follow up on these findings, we also performed post-hoc tests separately on data within the low- and high-depth-discriminators. We found that the high depth discriminators did better on the WM task when the items were separated in depth (main effect: $F(1,11) = 6.79$, $p = 0.024$), especially with larger set sizes (interaction: $F(4,44) = 3.53$, $p = 0.014$). This indicates that participants with better depth perception (> 72.9% accuracy) performed better on different-depth displays, but only at larger set sizes (Figure 8, top panel, $t(1,11) = -0.25, 0.06, 1.83, 1.44, 2.78$, $p = 0.81, 0.96, 0.09, 0.18, 0.02$ for set size 2, 4, 6, 8 and 12 respectively). For the low-depth-discriminators there was a small opposite trend such that performance was lower when memoranda were in different depth planes. However, the ANOVA did not reveal a significant main effect of separation in depth ($F(1,9) = 4.439$, $p = 0.064$) nor an interaction ($F(4,36) = 1.052$, $p = 0.394$). And post-hoc paired t-tests were also non-significant (Figure 8, bottom panel, $t(1,9) = -0.35, -1.35, -0.78, -1.14, -1.63$, $p = 0.73, 0.21, 0.46, 0.29, 0.14$ for set size 2, 4, 6, 8 and 12 respectively).

We also performed post-hoc tests separately on data from same-plane and different-plane conditions. Importantly, there was an interaction between low- and high-depth-discriminators and set-size when the memoranda were on different planes ($F(4,80) = 2.87$, $p = 0.028$) but not they were on the same plane ($F(4,80) = 0.75$, $p = 0.564$), indicating that the benefits of better depth perception were restricted to trials where the memory load was high load and memoranda were presented in separate depth planes. Moreover, the lack of an effect of depth perception ability on performance in the same-depth condition further suggests that differences in overall motivation between the two groups of participants cannot account for the observed differences in the different-depth condition.

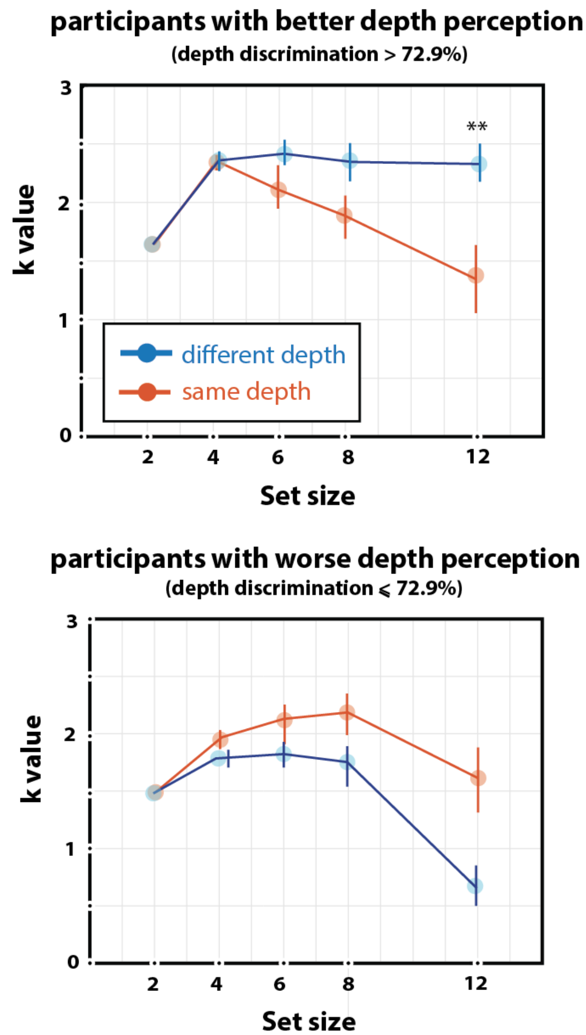

Figure 7. *Participants who exhibited better depth discrimination (upper panel), based on a median split of performance in the independent depth discrimination task, benefited more from the presence of depth information, particularly at high set sizes (** indicates p < 0.01. The error bars represent ±1 S.E.M.). For participants who exhibited worse depth discrimination (lower graph), the k value appeared to be lower when memoranda were on different depth plane, however, this did not reach significance. Note that the performance from both groups was comparable when the memoranda were on the same depth plane (compare red lines between the two panels).*

Discussion

Perceiving the world in 3D is a seemingly effortless endeavor, and depth information is fundamental to perceptual organization of the visual world into objects and surfaces, as well as guiding motor interactions with objects in the environment. However, the manner in which the visual system represents in-plane 2D information versus 3D depth information is fundamentally different. First, depth information must be indirectly inferred based on operations applied to the 2D input provided by the projection of light onto the retina. Thus, depth is a second order feature of visual representation that is indirectly constructed from a set of binocular and monocular cues. Second, the visual system is organized such that ordinal information about the 2D layout of a visual scene is preserved: stimuli that are closer to each other in the world are represented by neurons that are closer to each other in the retina and in later visual areas. In contrast, the extent of topographic representations of depth in visual cortex is not well understood, with only a few recent studies suggesting that a structured layout of depth exists in some visual areas (Finlayson et al., 2017). Here we show that separating memoranda in both the 2D plane and in 3D depth improves visual working memory performance, consistent with the idea that separating stimuli in depth attenuates inter-item competition and interference which affects how people perceive the display (Andersen, 1990; Finlayson & Golomb, 2016; Kooi, Toet, Tripathy, & Levi, 1994; Lehmkuhle & Fox, 1980; Papathomas, Feher, Julesz, & Zeevi, 1996). This is also in line with evidence that people remember real-world 3D objects better than drawings or photographs of the same objects, even when retinal images are roughly matched (Snow, Skiba, Coleman & Berryhill, 2014). Furthermore, separating memoranda in depth had the biggest impact on performance when set size increased, suggesting that at least some participants were able to exploit this additional 3D spatial information to help encode and maintain distinct representations of remembered items.

Previous work has produced mixed results regarding the impact of depth on VWM. For example, two recent studies using a change-detection task did not find any effect of separating memoranda in depth using a display in which all items were presented simultaneously (Qian et al., 2017; Reeves & Lei, 2014). An earlier study also found no benefits of depth using a simultaneous display, but did find that participants had a higher VWM capacity under stereoscopic viewing conditions when each item was presented sequentially on a different depth plane (Xu & Nakayama, 2007). The authors of this latter study hypothesized that perceiving items separated in depth might be inherently more difficult in a simultaneous display, as participants need to attend more than one depth plane at a time – in sequential displays this is presumably no longer an issue, unveiling the benefits of separation in depth. Interestingly, the same study showed that separation in depth had a benefit above and beyond other grouping cues, like changing the configuration of the memoranda by grouping sub-sets of memoranda into squares or circles (Xu & Nakayama, 2007). However, in everyday life we perceive depth information in stable and whole scenes, not in sequence. Because sequential presentation of depth information is one step removed from real-world conditions, it thus remains unclear from this previous work whether separation in depth yields any benefit without separation in time.

One alternative explanation for previous results which did not find a benefit to depth when using simultaneous displays is that participants simply differ in terms of how well they perceive the depth cues used in the experimental displays. In our Experiment 2, we independently measured individual differences in depth perception and found a clear benefit for separating memoranda in depth within the group of participants that were better able to exploit stereo cues to support depth perception. It is important to note that our depth discrimination task requires participants to be able to rapidly acquire depth information in order to accurately parse the array. Thus, even though all of the participants passed a basic stereo-vision screening test, there were still large individual differences in how efficiently they perceived depth information at the relatively brief exposure durations (i.e. 500ms) used in the depth perception and VWM tasks. For example, participants who have stereo-vision but who did poorly on the depth perception task might not be able to rapidly switch their attention between depth planes (or not be able to simultaneously attend to both depth planes), resulting in relatively worse performance in the 3D condition of the VWM task. The results from Experiment 2 also showed greater benefits of separation in depth at larger set sizes, consistent with the idea that separation in depth attenuates inter-item competition and possibly improves attentional filtering. As visual attention (the ability to selectively process visual information) and visual working memory (the ability to retain visual information) are related cognitive mechanisms, one possibility is that the separation of items in depth affects how visual attention is distributed (e.g. sequential focal attention rather than simultaneous more distributed attention). Consequently, interference (and thus error) could be reduced, the difference between items amplified (two colors were seen or remembered as more different, e.g. Finlayson & Golomb, 2016), and the relative position of items partially lost (more swap errors, e.g. mean non-target responses of 19% vs. 4% in sequential vs. simultaneous display respectively, Gorgoraptis, Catalao, Bays, & Husain, 2011)

It remains an open question the extent to which our results arise from differences in binocular disparity per se, differences in perceived depth, or more general properties of surface perception (e.g., Nakayama, He & Shimojo, 1995) regardless of the cues that give rise to such surfaces. Some work has suggested that perceptual benefits in related tasks are a result of binocular disparity rather than depth (Finlayson & Golomb, 2016), whereas many recognition tasks seem to largely benefit from coherent surface organization rather than binocular disparity (Nakayama, Shimojo, Silverman, 1989). Future research will be needed to dissociate these different factors and their respective influence on VWM performance

In summary, the present results demonstrate that separating memoranda in depth improves visual working memory. In Experiment 1, we show that separation in depth benefits visual working memory on a scale similar to separating memoranda in 2D. The similarity of these depth effects to effects observed with 2D space is particularly interesting given that spatial and depth information are fundamentally different, with 2D information encoded directly at the retina while 3D information needs to be indirectly inferred based on binocular and monocular cues. In Experiment 2, we show further that separation in depth confers the largest benefits when participants are better at exploiting stereo depth cues and when inter-item competition is highest due to larger set sizes. Together, these observations suggest that inter-item interference can occur after the computation of second order properties of the visual scene and not just at the level of retinotopically organized representations reflecting 2D in-plane separation. Showing items at varying depths may thus confer an important benefit to behavioral performance in psychophysical tasks.

Reference

Alvarez, G. A., & Cavanagh, P. (2005). Independent resources for attentional tracking in the left and right visual hemifields. *Psychological Science*, *16*(8), 637–643.

Andersen, G. J. (1990). Focused attention in three-dimensional space. *Perception & Psychophysics*, *47*(2), 112–120.

Andersen, G. J., & Kramer, A. F. (1993). Limits of focused attention in three-dimensional space. *Perception & Psychophysics*, *53*(6), 658–667.

Atchley, P., Kramer, A. F., Andersen, G. J., & Theeuwes, J. (1997). Spatial cuing in a stereoscopic display: Evidence for a “depth-aware” attentional focus. *Psychonomic Bulletin & Review*, *4*(4), 524–529.

Baddeley, A. (1986). Working Memory, Reading and Dyslexia. In E. Hjelmquist & L.-G. Nilsson (Eds.), *Advances in Psychology* (Vol. 34, pp. 141–152). North-Holland.

Bae, G.-Y., & Luck, S. J. (2017). Interactions between visual working memory representations. *Attention, Perception & Psychophysics*. https://doi.org/10.3758/s13414-017-1404-8

Bays, P. (2015). Evaluating and excluding swap errors in analogue report. *Journal of Vision*, *15*(12), 675–675.

Bays, P. M. (2016). Evaluating and excluding swap errors in analogue tests of working memory. *Scientific Reports*, *6*, 19203.

Bays, P. M., Catalao, R. F. G., & 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.

Bays, P. M., Gorgoraptis, N., Wee, N., Marshall, L., & Husain, M. (2011). Temporal dynamics of encoding, storage, and reallocation of visual working memory. *Journal of Vision*, *11*(10), 6–6.

Bays, P. M., & Husain, M. (2008). Dynamic shifts of limited working memory resources in human vision. *Science*, *321*(5890), 851–854.

Bays, P. M., Wu, E. Y., & Husain, M. (2011). Storage and binding of object features in visual working memory. *Neuropsychologia*, *49*(6), 1622–1631.

Brady, T. F., & Alvarez, G. A. (2011). Hierarchical encoding in visual working memory: ensemble statistics bias memory for individual items. *Psychological Science*, *22*(3), 384–392.

Brady, T. F., & Alvarez, G. A. (2015). Contextual effects in visual working memory reveal hierarchically structured memory representations. *Journal of vision*, *15*(15), 6-6.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436.

Cohen, M. A., Rhee, J. Y., & Alvarez, G. A. (2016). Limits on perceptual encoding can be predicted from known receptive field properties of human visual cortex. *Journal of Experimental Psychology. Human Perception and Performance*, *42*(1), 67–77.

Conway, A. R. A., Cowan, N., Bunting, M. F., Therriault, D. J., & Minkoff, S. R. B. (2002). A latent variable analysis of working memory capacity, short-term memory capacity, processing speed, and general fluid intelligence. *Intelligence*, *30*(2), 163–183.

Cowan, N. (2010). The Magical Mystery Four: How is Working Memory Capacity Limited, and Why? *Current Directions in Psychological Science*, *19*(1), 51–57.

Cowan, N., & Morey, C. C. (2006). Visual working memory depends on attentional filtering. *Trends in Cognitive Sciences*, *10*(4), 139–141.

Cowan, N., Morey, C. C., AuBuchon, A. M., Zwilling, C. E., & Gilchrist, A. L. (2010). Seven-year-olds allocate attention like adults unless working memory is overloaded. *Developmental Science*, *13*(1), 120–133.

Cusack, R., Lehmann, M., Veldsman, M., & Mitchell, D. J. (2009). Encoding strategy and not visual working memory capacity correlates with intelligence. *Psychonomic Bulletin & Review*, *16*(4), 641–647.

D'Esposito, M., & Postle, B. R. (2015). The cognitive neuroscience of working memory. *Annual Review of Psychology*, *66*, 115–142.

Downing, C., & Pinker, S. (1985). Attention and Performance. Earlbaum.

Emrich, S. M., & Ferber, S. (2012). Competition increases binding errors in visual working memory. *Journal of Vision*, *12*(4). https://doi.org/10.1167/12.4.12

Emrich, S. M., Riggall, A. C., Larocque, J. J., & Postle, B. R. (2013). Distributed patterns of activity in sensory cortex reflect the precision of multiple items maintained in visual short-term memory.

The Journal of Neuroscience: The Official Journal of the Society for Neuroscience, *33*(15), 6516–6523.

Engel, S. A., Glover, G. H., & Wandell, B. A. (1997). Retinotopic organization in human visual cortex and the spatial precision of functional MRI. *Cerebral Cortex* , *7*(2), 181–192.

Engle, R. W., Tuholski, S. W., Laughlin, J. E., & Conway, A. R. (1999). Working memory, short-term memory, and general fluid intelligence: a latent-variable approach. *Journal of Experimental Psychology. General*, *128*(3), 309–331.

Enns, J. T., & Rensink, R. A. (1990). Sensitivity to Three-Dimensional Orientation in Visual Search. *Psychological Science*, *1*(5), 323–326.

Finlayson, N. J., & Golomb, J. D. (2016). Feature-location binding in 3D: Feature judgments are biased by 2D location but not position-in-depth. *Vision Research*, *127*, 49–56.

Finlayson, N. J., & Grove, P. M. (2015). Visual search is influenced by 3D spatial layout. *Attention, Perception & Psychophysics*, *77*(7), 2322–2330.

Finlayson, N. J., Remington, R. W., Retell, J. D., & Grove, P. M. (2013). Segmentation by depth does not always facilitate visual search. *Journal of Vision*, *13*(8). https://doi.org/10.1167/13.8.11

Finlayson, N. J., Zhang, X., & Golomb, J. D. (2017). Differential patterns of 2D location versus depth decoding along the visual hierarchy. *NeuroImage*, *147*, 507–516.

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*(5), 673–679.

Golomb, J. D. (2015). Divided spatial attention and feature-mixing errors. *Attention, Perception & Psychophysics*, *77*(8), 2562–2569.

Gorgoraptis, N., Catalao, R. F. G., Bays, P. M., & Husain, M. (2011). Dynamic updating of working memory resources for visual objects. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *31*(23), 8502–8511.

Grill-Spector, K., & Malach, R. (2004). The human visual cortex. *Annual Review of Neuroscience*, *27*, 649–677.

Harrison, S. a., & Tong, F. (2009). Decoding reveals the contents of visual working memory in early visual areas. *Nature*, *458*(7238), 632–635.

He, Z. J., & Nakayama, K. (1995). Visual attention to surfaces in three-dimensional space. *Proceedings of the National Academy of Sciences of the United States of America*, *92*(24), 11155–11159.

Hollingworth, A. (2007). Object-position binding in visual memory for natural scenes and object arrays. *Journal of Experimental Psychology. Human Perception and Performance*, *33*(1), 31–47.

Hollingworth, A., & Rasmussen, I. P. (2010). Binding objects to locations: the relationship between object files and visual working memory. *Journal of Experimental Psychology. Human Perception and Performance*, *36*(3), 543–564.

Jiang, Y., Olson, I. R., & Chun, M. M. (2000). Organization of visual short-term memory. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *26*(3), 683–702.

Kooi, F. L., Toet, A., Tripathy, S. P., & Levi, D. M. (1994). The effect of similarity and duration on spatial interaction in peripheral vision. *Spatial Vision*, *8*(2), 255–279.

Lehmkuhle, S., & Fox, R. (1980). Effect of depth separation on metacontrast masking. *Journal of Experimental Psychology. Human Perception and Performance*, *6*(4), 605–621.

Linke, A. C., Vicente-Grabovetsky, A., Mitchell, D. J., & Cusack, R. (2011). Encoding strategy accounts for individual differences in change detection measures of VSTM. *Neuropsychologia*, *49*(6), 1476–1486.

Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature*, *390*(6657), 279–281.

Marshak, W., & Sekuler, R. (1979). Mutual repulsion between moving visual targets. *Science*, *205*(4413), 1399–1401.

Maunsell, J. H., & Newsome, W. T. (1987). Visual processing in monkey extrastriate cortex. *Annual Review of Neuroscience*, *10*, 363–401.

Ma, W. J., Husain, M., & Bays, P. M. (2014). Changing concepts of working memory. *Nature*

Neuroscience, *17*(3), 347–356.

McCarley, J. S., & He, Z. J. (2001). Sequential priming of 3-D perceptual organization. *Perception & Psychophysics*, *63*(2), 195–208.

Nakayama, K., He, Z. J., & Shimojo, S. (1995). Visual surface representation: A critical link between lower-level and higher-level vision. *Visual cognition: An invitation to cognitive science*, *2*, 1-70.

Nakayama, K., Shimojo, S., & Silverman, G. H. (1989). Stereoscopic depth: its relation to image segmentation, grouping, and the recognition of occluded objects. *Perception*, *18*(1), 55-68.

Nakayama, K., & Silverman, G. H. (1986). Serial and parallel processing of visual feature conjunctions. *Nature*, *320*(6059), 264–265.

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

Panichello, M. F., DePasquale, B., Pillow, J. W., & Buschman, T. (2018). Error-correcting dynamics in visual working memory. *bioRxiv*. Retrieved from https://www.biorxiv.org/content/early/2018/05/10/319103.abstract

Papathomas, T. V., Feher, A., Julesz, B., & Zeevi, Y. (1996). Interactions of Monocular and Cyclopean Components and the Role of Depth in the Ebbinghaus Illusion. *Perception*, *25*(7), 783–795.

Pashler, H. (1988). Familiarity and visual change detection. *Perception & Psychophysics*, *44*(4), 369–378.

Pasternak, T., & Greenlee, M. W. (2005). Working memory in primate sensory systems. *Nature Reviews. Neuroscience*, *6*(2), 97–107.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spatial Vision*, *10*(4), 437–442.

Pertzov, Y., & Husain, M. (2014). The privileged role of location in visual working memory. *Attention, Perception & Psychophysics*, *76*(7), 1914–1924.

Phillips, W. A. (1974). On the distinction between sensory storage and short-term visual memory. *Perception & Psychophysics*, *16*(2), 283–290.

Postle, B. R., Awh, E., Serences, J. T., Sutterer, D. W., & D'Esposito, M. (2013). The Positional-Specificity Effect Reveals a Passive-Trace Contribution to Visual Short-Term Memory. *PloS One*, *8*(12), e83483.

Qian, J., Li, J., Wang, K., Liu, S., & Lei, Q. (2017). Evidence for the effect of depth on visual working memory. *Scientific Reports*, *7*(1), 6408.

Rademaker, R. L., Bloem, I. M., De Weerd, P., & Sack, A. T. (2015). The impact of interference on short-term memory for visual orientation. *Journal of Experimental Psychology. Human Perception and Performance*, *41*(6), 1650–1665.

Rademaker, R.L., Chunharas, C., & Serences (2018). Simultaneous representation of sensory and mnemonic information in human visual cortex. *BioRxiv*, https://doi.org/10.1101/339200

Rademaker, R. L., Park, Y. E., & Sack, A. T. (2018). Evidence of gradual loss of precision for simple features and complex objects in visual working memory. *Journal of Experimental*. Retrieved from http://psycnet.apa.org/record/2018-08188-001

Rademaker, R.L., Tredway, C., & Tong, F. (2012). Introspective judgments predict the precision and likelihood of successful maintenance of visual working memory. *Journal of Vision*, 12(13), article 21: 1–13.

Rauber, H. J., & Treue, S. (1998). Reference repulsion when judging the direction of visual motion. *Perception*, *27*(4), 393–402.

Reeves, A., & Lei, Q. (2014). Is visual short-term memory depthful? *Vision Research*, *96*, 106–112.

Schurgin, Wixted, & Brady. (2018). Psychological Scaling Reveals a Single Parameter Framework For Visual Working Memory. *BioRxiv*. Retrieved from https://www.biorxiv.org/content/biorxiv/early/2018/05/18/325472.full.pdf

Scocchia, L., Cicchini, G. M., & Triesch, J. (2013). What's "up"? Working memory contents can bias orientation processing. *Vision Research*, *78*, 46–55.

Serences, J. T. (2016). Neural mechanisms of information storage in visual short-term memory. *Vision Research*, *128*, 53–67.

Serences, J. T., Ester, E. F., Vogel, E. K., & Awh, E. (2009). Stimulus-specific delay activity in human primary visual cortex. *Psychological Science*, *20*(2), 207–214.

Sereno, M. I., Dale, A. M., Reppas, J. B., Kwong, K. K., Belliveau, J. W., Brady, T. J., … Tootell, R. B. (1995). Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science*, *268*(5212), 889–893.

Sereno, M. I., Pitzalis, S., & Martinez, A. (2001). Mapping of contralateral space in retinotopic coordinates by a parietal cortical area in humans. *Science*, *294*(5545), 1350–1354.

Shin, H., Zou, Q., & Ma, W. J. (2017). The effects of delay duration on visual working memory for orientation. *Journal of Vision*, *17*(14), 10.

Simons, D. J., & Levin, D. T. (1997). Change blindness. *Trends in Cognitive Sciences*, *1*(7), 261–267.

Snow, J. C., Pettypiece, C. E., McAdam, T. D., McLean, A. D., Stroman, P. W., Goodale, M. A., & Culham, J. C. (2011). Bringing the real world into the fMRI scanner: Repetition effects for pictures versus real objects. Scientific reports, 1, 130.

Snow, J. C., Skiba, R. M., Coleman, T. L., & Berryhill, M. E. (2014). Real-world objects are more memorable than photographs of objects. *Frontiers in human neuroscience*, *8*, 837.

Sprague, T. C., Ester, E. F., & Serences, J. T. (2014). Reconstructions of information in visual spatial working memory degrade with memory load. *Current Biology*, *24*(18), 2174-2180.

Sreenivasan, K. K., Curtis, C. E., & D'Esposito, M. (2014). Revisiting the role of persistent neural activity during working memory. *Trends in Cognitive Sciences*, *18*(2), 82–89.

Störmer, V. S., Alvarez, G. A., & Cavanagh, P. (2014). Within-hemifield competition in early visual areas limits the ability to track multiple objects with attention. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *34*(35), 11526–11533.

Suchow, J. W., Brady, T. F., Fougnie, D., & Alvarez, G. A. (2013). Modeling visual working memory with the MemToolbox. *Journal of Vision*, *13*(10). https://doi.org/10.1167/13.10.9

Talbot, S. A., & Marshall, W. H. (1941). Physiological Studies on Neural Mechanisms of Visual Localization and Discrimination *. *American Journal of Ophthalmology*, *24*(11), 1255–1264.

Theeuwes, J., Atchley, P., & Kramer, A. F. (1998). Attentional control within 3-D space. *Journal of Experimental Psychology. Human Perception and Performance*, *24*(5), 1476–1485.

Treisman, A., & Zhang, W. (2006). Location and binding in visual working memory. *Memory & Cognition*, *34*(8), 1704–1719.

van den Berg, R., Shin, H., Chou, W.-C., George, R., & Ma, W. J. (2012). Variability in encoding precision accounts for visual short-term memory limitations. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(22), 8780–8785.

Vogel, E. K., McCollough, A. W., & Machizawa, M. G. (2005). Neural measures reveal individual differences in controlling access to working memory. *Nature*, *438*(7067), 500–503.

Wilken, P., & Ma, W. J. (2004). A detection theory account of change detection. *Journal of Vision*, *4*(12), 1120–1135.

Xu, Y., & Nakayama, K. (2007). Visual short-term memory benefit for objects on different 3-D surfaces. *Journal of Experimental Psychology. General*, *136*(4), 653–662.

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