The sensory strength of voluntary visual imagery predicts visual working memory capacity

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How much we can actively hold in mind is severely limited and differs greatly from one person to the next. Why some individuals have greater capacities than others is largely unknown. Here, we investigated why such large variations in visual working memory (VWM) capacity might occur, by examining the relationship between visual working memory and visual mental imagery. To assess visual working memory capacity participants were required to remember the orientation of a number of Gabor patches and make subsequent judgments about relative changes in orientation. The sensory strength of voluntary imagery was measured using a previously documented binocular rivalry paradigm. Participants with greater imagery strength also had greater visual working memory capacity. However, they were no better on a verbal number working memory task. Introducing a uniform luminous background during the retention interval of the visual working memory task reduced memory capacity, but only for those with strong imagery. Likewise, for the good imagers increasing background luminance during imagery generation reduced its effect on subsequent binocular rivalry. Luminance increases did not affect any of the subgroups on the verbal number working memory task. Together, these results suggest that luminance was disrupting sensory mechanisms common to both visual working memory and imagery, and not a general working memory system. The disruptive selectivity of background luminance suggests that good imagers, unlike moderate or poor imagers, may use imagery as a mnemonic strategy to perform the visual working memory task.

Introduction

The capacity limits of visual working memory (VWM) are highly predictive of many cognitive abilities, and are largely variable across individuals, yet the underlying cause of these capacity limits and their variance remains unclear (Bays, Catalao, & Husain, 2009; Fukuda, Awh, & Vogel, 2010; Rouder et al., 2008). The visual working memory literature is largely divided into two camps regarding the cause of these capacity limits: the discrete and flexible resource models. The discrete resource model generally proposes that there is a limited number of "slots" in memory that can each be occupied with a single item, whereas the flexible resource model posits that a finite memory resource can be spread out over many sensory items at differing degrees of precision determined by the number of items to be remembered (Bays & Husain, 2008; Fukuda et al., 2010; Rouder et al., 2008). There is substantial evidence for and against these theories, however neither theory focuses on why such large variations in capacity occur between individuals. In the neuroimaging literature there is likewise some debate as to which neural areas contribute to differences in visual working memory capacity. Some studies suggest that high-level brain areas are essential for holding visual information in working memory and it is the function or structure of these areas that influences visual working memory capacity (Bergmann, Genc, Kohler, Singer, & Pearson, 2014; Cornette, Dupont, Salmon, & Orban, 2001; Fuster, Bauer, & Jervey, 1981; Smith & Jonides, 1999). On the other hand, researchers have suggested that the early visual areas, as well as higher-level areas, are essential for maintaining highly detailed visual information in visual working memory (Albers, Kok, Toni, Dijkerman, & de Lange, 2013; Ester, Serences, & Awh, 2009; Harrison & Tong, 2009; Serences, Ester, Vogel, & Awh, 2009). A recent study using transcranial magnetic stimulation (TMS) (van de Ven & Sack, 2013) has shown that disrupting processing in early visual areas leads to an attenuation of visual working memory performance, lending support to the impor-

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tance of the early visual areas in creating, maintaining and manipulating detailed visual information in memory.

Similarly, studies using visual interference in the form of irrelevant pictures, uniform background luminance and dynamic visual noise have found similar disruptive effects on visual working memory performance (Darling, Della Sala, & Logie, 2007; Dean, Dewhurst, & Whittaker, 2008; Dent, 2010; Keogh & Pearson, 2011; McConnell & Quinn, 2000). It is thought that the presentation of irrelevant visual information leads to decreases in performance during visual working memory tasks as perceiving and remembering visual information occupy overlapping neural space (early visual cortex), which results in competition for neural resources attenuating the precision and strength of the mental representations.

When participants are asked to describe the strategies they use to complete visual working memory tasks they tend to describe one of two different types of strategies. Participants describe using one strategy that involves creating detailed mental images in their mind to compare to the subsequent test stimuli (Berger & Gaunitz, 1979; Gur & Hilgard, 1975; Harrison & Tong, 2009). These reports suggest that some participants may engage in the effortful generation of internal visual representations of the remembered items. These descriptions of the strategies employed by participants are synonymous with definitions of mental imagery, potentially implicating imagery as a possible cognitive strategy used to solve visual working memory tasks. The other type of strategy people report using in visual working memory tasks is to pick out particular details of a scene or array and encode them in a phonological or propositional form, which is then compared to the test scene or array (Berger & Gaunitz, 1979; Gur & Hilgard, 1975). This is different to the "imagery" strategy, as participants do not recreate a visual image in their mind to aide memory retention; instead they encode details of the stimulus in a more abstract or phonological form, perhaps using the language areas of the brain (i.e., Wernicke's or Broca's area).

These descriptions of strategies used for visual working memory mesh well with multicomponent theories of visual working memory. Multicomponent theories of visual working memory propose that visual working memory consists of two separate "components," the visual buffer and the visual cache (Baddeley & Hitch, 1974; Cocchini, Logie, Della Sala, MacPherson, & Baddeley, 2002; van der Meulen, Logie, & Della Sala, 2009). The visual buffer is thought to use the early visual areas to create detailed low-level sensory representations (also known as mental imagery) of the to-be-remembered items and is thought of as an "active" state that is easily interfered with by incoming sensory information due to the neural overlap of the visual buffer contents and visual perception (Borst, Niven, & Logie, 2012). The information in the visual buffer can be transferred to the visual cache, which is separate from mental imagery and is thought to be reliant on the posterior parietal cortex (Todd & Marois, 2004, 2005). The visual cache allows the temporary maintenance of the mental images and is protected from perceptual interference; however, the visual information is thought to be stored at a lower resolution or in a more abstract form than in the visual buffer (Borst, Ganis, Thompson, & Kosslyn, 2012). It is possible that the differences in strategies described by participants when completing visual working memory tasks may reflect an individual's differential use of these two components of the visual working memory system.

A recent study by Keogh and Pearson (2011) provides evidence supporting the theory that the internal voluntary creation of low-level sensory representations (also known as visual mental imagery, or the visual buffer) may be a strategy used by some participants to solve visual working memory tasks. This study found a significant positive correlation between visual imagery strength and visual working memory performance, but not with iconic memory. In addition, passively viewing background luminance, thought to interfere with the creation of low-level visual representations in the visual buffer (Borst, Niven, et al., 2012), during memory retention attenuated visual working memory performance. However, this effect was only observed for individuals with strong mental imagery, suggesting that perhaps only good imagers use their visual imagery (the visual buffer), to store visual information during visual working memory tasks. Interestingly some individuals in the poor imagery group still performed well on the visual working memory task suggesting that imagery was being used as a mnemonic to support visual working memory and not the other way around, because, if visual memory was being used in the imagery task, these participants should also have performed better on the imagery task.

Likewise, a recent functional imaging study demonstrated that it was possible to decode the content of visual working memory in primary visual cortex. Of particular interest here was the finding that they could still decode the content of visual working memory even when the algorithm was trained on visual imagery, not memory (Albers et al., 2013). This study provides a nice demonstration that voluntary visual imagery and visual working memory can overlap in their sensory representations.

However, these previous studies only examined participants' accuracy, not capacity, of visual working memory. Here we developed a task that requires

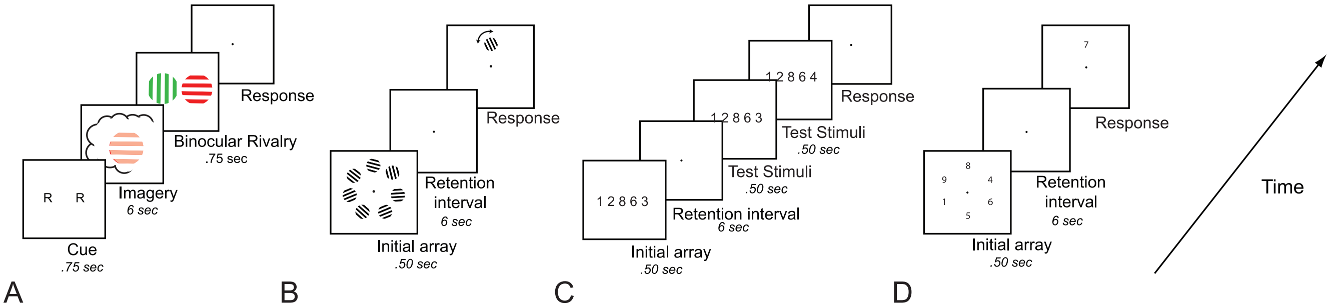

Figure 1. Experimental timelines. (A) During the imagery task, participants were instructed to imagine a red or green Gabor patch for 6 s; following this exercise, they were presented with a brief binocular rivalry display and were asked to indicate which image was dominate. (B) In the visual working memory (VWM) task, participants were presented with three to nine Gabor patches at varying orientations and were asked to remember these for 6 s. This was followed by a test Gabor patch and participants were asked to indicate whether it had been rotated 25° clockwise or anticlockwise compared to the corresponding Gabor patch in memory. (C) For the number working memory (NWM) task, participants were presented with a string of numbers anywhere from five to 11 digits long and were instructed to remember these for 6 s. Participants were then presented with two number strings consecutively, and were asked to indicate whether the first or second number string was the same as the one they were instructed to remember. (D) In the spatial number working memory (SNWM) task, participants were presented with five to 11 numbers in a circular array and were asked to remember these for 6 s. This was followed by a test number at one of the to-be-remembered number locations, and participants were asked to indicate whether this number was one number higher or lower than the number held in mind.

participants to hold three to nine oriented Gabor patches in visual working memory, to measure capacity limits of a participant's visual working memory (see Figure 1B). To measure imagery strength we used the previously documented binocular rivalry method (see Figure 1A; Keogh & Pearson, 2011; Pearson, Clifford, & Tong, 2008; Pearson, Rademaker, & Tong, 2011; Rademaker & Pearson, 2012; Sherwood & Pearson, 2010), see Pearson (2014) for an overview. Binocular rivalry involves presenting a different visual pattern to each eye, which results in one image becoming dominant while the other is suppressed from awareness. Previous studies have demonstrated that when participants are instructed to voluntarily imagine one of these two patterns, it has a higher probability of becoming the dominant image during a subsequent brief binocular rivalry display (Keogh & Pearson, 2011; Pearson et al., 2008; Sherwood & Pearson, 2010). Both trial-by-trial and subsequent questionnaire measures of subjective imagery vividness have been shown to correlate with imagery strength measured by percent primed during the binocular rivalry task. Many experiments have now shown that these behavioral measures are independent of response bias by using different types of catch trials (Pearson et al., 2011), are reliable when assessed over time (Rademaker & Pearson, 2012), and have demonstrated that imagery conforms to the known characteristics of early visual cortex that are unknown to naïve participants (Pearson et al., 2008). Research using this method has also shown that imagery can be dissociated from visual attention (Pearson et al., 2008), and that the surrounding environmental conditions can affect the strength of imagery generation (Chang, Lewis, & Pearson, 2013; Keogh & Pearson, 2011; Pearson et al., 2008; Sherwood & Pearson, 2010).

Luminance was again included in the current study as a causative or perturbation method to investigate the different strategies, or components, of visual working memory participants' use. Luminance is thought to have obligatory access to the visual buffer, and as such will interfere with the creation and maintenance of low-level sensory representations held in mind (Borst, Ganis, et al., 2012). If participants are using imagery, or the "visual buffer," as a mnemonic for solving the visual working memory task we might expect that luminance would attenuate their performance on the visual working memory task and reduce the number of items they are able to hold in mind. However, if participants are using the visual cache to maintain visual information luminance should have no effect on the capacity limits of visual working memory.

The current results support the previous study by Keogh & Pearson (2011), imagery strength correlated with visual working memory capacity. "Good imagers" were found to have superior capacity for visual working memory; however, in the presence of luminance good imagers no longer performed any differently to either moderate or poor imagers on the memory task. Our findings suggest that imagery, or the use of the visual buffer, may be a cognitive tool of sorts, used in visual working memory tasks, which allows for superior performance. However, the attenuating effect of luminance suggests that only some participants (good imagers) use imagery, or use it to a useful degree, during visual working memory.

Method

Participants

Thirty-six undergraduate students (24 females, aged 18–35) participated in the first study in exchange for course credit. Twenty-one undergraduate students (11 females, aged 18–40) participated in the spatial number working memory experiment. All participants had normal or corrected to normal vision. All participants completed each measure of memory and imagery. Three participants were not included in the analysis, as the exponential decay model did not fit their data.

Informed written consent was obtained from all participants, and all experiments were approved by the UNSW Human Research Ethics Advisory Panel (Psychology).

Apparatus

All of the tasks were performed in darkened rooms with black walls on a 19-inch Philips Brilliance 109P4 monitor with a resolution of 1,280 × 960 pixels and a refresh rate of 75 Hz (Philips, Amsterdam, Netherlands), driven by an iMac computer (Apple, Cupertino, CA). Experiments were run in MATLAB (MathWorks, Natick, MA), using Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). A fixed viewing distance of 57 cm for all experiments was obtained using a chinrest, and participants were instructed to maintain fixation on the bull's-eye (a fixation point) at all times throughout the experiment, which acted as a fusion lock in the rivalry conditions to maintain the binocular rivalry illusion. For the binocular rivalry experiment participants wore red–green anaglyph glasses.

Stimuli

In the imagery task the binocular rivalry stimuli consisted of red horizontal (CIE $x = .277$, $y = .613$) and green vertical (CIE $x = .601$, $y = .368$) Gabor patterns, 1 c/°, Gaussian $\sigma = 1.25°$. The patterns were presented in an annulus around the fixation point and both Gabor patterns had a mean luminance of 7.8 cdm^2. The background was black throughout the entire task during the no luminance conditions. For the imagery luminance condition the background ramped up to yellow (a mix of the green and red colors used for the rivalry patterns, with luminance at 7.8 cdm^2) during the 6-s imagery period. During this period the background luminance was smoothly ramped up and down to avoid visual transients, which may result in attention being directed away from the task.

Mock rivalry displays were included to assess any effects of decisional bias in the imagery task. One half of the mock rivalry stimulus was a red Gabor patch with the other half being a green Gabor patch (a spatial mix) and they shared the same parameters as the green and red Gabor patches mentioned in the previous paragraph. The mock rivalry stimuli were spatially split with blurred edges and the exact path differed on each catch trial (random walk zigzag edge) to resemble actual piecemeal rivalry.

The stimuli in the visual working memory task consisted of three to nine Gabor patterns (1 c/°, Gaussian $\sigma = .75°$) at 70% contrast. The Gabor patterns were presented in a circular annulus around the bull's-eye fixation point. The background was black for the duration of the experiment, with the exception of the retention interval during the luminance condition where the background ramped smoothly up and down to white during the 6-s retention interval.

All numbers in the verbal number-string working memory experiment were white, presented on a black background (Times New Roman; .6° in height). In the number-string memory task the numbers were presented centrally in a straight line. During the retention interval, the background was black for the no-luminance condition and ramped up to white in the luminance condition.

All numbers in the spatial number working memory experiment were white presented on a black background (Times New Roman; .5° in height). The numbers were presented in a circular annulus around the bulls eye fixation point.

Procedure

Binocular rivalry

Individual differences in eye dominance can lead to a perceptual bias for one eye. For this reason, participants underwent an eye-dominance test procedure prior to the imagery task, as previously documented (Pearson et al., 2008; Pearson, Rademaker, & Tong, 2011; Rademaker & Pearson, 2012; Sherwood & Pearson, 2010).

During all tasks, participants were instructed to maintain fixation on a bull's-eye at all times. Participants were presented centrally with an "R" or "G" at the beginning of each trial which cued them to imagine either a red horizontal (R) or green vertical (G) Gabor patch (see Figure 1A). This cue was randomized on each trial and each cue appeared an equal number of times. Participants were instructed to imagine this image for the entire imagery period (6 s). Participants were then presented with a rivalry display for 750 ms and asked to indicate which pattern was dominant by pressing the corresponding key (1 = green vertical, 2 = equally mixed percept, 3 = red horizontal). Mixed nonrivalrous mock rivalry trials were included to check for any possible effects of demand characteristics.

For a quarter of all trials participants were presented with a mock rivalry catch trial stimulus (consisting of half green vertical and half red horizontal displays). Participants should always respond to these displays as being a mix (i.e., they should always press number "2" as this stimulus is completely stable, nonambiguous, and hence, is not liable to perceptual priming from imagery). If subjects report the mock rivalry stimulus as unitary (e.g., all red), this can indicate that participants may not be completing the task properly or demonstrating participant bias. Participants completed a total of 80 imagery trials, with 40 in the luminance condition and 40 in the no luminance condition. The order of conditions was counterbalanced across participants.

Visual working memory

The visual working memory (VWM) task used in this experiment measures individuals' visual working memory capacity (see Figure 1B). Participants were presented with three to nine Gabor patterns for 500 ms and were asked to remember all of the Gabor patterns' spatial locations and orientations for a retention interval of 6 s. Following this, participants were presented with a single test pattern in one of the locations in the original array. The test pattern was always rotated either clockwise or anticlockwise by 25° compared to the corresponding pattern in memory. Participants were told to identify whether the pattern had been rotated 25° clockwise or anticlockwise compared to the remembered image by pressing the right or left arrow keys, respectively. All participants completed six trials of each set size (three to nine or one to seven [in the control spatial number memory experiment]) in a randomized order resulting in a total of 84 trials, with 42 in the luminance and 42 in the no luminance condition.

Number-string working memory

The number-string working memory (NWM) task used here is an adaptation of the one used in Keogh and Pearson's (2011) study. Here we changed the task to measure capacity instead of accuracy (see Figure 1C). In this task participants were presented with a number string of five to 11 numbers and are instructed to remember them for 6 s. Following this exercise, two strings of numbers were presented sequentially. One of these numbers was identical to the to be remembered string while one was different by one number in the string. Participants were to indicate which number was the *same* by pressing "1" if they thought the number string presented first was the same or "2" if they thought the second was the same. All participants completed six trials of each set size (five to 11) in a randomized order resulting in a total of 84 trials, with 42 in the luminance and 42 in the no luminance condition.

Spatial number working memory

The spatial number working memory (SNWM) task was included in a second experiment. We wanted to make sure results were not due to differences in the task design (the number working memory task presented participants with two full test displays while the visual working memory task presented one test item). To make the number working memory task more similar to the visual working memory task, participants were presented with five to 11 numbers in a circular array (see Figure 1D). Participants were instructed to remember the numbers and their spatial locations for 6 s. Following this, participants were presented with a single number at one of the locations of the original array. This number was either one number higher or lower than the remembered number at that spatial location. Participants were instructed to indicate whether this new number was one number higher or lower than the to-be-remembered number by pressing ">" arrow or "<" arrow, respectively. All participants completed six trials of each set size (five to 11) resulting in a total of 42 trials.

Results

Correlational data

Figure 2A shows a significant positive correlation, $r(32) = 0.57$, $p < 0.001$, between imagery strength (measured as percent primed) and visual working memory (measured as percent correct at the set size three). We have shown the results for set size three (Figure 2) as this is the set size at which working memory fidelity typically reaches asymptote (Anderson, Vogel, & Awh, 2011; Zhang & Luck, 2008), and was the set size that showed the most variation across out participants. Four participants perform below chance at set size three, and when they were removed from the analysis, the correlation between imagery strength and visual working memory at set size three remains strong and significant, $r(28) = 0.71$, $p < 0.0001$. Imagery strength was also positively correlated with

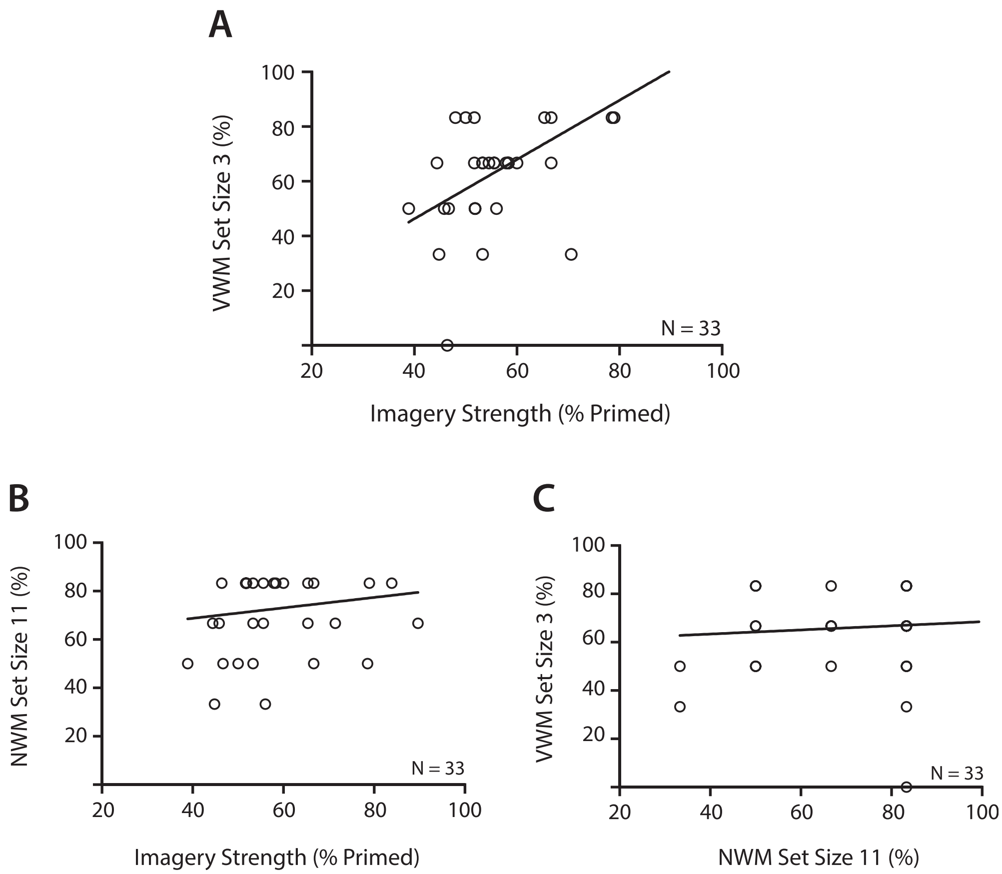

Figure 2. Correlation results. Each dot shows an individual participant ($N = 36$) and the trend lines show a linear fit to the data. (A) Imagery ability was predictive of visual working memory at a set size of three. (B) There was no significant correlation between imagery ability and number working memory at a set size of 11. (C) Similarly, there was no correlation between participants' visual memory or number working memory performance at a set size of three and 11, respectively.

performance at set size four for visual working memory, $r(32) = 0.48$, $p < 0.01$, but was not significant at any higher set sizes (all $p > 0.36$). Figure 2B and C show performance at set size 11 on the verbal number working memory as this set size had the most variation across participants. We found that there was no significant correlation between number working memory performance at set size 11 and either imagery strength, $r(32) = 0.18$, $p = 0.33$ (Figure 2B), or visual working memory performance, $r(32) = 0.03$, $p = 0.86$, (Figure 2C). Both of these r values were significantly different from the r value for the positive correlation between visual working memory (set size three) and imagery strength (Williams, t-test between nonindependent Rs for: NWM and imagery, $t(32) = 1.82$, $p < 0.05$; and NWM and VWM, $t(32) = 2.77$, $p < 0.05$. There were no significant correlations for any set size of number working memory and imagery (all $p > 0.12$) or visual working memory (all $p > 0.06$), except for visual working memory at set size four and number working memory at set size nine, $r(32) = 0.38$, $p = 0.03$. Taken together, these data suggest that those participants who have good visual mental imagery also have larger visual working memory capacity; however, good imagers perform no better than poor imagers on a general working memory task.

We were worried that the lack of correlation between imagery and number memory may be due to differences in the task design, rather than the use of a different component of working memory. To assess this, we designed a new experiment to test numerical working memory that was more similar to the visual working memory task (see Figure 1D). Participants also completed the same visual memory and imagery tasks. We again found that with the new number memory task there was no correlation between performance in this task and the imagery strength (all ps > 0.08). Likewise, there were no correlations between this task and performance on the visual working memory task (all ps > 0.08) except for visual working memory at set size one and number working memory at set size five and six, $r(20) = 0.68$, $p < 0.01$ and $r(20) = 0.48$, $p < 0.05$. These results suggest that the lack of correlation between imagery and the number working memory task is not due to task differences but instead due to

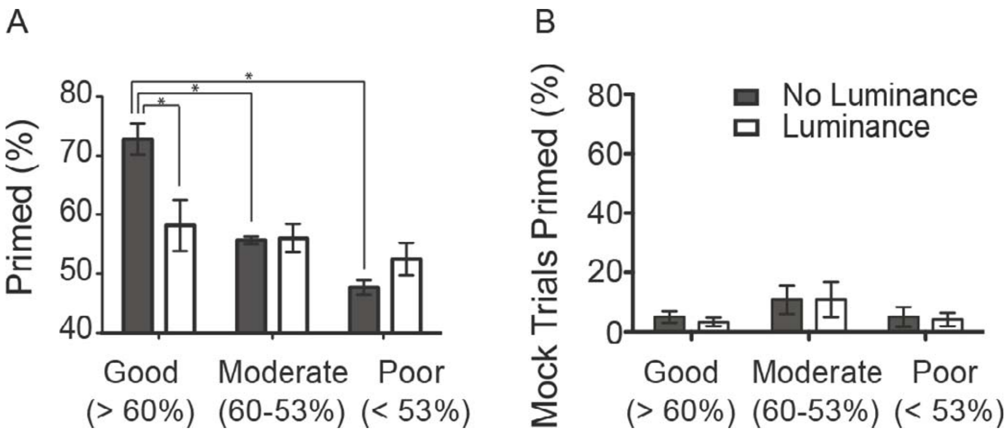

Figure 3. Imagery and mock trial data. (A) Good imagers show significantly more priming from imagery than moderate or poor imagers. Luminance attenuates imagery priming but only for good imagers. (B) There are no significant differences across any of the groups for the percent of mock trials primed.

participants' use of different components of the working memory system.

Background luminance manipulations

We hypothesized that superior performance by good imagers on the visual working memory task might be due to the use of imagery as a mnemonic to solve the visual working memory task. Previous studies have shown that including background luminance during imagery generation disrupts imagery formation and maintenance (Keogh & Pearson, 2011; Pearson et al., 2008; Sherwood & Pearson, 2010). If participants are using visual imagery to assist in the visual working memory task, the presence of luminance during the retention period might likewise result in a decrease in visual working memory capacity. However, if imagery is not being used as a strategy by participants we should see no difference in performance on the visual working memory task in regards to background luminance.

To investigate different strategies used by individuals we split our participants into good, middle, and poor imagers (an even ranked split into three groups), based on their score in the imagery task (imagery strength; see Figure 3A). If good imagers' higher capacity in the visual working memory task is due to the use of imagery/visual buffer, we should see a decrease in their performance in the presence of background luminance. Likewise, if poor and moderate imagers' lower accuracy is due to a heavier reliance on the visual cache and not imagery, we should expect little to no effect of luminance on their visual working memory performance. Imagery strength was measured by the percent of trials that were primed in accordance with the imagery cue. A high level of priming indicates that a participant has strong visual imagery. A significant interaction between imagery strength and the presence of luminance was found, $F(2, 30) = 24.57$, $p < 0.0001$. Without luminance, post hoc analysis using the Bonferroni correction found that good imagers performed significantly better than both moderate ($p < 0.0001$) and poor ($p < 0.0001$) imagers (Figure 3A). However, when luminance was present there was no difference in performance for any of the groups of participants on the imagery task ($p > 0.05$ for all comparisons). Luminance was also found to selectively reduce performance on the imagery task only for good imagers (pairwise comparison $p < 0.0001$ with Bonferroni correction for multiple comparisons). Figure 3B shows the percent of mock trials showing a bias in the direction of priming (i.e., inline with the imagery cue). Mock trials were included to identify any possible nonperceptual bias effects. There were no differences for nonperceptual priming between the imagery groups, $F(2, 30) = 1.78$, $p = 0.18$, nor was there an effect of luminance, $F(2, 30) = 0.06$, $p = 0.81$, demonstrating that it is unlikely that our results are due to nonperceptual bias.

Figure 4 shows participants' performance on the visual working memory and number working memory capacity tasks. In Figure 4A, the x-axis shows set size while the percent correct is displayed on the y-axis. Data are split by imagery strength into three groups; good imagers (green line), moderate imagers (blue line), and poor imagers (red line). The top left panel of Figure 4A shows a main effect of set size when averaging across all participants, $F(6, 180) = 2.45$, $p < 0.05$. Post hoc analysis using the Bonferroni correction for multiple comparisons shows that good imagers performed significantly better than both poor and moderate imagers at a set size of three: moderate ($p < 0.05$), poor ($p < 0.05$); and set size of four, moderate ($p < 0.05$), poor ($p < 0.01$). However, there were no significant differences across imagery groups for any other set sizes.

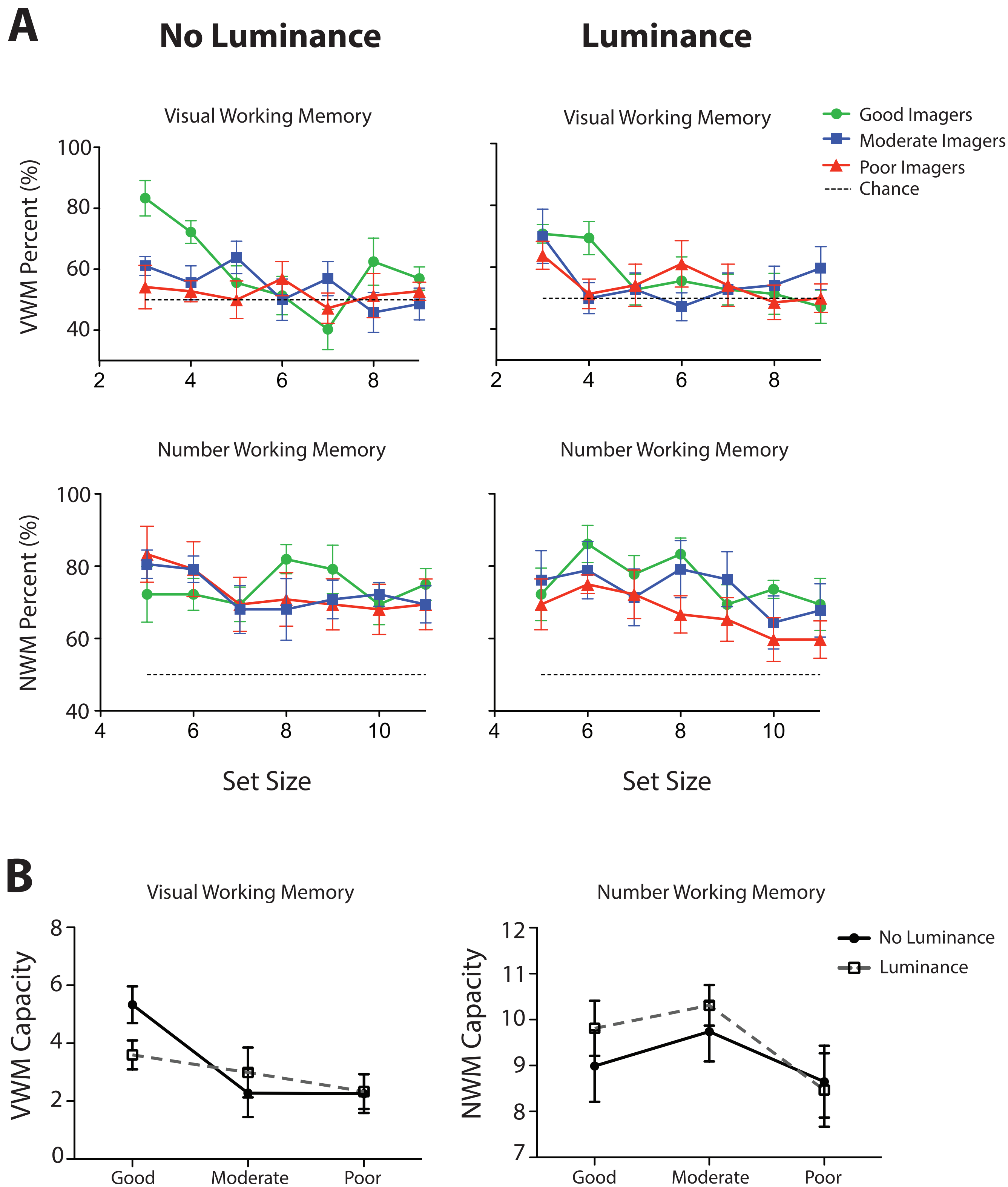

Figure 4. Visual working memory and number working memory set size and capacity graphs. (A) The top row of the graph shows good, moderate, and poor imagers' performance on the visual working memory capacity task without (left panel) and with luminance (right panel). The bottom row of the graph shows good, middle, and poor imagers' performance on the number working memory capacity task without (left panel) and with luminance (right panel). (B) The left panel shows good, moderate, and poor imagers' visual working memory capacity with (gray dotted line) and without (black line) luminance. The right panel shows good, moderate, and poor imagers' number working memory capacity with (gray dotted line) and without (black line) luminance.

A number working memory task was also included to see if this pattern extended to other forms of working memory. The bottom row of Figure 4A shows the results for participants on the number working memory task. The left bottom panel shows that there are no differences in accuracy for the three imagery groups when the background was a constant black, with no significant interaction, $F(12, 180) = 0.66$, $p = 0.79$, or main effects of imagery strength, $F(2, 30) = 0.128$, $p = 0.29$, or set size, $F(6, 180) = 1.58$, $p = 0.16$.

Luminance was also included to assess whether participants were using imagery as a strategy to solve the visual working memory task. When luminance was presented during the retention period of the visual working memory task, good imagers no longer performed differently to the moderate or poor imagers (top right of Figure 4A) with no significant interaction between imagery strength and set size, $F(12, 180) = 1.48$, $p = 0.13$, or a main effect of imagery strength, $F(2, 30) = 0.06$, $p = 0.94$. A main effect of set size was observed, $F(6, 180) = 2.24$, $p < 0.05$; however, post hoc analysis using the Bonferroni correction for multiple comparisons found no differences on performance for any of the set sizes.

To confirm that the effect of luminance is specific to low-level visual representations held in mind, we included the luminance manipulation during the number working memory task (Figure 4A: bottom row, right column). There was no effect of luminance on performance for this task with no significant interaction between imagery strength and set size, $F(12, 180) = 0.51$, $p = 0.91$, or any significant main effects for either imagery strength, $F(2, 30) = 1.77$, $p = 0.19$, or set size, $F(6, 180) = 1.89$, $p = 0.08$. This lack of interference from luminance suggests that luminance was only having an effect on low-level sensory representations held in mind, and does not interfere with the general mechanisms of working memory.

To ensure our findings are not specific to, or only driven by participants' accuracy, at set size of three and four we examined a different measure of capacity for each individual for both types of memory. To attain a single value estimate of each individual's memory capacity that takes all their data points into account, we fit an exponential decay function through each subject's accuracy versus set size data. We then found the set size value at which participants were performing at 66.7% correct, and this set size was used as a participant's memory capacity value. A score of 66.67% correct was used as a threshold as this was the value where participants were performing just above chance. Figure 4B shows the capacity values for good, moderate, and poor imagers on the visual working memory task (left panel) and the number working memory task (right panel).

A main effect of imagery strength was found for visual working memory capacity (left side of Figure 4B: $F(2, 30) = 4.48$, $p < 0.05$. Pairwise comparisons (Bonferroni correction) revealed that good imagers had greater visual working memory capacity than both poor and moderate imagers ($p < 0.016$ for both comparisons) when performing the task without background luminance.

In line with the findings for number working memory's accuracy versus set size functions, good, moderate, and poor imager's number working memory capacities were no different from each other (see right side of Figure 4B), with no significant interaction, $F(2, 30) = 0.44$, $p = 0.65$, or main effects of imagery strength, $F(2, 30) = 1.68$, $p = 0.20$, or luminance, $F(1, 30) = 0.8$, $p = 0.38$. This suggests that the good imagers superior performance is restricted to visual working memory and not just a general memory superiority.

The same attenuation effect of luminance, seen in the full set size functions, was also found for visual working memory capacities. Good imagers no longer had significantly larger VWM capacities than poor or moderate imagers in the presence of luminance (see Figure 4B, all $p > 0.57$). Good imagers were also the only group to show any effect of luminance, with their performance being significantly worse in the luminance condition (pairwise comparison $p < 0.05$ with Bonferroni correction for multiple comparisons). In line with the number working memory accuracy versus set size functions, number working memory capacities were unaffected by the presence of luminance with no significant interactions or main effects for imagery strength or luminance (all $p > 0.2$, see left of Figure 4B). Pairwise comparisons also showed no reduction in performance for any of the groups when luminance was or wasn't present (all $p > 0.30$). This indicates that the luminance is primarily having an effect on low-level visual representations and not a general attentional interference effect.

Discussion

Our results dovetail nicely with the previous findings of Keogh and Pearson (2011), demonstrating that imagery strength predicts visual working memory ability. However, the current results go beyond previous findings linking stronger mental imagery with greater visual working memory capacity. Importantly, there were no significant differences in performance on a number working memory task for any of the groups of imagers, suggesting that the good imagers' superior performance on the visual working memory task is specific to sensory-based mechanisms. In line with these findings, the previous study by Keogh and Pearson

(2011) found no correlation between iconic memory, a number working memory task, or a rapid letter detection task. Taken together it seems highly unlikely that the significant correlation between imagery and visual working memory is due to differences in general working memory mechanisms, general task effort, or attention.

Interestingly, good imagers perform significantly better than both middle and poor imagers in the no luminance condition. To assess why good imagers' performance was superior to the moderate and poor imagers on the visual working memory task, we included a background luminance condition. Luminance, during the retention period of the visual working memory and imagery generation period (but not during the test stimulus), was included as a causal means to assess whether participants were using different strategies or different components of visual working memory to complete this memory task. Previous studies have shown that seemingly irrelevant passive visual information disrupts visual imagery tasks (Baddeley & Andrade, 2000; Keogh & Pearson, 2011; Pearson et al., 2008; Sherwood & Pearson, 2010). However, the literature has been split as to whether irrelevant visual information disrupts visual working memory or not, with some studies showing interference (Darling et al., 2007; Dean et al., 2008; Dent, 2010; McConnell & Quinn, 2000), while others report no degradation in participants' performance (Darling et al., 2007; Darling, Della Sala, & Logie, 2009; van der Meulen et al., 2009). These findings, although seemingly inconsistent, support the multicomponent theory of visual working memory.

The multicomponent theory of visual working memory suggests that there are two components to visual working memory—the visual buffer and the visual cache. The visual buffer allows for the retention of highly detailed and rich visual information using the early visual areas. However, incoming visual information, which has obligatory access to the early visual areas, can interfere with these internal sensory representations. Information in the visual buffer can be transferred to another component of visual working memory, the visual cache. The visual cache protects visual information from being degraded by incoming sensory information, however this protection results in a tradeoff: security from afferent sensory signals at the cost of a loss in fidelity.

It has been suggested that the contradictory findings regarding interference by irrelevant sensory information may be due to differences in task difficulty or stimuli complexity (Andrade, Kemps, Werniers, May, & Szmalec, 2002; Borst, Niven et al., 2012; Dent, 2010). These works suggest that studies demonstrating interference required participants to maintain highly detailed visual information in order to complete the tasks and, as such, required participants to use the visual buffer in order to do so. For example Dent (2010) required participants to keep the precise color of objects in mind to perform the memory task. This study required very detailed mental representations in order to complete the task and, as such, found interference from irrelevant visual stimuli. The studies that failed to find interference from irrelevant sensory stimuli did not require participants to maintain highly detailed visual information (Darling et al., 2007, 2009; van der Meulen et al., 2009). For instance, van der Meulen et al. (2009) found no disruption from static interference on their memory task; however, their task used memory for letters, which do not need to be retained with high precision in order to be remembered. As such, participants may have been able to use the visual cache, which is less prone to interference, to store visual information. It is possible that the lack of visual interference found in some studies reflects participants' use of the visual cache instead of the visual buffer to remember information. Alternately, the mixed findings regarding disruption by irrelevant visual stimuli may be due to individual differences in the strategies employed by the participants. For example, if the majority of participants in a study used the visual buffer as a mnemonic for task performance, we should expect interference from irrelevant visual information to occur. However, if a large proportion of participants were using the visual cache for task completion, we would not expect to see any effect on performance from irrelevant visual information.

Our study found individual differences in the effect of irrelevant passive visual information on a visual working memory task. For those participants with good imagery, irrelevant visual information in the form of increased background luminance, reduced participants' visual working memory capacity. However, luminance had no effect on moderate or poor imagers' visual working memory capacities. These findings may reflect the different strategies or components of visual working memory used by participants. Perhaps good imagers used the visual buffer to maintain very detailed information during the task and, as such, performed better than their counterparts who used the visual cache to store less precise information. However, when luminance was introduced, good imagers performance drops to the same level as moderate and poor imagers, due to the deterioration of their internal images by the irrelevant visual information. Alternatively, the introduction of irrelevant information may lead to the inability to use the visual buffer and results in good imagers having to use the visual cache in the same way moderate and poor imagers do. It will be interesting to see if future research can tease apart these two hypotheses.

The current results suggest that the use of the visual buffer, or visual imagery, as a strategy during visual working memory results in better performance when highly detailed information is necessary for task completion. It will be interesting to find out why some participants do not, or perhaps cannot, use the visual buffer when completing visual working memory tasks when it may offer an advantage. Whether or not moderate and poor imagers use a different strategy (and neural machinery) compared to good imagers during visual working memory tasks, or just perform poorly due to poor imagery "machinery" cannot be answered by the current data. Exploring the different neural substrates of imagers of varying abilities may help answer this question. A recent study has shown that when participants complete a mental rotation task there are interindividual differences in the neural networks involved. Good imagers had greater activation in the visual cortex, whereas poor imagers show greater activity in the fronto-parietal network. The authors suggest that different participants used different cognitive strategies for the same task (Logie, Pernet, Buonocore, & Della Sala, 2011).

Examining differences in strategies and neural networks for visual working memory may help discern whether good imagers use different neural areas (namely the early visual areas), to their poor and moderate counterparts, or if they use the same neural areas in a superior way. This line of research may also explain some of the contention in the literature regarding neural correlates of visual working memory. It is no surprise that if individuals use different strategies and, as such, different neural areas, this would result in conflicting results between studies, especially if they have a disproportionate number of either good or poor imagers in a study. Understanding the individual differences in strategies and neural correlates used by people may help to inform possible future training programs for improving visual working memory and help to enrich our current understanding of working memory as a whole.

If individuals use different strategies, or rely more heavily on either the visual buffer or cache during visual working memory tasks this may have ramifications for discrete and fixed theories of visual working memory. If there are two components to visual working memory, it may be that one component of visual working memory is a dynamic system while the other is fixed. It is possible that the visual buffer has a fixed number of "slots" that can be maintained, due to the retinotopic architecture of the early visual cortex (Franconeri, Alvarez, & Cavanagh, 2013), whereas the visual cache may have its own discrete limits, due to its nonsensory characteristics. Understanding the interplay and interindividual differences in the use of these two components of visual working memory will ultimately result in more complete, robust theories of visual working memory.

Keywords: mental imagery, visual working memory, individual differences, memory capacity, verbal working memory, perceptual disruption

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