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The bandwidth of consolidation into visual short-term memory depends on the visual feature

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We investigated the nature of the bandwidth limit in the consolidation of visual information into visual short-term memory. In the first two experiments, we examined whether previous results showing differential consolidation bandwidth for colour and orientation resulted from methodological differences by testing the consolidation of colour information with methods used in prior orientation experiments. We briefly presented two colour patches with masks, either sequentially or simultaneously, followed by a location cue indicating the target. Participants identified the target colour via buttonpress (Experiment 1) or by clicking a location on a colour wheel (Experiment 2). Although these methods have previously demonstrated that two orientations are consolidated in a strictly serial fashion, here we found equivalent performance in the sequential and simultaneous conditions, suggesting that two colours can be consolidated in parallel. To investigate whether this difference resulted from different consolidation mechanisms or a common mechanism with different features consuming different amounts of bandwidth, Experiment 3 presented a colour patch and an oriented grating either sequentially or simultaneously. We found a lower performance in the simultaneous than the sequential condition, with orientation showing a larger impairment than colour. These results suggest that consolidation of both features share common mechanisms. However, it seems that colour requires less information to be encoded than orientation. As a result, two colours can be consolidated in parallel without exceeding the bandwidth limit, whereas two orientations or an orientation and a colour exceed the bandwidth and appear to be consolidated serially.

Keywords: Visual memory; Consolidation; Bandwidth.

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Successful visual behaviour requires the ability to process information from dynamic, continuously changing surroundings. Visual information processing thus entails the creation and storage of durable representations of the fleeting characteristics of a given fixation. This durable storage is commonly referred to as visual short-term memory (VSTM). It is generally accepted that VSTM can hold about 3–4 items for simple visual features (Luck & Vogel, 1997; Pashler, 1988), although whether such a capacity limit reflects limits in discrete slots or continuous resources is currently under intense debate (Bays & Husain, 2008; Wilken & Ma, 2004; Zhang & Luck, 2008). Regardless of the nature of such capacity limit, the need to process highly dynamic input has led to the suggestion that the visual system can rapidly encode and consolidate new items into VSTM, although at the expense of losing old items (Ballard, Hayhoe, & Pelz, 1995; Becker & Pashler, 2002; O'Regan, 1992; Wolfe, Klempen, & Dahlen, 2000).

Previous research suggests that the consolidation process itself has a limited capacity, or bandwidth. For example, several studies varied the set size of a briefly presented memory array and found worse performance as the set size increased, despite the fact that even the larger set sizes were small enough that they should not have exceeded the storage limit of VSTM (Jolicœur & Dell' Acqua, 1998; Vogel, Woodman, & Luck, 2006; West, Pun, Pratt, & Ferber, 2010). These findings are consistent with the view that the bandwidth of VSTM consolidation is limited. However, varying set size might also introduce different amounts of decision noise or interference among items (Eckstein, Thomas, Palmer, & Shimozaki, 2000; Palmer, Verghese, & Pavel, 2000). As the number of items in the memory set increases, the number of decisions at test also increases (e.g., in change detection task, participants need to decide whether each item changed). In addition, memory representations for different items could interfere with each other (e.g., due to similarity), and the more items to be maintained, the more likely that interference will occur. Thus, the findings of worse performance with higher set sizes could be attributable to either consolidation limits or limits in postconsolidation processes.

We recently employed a sequential/simultaneous paradigm to investigate the bandwidth limit of consolidation (Becker, Miller, & Liu, 2013; Liu & Becker, 2013; Mance, Becker, & Liu, 2012). This method allows an investigation of consolidation while holding the memory load, decision noise, and interference constant. In this paradigm, two items are briefly presented and masked, either sequentially or simultaneously (Duncan, 1980; Hoffman, 1978; Shiffrin & Gardner, 1972). Comparing performance in the sequential and simultaneous condition allows one to infer whether or not multiple items can be consolidated in parallel (Scharff, Palmer, & Moore, 2011a, 2011b). In both conditions, the memory load is the same, while the number of items that need to be *concurrently* consolidated differs. Better performance in the sequential condition implies either a serial or limited-capacity parallel process, whereas equivalent performance in the two conditions implies a parallel process.

Using the sequential/simultaneous paradigm, we have investigated the consolidation of orientation and colour information and have obtained different results. In the colour experiments, we found equivalent performance in the sequential and simultaneous condition, suggesting a parallel process up to two items (Mance et al., 2012). However, in the orientation experiments, we found better performance in the sequential than the simultaneous condition (Becker et al., 2013), suggesting a serial (or limited-capacity parallel) process. Furthermore, using a continuous measure of memory precision, we were able to demonstrate that consolidation of orientation information is strictly serial (Liu & Becker, 2013).

These results suggest that the bandwidth of consolidation depends on the visual feature and provide strong constraints on theories of VSTM consolidation. However, before accepting the notion that colour and orientation have different consolidation bandwidths, it is necessary to exclude procedural differences that might have contributed to our initial observations. Specifically, most of our orientation experiments (Becker et al., 2013; Liu & Becker, 2013) required the orientations to be bound to a specific spatial location, whereas our colour experiments did not require this binding (Mance et al., 2012). It is possible that this methodological difference accounts for the observed bandwidth difference. To investigate this possibility, Experiment 1 investigated the consolidation of colours using a method that required the colours to be bound to a specific spatial location, thereby replicating our orientation methods. In Experiment 2, we measured memory precision and used a mixture model (Liu & Becker, 2013; Zhang & Luck, 2008) to provide converging evidence regarding the nature of the consolidation process for colour. Finally, in Experiment 3, we paired a colour stimulus with an orientation stimulus in the sequential–simultaneous paradigm to further probe the dependence of VSTM consolidation on visual features.

EXPERIMENT 1

Our prior experiments suggesting the parallel consolidation of two colours (Mance et al., 2012) involved the presentation of two test stimuli followed by a probe stimulus at fixation. Participants were required to indicate whether or not the probe colour matched either of the test stimuli. By contrast, most of our previous experiments suggesting the serial consolidation of orientation (Becker et al., 2013, Exps. 1a, 1b, and 2; Liu & Becker, 2013) presented a box outline at the location of one of the test stimuli, and participants had to indicate the orientation of that probed item. Thus, a key difference between these methods was that the orientation experiments required observers to bind each orientation to a specific spatial location, but the colour experiments did not. Although features may necessarily be bound to their spatial locations during initial encoding (Treisman & Zhang, 2006), this spatial binding may dissipate once the item is fully consolidated into working memory (Logie, Brockmole, & Jaswal, 2011; Woodman, Vogel, & Luck, 2012). Thus, it is possible that the orientation experiments found lower consolidation bandwidth because they required the orientation to be bound to spatial locations at the time of report. If the feature-location binding was lost between consolidation and report, the requirement to use the location cue may necessitate additional processing. The colour experiments did not require this additional processing, which may have produced a greater consolidation bandwidth. To investigate this possibility, in Experiment 1 we examined the consolidation of colour information using the same type of location probe that we have previously used in our orientation experiments.

Methods

Participants. Participants were 12 students from Michigan State University (three male, nine female). In all experiments, the sample size was based on our previous studies using the same experimental paradigm (Becker et al., 2013; Liu & Becker, 2013; Mance et al., 2012). All gave written informed consent and were naïve as to the purpose of the study. Participants were compensated $10 per session.

Stimuli and display. The stimuli were circular coloured patches (2°) and appeared in one of four possible locations at the corners of an imaginary square centred on fixation (eccentricity = 6°). They could be one of four colours: red, green, blue, or yellow, set at the maximum saturation achievable by the monitor (e.g., red is [255 0 0]). Both the colours and locations of the stimuli were randomly selected, without replacement, from their four possible values. The masks were 2.4° circular 10 × 10 checkerboard patterns, with the colour of each check randomly sampled from the four colour values. The background was black, and a small white circular fixation point (0.3°) was presented in the centre of the screen throughout the experiment. Participants were instructed to keep their gaze on this point.

The experiment was programmed in MGL (http://gru.brain.riken.jp/doku.php?id=mgl:overview), a set of OpenGL libraries running in MATLAB (The MathWorks, Natick, MA) on an Apple iMac computer. The stimuli were displayed on a 19-inch cathode ray tube (CRT) monitor with a refresh rate of 96 Hz. The monitor was positioned 57 cm away from the chinrest, which was aligned with the centre of the screen.

Main task. Participants performed a colour identification task in one of three conditions (Figure 1). In the Set Size 1 (SS1) condition, a single colour patch was presented and followed by a mask. In the Sequential (Seq) condition, one colour patch was presented (and masked), then a second colour patch was presented (and masked) in a different location. In the Simultaneous (Simu)

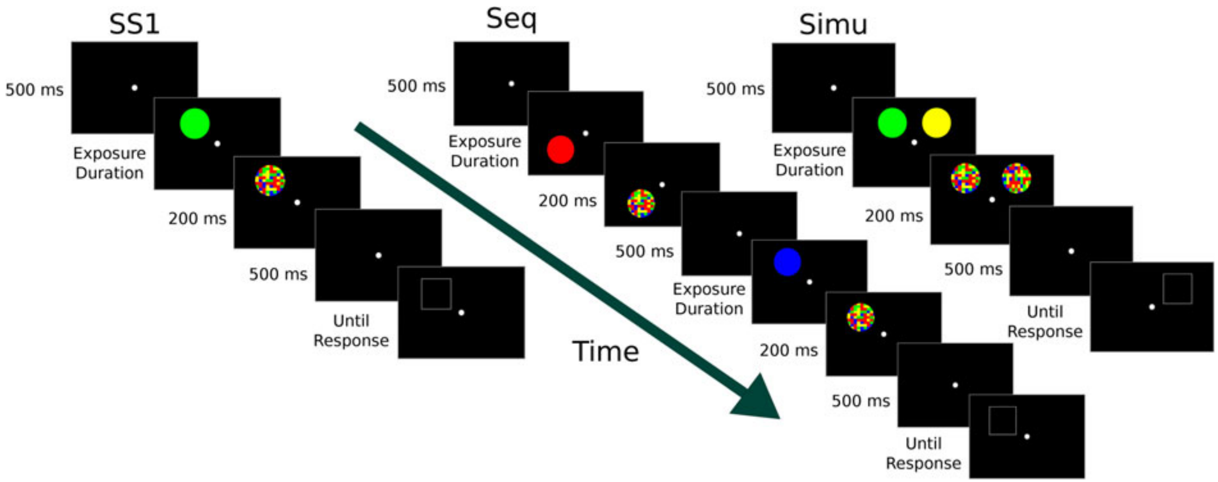

Figure 1. The schematics of trials in Experiment 1. The exposure duration was determined individually for each participant in the thresholding task. To view this figure in colour, please see the online issue of the Journal.

condition, two colour patches were presented (and masked) at the same time in two different locations. Each trial began with a 500 ms fixation period followed by the onset of the stimuli, which were presented for the appropriate exposure duration determined for each participant via the thresholding procedure (see later). All colour patches were followed by a 200 ms mask. At the end of the trial, the cue (a gray square outline) appeared to indicate the location of the target stimulus. The cue remained on the screen until response. Participants were instructed to report the target colour via buttonpress. Responses were made using the A, S, 4, and 5 keys (4, 5 on the number pad) to indicate red, green, blue, and yellow, respectively. The first letters of the colours' names ("R", "G", "B", "Y") were posted in that order directly above the keyboard for reference. Feedback was provided after incorrect responses via low-pitched tones.

The three presentation conditions (SS1, Seq, and Simu) were run in blocks of 75 trials, with a prompt at the beginning of each block informing participants of the block type. The blocks were arranged into two superblocks, each containing a random sequence of the three block types, for a total of six blocks.

Thresholding procedure. A thresholding tasks was performed by all participants prior to participation in the main task. The thresholding task was identical to the Seq and Simu conditions described earlier, except that the stimulus exposure duration was varied using the method of constant stimuli to manipulate difficulty. One of the following seven durations was used for any given trial: 10.4, 20.8, 41.7, 85.3, 125, 166.7, or 333.3 ms. Participants ran two blocks of both the Seq and Simu conditions to equate any practice effects. We used the data from the Seq blocks to determine the exposure duration. The proportion correct was calculated for each duration, and the data were fitted with the exponential function:

$$Pc = \delta + \gamma\left(1 - e^{-\beta t}\right)$$

Pc is percentage correct, *t* is exposure duration, and δ, λ, β are free parameters that control the shape of psychometric function. Data were fitted with standard maximum likelihood methods and the duration that produced ~85% correct for these sequential trials was used for the stimulus presentation duration for all conditions in the main task.

Results

The average exposure duration across participants was 67.7 ms (range 41.7–114.6 ms). A one-way repeated-measures ANOVA was performed on the proportion correct (Figure 2). There was a main effect of condition, $F(2, 22) = 26.15$, $p < 10^{-4}$, $\eta_p^2 = .28$. Most relevant to our main research question, follow-up paired *t*-tests revealed that there was no significant difference between the Simu and Seq conditions, $t(11) = 0.86$, $p = .41$. The main effect resulted because

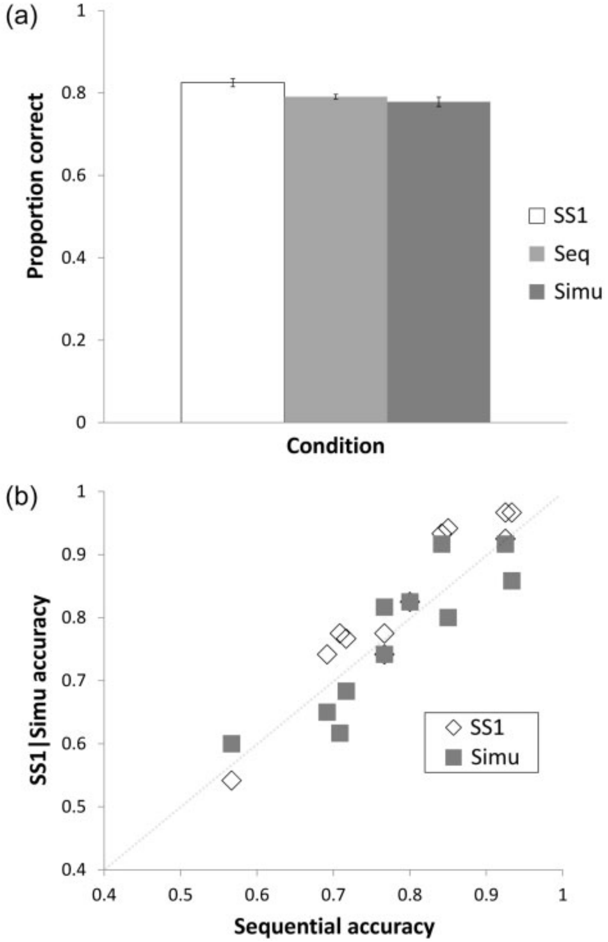

Figure 2. Results of Experiment 1. (a) The proportion correct for each condition. Error bars display the within-subjects standard error of the mean (Cousineau, 2005). (b) Individual data plotting Seq performance on the x-axis and Simu and SS1 performance on the y-axis values. Most diamonds are above the identity line (dashed line going through the origin), indicating most participants had better performance in SS1 than Seq. Most squares are around the identity line, indicating overall equivalent performance in Seq and Simu across participants.

performance in the SS1 condition was better than both the Seq and Simu conditions (both *p*s < .05). For the Seq condition, we also compared accuracy for target stimuli that appeared first versus target that appeared second in the sequence and found no significant difference, target first: 0.81, target second: 0.77, $t(11) = 1.76$, $p = .10$, indicating there was no order effect. This was expected given our SOA in the sequential display (>700 ms) was greater than typical estimates of attentional dwell time (200–500 ms) using similar displays (e.g., Duncan, Ward, & Shapiro, 1994; Kyllingsbaek & Bundesen, 2007).

Comparison to previous orientation data. To further verify that there is a genuine difference between colour and orientation, we directly compared the results across experiments. In Becker et al. (2013), we asked participants to remember and report the orientation of briefly presented grating stimuli in the same Sequential/Simultaneous protocol. In Experiment 1b of that paper, grating stimuli were selected from a set of 10 possible orientations and participants (n = 10) reported whether the target grating was tilted to the right or left of vertical. In Experiment 2, the number of possible gratings was reduced to four (horizontal, vertical, and the two diagonal 45° tilted gratings), and participants (n = 10) responded by indicating whether the target grating was oblique or cardinal. Figure 3 replots performance for those two experiments from Becker et al. along with the current Experiment 1. It is apparent that performance in the simultaneous condition is worse than in the sequential condition for the previous orientation experiments, but there is a negligible difference for colour. Separate mixed-factor ANOVAs were conducted with the presentation condition and experiments as factors. Comparing the current Experiment 1 and Experiment 1b in Becker et al., there was a significant main effect of presentation condition, $F(1, 20) = 29.5$, $p < 10^{-4}$, $\eta_p^2 = .43$, and experiment, $F(1, 20) = 16.6$, $p < .001$, $\eta_p^2 = .45$, as well as a significant interaction, $F(1, 20) = 19.4$, $p < .001$, $\eta_p^2 = .28$. The significant interaction occurred because simultaneous presentation only reduced performance in the orientation experiment. Comparing the current

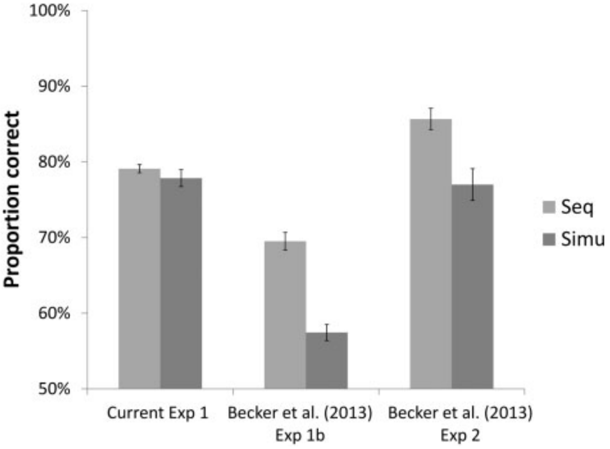

Figure 3. Comparing colour results from current Experiment 1 to orientation results from Becker et al. (2013).

Experiment 1 with Experiment 2 in Becker et al. also yielded a significant main effect of presentation condition, $F(1, 20) = 7.98$, $p < .01$, $\eta_p^2 = .25$, and presentation by experiment interaction, $F(1, 20) = 4.47$, $p < .05$, $\eta_p^2 = .14$, again confirming that simultaneous presentation only impaired performance for orientation stimuli. In addition, this pattern remained even when the overall task difficulty was relatively consistent across experiments, as was demonstrated by a nonsignificant main effect of experiment, $F(1, 20) < 1$.

Discussion

These analyses established that performance was equivalent for the colour feature in the sequential and simultaneous conditions when we used the same location cue as in our previous orientation experiments. The results suggest that the different findings between earlier colour and orientation experiments were due to the consolidation process and not due to differences in the methodology that had been applied. Our results demonstrated that both colours in the Simu condition were consolidated as well as in the Seq condition. Given the extreme temporal constraints placed on the exposure durations, the data suggest a parallel consolidation process even though participants had to encode both the location and colour values. These results thus extend our previous findings from the probe-matching experiments where it was not necessary to bind colour and location (Mance et al., 2012).

Equivalent performance for the simultaneous and sequential conditions suggests parallel consolidation of two colours, but it is still possible that this parallel consolidation is rather limited. The response required in Experiment 1 was a four-alternative forced choice categorization of highly discriminable colours. Under these circumstances, an impoverished representation of both colours could be sufficient for a correct response. Hence, it is possible that parallel consolidation of colour results in only imprecise representations, whereas forming more precise representations of the colours may require a limited-capacity or serial consolidation process. If so, we would expect a more precise memory representation in the Seq than the Simu condition, but the measurements in Experiment 1 may have been too insensitive to detect a difference in precision. By contrast, if two colours can be consolidated in parallel, the precision of the memory representation should be equivalent in the Seq and Simu conditions. Experiment 2 was designed to further investigate the nature of this parallel consolidation process by assessing the precision of the memory representation.

EXPERIMENT 2

In all of our experiments with colour (Experiment 1 and our previous experiments in Mance et al., 2012), we have used highly discriminable colours with a discrete response and found evidence for parallel consolidation for two colours. As stated earlier, these tasks only required a low-resolution representation, such that representing the approximate feature would be sufficient for a correct response. It is possible that forming low-resolution VSTM representations requires less bandwidth such that two approximate colours can be consolidated in parallel. However, if the task requires high-resolution information, then consolidation could consume more bandwidth such that two colours would need to be consolidated in a serial manner.

To further probe the bandwidth limit in consolidation of colour information, in Experiment 2, participants were asked to recall the precise hue of the colour stimuli. If consolidation of high-resolution colour information requires a limited-capacity process, performance should be more precise in the sequential than the simultaneous presentation condition. By contrast, if the consolidation of two colours is truly a parallel process, then the precision of the recall performance should be equivalent for both presentation conditions. A continuous measure of colour memory also allowed us to perform a mixture model analysis (Zhang & Luck, 2008), which is capable of distinguishing between unlimited parallel, limited-capacity parallel, and strictly serial processes (see Liu & Becker, 2013). We previously used this method to investigate the consolidation of orientation and found strong evidence that orientations were consolidated via a strictly serial process (Liu & Becker, 2013). The application of the same type of model to colour data should provide insight into the nature of any possible differences in the consolidation processes for colour and orientation.

Finally, we note that a serial process can mimic a parallel process if the presentation time is so long that the serial process is allowed to complete multiple iterations. To rule out this possibility, we used two exposure durations. If consolidation was implemented via a serial process that switched between stimuli in the simultaneous condition, reducing the presentation duration should produce a more pronounced drop in performance for the simultaneous than the sequential condition. If, however, consolidation was implemented via a truly parallel process, shortening the duration should affect both conditions to similar extent.

Methods

Participants. There were 14 participants in total (13 females, one male), five of whom also participated in Experiment 1. Participants were compensated with $10 per session.

Stimuli and display. Stimuli were colour patches of the same shape, size, and eccentricity as in Experiment 1. However, the colours of the patches were randomly sampled from a circle in the CIE L*a*b* colour space (radius = 60, a = 20, b = 38, luminance = 70). The only constraint on colour selection was that in the Seq and Simu conditions the two colours could not be within 45° of one another on the colour circle. The masks were 8 × 8 checkerboard patterns with the colour of each check randomly sampled from the same colour circle.

The stimuli were displayed on a 21-inch CRT monitor refreshed at 100 Hz. The monitor was calibrated with an i1Pro spectrophotometer (X-Rite, Grand Rapids, MI), to derive the transformation from the CIE L*a*b space to the monitor RGB space (Westland & Ripamonti, 2004).

Task and procedure. Participants again were presented with a single colour patch, or two colour patches either sequentially or simultaneously (Figure 4). The trial structure was similar to that of Experiment 1, except at the end of the trial, a colour ring (thickness: 2°, eccentricity: 11°), depicting the colour circle in the CIE L*a*b space, was presented. Participants were instructed to click on the ring where the colour matched the target's hue. Targets were again indicated by the same location cue used in Experiment 1.

Two fixed exposure durations, 70 ms and 150 ms, were used in separate sessions for each participant. In each session, the three presentation conditions (SS1, Seq, Simu) were run in blocks of 75 trials, with block order sequenced the same as in Experiment 1. Six participants ran the short duration (70 ms) session first, and the other eight ran the long duration (150 ms) session first.

Data analysis. For each trial, we calculated the offset (error) in the participant's colour setting as the circular deviation between the reported and the true target colour on the colour wheel. For descriptive data analyses, we computed the mean and the variance of the offset using circular statistics (Berens, 2009). We used the log of the variances for statistical tests because they are more normally distributed. We also fitted the offset data with a model that assumes performance results from the mixture of a proportion of "guess" trials (g) in which participants did not consolidate the target into VSTM, and a second proportion of "known" trials (1 – g) in which the item was consolidated into memory (Zhang & Luck, 2008). Under this model, guess trials conform to a uniform distribution and known trials conform to a circular normal distribution with a mean (κ) and standard deviation (σ). The model was fitted to the observed colour offset data (for both individual and aggregate data) using standard maximum likelihood methods (Myung, 2003). These analyses mirror the analyses we performed to investigate the consolidation of orientation information in Liu and Becker (2013).

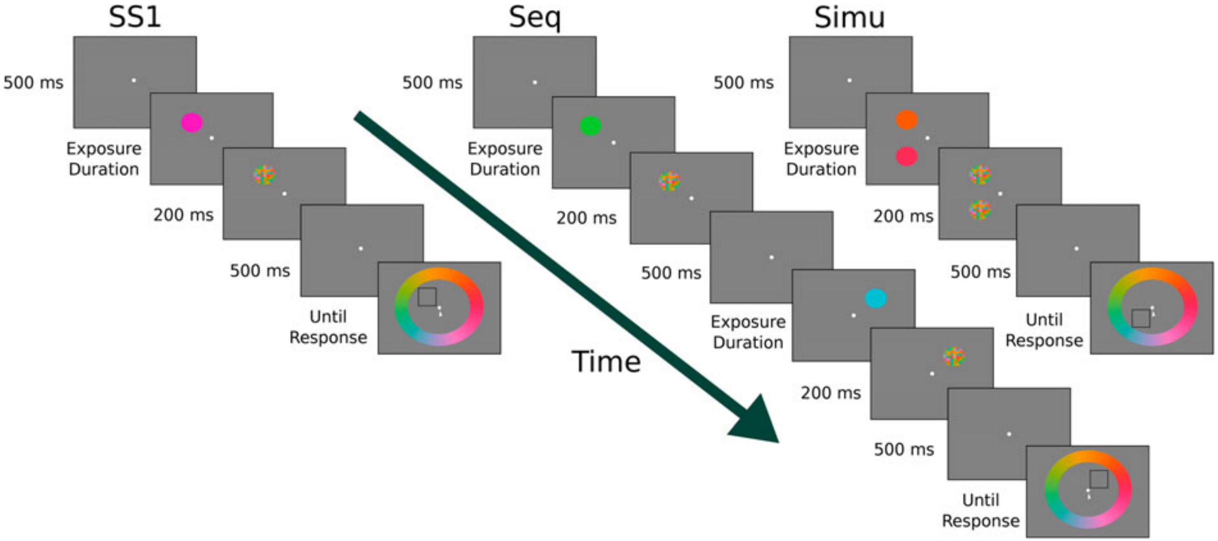

Figure 4. The schematics of trials in Experiment 2. To view this figure in colour, please see the online issue of the Journal.

Results

Descriptive analysis. On average, participants' colour settings were centred on the colour of the cued item and did not show systematic bias (Figure 5a). A 2 (duration) × 3 (condition) repeated-measures ANOVA on the mean offsets found no significant main effect nor their interaction: duration, $F(1, 13) = 2.97$, $p = .11$; condition, $F(2, 26) = 1.69$, $p = .20$; interaction, $F(2, 26) < 1$. A second 2 (duration) × 3 (condition) repeated-measures ANOVA was performed on the log variance data (Figure 5b). There were significant main effects of both duration, $F(1, 13) = 11.68$, $p < .01$, $\eta_p^2 = .47$, and condition, $F(2, 26) = 33.83$, $p < 10^{-4}$, $\eta_p^2 = .72$, with no interaction effects, $F(2, 26) < 1$. The main effect of duration resulted from lower precision (higher variance) in the shorter duration. This evidence for lower precision with less encoding time suggests that reducing the time available for encoding decreased the amount of information that one could extract from the display.

The main effect of condition resulted from a higher precision (lower log variance) in the SS1 condition relative to the Simu and Seq conditions. Planned comparisons (paired *t*-tests) confirmed that the SS1 condition differed from both the Simu and Seq conditions for both durations (all *p*s < .001). More importantly, there was no significant difference between the Simu and Seq conditions for either duration: short, $t(13) = 0.64$, $p = .53$; long, $t(13) = 0.28$, $p = .78$. The equivalent performance in the Seq and Simu conditions suggest that two colours can be consolidated in parallel, which is consistent with the results of Experiment 1 and our earlier colour results (Mance et al., 2012). We also examined accuracy for target stimuli that appeared either first or second in the Seq condition, and found no significant difference in log variance for either the short duration condition, target first: 6.01, target second: 6.16, $t(13) = 1.23$, $p = .24$, or the long duration condition, target first: 5.73, target second: 5.27, $t(13) = 2.15$, $p = .051$.

Model fitting. The three parameters of the mixture model include a measure of bias of the memory representation (κ), precision of the memory representation (σ), and guess rate (g). The purpose of fitting the mixture model to the data is to further evaluate the parallel nature of colour consolidation. If two concurrent stimuli are consolidated into VSTM in parallel, then there would be no more random guessing (g) in Simu than in the Seq condition. If this parallel process was unlimited then there should be no difference in the precision of the memory representations between the Simu and Seq conditions. By contrast, if the process was a limited-capacity parallel process, then memory representations should be less precise in the Simu than in the Seq condition. A strictly serial process, such as was found using a similar model to examine the consolidation of orientation information (Liu & Becker, 2013), should produce higher guess rates in the Simu than the Seq condition but no difference in precision between the two conditions.

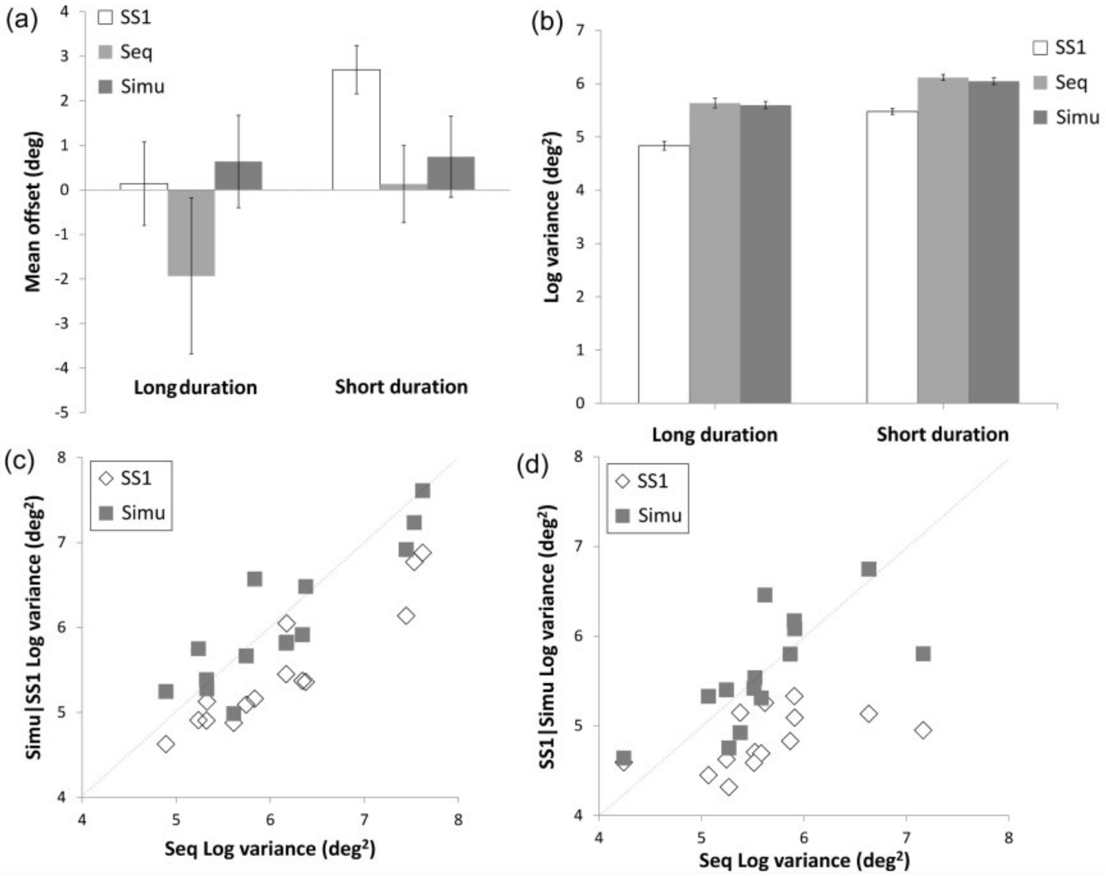

Figure 5. Results of Experiment 2. (a) The average bias in participant's colour recall. (b) The log of the variance of each condition. Error bars display the within-subject standard error of the mean. (c) The log variance of the SS1 and Simu condition against that of the Seq condition, for the short duration presentation. (d) The same scatter plot for the long duration presentation. In both cases, the diamonds tend to be below the identity line, indicating smaller variance for SS1 than Seq, but the squares cluster around the identity line, indicating equivalent variance for Simu and Seq.

We fitted individual participant data with the mixture model and obtained three parameter estimates for each participant: bias (κ), standard deviation (σ), and guess rate (*g*) (Figure 6). We then performed two-way repeated-measures ANOVAs on these model parameters with factors of duration (short, long) and presentation condition (SS1, Seq, Simu). For the bias, we found no significant main effects nor their interaction: duration, $F(1, 13) = 1.05$, $p = .32$; condition, $F(2, 26) = 1.26$, $p = .30$; interaction, $F(2, 26) = 2.88$, $p = .07$. For the guess rate, there was a main effect of condition, $F(2, 26) = 9.06$, $p < .001$, $\eta_p^2 = .86$, but neither duration, $F(1, 13) = 3.12$, $p = .10$, nor their interaction, $F(2, 26) < 1$, was significant. For the standard deviation, there were significant main effects for both condition, $F(2, 26) = 15.06$, $p < 10^{-4}$, $\eta_p^2 = .83$, and duration, $F(1, 13) = 18.82$, $p < .001$, $\eta_p^2 = .20$, but not their interaction, $F(2, 26) = 1.17$, $p = .33$. The fact that there was a main effect of duration suggests that limiting the time for encoding made the task more difficult.

To isolate the source of the main effects of condition for the standard deviation and guess rate parameters, we ran paired *t*-tests comparing the three conditions within a given exposure duration. For the short duration, SS1 had a lower guess rate and a smaller standard deviation (higher precision) than both the Seq and Simu conditions (all *p*s < .02). More importantly, there was no difference between the Seq and Simu condition in terms of either their guess rate ($p = .21$) or standard deviation ($p = .70$), consistent with the consolidation of both colours in parallel. For the long duration, we again found that SS1 had a lower guess rate and smaller standard deviation than both the Seq and Simu conditions (all *p*s < .04). Again there was no difference in the guess rate ($p = .47$) between Seq and Simu conditions; however, the standard deviation for the Seq condition was significantly smaller than the Simu condition ($p < .01$).

Comparison to previous orientation data. We compared the model parameters from the short duration condition to our previous experiment using orientation stimuli (Liu & Becker, 2013). In that study, we asked participants ($n = 12$) to recall the orientation of briefly presented grating stimuli in the same Sequential/Simultaneous protocol and used the mixture model to analyse their recall data. The guess rate and precision parameters for the current Experiment 2 and the orientation experiment from Liu and Becker (2013) are replotted in Figure 7(a) and (b), respectively. Mixed-factor ANOVA showed that there were no significant effects for the precision parameter (all *F*s < 1). However, for the guess rate parameter, there were significant effects for presentation condition, $F(1, 24) = 15.0$, $p < .001$, $\eta_p^2 = .24$, experiment, $F(1, 24) = 7.18$, $p < .05$, $\eta_p^2 = .23$, as well as their interaction, $F(1, 24) = 24.4$, $p < 10^{-4}$, $\eta_p^2 = .39$. This interaction resulted because simultaneous presentation reduced performance for orientation stimuli, but not for colour stimuli.

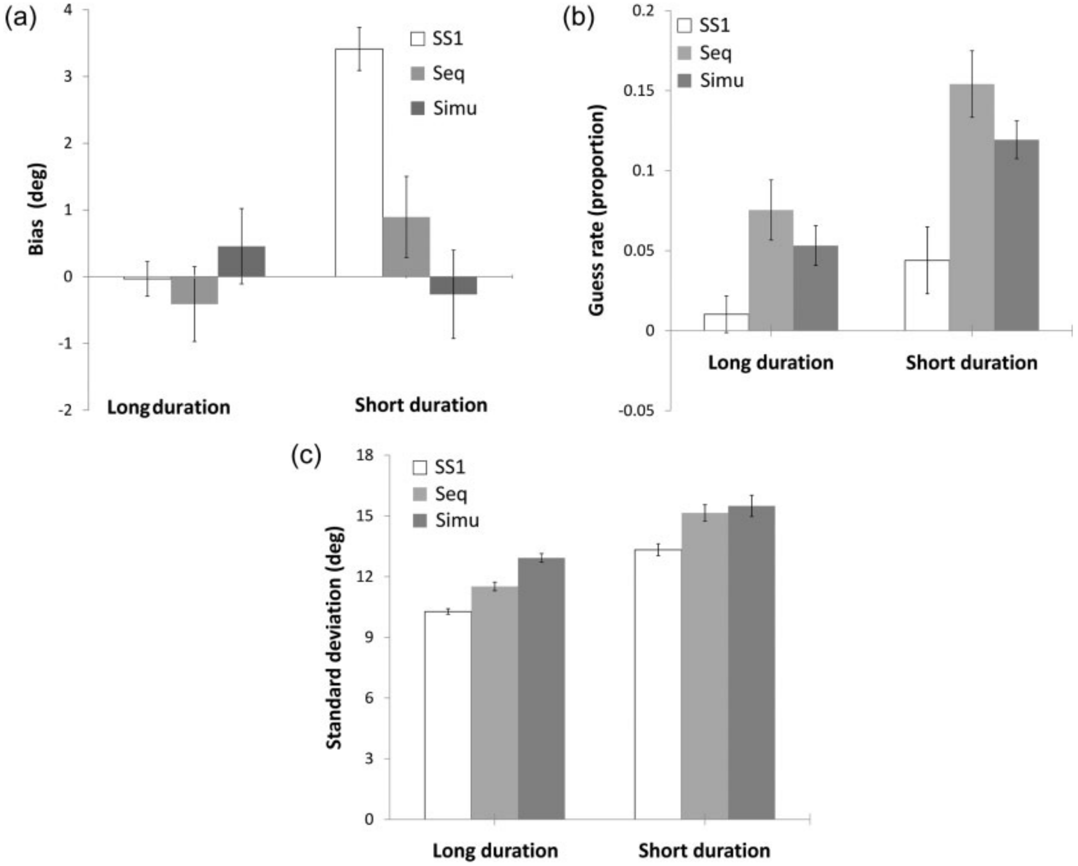

Figure 6. Model fitting results to Experiment 2 data. A mixture model was fitted to individual participant data and the mean parameter values are plotted. (a) The bias parameter θ, (b) the guess rate (g), and (c) the standard deviation of the circular normal distribution (σ). Error bars display the within-subjects standard error of the mean.

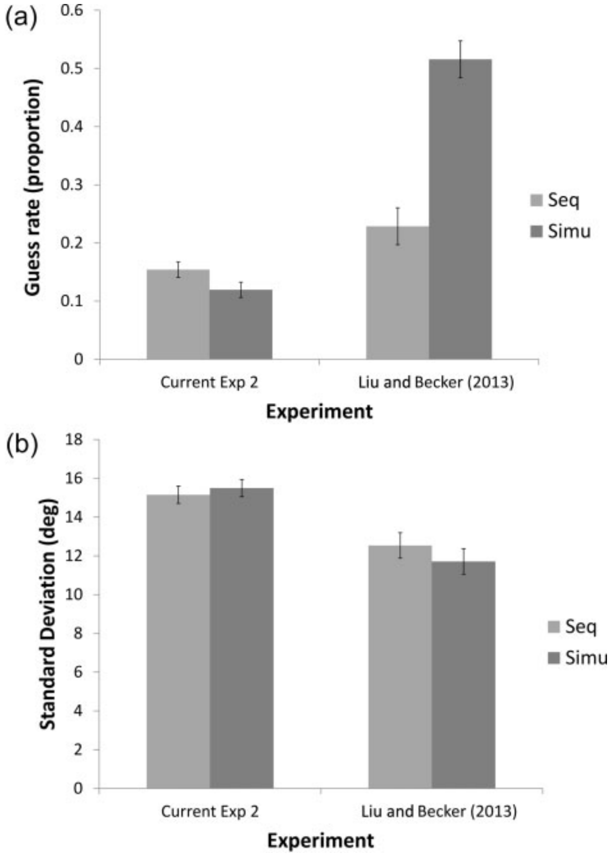

Figure 7. Comparing colour results from the current Experiment 2 to orientation results from our previous experiment in Liu and Becker (2013), (a) guess rate and (b) standard deviation.

Discussion

The descriptive statistics demonstrate almost identical performance and memory precision (log variance) for the Seq and Simu conditions. There are two interpretations for this finding of equivalent performance for consolidating one or two items into VSTM during a brief period. The first is that two colours can be consolidated in parallel without taxing capacity limits. The second is that the duration of the stimulus presentation was long enough to allow for either a limited-capacity parallel process to complete processing of both items, or for a serial process to complete processing of the first item and then switch to and complete processing of the second item. However, our use of two presentation durations allows us to rule out this latter interpretation. Overall performance and memory precision (log variance) was reduced when the presentation duration was shortened. This reduction in performance provides evidence that, at least at the shorter duration, there was insufficient time to complete processing of the items. Under a limited-capacity parallel or serial scenario, the drop in performance we saw with the shorter duration should have been more severe in the simultaneous condition. However, this was not the case. Even in the short duration, performance was equivalent for simultaneous and sequential presentation. This provides strong evidence that two colours can be consolidated in parallel just as well as a single colour can be consolidated.

This conclusion is further bolstered by the modelling results. First, we found no difference in guess rate between the simultaneous and sequential conditions at either duration. Second, we also found no difference in the memory precision parameter between these two conditions at the short duration. All of these patterns are consistent with the parallel consolidation of two colours into VSTM. Interestingly, we did find that the sequential condition had higher memory precision under the long presentation duration. This finding suggests that, given enough time, a second process that might be serial or limited-capacity can be used to improve memory precision. This second process might be eye movements to the stimulus, or verbal encoding. We do not believe this finding is problematic for our overall claim that the initial consolidation of two colours is performed in parallel. For this claim, the short duration is the most informative condition. However, this finding suggests it is critical to use a duration that is adequately short to assess the initial consolidation phase.

Interestingly, our finding of increased memory precision with longer stimulus duration is at odds with results from Experiment 4 of Zhang and Luck (2008). These authors presented three coloured squares for a fixed duration (100 ms) but varied the delay between stimulus and mask (either 10 ms or 240 ms). They found decreased guess rate but similar precision with longer SOA, suggesting that consolidation into VSTM was a discrete process, because additional processing time did not lead to improved precision. Our short and long durations were 70 ms and 150 ms, respectively, and we found increased precision with the longer duration (Figure 6c). Thus, the consolidation process seems to be continuous rather than discrete, and it is possible that the 110 ms SOA used in the previous study was too long such that precision has already reached the asymptotic level.

Last, it is worth noting that performance in the SS1 condition was always better than performance in either of the presentation conditions for two items. This finding replicates our earlier work. In that work and here, we attribute this SS1 superiority to postconsolidation processes such as reduced interference and/or reduced decision noise.

EXPERIMENT 3

Experiments 1 and 2 further extended our previous finding of equivalent performance in the sequential and simultaneous conditions for colour stimuli (Mance et al., 2012). This was the case both when the task required colour-location binding and when the task required high-resolution memory representation. These results stand in stark contrast to our previous work on orientation (Becker et al., 2013; Liu & Becker, 2013), which demonstrates that two orientations were consolidated in a serial fashion. In sum, there is compelling evidence that two orientations are processed in a serial manner while two colours can be processed in an unlimited capacity, parallel manner.

One straightforward interpretation of these discrepancies is that there are two independent mechanisms, a serial process for the consolidation of orientations and a parallel process for consolidating colours. We have previously speculated that consolidation into VSTM requires establishing distinct neuronal assemblies for each item (Becker et al., 2013). Recent neuroimaging studies have suggested that working memory representations are maintained in sensory areas (Harrison & Tong, 2009; Riggall & Postle, 2012; Serences, Ester, Vogel, & Awh, 2009). If so, the different results for colour and orientation could be due to these features being processed primarily by distinct visual areas. For example, colour may rely more on V4, whereas orientation may rely more on V1. If this is the case, then consolidation of colour and orientation might proceed in largely independent manner. Experiment 3 was designed to test this hypothesis by testing the bandwidth of consolidating a colour stimulus and an orientation stimulus simultaneously. If the consolidation processes for these two feature dimensions are independent, we should observe similar performance in sequential and simultaneous presentation. If, however, the two processes rely on some common mechanisms, we would expect interference between the two feature dimensions such that a lower performance should be observed for the simultaneous than the sequential condition.

Methods

Participants. Sixteen students from Michigan State University participated for compensation at a rate of $10/hour. Three participants were excluded due to large thresholds (for more details, see later), so results were based on 13 participants. All participants were naïve as to the purpose of the study.

Stimuli and display. The stimulus presentation of Experiment 3 followed the same display setup as the first two experiments, except that the stimuli were different. Stimuli consisted of four colour patches and four sinusoidal gratings (contrast: 0.7, spatial frequency: 2 cycles/deg). The colour patches were identical to those in Experiment 1, and the grating orientations were horizontal, vertical, and the two diagonals (45° and 135°). The gratings were rendered in a circular aperture presented on a grey background. The edge of the aperture was smoothed to ensure a gradual transition in luminance at the border of the grating (see Figure 8a for an example of the grating stimulus). Due to the smooth edge of the aperture, the diameter of the gratings was set to 2.3°, 0.3° larger than the colour patches, to approximately equate the perceived size of the two types of stimuli. On each trial participants were presented with both a grating and a colour patch. Both stimuli were then masked, with the colour masks identical as Experiments 1 and 2 and the gratings masked by circular apertures containing pixel noise pattern generated with a random uniform distribution over all possible luminance levels (see Figure 8a for an example of the mask). Again, a square outline was used to indicate the target's location after the stimulus presentation.

Main task. The task and procedure were identical to those of Experiment 1, with the following exceptions. Participants reported the feature of the target indicated by the location cue by pressing one of eight possible keys on a computer keyboard. The "A", "S", "D", and "F" keys were used for horizontal, 45°, vertical, and 135° orientation, respectively, and "4", "5", "6", and "+" keys (on the numeric keypad) were used for red, green, blue, and yellow colour, respectively. The response mapping was posted above the keyboard for reference throughout the experiment. For colours, the reminders were the first letter of each colour ("R", "G", "B", "Y"); for orientations, the reminders were lines drawn in the corresponding orientation. Stimuli were presented for the duration that was individually determined for each participant (see "Thresholding task"). We did not include the SS1 condition in Experiment 3, as it did not have direct bearing on our predictions. We note here that we have consistently found a superior performance in SS1 compared to both the sequential and simultaneous conditions. Sequential and simultaneous trials were blocked (100 trials/block) for a total of four blocks (two blocks per condition). The block order was randomized with the constraint that two of the same type could not be run consecutively.

Thresholding task. Before the main task, each participant performed a thresholding task very similar to that used in Experiment 1. On each trial, only one stimulus was presented, either a colour patch or an orientated grating. Colour and orientation thresholding were conducted in separate blocks (a total of 120 trials were obtained for each feature), within which the stimulus exposure duration was varied across trials. The proportion correct data were fitted separately for each stimulus type with an exponential function as in Experiment 1. A 85% threshold was calculated for each stimulus type and the mean of those two thresholds was used in the main experiment as the stimulus exposure time.

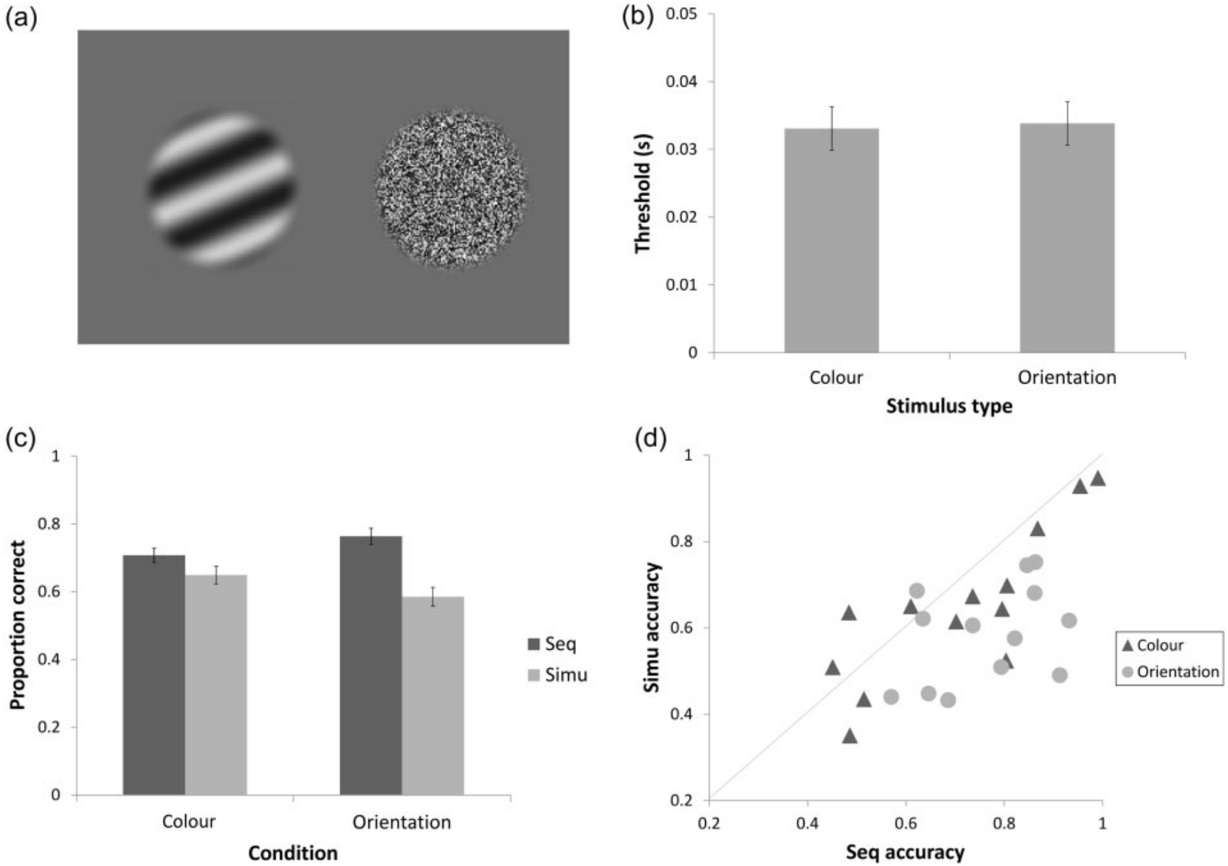

Figure 8. Stimuli and results of Experiment 3. (a) Examples of orientation stimuli used in Experiment 3 (left: grating, right: mask). (b) The average duration threshold for the orientation and colour stimuli. (c) The average proportion correct for each condition. Error bars display the within-subjects standard error of the mean (Cousineau, 2005). (d) The scatter plot of individual participant data, plotting accuracy in the simultaneous condition against the sequential condition for both the colour and orientation stimulus.

Results and discussion

We first examined data from the thresholding task. In general, duration thresholds were similar for colour and orientation. However, three participants showed extremely long duration threshold for orientation (>300 ms). We suspect they might have difficulty using the response mapping for orientation—our own experience is that it took more effort to learn the response mapping for orientation than that for colour. We hence removed data from these participants from our analyses, such that the results reported here were based on 13 participants. We should note, however, that including these three subjects in our analyses produced essentially the same overall pattern of results. Across the 13 participants, the measured duration threshold was very similar for colour and orientation (Figure 8b), and there was no significant difference between the two thresholds, *t*-test, $t(12) = 0.12$, $p = .91$. The lack of difference between colour and orientation threshold also justified our approach to use the average threshold as the stimulus exposure time in the main task. The average stimulus exposure time across participants was 35 ms (range: 20–80 ms).

Average proportion correct across participants in the main task is shown in Figure 8c. We performed a 2 (stimulus type) × 2 (condition) repeated-measures ANOVA on the proportion correct data and found a significant main effect of condition, $F(1, 12) = 7.77$, $p < .05$, $\eta_p^2 = .39$, as well as a significant interaction effect between stimulus type and condition, $F(1, 12) = 6.36$, $p < .05$, $\eta_p^2 = .35$. The main effect of stimulus type was not significant, $F(1, 12) < 1$. To further test our prediction of independent consolidation for colour and orientation, we performed separate *t*-tests to compare sequential and simultaneous performance within each feature dimension. For colour, performance was marginally, $t(12) = 1.99$, $p = .07$, better for the sequential than simultaneous presentation. For orientation, performance was significantly better for sequential than simultaneous presentation, $t(12) = 4.97$, $p < .001$. Thus, simultaneous presentation impaired performance for orientation more than colour. This differential effect of stimulus type on presentation condition accounted for the interaction effect in the overall data. Here, we again did not find a significant difference in performance for targets appearing in the first versus second interval in the Seq condition, target first: 0.76, target second: 0.71, $t(12) = 1.84$, $p = .09$. No significant difference was observed when we examined colour and orientation data separately.

These results showed that consolidating colour and orientation simultaneously incurred a cost relative to consolidating them sequentially. We would like to note that performance for both stimulus types was numerically lower in the simultaneous than the sequential condition, although this decrement was less reliable for colour than for orientation, leading to the interaction effect. Overall, these results argue against our original hypothesis that the consolidation of colour and orientation rely on independent mechanisms, as that should produce equivalent performance in the sequential and simultaneous condition for both stimulus types. Thus, the consolidation of colour and orientation likely shares a common mechanism at some level. Furthermore, this common mechanism exhibits differential efficiency in processing colour and orientation information. We will discuss possible reasons for this differential efficiency in the General Discussion. For now, we conclude that consolidation of colour and orientation are nonindependent processes.

GENERAL DISCUSSION

Our data provide strong evidence that two colours can be consolidated into VSTM just as quickly and accurately as a single colour. In our earlier work, we also found evidence for parallel consolidation of two colours, but this ability did not extend to two orientations. In fact, when investigating orientation we found strong evidence for strictly serial processing. One potential confound was the fact that different methods were used to assess memory of colour and orientation. So it was possible that the observed difference in consolidation ability between features was an artifact of methodological differences.

Here we used the same methods that we have previously used in our orientation studies to investigate the consolidation of colour. Experiment 1 used a location cue that was similar to Experiments in Becker et al. (2013), and Experiment 2 used a similar type of continuous response and the same modelling techniques as Liu and Becker (2013). Yet here we come to the exact opposite conclusions as those orientation experiments. Our cross-study comparisons provide strong evidence that there is a real difference in the bandwidth to consolidate colours and orientations, with at least two colours being able to be consolidated in parallel, whereas two orientations are consolidated in a strictly serial manner.

Why should there be this difference in the consolidation process of colour and orientation? A simple hypothesis would be that consolidation of colour and orientation relies on independent processes. This would predict that one colour and one orientation can be consolidated as well in sequential as in simultaneous presentation. In Experiment 3, we tested this prediction by presenting a colour patch and an oriented grating either sequentially or simultaneously. However, we found worse memory performance for both features in the simultaneous condition than the sequential condition, with orientation showing a larger decrement than colour. This finding suggests that consolidation of colour and orientation shares common processes. Thus, a single mechanism might be responsible for consolidating different features, but the bandwidth of consolidation varies for different features.

We speculate that this differential bandwidth arises due to differential informational demand when encoding different features. Specifically, colour may require less information to be encoded, thus consuming less bandwidth, than orientation. For a uniform colour patch, encoding of any local region is sufficient to derive the stimulus colour, whereas for a circular grating, a larger region needs to be encoded to compute the stimulus orientation. In other words, any single pixel in a colour patch has sufficient information about the stimulus colour, whereas a single pixel in a grating does not contain information about its orientation. This argument is similar to the distinction between boundary feature and surface feature discussed by Alvarez and Cavanagh (2008).

From a functional point of view, the accurate perception of colour requires colour constancy, whereas simple orientations do not require constancy. Colour constancy requires a light source with multiple wavelengths, and multiple objects that have different reflectance properties. Most models of colour constancy assume that it is achieved by coding the relative L, M, and S cone activity across multiple independent objects or surfaces that have different surface reflectance (see Brainard, 2004, for a review). This requirement to simultaneously represent multiple coloured surfaces may have resulted in a system that can simultaneously consolidate colour information from multiple distinct objects at once, thereby ensuring the rapid computation underlying colour constancy.

Another difference between colour and orientation is the fact that, although both features are based on the continuous variation of physical properties (wavelength and angle), colour is perceived more categorically than orientation. It is possible that the categorical coding of colour requires less information to be encoded and hence consumes less consolidation bandwidth. In addition, colour categories have easy access to verbal labels and perhaps verbal encoding provides an additional channel for memory consolidation. However, we think verbal encoding alone cannot explain all of our results. First, verbal codes would be less useful in the current Experiment 2 where stimuli colours were randomly selected on the colour wheel and participants need to recall the precise hue of the target. Second, in our previous study (Becker et al., 2013), we facilitated verbal encoding of orientation information by making the stimuli and judgement more categorical (e.g., left- vs. right-tilted, cardinal vs. oblique; see also Wolfe, Friedman-Hill, Stewart, & O'Connell, 1992). In all these experiments, we consistently found a lower consolidation bandwidth for orientation than colour. Finally, we should note that having the possibility of verbal encoding does not necessarily lead to better performance. For example, Stevanoski and Jolicœur (2007) tested working memory consolidation of colour stimuli and found that activating a verbal code for colour was more, rather than less, capacity demanding in terms of the use of a central mechanism. For these reasons, we do not think verbal encoding plays a significant role in our findings.

All of these factors could contribute to a more efficient processing of colour than orientation. Regardless of the exact reason for the disparity in efficiency, a possible interpretation of our results is that consolidation has a fixed bandwidth in terms of the amount of information that can be simultaneously processed, and this amount is sufficient to accommodate two colours, but only one orientation. Thus, two colours can be consolidated in parallel, whereas two orientations can only be consolidated serially. This scenario is depicted in Figure 9, where consolidation is shown as the process that connects perceptual analysis to working memory stores. The bandwidth of consolidation (depicted as the height of the rectangle) is large enough to accommodate two colours but only one orientation at a time (for more detailed explanations, see figure caption). Under this scenario, one colour and one orientation will also exceed the bandwidth (not depicted), leading to a lower performance in the simultaneous than the sequential condition. However, the item that requires less information to be encoded (colour) is less affected by a limit in consolidation than the item that requires more information to be encoded (orientation). It is worth pointing out that our experimental protocol limits encoding time (via the thresholding procedure), which is necessary to prevent serial shift of processing among items before the mask terminates consolidation. We think the bandwidth limit we revealed is a set

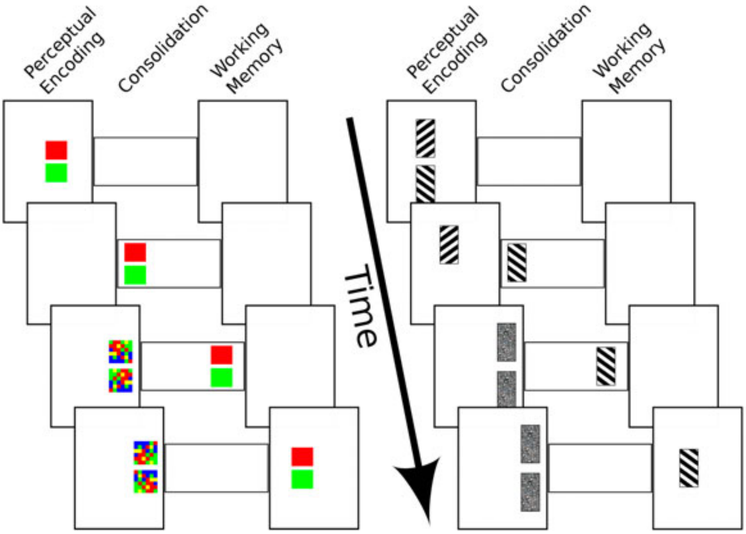

Figure 9. Schematic of the consolidation bandwidth limit. We envision the consolidation as the intermediate step in transferring the results of perceptual analysis to working memory stores. However, the bandwidth, or the amount of information that can be transmitted at once, is limited, which is depicted by the height of the central rectangle. The figure shows hypothetical scenarios when two colours (left side) or two orientations (right side) are shown simultaneously. Both stimuli can be encoded in parallel by the perceptual system, but, because of the brief and masked presentation, the system cannot consolidate one item and then switch to the other item. Because colour requires less information to be encoded, two colours can be consolidated at the same time such that they can be transferred to the working memory store before the mask. However, orientation requires more information to be encoded, so that only one stimulus can be consolidated at a time before the mask onset, which effectively eliminates the other stimulus from entering into working memory store. To view this figure in colour, please see the online issue of the Journal.

capacity limit of the amount of information that can be consolidated at once, and it is distinct from temporal limits due to limited processing time. If more time is available, it could allow multiple iterations of this consolidation process to occur, which could increase performance levels as more samples/instances of the items are stored.

Our results seem to rule out explanations based on differences in the nature of early perceptual representations between colour and orientation. We have previously suggested that a larger perceptual space for colour than orientation (i.e., three-dimensional space of brightness, hue, saturation vs. one-dimensional space for orientation) may make it easier to represent multiple colours than multiple orientations simultaneously without interference among representations (Becker et al., 2013). At the neurological level this might mean that the consolidation of each of the two colours is supported by a distinct neural ensemble, whereas the consolidation of each of the two orientations could rely on overlapping neural ensembles. In light of our new results, this explanation seems less viable as one would expect that the neural ensemble for a colour and an orientation should be at least as distinct as those for two colours, which would predict efficient consolidation of one colour and one orientation. Instead, our results hint at a common central mechanism that sets the bottleneck of consolidation that works independently of specific sensory representations. The key factor is how much information a particular feature requires to be encoded in order to consolidate the information into VSTM. Our results also have implications for research on VSTM storage, as one needs to take into account of the limited consolidation bandwidth when studying storage limit. Our results show that if the memory array is presented very briefly and masked, only a few items can be consolidated. Under these conditions, performance may reflect a limit in consolidation, in addition to (or instead of) a limit in storage. For this reason, we recommend sufficiently long exposure time or stimulus-mask SOA (e.g., 100 ms per item) when investigating VSTM storage.

Clearly, addition research will be necessary to determine the source and functional significance of the difference in consolidation bandwidth between colour and orientation. Even so, our current results provide clear evidence that this consolidation limit is not equal for all visual features. Furthermore, our results suggest that a common central mechanism is the rate-limiting factor for consolidation of features into VSTM.

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