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Lack of colour integration in visual short-term memory binding

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Abstract

Bicoloured objects are retained in visual short-term memory (VSTM) less efficiently than unicoloured objects. This is unlike shape-colour combinations whose retention in VSTM does not differ from that observed for shapes only. It is debated whether this is due to a lack of colour integration and whether this may reflect the function of separate memory mechanisms. Participants judged whether the colours of bicoloured objects (each with an External and an Internal colour) were the same or different across two consecutive screens. Colours had to be remembered either individually or combined. In Experiment 1, External colours in the combined colours condition were remembered better than the Internal colours and both were performed worse than the individual colours condition. The lack of colour integration observed in Experiment 1 was further supported by a reduced capacity of VSTM to retain colour combinations relative to individual colours (Experiment 2). An additional account was found in Experiment 3 which showed spared colour-colour binding in the presence of impaired shape-colour binding in a brain damaged patient, thus suggesting that these two memory mechanisms are different.

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Introduction

Visual short-term memory (VSTM) represents multi-feature objects either as integrated units (Luck & Vogel, 1997; Vogel, Woodman, & Luck, 2001) or as sets of individual features (Wheeler & Treisman, 2002). Some authors have found that uni-feature and multi-feature objects can be retained in VSTM with similar efficiency (e.g., Brockmole, Parra, Della Sala, & Logie, 2008; Gajewski & Brockmole, 2006; Luck & Vogel, 1997; Vogel et al., 2001), suggesting that multi-feature objects are represented in VSTM as integrated units and that their binding is cost-free (i.e., object-based format). Other authors have shown that VSTM performance for multi-feature objects is significantly poorer than VSTM performance for uni-feature objects (e.g., Olson & Jiang, 2002; Parra, Abrahams, Logie, & Della Sala, 2009a; Wheeler & Treisman, 2002; Xu, 2002), suggesting that VSTM represents individual features and that the binding between these features requires additional memory capacity (i.e., feature-based format).

These different results seem to depend on the kind of features to be bound, which could belong either to the same dimension or to different dimensions. Typically, studies showing no differences compared VSTM performance for object-colour bindings and objects only (Brockmole et al., 2008; Gajewski & Brockmole, 2006; Vogel et al., 2001). In contrast, studies reporting differences compared VSTM for colour-colour bindings and single colours (Olson et al., 2002; Parra et al., 2009a; Wheeler & Treisman, 2002; Xu, 2002).

One way to reconcile this discrepancy is to posit that resources drawn from a single dimension would be depleted quickly (i.e., more interference), whereas resources drawn from different dimensions would be shared, and memory operations

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would be less constrained by capacity limitations (Olson et al., 2002; Wheeler & Treisman, 2002). However, the observation that retaining bicoloured objects in VSTM requires more memory capacity than retaining unicoloured objects does not rule out the possibility that colours are integrated within single units. For example, Parra et al. (2009a) used a change detection task to measure recognition of bicoloured objects across study and test display. In one condition, one colour of two bicoloured objects was replaced by a new colour in the test display. Hence, memory for the individual colours presented at study was enough to perform the task. In a second condition one colour of two bicoloured objects swapped between objects at test, hence the way the colours were combined at study (i.e., binding) was the crucial piece of information. Participants performed the former condition significantly better than the latter (Parra et al., 2009a). The only difference between these two conditions is the additional requirement in the second condition to remember how colours combine. These results do not rule out that colour combinations can be represented in VSTM in an object-based format. They only suggest that, in doing so, more resources might be required.

Gajewski and Brockmole (2006) distinguished between the object-unit hypothesis and the independent-stores hypothesis. The object-unit hypothesis assumes that the proportion of trials where participants report both features correctly is a function of the probability of remembering the item (whole unit), and the probability of guessing both features correctly when the item is not remembered. From this perspective, the item would only be remembered if information about both constituent features is accessible in memory. On the contrary, the independent-stores hypothesis assumes that features can be remembered and guessed independently. Therefore, there should be no need for representing the object as a whole in order to have access to its

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constituent parts. They found that when people have to retain in VSTM objects defined by shape-colour bindings, they can remember the objects only if they correctly remember both constituent features (i.e., an all-or-none principle). Hence, remembering only one feature does not grant access to the object representation. In the unified object representation, once features are bound, they lose their individual properties and adopt the properties that define the new object. Gajewski and Brockmole (2006) investigated VSTM only for shape-colour bindings. Therefore, it is not known whether colour binding leads to the formation of new object representations and whether this occurs following the all-or-none principle.

Previous studies on colour-colour binding in VSTM (Olson et al., 2002; Parra et al., 2009a; Wheeler & Treisman, 2002) do not permit the identification of the type of format used to represent colour combinations in VSTM. This is because the tasks used in these studies did not allow ascertaining whether memory for colour parts of bicoloured objects yielded different behavioural results. Taken together the approach proposed by Gajewski and Brockmole (2006) and the methodology used by Parra et al. (2009a) might enable the investigation of whether or not colours are bound into integrated units in VSTM. Parra et al. (2009a) used a change detection task which presented bicoloured objects in two conditions which only differed in their binding requirement. Because any changes occurred in the same part of two of the objects (i.e., Internal or External colours), this design might allow the assessment of memory for objects' parts, should this principle apply to bicoloured objects (instead of being remembered as integrated units).

The independent-stores hypothesis would predict a greater cost to represent combined colours in VSTM than to represent the same number of individual colours (see Figure 1, AB > A&B). Because colours are represented in VSTM not as

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integrated units but as individual entities, retaining how colours combine would require extra memory capacity. If this were the case, each colour of bicoloured objects could be differentially remembered whether they have to be remembered together or individually. The rationale is that if colour parts of bicoloured objects are not bound into unified representation, they would be retained separately in VSTM and this may lead to different patterns of errors when either part changes. Alternatively, if colours are bound in a way that leads to the formation of new objects, memory accuracy for each individual colour would not differ, as changing either colour would result in a new object (as predicted by the object-unit hypothesis). Experiment 1 is set up to determine which of these two hypotheses better accounts for VSTM performance during feature binding within the colour dimension (see Figure 1 for experimental hypotheses).

-------- Insert Figure 1 about here --------

Experiment 1

A novel change detection task was used to investigate whether VSTM performance for bicoloured objects differed when changes occur in either of the two colours, and when colours have to be remembered together or as individual features. This design enables the assessment of the type of representation used to retain colour combinations in VSTM as memory for each colour part can be separately measured. This would permit us to test the hypothesis regarding the lack of colour integration which has been suggested previously (Parra et al., 2009a; Wheeler & Treisman, 2002). If colour parts of bicoloured objects are retained in VSTM as separate entities

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and not as features bound into unified representations, different patterns of performance would be expected when either part of bicoloured objects changes (e.g., more hits or misses for a given part).

Participants

Twenty six healthy young volunteers entered Experiment 1 (Age: M = 20.27, SD = 1.31; Years of education: M = 14.81 SD = 1.23; Sex: M = 7, F = 19). All gave their written consent prior to participation.

Stimuli

Stimuli consisted of objects with an Internal and an External area. Each area comprised 50% of the surface of the object and was filled with one of eight colours (for RGB values see http://www.era.lib.ed.ac.uk/bitstream/1842/2441/1/08-278-MAP.doc). Four objects were presented in random positions on a 15" PC screen using a 3x3 virtual grid. To construct the visual arrays for each trial one object was selected from the set used by Parra et al., (2009a). At the viewing distance of 65 cm, objects subtended 0.75^{o} and the minimum distance between them was 0.5^{o}.

Design and Procedure

Using a change detection task, participants were requested to judge two consecutive displays (i.e., study and test) which presented the stimuli described above. The design of the change detection task and its experimental conditions are shown in Figure 2. For each condition in half of the trials the objects on both displays were the same ("Same" trials). In the other half, two of the objects in the test display showed

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different colours from those in the study display ("Different" trials). Colour changes were either in the Internal area (50%) or in the External area (50%). Participants were requested to respond "different" or "same" depending on whether or not they have detected changes between displays.

Two memory conditions were assessed (Figure 2). In the Colour Change condition, the External and the Internal area of each object were shown in different colours. In the different trials one colour either from the Internal of from the External area in two of the objects was replaced by a new colour that had not appeared in the study display. The colours of the other two objects remained the same. Participants were told to focus on colours and not on their associations as the change would consist of new colours. In the Combined Colours condition, both the Internal and the External area were of different colours. In the different trials two objects swapped one colour either from the External or from the Internal area. The colours of the other two objects remained the same. Participants were told that colours and their associations were both relevant as sometimes colours would be rearranged in different combinations during the test display. For the Colour Change and Combined Colours conditions, colours could be repeated no more than twice within a display but not within objects.

Participants performed 15 practice trials followed by 48 trials out of which 24 were "same" and 24 were "different". The "same" and "different" trials were fully randomized and conditions were blocked and counterbalanced across participants.

-------- Insert Figure 2 about here --------

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Analysis

Two dependent variables were computed for Experiment 1. Percentage of Correct Recognition defined as (Hits/No. Different Trials) * 100 (i.e., Hits = changes correctly recognised when either area changed) and Response Bias (Beta). Response bias (Beta) in a "yes/no" or "same/different" tasks is often quantified based on a ratio of the probability of hits and the probability of false alarms, (Probability(Hits) + Probability(False Alarms))/2, Stanislaw & Todorov, 1999). Using the natural logarithm of this ratio, negative values of ln(Beta) indicates bias toward "no/same" responses (rejecting the change hence more Misses or Correct Rejection), whereas positive values of ln(Beta) indicates bias toward "yes/different" responses (accepting the change hence more Hits or False Alarms). A value of 0 indicates no response bias (McNicol, 1972). Percentage of correct recognition would be informative of the accuracy in remembering either colour combinations or individual colours. Response bias would reveal any preferential processing across memory conditions and type of changes. For both variables, two-way repeated-measures ANOVA was carried out. The repeated measures were Condition (Colour Change vs. Combined Colours) and Change (External vs. Internal).

Results

Percentage of Correct Recognition

Mean performance data is shown in Figure 3A. Significant main effects were found for Condition [$F(1,25) = 42.47$, $p < 0.001$] whereby Combination Change resulted in worse performance than Colour Change. Change also resulted in a significant main effect [$F(1,25) = 5.78$, $p < 0.05$] whereby colours of the External area were more accurately remembered than colours of the Internal area. The interaction of Condition

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by Change was found to be significant [$F(1,25) = 5.79$, $p < 0.05$]. Paired-samples t-tests showed that the interaction was driven by better memory performance for External Colour changes relative to Internal Colour changes in the Combination Change condition ($t(25) = 2.41$, $p < 0.05$) as compared to the Colour Change condition.

Response Bias (Beta)

Mean Response Bias is shown in Figure 3A. A significant main effect was found for Condition [$F(1,25) = 10.25$, $p < 0.01$] whereby Combination Change resulted in more preference for the response "same" (i.e., more negative Beta) than Colour Change. Change also resulted in a significant main effect [$F(1,25) = 5.11$, $p < 0.05$] whereby bias for "same" responses was more pronounced for colours presented in the Internal area than colours presented in the External area. The interaction of Condition by Change was non-significant [$F(1,25) = 0.18$, n.s.] suggesting that the negative bias for Internal colours was similar in both conditions.

-------- Insert Figure 3 A and B about here --------

Comments

Remembering combinations of colours was a more demanding task than remembering the same number of individual colours (see also Olson & Jiang, 2002; Parra et al., 2009a; Wheeler & Treisman, 2002; Xu, 2002). Notably, colours presented in the External area were remembered better than colours presented in the Internal area only in the Combination Change condition. These results provide direct evidence that colours are not integrated into single object representations in VSTM but are held as

associations of individual features. It is worth noting that the differences across conditions could not be accounted for by saliency effects (see Table S1 in Supplementary Material).

These results are challenging. The independent-stores hypothesis would support the prediction that colours which are processed within a single dimension but are presented as different parts of multicoloured objects may yield increased errors in changing trials in the Combination Change condition (i.e., as each part is processed separately). However, this hypothesis would not lend support to a prediction on a pattern of preference (i.e., bias) for External or for Internal colours. The analysis of Response Bias shed some light on this pattern of performance. It seems that participants are more likely to retain colours presented in the External than in the Internal area of bicoloured objects. This makes changes in the Internal area more likely to be missed (i.e., negative Beta), providing evidence in favour of the lack of colour integration in VSTM.

The better accuracy for External colours together with a bias toward detecting changes in this area support the hypothesis that colours of bicoloured objects are held in memory as two independent and associated, rather than integrated, pieces of information. If this is the case, retaining two colours together should require more memory capacity than retaining the same number of colours which have to be remembered individually. This hypothesis could be inferred from the outcomes of Experiment 1; however, it cannot be supported by these data. Differences in performance across conditions and type of changes suggest that capacity limitations may underpin the significant effects observed. Experiment 1 does not allow us to assess whether the procedures enable participants to group items into higher order chunks (e.g., remembering colours in the Combination Change as unified items

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instead of as the association of individual colours) which is an important index of STM capacity as posited by Cowan (2001).

This hypothesis needs further investigation. First, memory performance in Experiment 1 was assessed at the level of VSTM capacity (i.e., 4 items, see Cowan, 2001; Vogel et al., 2001). Second, memory accuracy expressed as the Percentage of Correct Recognition informs us about the demands of the tasks on the assessed functions but is not a direct measure of memory capacity (see Cowan, 2001). Third, in Experiment 1, the location of items was kept constant across study and test display. Participants could have used location as a memory cue (Treisman & Zhang, 2006) which made this piece of information relevant to the task and likely to be bound to the remembered items.

Experiment 2

Experiment 2 investigated whether the lack of colour integration previously suggested by other authors (Olson et al., 2002; Parra et al., 2009a; Wheeler & Treisman, 2002) and directly assessed for the first time in Experiment 1 could also be unveiled through the assessment of capacity limitations in VSTM. Our prediction was that if in order to correctly remember the bicoloured objects the link between colours should be retained in memory in addition to the constituent colours, the effect of this additional cost should be observed regardless of the number of objects that had to be remembered. (see Figure 1).

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Participants

Twenty eight new healthy young volunteers took part in Experiment 2 (Age: M = 21.68, SD = 1.49; Years of education: M = 17.19 SD = 2.12; Sex: M = 13, F= 15). All gave their written consent prior to participation.

Design and Procedure

For Experiment 2 we used the same task devised by Parra et al. (2009a), which differed from the task used in Experiment 1 in the following ways: (1) the location of the items randomly changed from the study to the test display and (2) the set sizes were 2, 4 and 6. The other task parameters and conditions were as in Experiment 1. As in Experiment 1, participants were told to focus on colours and not on their associations in the Colour Change condition or on colours and their associations in the Combined Colours condition. Each condition (Colour Change and Combined Colours) consisted of 32 trials out of which 16 were “same” and 16 were “different”. Conditions were blocked and counterbalanced across participants. The same and different trials were fully randomized. This design did not allow assessing memory for parts of bicoloured objects (i.e., External and Internal) as this manipulation becomes irrelevant in the Combined Colours condition when objects change their spatial locations. For the Colour Change condition the design was the same as described in Experiment 1. However, because the main finding of Experiment 1 concerned the Combined Colours condition and the main hypothesis for Experiment 2 concerns VSTM capacity as an additional underpinning of the lack of colour integration in that condition, the effect of Change (i.e., External area vs. Internal area) was not considered in Experiment 2.

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Analysis

To assess the hypothesis set forth in this experiment, we chose the approach devised by Pashler (1988) and used by Luck et al. (1997) which considers the capacity of VSTM as the number of items effectively retained as a function of the total number of items to-be-remembered (set size) also controlling for the effects of guessing (i.e., false alarm rate). Following this approach, VSTM capacity was computed using the expression: K = [S * (H - F)] / (1 - F), where K is capacity, S the set size, H is the observed hit rate (H = hits / [hits + misses]), and F is the observed false alarm rate (F = false alarms / [false alarms + correct rejections]). Capacity (K) was analysed using two-way repeated-measures ANOVA with Condition (Colour Change vs. Combined Colours) and Set Size (2 vs. 4 vs. 6) as the within-subjects factors.

Results

Mean capacity data are shown in Figure 4. There was a significant effect of Condition [$F(1,27) = 21.42$, $p < 0.001$] whereby VSTM capacity was smaller for Combination Change than for Colour Change. Set Size also resulted in a significant main effect [$F(2,54) = 13.53$, $p < 0.001$] whereby VSTM capacity increased as the memory load increased (all $p < 0.001$) except for set size 6 as compared to set size 4. The Condition by Set Size interaction was also significant [$F(2,54) = 2.74$, $p < 0.05$]. Further assessment of the interaction revealed that it was driven by a reduced memory capacity for Combination Change at set sizes 2 and 4 but not at set size 6. The results showed that two seems to be the maximum number of bicoloured objects that one can held in VSTM when colours have to be remembered together.

-------- Insert Figure 4 about here --------

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Comments

More capacity was needed to retain colour combinations in VSTM even when only two items were presented. At set size 4 the cost of remembering how colours combined at study (i.e., Combination Change condition) exceeded that required to retain one bicoloured object (K for Combination Change = 1.95 and for Colour Change was 2.99). This additional capacity should be that required to retain the information about how colours were combined. When the capacity of VSTM was exceeded (i.e., set size 6), the cost for the Combination Change condition was greater than that for the Colour Change condition though not significantly. Hence, once the capacity of VSTM is overloaded, retaining the information on how colours combined becomes more challenging and performance on the Combination Change condition rapidly deteriorates (see Parra et al., 2009a; Wheeler & Treisman, 2002; see also supplementary material for accuracy data). It might be possible that under this condition, the participants chose to focus on a subset of items in order to alleviate the extra load imposed by the need of retaining the binding between the colours of the items chosen. It is worth mentioning that the experimental manipulation introduced in Experiment 2 to make item location random could not account for the effects observed in Experiment 1 (See Table S2 in Supplementary Material). These findings demonstrate that colours that have to be retained within bicoloured objects in VSTM are not represented as integrated units but are remembered as two separate pieces of information which are associated within complex experiences. Differential memory accuracy for colour parts of bicoloured objects, a processing bias for External colours

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and an additional capacity required to store the association between colours within bicoloured objects seem to underpin the lack of colour integration.

Taking together the results of the present study and those of previous studies, we suggest that binding information in VSTM across the shape and colour dimension and within the colour dimension are functions supported by different processes. Binding shape-colour information leads to the formation of integrated units, the retention of which requires no more resources than those required to retain shapes only (Brockmole et al., 2008; Gajewski & Brockmole, 2006; Luck et al., 1997; Vogel et al., 2001). Holding associations of colours within bicoloured objects in VSTM requires considerably more capacity than holding the same number of individual colours. This evidence suggests that the two processes may reflect the function of different memory mechanisms. If this were the case, we may predict dissociations for shape-colour and colour-colour binding in VSTM (see Figure 1). In Experiment 3 we investigated this hypothesis in E.S., a brain damaged patient who presents with profound impairments to process shape-colour bindings in VSTM. The case of this patient is fully reported in Parra, Della Sala, Logie, and Abrahams (2009b).

Experiment 3

Experiment 3 investigated whether the type of representational format (i.e., conjunctions vs. associations) used to retain multifeature objects in VSTM may differ according to the material to be bound. Based on the data from Experiment 1 and 2 we would predict that a differential impairment may be observed for memory representations either based on integrative mechanisms (i.e., shape-colour) or based

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on associative mechanisms (i.e., colour-colour). If this hypothesis were valid, it would be possible to observe dissociations within VSTM for within and across dimension binding in individuals with brain damage. As E.S. had already showed a severe impairment in cross-dimension binding, it would be useful to investigate whether within dimension binding remains spared in this patient.

Participants

E.S. and ten healthy controls matched with E.S. by age (E.S.: 69; Controls: M = 67.4, SD = 6.41; t = 0.24, n.s.) and years spent in formal education (E.S.: 10; Controls: M = 14.1, SD = 2.68; t = 1.26, n.s.) entered Experiment 3. E.S. is a right-handed woman who had a meningioma in the left wing of the sphenoid which, before surgery, impinged upon her left temporal lobe. She showed normal performance in a large neuropsychological battery assessing memory, attention, executive, and language functions. However, E.S.'s VSTM for shape-colour bindings was dramatically impaired. Full clinical and neuropsychological profile of E.S. is detailed in Parra et al. (2009b). A summary of her neuropsychological assessment is also presented as Supplementary Material (Table S3).

Design and Procedure

E.S. and controls performed the same task described in Experiment 2 including set sizes 2 and 4. Performance of E.S. and controls on the shape-colour binding task was assessed using the same task described by Parra et al.'s Experiment 1 (2009b). In this task, shape-colour bindings are presented in both displays. In the different trials, two shapes swapped their colours in the test display. Participants are requested to report whether or not they detected a change between displays (see Parra et al., 2009b for a

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full description of this task). Set size 6 was not included in Experiment 3 because E.S.´s performance on the shape-colour binding task with this set size was at floor. All gave their written consent prior to participation.

Analysis

Percentage of Correct Recognition and VSTM Capacity (K) were computed. Set sizes two and four only from the Combination Change condition were used.

To compare the performance of E.S. and controls we used the statistics devised by Crawford and Garthwaite (2002) to investigate selective impairments in single-case studies. We calculated the point estimate (PE)[1] of abnormality which indicates the percentage of the control population that would be expected to obtain a score lower than that of E.S. Then we assessed whether the pattern of performance analysed across forms of binding fulfilled the criteria for classical dissociation (Crawford, Garthwaite, & Gray, 2003; Crawford & Garthwaite, 2005a). For all statistics we report the PE, one-tailed t-values (a poorer performance by E.S. relative to controls was predicted), and the probability that E.S.'s scores fell outside the normal range.

Results

Percentage of Correct Recognition

Figure 5A shows the mean Percentage of Correct Recognition for E.S. and controls across types of binding and set sizes (see Table S4 in Supplementary Material for the descriptive statistics). When E.S.'s and controls' scores in the shape-colour binding

[1] Crawford and Garthwaite (2002) developed a method for obtaining a point estimate of the abnormality of a difference between a patient's score and the average score of a modest sample which treats the normative sample statistics as statistics rather than as parameters. This is achieved by obtaining a point estimate of the abnormality of a pair of test scores.

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condition were compared, E.S. showed a clear impairment with both set sizes [2: PE = 1.38, $t(9) = 2.62$, $p = 0.014$; 4: PE = 0.05, $t(9) = 4.74$, $p < 0.001$]. No significant differences were observed when E.S.'s and controls' scores were compared across set sizes in the Colour-Colour binding task [set size 2: PE = 6.1, $t(9) = 1.7$, $p = 0.06$; set size 4: PE = 31.9, $t(9) = 0.49$, ns].

-------- Insert Figure 5 A and B about here --------

VSTM Capacity (K)

Figure 5B shows mean Capacity data for E.S. and controls across types of binding and set sizes. When E.S.'s and controls' capacity scores in the shape-colour binding condition were compared, E.S. showed a dramatic reduction in her VSTM capacity at both set sizes [2: PE = 0.00, $t(9) = 13.63$, $p < 0.001$; 4: PE = 0.00, $t(9) = 6.82$, $p < 0.001$]. No one from the normal population would be expected to show smaller VSTM capacity than E.S. No significant differences in capacity were observed when E.S.'s and controls' scores were compared across set sizes in the Colour-Colour binding task [2: PE = 18.3, $t(9) = 0.96$, ns; 4: PE = 32.0, $t(9) = 0.49$, ns].

Assessing dissociations in VSTM

The outcome from the analyses above suggests that VSTM for shape-colour bindings could be impaired in the presence of preserved colour-colour binding functions. This supports the hypotheses originating Experiment 3. However, in order to assess whether this pattern of impairment fulfils the classical criteria for dissociation, we entered this data into the formula devised by Crawford and Garthwaite (2005b). The

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outcome shows a PE = 0.05, $t(9) = 4.72$, $p < 0.001$, indicating that E.S.'s pattern of performance fulfilled the criteria for a classical simple dissociation.

Comments

In Experiments 1 and 2 we have shown that the processes responsible for binding features within and across dimensions in VSTM seem to be supported by different cognitive mechanisms. In contrasts to shape-colour binding (Brockmole et al., 2008; Gajewski & Brockmole, 2006; Luck et al., 1997; Vogel et al., 2001), colour-colour binding does not lead to the formation of unified representation (Experiment 1) and requires additional capacity to retain the relation between features within objects (Experiment 2). The segregated nature of these memory operations was further supported by the outcomes of Experiment 3 which reported the case of a patient showing a dramatic impairment in binding shape with colours in VSTM, whereas her performance in binding colours within bicoloured objects was preserved. It is worth noting that colour-colour binding is the more demanding of the two tasks (see Introduction), and that in the paradigm used in Experiment 3, healthy participants do not find colour-colour binding overall easier to perform than shape-colour binding, as evidenced by their performance (see Figure 5).

General Discussion

The results from the series of experiments presented here confirm the hypotheses that colours are not integrated in VSTM into unified objects (Olson et al., 2002; Parra et al., 2009a; Wheeler & Treisman, 2002; Xu, 2002) but are rather retained as

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associations in VSTM. Three different sets of evidence support this proposal. They will be discussed in turn.

Memory bias

The observation of memory superiority for colour parts of bicoloured objects (i.e., External colours better remembered than Internal colours) offers evidence in support of a lack of colour integration in VSTM. We predicted that, if colours are represented in VSTM not as integrated units but as individual entities, each colour of the bicoloured objects could be differentially remembered. We did not assume, however, that the differential memory for colour parts would reflect a processing bias for External colours. Should the independent-stores hypothesis hold true for bicoloured objects, one would expect to observe differential performance for External or Internal colours, but not necessarily a consistent pattern for either part, as observed in Experiment 1.

There is no account available in the VSTM literature to explain this processing bias for External colours in the Combination Change condition. Considerable evidence however could be gleaned from the memory and perception literature concerning figure/background representation. If we were to assume that the External colours of our stimuli could be interpreted as background colours, the effect appears to be consistent with evidence from the literature on memory (Isarida & Isarin, 2007; O'Herron & von der, 2009; Peterson & Grant, 2003) and perception (Hecht & Vecera, 2007; Vecera & Palmer, 2006; Vecera, 2004; but see Lester, Hecht, & Vecera, 2009). According to this literature, background information plays a crucial role in forming and accessing complex representation in memory and perception. Should these organizational principles also apply to VSTM, one might suggest that the background

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processing superiority reported in previous studies and the memory superiority for External colours of bicoloured objects observed in the present study may reflect the outcomes of related functions.

The memory superiority for External colours allowed us to empirically demonstrate that colours are not integrated into inseparable units. However, further research is needed to characterise this processing bias. Future studies should investigate this processing bias using recall instead of recognition paradigms whereby participants would be asked to report the changing area/colour (i.e., External or Internal) during Combination Change and Colour Change instead of recognising changes occurring in whole arrays.

Capacity limitations

The tasks used in the present study enabled the assessment of the extra capacity required to retain colour bindings in VSTM as the Colour Change condition provides a clear cut baseline performance. As Combination Change and Colour Change conditions presented exactly the same amount of information, performance drop in the Combination Change condition could be interpreted as the need for retaining the additional information on how colours combined (i.e., the binding). This was found to be case when the number of items did not overload the memory capacity. In fact, the binding between colours within bicoloured objects seems to be a function supported by processes other than those involved in colour processing. For example in Experiment 2, the VSTM capacity in the Combination Change and Colour Change condition was greater than two items and at the same level with set size 6. The amount of colour information to be processed overloaded the capacity of this single dimension (Olson et al., 2002; Parra et al., 2009a; Wheeler & Treisman, 2002; Xu,

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2002). However, the finding that performance was above chance in both conditions (see Table S5 Supplementary Material) suggests that binding operations required to perform the Combination Change condition, which we have demonstrated to require extra resources, were not supported by the same mechanisms involved in colour processing. The data presented here suggest that resources within the colour dimension were depleted more in the Combination Change condition than in the Colour Change. Hence, to achieve above chance performance in the Combination Change condition resources other than those provided by the colour dimension should have been used.

Recent fMRI studies suggest that individual and bound features are processed in different brain regions. Prefrontal regions seem to be important for binding functions (Prabhakaran, Narayanan, Zhao, & Gabrieli, 2000), whereas posterior parietal regions seem to be involved in feature processing (Xu, 2007). Furthermore, there is currently a debate in the literature regarding the conditions in which attention is required for shape-colour bindings, with recent studies demonstrating an involvement of attention (Brown & Brockmole, 2010; Elsley & Parmentier, 2009). However, recent studies suggest that binding shapes and colours within single items in working memory does not require more attentional resources than those required to process individual features (see Allen, Hitch, & Baddeley, 2009; Allen, Baddeley, & Hitch, 2006; Johnson, Hollingworth, & Luck, 2008). This evidence together with the results presented here support the proposal that whereas shape-colour bindings could be processed automatically in VSTM, the link between colours within bicoloured objects has to be actively maintained in order to accurately remember these complex stimuli.

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Dissociation within VSTM binding and its implications

If the link between colours within bicoloured objects has to be actively retained in VSTM in order to accurately remember the objects, these binding processes would be different to those we have been presented with in literature supporting the object-based hypothesis of VSTM (Allen et al., 2006; Brockmole et al., 2008; Gajewski & Brockmole, 2006; Luck et al., 1997; Vogel et al., 2001). This literature suggests that in the unified object representation, bound features lose their individual properties and adopt those defining the new object. Hence, remembering only one feature would not grant access to the other features that belong to a specific object representation. If we were to interpret this as a conjunction of features in VSTM, then the current data with colour-colour binding would be interpreted as a relation of features in VSTM.

There seems to be similarities between the functional constructs of the object-unit hypothesis and the independent-stores hypothesis proposed by Gajewski and Brockmole (2006) and contrasted in the present study, and the conjunctive and relational hypotheses discussed by Moses and Ryan (2006). The first two hypotheses have been postulated to investigate working and short-term memory binding functions whereas the second two hypotheses mainly concern long-term memory binding functions. The conjunctive hypothesis proposes that features are bound into integrated units (e.g., features within faces, colours within shapes) in a way that leads to changes in objects' identity (similar to the object-unit hypothesis). The relational hypothesis suggests that features are associated within complex memory networks; however each retains its own identity (similar to the independent-stores hypothesis). The outcomes from previous studies investigating VSTM performance with shape-colour bindings suggest that the predictions of the conjunctive and the object-based hypotheses could both account for this VSTM function (Allen et al., 2006; Brockmole et al., 2008;

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Gajewski & Brockmole, 2006; Vogel et al., 2001). The results presented here suggest that VSTM performance with colour-colour bindings could be accounted for by the independent-stores hypothesis whose predictions are similar to those of the relational hypothesis. That is, colours are not bound into single objects but their relation within objects is held in memory when the task requires such an association.

Taken together the data collected from E.S. in a previous study (Parra et al., 2009b) and in the current study suggest that shape-colour bindings and colour-colour bindings are stimuli processed in VSTM via different mechanisms. Parra et al. (2009b) proposed that the binding between shapes and colours represents an additional piece of information which seems to be processed by mechanisms distinct from those responsible for feature processing and feature memory. Current data from healthy individuals with colour-colour bindings also support this view and in the case for E.S., they suggest that this form of memory representation is processed by mechanisms other than those responsible for processing shape-colour bindings. Colour-colour bindings are processed in VSTM by mechanisms that may be more accurately accounted for by the independent-stores hypothesis (or relational hypothesis) whereas shape-colour bindings seem to be represented via mechanisms more linked to the predictions of the object-based hypothesis (or conjunctive hypothesis). The scarce literature available on VSTM and Working Memory binding suggests that holding conjunctions of features (i.e., shape-colours) and holding relations between features as associations in memory are processes supported by different mechanisms and brain regions (Baddeley, Allen, & Vargha-Khadem, 2010; Parra et al., 2010; 2011; Piekema, Kessels, Mars, Petersson, & Fernandez, 2006). Baddeley et al. (2010) assessed Jon, a patient with developmental amnesia whose pathology appears to be limited to the hippocampus. Jon showed preserved Working

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Memory functions for shape-colour binding while E.S.'s presented with a severe impairment. E.S.' lesion impinged upon the anterior pole of the left temporal lobe. It might be possible that medial temporal lobe structures other than the hippocampus could be involved in this form of binding. This together with the data presented here support the idea that some of the properties of binding processes in VSTM are dissociable.

Conclusions

The results presented here provide novel evidence which can help to explain why colour-colour bindings (i.e., within dimension binding) are retained in VSTM less efficiently than shape-colour bindings (i.e., across dimensions binding). Colour combinations are subserved by associative memory mechanisms while shape-colour combinations are subserved by conjunctive mechanisms. These mechanisms seem to pose different memory demands and are differentially vulnerable to brain damage.

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Figure Captions

Figure 1. Hypotheses assessed in Experiments 1 to 3. Experiment 1 investigated whether colour combinations could be retained in VSTM as integrated objects or as individual features which are associated within objects. Experiment 2 investigated if the additional cost of retaining colour-colour binding in VSTM (AB > A&B) holds when the number of to be remembered objects increased. Experiment 3 assessed the hypothesis that if colours are not bound into unified representations, this memory function should dissociate from that supporting shape-colour binding as the last one does lead to integrated objects in VSTM. This hypothesis was tested in a patient who had previously shown severe impairment in the latter function.

Figure 2. Experimental procedure used to asses VSTM for colour combinations (CC) and for non-combined colours (Colour Change). The set size shown is for illustration purposes. 1000 msec was chosen as the presentation time in previous studies suggests that shorter times may yield near floor performance (Parra et al., 2009a).

Figure 3. (A) Mean Percentage of Correct Recognition and **(B)** Response Bias (Beta) in the two experimental conditions (Colour Change and CC) across the type of changes (Internal and External) (Error bars represent the standard error of the means).

Figure 4. Mean capacity in the two experimental conditions (Colour Change and CC) across the three set sizes (Error bars represent the standard error of the means).

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Figure 5. (A) Mean Percentage of Correct Recognition and **(B)** Capacity (K) for E.S. and controls across types of binding and set sizes (Error bars represent the standard error of the means).

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Figure 1.

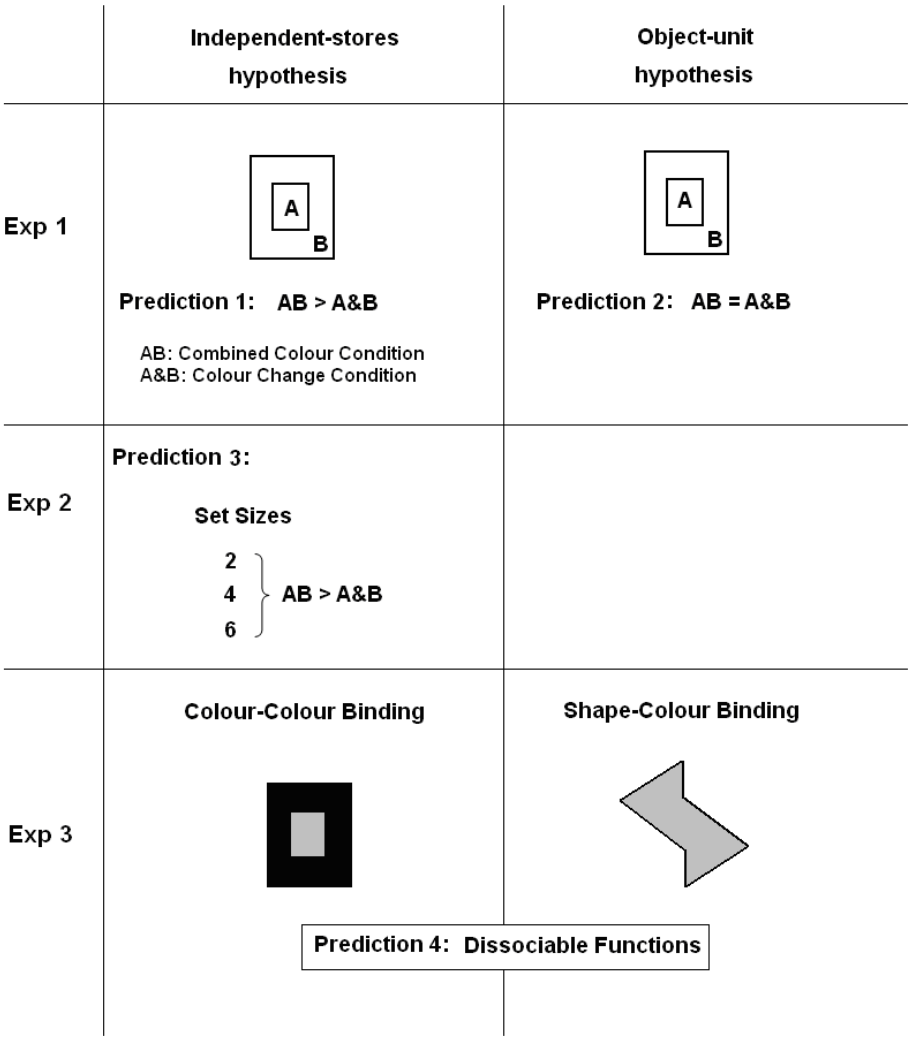

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Figure 2.

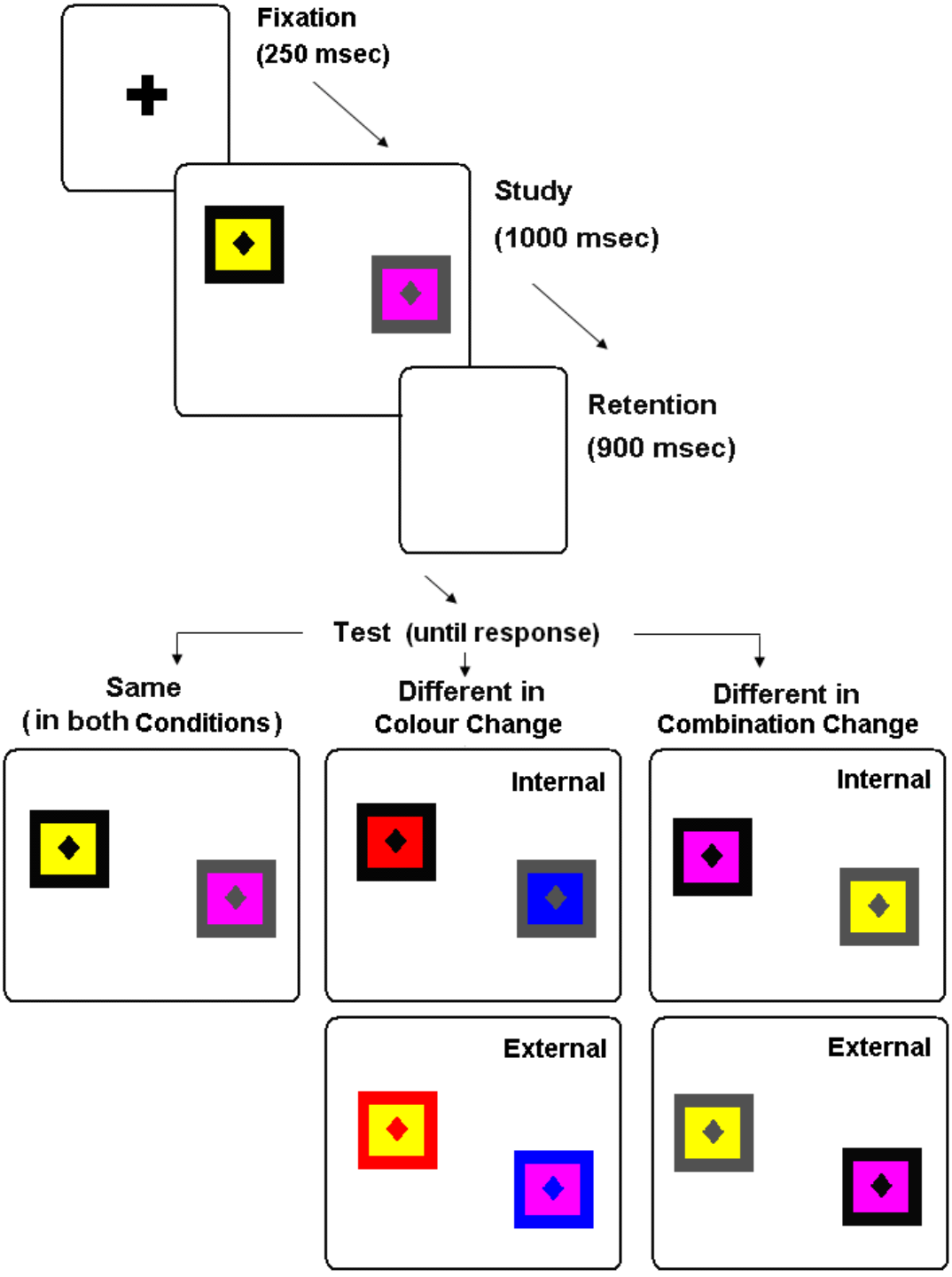

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Figure 3.

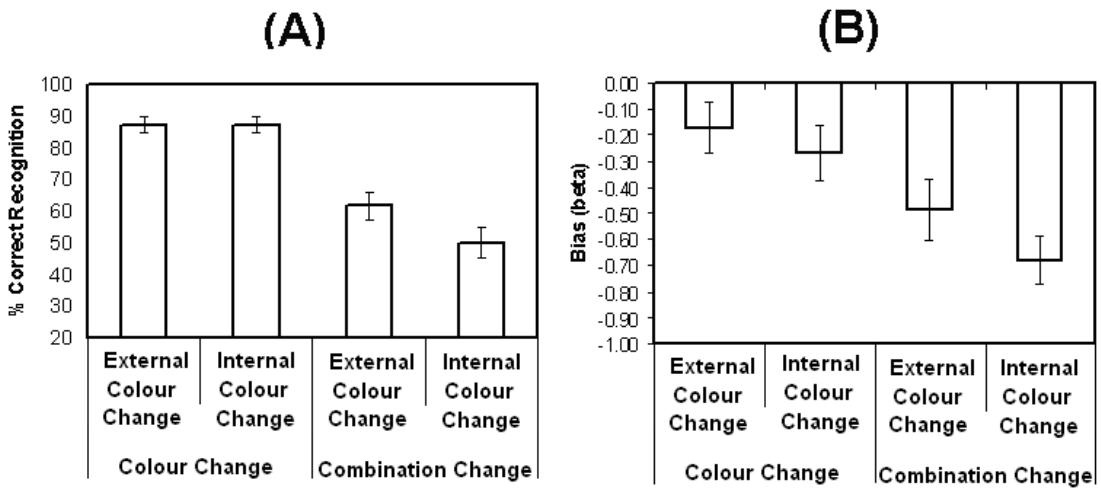

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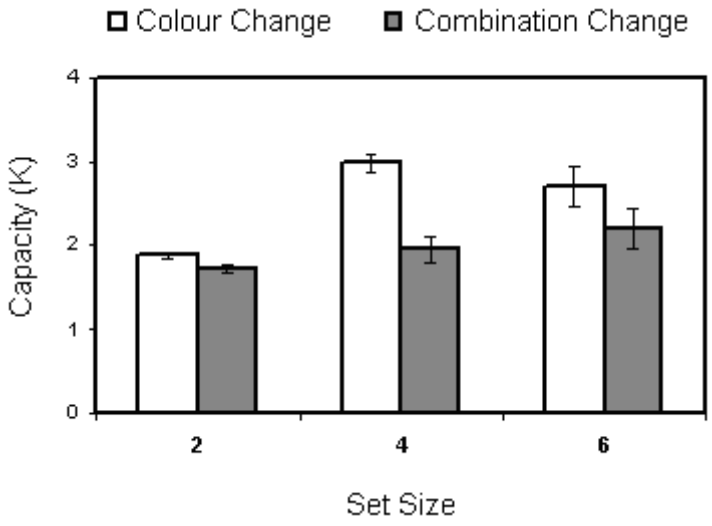
Figure 4.



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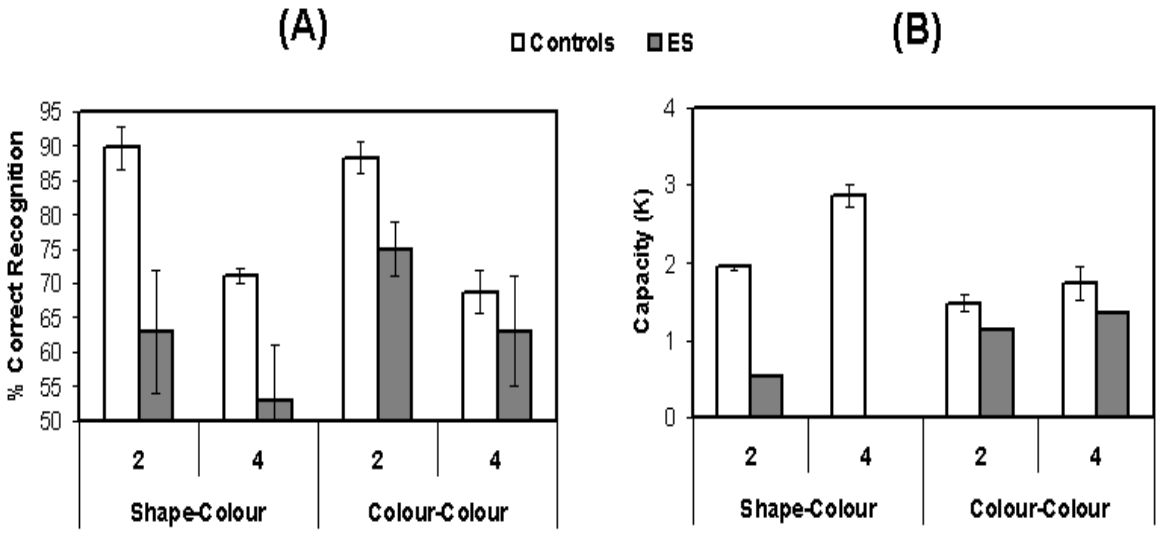
Figure 5.