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Citation for published version:
Parra, M, Della Sala, S, Logie, RH & Abrahams, S 2009, 'Selective impairment in visual short-term memory binding', *Cognitive Neuropsychology*, vol. 26, no. 7, pp. 583-605.
https://doi.org/10.1080/02643290903523286

Digital Object Identifier (DOI):
10.1080/02643290903523286

Link:
Link to publication record in Edinburgh Research Explorer

Document Version:
Peer reviewed version

Published In:
Cognitive Neuropsychology

Selective impairment in visual short-term memory binding

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Short Title: Impairment in VSTM binding

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Key words: Short-term memory, memory binding, feature integration, working memory, episodic buffer.

Acknowledgements

We thank Dr. Patrick Statham, Neurologist from the Western General Hospital, who granted us access to the clinical notes and MRI scans of ES. M.A.P.'s work during the accomplishment of this project was supported by the Programme Alban, the European Union Programme of High Level Scholarships for Latin America, Scholarship No. E04D048179CO (Supervisor S.D.S).

Abstract

Dissociations within binding in perception have been reported after brain damage. In short-term memory (STM), feature binding and feature processing appear to rely on separate processes. However, dissociations within binding in STM following brain damage have not been reported to date. We report on the case ES who, after removal of a left medial sphenoid ridge meningioma, developed a selective impairment of visual STM (VSTM) binding. We found that, despite having normal perceptual binding, ES was unable to retain in VSTM features bound into objects while she could retain individual features as well as controls (Experiments 1-2, 4, and 6). Her verbal STM for bound and single features remains intact (Experiments 3 and 5). ES's performance suggests that STM binding can be dissociated from STM for single features across visual and verbal domains. The results are discussed in the light of current models of STM.

Introduction

Research on perception and visual attention has demonstrated that the issue of how to bind the multiple features that characterize individual objects or scenes (e.g., shape, colour, motion, luminance, depth), which are processed in separate brain regions (Denys et al., 2004; Kandel & Wurtz, 2000; Van & Drury, 1997), represents not only a theoretical but a practical problem (Treisman, 1996; 1998; 1999; Treisman & Gelade, 1980). The Feature Integration Theory (Treisman & Gelade, 1980) and the role of attention in feature integration have been proposed to explain data from both normal and brain damaged individuals (e.g., illusory conjunctions) (Cohen & Rafal, 1991; Corbetta, Shulman, Miezin, & Petersen, 1995; Friedman-Hill, Robertson, & Treisman, 1995; Wojciulik & Kanwisher, 1998). The literature on perception suggests that attention acts as the "cognitive glue" which keeps features together (Treisman, 1996; 1998; 1999; Treisman & Gelade, 1980). According to the Feature Integration Theory, as long as objects fall within the focus of attention and their features share the same spatial locations, they will be interpreted as belonging together and represented in perception as unified objects (Treisman & Gelade, 1980).

Less is known about binding in memory (Luck & Vogel, 1997; Treisman, 2006; Vogel, Woodman, & Luck, 2001; Wheeler & Treisman, 2002; Zimmer, Mecklinger, & Lindenberger, 2006). Attempts have been made to investigate whether this object-based organization that characterizes perception also applies to visual short-term memory (VSTM) (Luck & Vogel, 1997; Vogel et al., 2001; Wheeler & Treisman, 2002). As attention has been used to provide accounts of binding in perception, an Episodic Buffer (Baddeley, 2000) has been added to the working memory (WM) model proposed by Baddeley and Hitch (1974) to account for this process in memory. The Episodic Buffer has been thought of as a memory device able to bind multimodal information (Allen, Baddeley, & Hitch, 2006; Baddeley, 2000; 2007a & b), yet two issues still remain unresolved; firstly whether WM stores individual features or integrated objects (Luck & Vogel, 1997; Vogel et al., 2001; Wheeler & Treisman, 2002), and secondly what brain mechanisms underpin these forms of WM representation (Piekema, Kessels, Mars, Petersson, & Fernandez, 2006; Prabhakaran, Narayanan, Zhao, & Gabrieli, 2000; Uncapher, Otten, & Rugg, 2006; Xu, 2007).

Two alternative hypotheses have been proposed to explain how conjunctions of features are represented in the visual component of WM (i.e., VSTM). One suggests that VSTM is object-based (Luck & Vogel, 1997; Vogel et al., 2001) while the other proposes a feature-based organization for VSTM (Treisman, 2006; Wheeler & Treisman, 2002). In fact, the representation format of VSTM has been found to depend on factors such as memory load, type of bound features, influences from long-term knowledge, and others (Alvarez & Cavanagh, 2004; Brockmole, Parra, Della Sala, & Logie, 2008; Logie & van der Meulen, 2009; Parra, Abrahams, Logie, & Della Sala, 2009a; Wheeler & Treisman, 2002). Therefore, whereas in perception the analysis of the external world seems to be object-based, in VSTM either objects or features may be the unit of representation.

Neuropsychological evidence suggests that representing single and bound features in perception may be supported by different brain mechanisms. Studies of single cases with focal brain damage have shown that the occipital, parietal and temporal regions are all important for perceptual feature binding (Cohen & Rafal, 1991; Friedman-Hill et al., 1995; Wojciulik & Kanwisher, 1998; see also Corbetta et al., 1995 for fMRI evidence in normal individuals). Friedman-Hill et al. (1995) and

Wojciulik and Kanwisher (1998) assessed RM, a patient with an extensive vascular lesion affecting the occipito-parietal and temporal regions which expressed clinically as Balint's syndrome. Even though RM was able to perceive individual features such as letter shapes, colours or locations, and had implicit access to integrated representations of these features, when asked to report these conjunctions explicitly, he performed at chance showing a significant number of binding errors (e.g., illusory conjunctions) (Friedman-Hill, et al., 1995; Wojciulik & Kanwisher, 1998). These results led the authors to suggest that the attentional mechanisms subserved by the brain regions damaged in RM, are important for correct feature binding. Similar findings had been reported by Cohen and Rafal (1991) in an earlier single case study.

The neuropsychology literature on VSTM binding is sparse. The results from behavioural and fMRI studies involving both visual and verbal STM support the proposal that as for perception, STM may be equipped with independent mechanisms to process integrated objects and individual features. Behavioural studies on language have shown that lists of words can be represented in verbal STM as integrated units (e.g., binding words into sentences), and that this process considerably boosts the capacity of this memory system (Cowan, 2001; Miller, 1956). In the language literature this process is known as chunking (Cowan & Chen, 2009), and relies mainly on binding operations (Burtis, 1982; Cowan, 2001; Gobet et al., 2001; Gobet & Clarkson, 2004). Furthermore, recent studies with Alzheimer's disease patients (Parra, Abrahams, Fabi, Logie, Luzzi, & Della Sala, 2009b) and healthy older adults (Brockmole et al., 2008; Parra et al., 2009a) have revealed that STM binding is impaired in the former group to a much greater extent than STM for single features, whereas in the latter group both forms of STM representations are preserved.

Neuroimaging studies have suggested that processing objects and features in WM may involve different brain regions. The prefrontal cortex has been found to be activated when WM for conjunctions of features was explored (Mitchell, Raye, Johnson, & Greene, 2006; Prabhakaran et al., 2000). Posterior parietal regions however, are considered to be responsible for feature processing in VSTM (Shim, Alvarez, & Jiang, 2005; Xu, 2007). In PET studies assessing perceptual binding, the parietal regions have been found to be activated during visual search for conjunctions of features (Corbetta et al., 1995). This suggests that the networks subserving object and feature processing in perception and VSTM may be different but they might share resources. More recently the hippocampus, a structure largely thought of as being involved in long-term memory binding (Holdstock, Mayes, Gong, Roberts, & Kapur, 2005; Mayes, Montaldi, & Migo, 2007; Mayes et al., 2004), has been found to be activated during WM tasks involving feature binding (Hannula & Ranganath, 2008; Hannula, Tranel, & Cohen, 2006; Mitchell, Johnson, Raye, & D'Esposito, 2000; Mitchell et al., 2006; Piekema et al., 2006). However, the involvement of the hippocampus seems to depend on the requirement of binding to spatial locations (Piekema et al., 2006). Hence, STM binding seems to rely on a network which comprises prefrontal, parietal, and temporal regions. These regions show different levels of activation during the processing of single features and integrated objects.

In sum, objects and features seem to be processed in perception and VSTM through separate mechanisms. In perception, this proposal has been assessed in both normal and brain damaged individuals including single case studies. Even though the available literature on STM involving behavioural and neuroimaging studies suggests that this may also be the case for this cognitive system, this hypothesis has never been directly tested. Considering the results from behavioural and neuroimaging studies on

STM discussed above, it may be possible to predict that a pattern of dissociation similar to that found in perception (i.e., compromised object processing with preserved feature processing) (Friedman-Hill, et al., 1995; Wojciulik & Kanwisher, 1998) might also be found in STM. In this paper we report on single case who shows a dissociation within binding in STM. We present case ES who has a selective impairment in VSTM for bound objects whereas her VSTM for individual features as well as verbal STM for bound objects and individual features is intact. The assessment of ES was aimed at providing new insights into the functional organization of STM for features and objects.

Case ES

We saw ES for the first time in September 2006. She was a member of the Edinburgh Psychology Department panel of volunteers, originally recruited as a control participant for a different experiment (Parra et al., 2009a). However, after a few trials of the paradigm for that experiment (Experiment 1 in the current paper), it was clear that she was having great difficulty in holding the bindings of features in VSTM as compared with her VSTM for single features. This pattern was quite unlike other control participants in that experiment. In the debriefing session it became apparent that she had previously undergone brain surgery to remove a left medial sphenoid ridge meningioma. She was therefore not included as a control participant in that study (Parra et al., 2009a) and was instead invited to take part in a single case study to assess her STM for binding. At the time of the assessment, she maintained she was free of symptoms and she had noticed no memory problems in her everyday life.

Case history

ES is a right handed woman who completed 9 years of formal education. She was 69 years old at first interview. At the age of 64 she had been diagnosed with a meningioma pressing against her left temporal lobe. This was surgically removed. A follow-up MRI scan 3 months after surgery is shown in Figure 1.

Figure 1 about here

General neuropsychological assessment

Her colour vision as assessed by the Colour Blindness Test (Dvorine, 1963) was found to be normal (15/15). As can be seen from Table 1, ES performed within normal range in an extensive neuropsychological battery**.** Her memory functions including the recall and recognition of verbal and nonverbal material (Logical Memory Test, Doors and People Test, Rey Osterreith Figure) was intact. She performed well in attention tasks (Ruff 2 & 7 Selective Attention task and Trail Making Test parts A and B). On tests of executive functions she was in the normal range for number of categories achieved at the Wisconsin Card Sorting Test although she showed abnormally high number of perseverations. However, she performed within the normal range in the Hayling and Brixton Test and Word Fluency Tests. Visual and perceptual functions as measured by the Visual Object and Space Perception Battery and copy of the Rey Osterreith Figure showed no impairment. Notably, her performance on the Visual Patterns Test (Della Sala, Gray, Baddeley, Allamano & Wilson, 1999) was unimpaired, indicating intact visual span.

Table 1 about here

Experiment 1

Aims

Experiment 1 investigated memory binding and more specifically memory for bound information (i.e., objects) as compared with memory for single information (i.e., features) in ES and a group of controls.

Methods

ES and eight controls matched on age (M = 69.0, SD = 8.3; t = 0, df = 7; n.s.), education (M = 12.1, SD = 2.2; t = -0.90, df = 7; n.s.) and premorbid Verbal IQ (M = 107.5, SD = 5.06; t = -1.77, df = 7; n.s.) as measured by the Wechsler Test of Adult Reading (Wechsler, 2002) entered Experiment 1. All participants gave their informed consent to take part in this study.

The task used in this experiment was based on a change detection paradigm and was devised to assess memory for single features (i.e., abstract shapes and colours) and for the binding of these features. The experimental conditions included in this task as well as the trial design are shown in Figure 2. Using a 15” personal computer screen participants were presented on each trial with a study array followed by a test array, each consisting of 2 or 4 shapes (shape only condition), or colours (colour only condition), or coloured shapes (shape-colour binding condition). Items subtended 1.5 cm horizontally and vertically and they were separated by no less than 1 cm. Viewing distance was not constrained.

As we wanted to avoid the use of articulatory suppression, we selected a set of abstract shapes and a set of colours which RGB values were modified as to make them different from primary colours. A pilot study proved that the stimuli chosen within each set were perceptually different but difficult to name. This together with the suggestion by Vogel, Woodman, and Luck (2001) and Treisman (2006) about the non-significant contribution of verbal STM to successful VSTM performance during change detection tasks supported the decision of not including articulatory suppression in our experiments.

As indicated in Figure 2, the task was to compare the test array with memory for the previously presented study array. In 50% of the trials the study and test array consisted of different items; for shape only or colour only conditions, the test array showed two new shapes or two new colours respectively; for the shape-colour binding condition, the test array showed the same shapes and colours as before, but with two colours swapped between shapes. In the other 50% of trials, the items were the same in both arrays. For both the “same” and “different” trials, item locations between study and test arrays were randomly changed. This procedure was aimed at rendering location an uninformative feature during the task (see Wheeler & Treisman, 2002). Participants were explicitly instructed to remember the information visually as any attempt to use verbal labels might result in unsuccessful performance. They were also instructed to respond verbally “different” or “same” depending on whether or not they detected a change between the two arrays. Each condition was blocked and started with 10 practice trials followed by 64 test trials (32 trials per array size).

Figure 2 about here

Statistical Analysis

The statistical analysis is based on that devised by Crawford and Garthwaite (2002) to investigate neuropsychological impairments in single case studies. Using the formulae provided by the authors (http://www.abdn.ac.uk/~psy086/dept/), we first investigated whether there were statistically significant difference between ES's and controls' memory scores for integrated objects and individual features. The method devised by Crawford and Garthwaite (2002) provides a point estimate (PE) of abnormality. The PE indicates the percentage of the control population that would be expected to obtain a score lower than that achieved by the patient in the assessed function (Crawford & Garthwaite, 2002). Hence, small values of PE are indicative of abnormality. We then assessed whether the difference between ES' performance in the impaired condition and her average performance differed statistically from this same contrast calculated in the controls. For all statistics we report the PE, the one-tailed t-value, and the probability that her scores were outside the normal range.

Results

Mean scores across experimental conditions for ES and Controls are shown in Figure 3. Compared to controls, ES had no difficulties in remembering abstract shapes [PE = 15.99, t = -1.07, df = 7; n.s.] or colours [PE = 47.88, t = -0.05, df = 7; n.s.] presented as individual features. However, ES showed a significant deficit in memory for bound features [PE = 0.66, t = -3.30, df = 7; $p < 0.05$] (Figure 3A). This binding deficit was observed when she had to remember either 2 objects [PE = 2.38, t = -2.40, df = 7; $p < 0.05$] or 4 objects [PE = 1.64, t = -2.66, df = 7; $p < 0.05$] (Figure 3B). Only 0.66% of the population would be expected to score lower that ES in the condition assessing memory for shapes bound with colours, indicating a profound impairment. Finally, the discrepancy analysis across conditions showed that only 3.04% of the population (t = -2.23, df = 7) would be expected to score lower that ES when memory for the binding of shapes with colours is compared to her average performance. In contrast, 68.0% (t = 0.49, df = 7) and 93.71% (t = 1.74, df = 7) of the population would be expected to score lower that ES when her performance in conditions assessing memory for shapes only and colours only respectively are compared to her average performance.

Figure 3 – A and B - about here

Comments

ES displayed a selective deficit for memory of bound features, with spared memory for single features. It might be argued that limited VSTM resources (i.e., approximately 4 items, Cowan, 2001; Luck & Vogel, 1997; Vogel et al., 2001) are enough for processing single feature but not for processing multi-feature objects. However, Brockmole et al. (2008) used a version of the current task to assess VSTM for arrays of 4 items in older adults with a mean age (67.3 years) which was comparable to ES's age. The authors reported that performance in the shape only and shape-colour binding conditions did not differ in this group. In fact, Bonferroni-corrected paired-sample t-tests showed that this was also the case for performance of the control participants in the current experiment. Therefore, limited VSTM resources alone cannot be the cause of the poor performance observed in ES in the binding condition only.

An earlier case (RM -Friedman-Hill et al., 1995; Wojciulik & Kanwisher, 1998) shows some resemblance to ES. RM performed at chance when he was asked to report verbally conjunctions of features visually presented even though he showed a normal priming effect to these conjunctions. The authors suggested that RM had a specific difficulty in binding features into objects. There are however, a number of differences between these earlier single case studies and the current study which suggest that the impairments found in RM and ES may arise from damage to different processes. In the study by Wojciulik and Kanwisher (1998) the explicit access to feature binding was assessed with a task that presented two coloured words. The coloured words were initially presented for 300 msec. The presentation time was then reduced in a control phase until RM's explicit performance reached chance level (e.g., in Experiment 1 the mean presentation time over ten blocks of valid trials was 159 msec). Under this condition, RM showed a normal priming effect. Additionally, in the task used by Wojciulik & Kanwisher (1998), the implicit and explicit tests were paired. That is, the patient's implicit recognition was assessed after the control phase described above, and immediately after he had to report the requested feature verbally. Therefore, with the short presentation time, the lack of retention interval between the implicit and explicit tests, and the small number of items used in that task, it is very likely that the impairment shown by RM results from a deficit in visual perception rather than in VSTM. The authors argued that the parietal regions, which were damaged in RM, subserve the attentional mechanisms necessary for feature binding. These attentional mechanisms do not seem to be necessary for feature binding in VSTM (Gajewski & Brockmole, 2006; Johnson, Hollingworth, & Luck, 2008).

However, the results of the study by Wojciulik and Kanwisher (1998) led to the question of whether ES's impairment arose from difficulties in holding in VSTM conjunctions of features or in forming these bindings in perception. As in our Experiment 1 there was a gap between the study and test displays, hence this task did not assess whether these features were correctly grouped in perception. In order to investigate whether ES's impairment was specific to binding in VSTM it was important to assess the potential contribution of perceptual binding to this impairment.

Experiment 2

Aims

Experiment 2 investigated whether the deficit shown by ES in the condition assessing memory for bound features of Experiment 1 could be accounted for by deficits in binding in perception. If the process of forming conjunctions of features in perception is unaffected in ES, we would have more confidence in our interpretation that the impairment observed in Experiment 1 arose from difficulties in retaining feature bindings in VSTM.

Methods

The same participants from Experiment 1 took part in this experiment. The task was constructed using the stimuli and apparatus described in Experiment 1. In this new task participants were simultaneously presented with two arrays of four items each in the upper and lower half of a PC screen. Items consisted of the same shapes (shape only condition), colours (colour only condition), or coloured shapes (shape-colour binding condition) used in Experiment 1. In 50% of the trials both arrays presented identical items whereas in the other 50%, two items changed either in the upper (25%) or in the lower (25%) array. Changes between arrays were the same as described in Experiment 1. Participants were requested to search for differences between the two arrays and to respond, by pressing two keys, as to whether they consisted of the same or different items. Participants were instructed to do this as accurately as possible while also responding as quickly as possible. Percentage of correct detection was used as the dependent variable. Each condition involved presenting 32 trials in a random order.

Results

Compared to controls, ES had no difficulties in searching for differences between arrays of shapes [PE = 74.75, $t = 0.07$, $df = 7$; n.s.], colours [PE = 72.21, $t = 0.619$, $df = 7$; n.s.], or coloured shapes [PE = 56.24, $t = 0.163$, $df = 7$; n.s.].

Comments

When the same type of stimuli were used for searching for differences between arrays rather than for holding these arrays in VSTM, ES and controls did not differ. Had ES had any difficulty in forming bindings in perception, she would have performed poorly in this perceptual task. This result suggests that RM's (Wojciulik & Kanwisher, 1998) and ES's impairments result from damage to different processes. Taken together, the results from Experiments 1 and 2 suggest that ES can accurately integrate features in perception but she cannot hold these bindings in VSTM. Given the results of Experiment 2, we therefore maintain that the current paper presents the first report of a selective deficit in temporary memory for conjunctions of features following brain damage.

ES's meningioma was in the left hemisphere, which is usually associated with verbal processing (Milner, 1971; 1982; Milner & Taylor, 1972). However, her visual STM binding functions were found to be impaired in Experiment 1. This is not per se surprising (see e.g. dissociation in Della Sala et al., 1999). In the neuropsychological assessment ES performed tasks assessing visual and verbal memory within the normal limits (i.e., Logical Memory, Visual Pattern Span, Doors and People Test, Recall of Rey-Osterrieth Complex Figure, and VOSP). This led to the question of whether ES's STM impairment was confined to visual binding or whether it also extended to verbal binding. Therefore, Experiment 3 was designed to assess whether ES might also show a deficit in binding that involved verbal codes.

Experiment 3

Aims

Experiment 3 investigated if ES's memory deficit for non-verbal bound information would also encompass her verbal memory for integrated objects. This was addressed by assessing memory for nameable features and conjunctions of these features using a task that explicitly required holding the information in STM using verbal codes.

Methods

Eight new participants served as controls for ES in this experiment. Participants were matched to ES on age (M = 69.8, SD = 6.22; t = -0.122, df = 7; n.s..), education (M = 12.2, SD = 1.75; t = -1.185, df = 7; n.s.), and VIQ (M= 105.0, SD = 4.34; t = -1.56, df = 7; n.s.). All participants gave their signed consent to take part in this study.

For Experiment 3 we devised a new task to assess recognition of verbal information. Figure 4 shows the experimental conditions and trial designs used in this experiment. Two sets of 11 nameable colours (Red, Blue, Green, Brown, Orange, Yellow, Purple, Gray, Turquoise, Pink, and Black) and 11 nameable objects (Bed, Apple, Banana, Bell, Shoe, Car, Book, Chair, Cup, Guitar, and Button) were used to construct the stimuli arrays. Nameable objects were taken from the International Picture Naming Project (http://crl.ucsd.edu/~aszekely/ipnp/). In Experiment 1 we kept constant the number of objects and we varied the number of features. That is, 2 or 4 objects with one feature each in conditions assessing memory for colours or shapes, and 2 or 4 objects with two features each in the condition assessing the binding of shapes with colours. As the total amount of information as determined by the number of features was greater in the binding condition than in conditions assessing memory for individual features, there may have been an effect of memory load. In order to remove this effect from further experiments we varied the task design. In Experiment 3 we kept constant the number of features across conditions and we only varied the number of objects holding these features, therefore, participants were presented with study arrays consisting of 4 or 6 objects (object only condition), 4 or 6 colours (colour only condition), or 2 or 3 combinations of objects and colours (object-colour binding condition).

The study array was presented for 1.5 sec per feature, that is, when 6 single objects or 3 coloured objects were presented on the screen, the presentation time was 9 sec for each display. This equated the presentation time for the amount of information to be remembered as determined by the number of features. After the study array participants were given a booklet which contained lists of names of objects, colours, or pairs of objects and colours. The retrieval cues used in this experiment were written words rather than visual objects to ensure that the visual information presented in the initial display would be transposed into verbal codes in order to make the correct selection during the recognition phase. The lists consisted of twice as many items as presented in the study array. For conditions assessing memory for individual items, 50% of the items in the lists were the names of the objects presented in the study display and 50% were distracters. In the condition assessing memory for bound items, 50% of the object-colour pairs in the lists corresponded to the items previously presented, 25% were constructed using the names of the objects previously seen coupled with distracter colour names, and the other 25% were constructed using the names of the colours previously seen coupled with new distracter object names. As we wanted to avoid semantic STM facilitation, in the binding condition objects were never presented at study in prototypical colours. Participants were requested to tick the items that corresponded to the objects previously seen. The task consisted of 18 trials per experimental condition (9 trials per array size).

Figure 4 about here

To ensure that participants were able to name the items in the experiment, prior to the first trial they were presented with two arrays one containing 22 objects and another one containing 22 colours. Fifty percent of the objects and colours presented in these arrays corresponded to the actual stimuli used in the experiment while the other 50% were not used in the experiment. Participants were requested to name the objects and the colours aloud. All the participants that entered the experiment, including ES, named 100% of the objects and colours correctly.

Results

Figure 5 shows mean performance of ES and controls in Experiment 3. As compared to controls, ES had no difficulties in remembering objects [PE = 5.44, t = -1.83, df = 7; n.s.], colours [PE = 36.32, t = -0.36, df = 7; n.s.], or objects bound with colours [PE = 55.58, t = 0.14, df = 7; n.s.].

Figure 5 about here

Comments

ES was able to use verbal codes to retain information on bound features that were visually presented. Taken together with the results from Experiment 1, this suggests that ES is specifically unable to hold conjunctions of information in VSTM. The fact that in the task for Experiment 3 the number of items in the binding condition was half the number of items presented in the single feature conditions may suggest that ES was better simply because this binding task was less demanding than the binding task used in Experiment 1. However, we do not consider the task demands as the mechanism responsible for ES's impaired visual and preserved verbal binding functions observed in Experiments 1 and 3 respectively.

ES was unable to retain 2 coloured shapes in VSTM (Experiment 1) while she could retain 3 coloured objects in verbal STM (Experiment 3). The binding condition may have resulted in better scores than in the single feature conditions just because long-term representations of the items used in Experiment 3 may have been more accessible than those for the items used in Experiment 1 (see Hollingworth, 2005; Logie, 2003; Logie & van der Meulen, 2008). This may explain why in Experiment 3, performance of ES and controls was better in the binding condition than in the single feature conditions, a pattern that was not observed in Experiment 1. This does not rule out the binding requirements of the task used in Experiment 3. If we were to assume the task demands as the mechanism responsible for ES's preserved verbal and impaired VSTM binding, we should expect to find normal visual binding functions in ES if the same task used in Experiment 3 required holding information in a visual rather than in a verbal format. Alternatively, if our interpretation of ES's deficit is correct, then we should find the same pattern of results observed in Experiment 1. We tested these hypotheses in the next experiment, with an adaptation of the paradigm from Experiment 3 in which visual information was used in both the study and test phases (instead of words as recognition cues).

Experiment 4

Aims

Experiment 4 addressed memory for nameable features and conjunctions of these features using a task that required the maintenance of this information in STM using mainly visual codes.

Methods

The same participants who undertook Experiment 3 took part in Experiment 4. The study arrays were the same as described in Experiment 3. However, the test arrays consisted of objects rather than words (see Figure 6). In the condition assessing memory for single features the test array presented twice as many items as the study array. Half of these items corresponded to those previously seen while the other half were items not presented in the study array. Participants were requested to select, using the mouse, the objects or colours they had seen in the study array. The objects or colours selected were subsequently removed from the test array. In the condition assessing memory for the binding of objects with colours, the test display presented two separate arrays of items. One array consisted of the same objects previously seen plus the same number of new distracter objects, and the second array consisted of the same colours previously seen plus the same number of new distracter colours. Participants were requested to select, using the mouse, the objects they had seen in the study array with their corresponding colours. The selected combinations were shown at the bottom of the screen. The task consisted of 18 trials per experimental condition (9 trials per array size).

Figure 6 about here

Results

Figure 7 shows mean performance from Experiment 4. ES had no difficulties in remembering objects [PE = 29.32, t = -0.57, df = 7; n.s.] or colours [PE = 41.30, t = -0.23, df = 7; n.s.] presented as individual features. However, ES's memory for these features integrated into objects was impaired [PE = 0.05, t = -5.41, df = 7; p < 0.01] (Figure 7A). When her performance in the condition assessing memory for bound features was analyzed across set sizes (see Figure 7B), these differences fell short of significance [2 items: PE = 8.37, t = -1.54, df =7; p = 0.08; 3 items: PE = 8.39, t = -1.54, df = 7; p = 0.08]. Only 0.05% of the population would be expected to score lower than ES in the condition assessing memory for objects bound with colours.

However, 29.32% and 41.30% would be expected to score below ES in tasks assessing VSTM for objects or colours only respectively. The discrepancy analysis showed that 0.23% of the population ($t = -4.09$, $df = 7$) would be expected to score lower than ES when memory for the binding of objects with colours was compared to her average performance. In contrast, 94.54% ($t = 1.83$, $df = 7$) and 97.06% ($t = 2.25$, $df = 7$) of the population would be expected to score lower than ES when performance in conditions assessing memory for objects only and colours only respectively, are compared to her average performance.

Figure 7 – A and B - about here

Comment

Taken together, the results of Experiments 1, 3 and 4 suggest that ES's impairments reflect an inability to represent bound information in VSTM while her memory for visual unbound information and for verbal bound and unbound information seems to be intact. The results of Experiment 4 allow us to propose with more confidence that the preserved verbal and impaired VSTM binding functions observed in ES do not seem to be accounted for by differences in task demands. However, the verbal nature of the stimuli used in Experiments 3 and 4 could explain why comparisons between ES's and controls' scores across set sizes in Experiment 4 resulted in non-significant effects. ES might have been able to use some of her verbal resources to aid VSTM.

However, as Figure 7B shows, these resources were not enough to overcome her specific VSTM binding impairment.

As the previous experiments assessed recognition memory for verbal and non-verbal information, we were also interested in assessing whether the selective deficit shown by ES in memory for objects would be replicated when recall was used as the retrieval strategy. Experiment 5 and 6 were devised to investigate memory for bound and unbound information using a free recall paradigm. Experiment 5 investigated free recall of single and bound words that were aurally presented. Experiment 6 investigated free recall of shapes and colours that were visually presented as individual or combined features.

Experiment 5

Aims

We predicted that ES would perform well on tasks assessing memory for single and bound features that were presented aurally, which would mainly rely on verbal STM.

Methods

The same participants who participated in Experiments 3 and 4 took part in Experiment 5. For this experiment we created lists consisting of two or three syllable words that corresponded to the names of pictures taken from the same database used in Experiments 3 and 4 (http://crl.ucsd.edu/~aszekely/ipnp/). Objects with high naming frequencies were selected from the database (e.g., Accordion, Basket, Button, Doorknob, Hanger, etc.). Additionally, we created a list of adjectives which were selected on the basis of their semantic relation to the objects chosen. Although a semantic relation may facilitate STM for the two elements in the pairs (e.g., Folded-Accordion, Knitted-Basket, Flashing-Button, Round-Doorknob, Metallic-Hanger), the fact that within each list the adjectives held semantic relations with more than one object (e.g., the Basket may be Knitted but may also be Round) should have demanded extra effort to keep both elements correctly bound. This is particularly true when larger lists are used.

Lists of 4 or 6 nouns (noun only condition), 4 or 6 adjectives (adjectives only condition), or 2 or 3 combinations of nouns and adjectives were presented aurally using loud speakers. The presentation rate was 1 word per sec (2 sec for the pairs) with an interval of 1 sec between words or combinations. Participants were requested to remember these words or word pairs and to recall them in any order. The task consisted of 18 trials per experimental condition (9 trials per array size).

Results

Mean performance is shown in Figure 8. ES had no difficulties in recalling nouns [PE = 65.39, t = 0.41, df = 7; n.s.], adjectives [PE = 63.02, t = 0.35, df = 7; n.s.], or combinations of nouns with adjectives [PE = 85.13, t = 1.13, df = 7; n.s.].

Figure 8 about here

Comments

The finding of preserved memory for bound verbal information observed in the recognition task of Experiment 3 was replicated in this recall experiment. Note that Experiment 5 extends this finding not only to a new retrieval strategy (i.e., recall) but also to a new modality as the stimuli were aurally presented. These results suggest that whenever ES can rely on verbal codes to assist her memory for bound features she can remember this information as well as controls.

Experiment 6

Aims

If ES's impairment for visual binding extends to memory recall, ES should perform poorly on tasks assessing visual recall (i.e., drawing) of bound visual features while she would perform well on tasks assessing visual recall of single features.

Methods

The same participants who entered Experiments 3 to 5 took part in Experiment 6. In this experiment the stimuli used were nameable shapes and colours. Figure 9 shows the experimental conditions and trial sequences used in Experiment 6. A set of 8 nameable shapes (Square, Triangle, Circle, Diamond, Rectangle, Oval, Arch, and Cross) and a set of 8 colours (Red, Pink, Blue, Turquoise, Green, Yellow, Orange, and Brown) were used to construct arrays for this task. Arrays of 2 or 4 shapes (shape only condition), 2 or 4 colours (colours only condition), or 1 or 2 combinations of shapes with colours (shape-colour binding condition) were presented in the initial display. The display was presented for 1.5 sec per feature as in Experiment 3 and 4. Participants were instructed to remember as many items as possible. In conditions assessing memory for shapes or colours participants were provided with a booklet and a pencil for the shape only condition or 8 colouring pencils for the colour only condition (pencils corresponding to the colours used in the task) once the array had disappeared. In the case for shape only, participants were requested to draw the shapes seen before using a black pencil provided. In the case for colour only, participants were requested to select the pencil for each of the colours presented (from the set of colouring pencils provided) and to draw a line on the booklet with each of them.

For the condition assessing the binding of shapes with colours we used two different procedures. As the specific deficit shown by ES in holding bound information in VSTM vanishes whenever she can use verbal labels for rehearsing, we asked ES and controls first to study the coloured shapes visually and to draw them down as soon as the initial display had disappeared (we called this block “without verbal aid”). We then presented a second block of coloured shapes but on this occasion ES and controls were asked to name them aloud when they were studying them and to keep rehearsing them until they had drawn them on the booklet (we called this block “with verbal aid”). The results of Experiments 3 and 4 revealed that when the same type and number of stimuli were to be held in verbal and visual STM respectively, ES could perform the first task without difficulties while she had significant problems in performing the second task. This suggests that the verbal nature of the recognition phase of the task used in Experiment 3 encouraged ES to transpose the to-be-remembered information from her impaired visual to her preserved verbal STM. Although ES and controls were not instructed to avoid verbal rehearsal nor were they required to suppress articulation, the results of Experiment 4 suggest that they did not choose verbal coding as a strategy to perform this task or at least that they did not use it as effectively as they did in Experiment 3. Relying on this evidence, this new experiment was aimed at assessing the effectiveness of the strategy developed by ES when the instructions of the task explicitly encourage such information transfer from visual to verbal STM. The rationale is that by encouraging verbal rehearsal, the impact of ES's lesion on her visual STM should be reduced, and she would be able to perform the task without difficulties.

In both blocks, participants were provided with a booklet and a set of eight colouring pencils and they were requested to select the colours of the shapes previously seen and to draw the corresponding shapes as soon as the study display disappeared. Six trials (3 trials per array size) were used for each experimental condition, including the two blocks of stimuli used in the binding condition.

Figure 9 about here

Results

Figure 10 shows the mean scores of ES and controls in Experiment 6. The analysis carried out on the data collected during the "without verbal aid" block showed that ES had no difficulties in recalling shapes [PE = 19.41, t = -0.92, df = 7; n.s.] or colours

[PE = 38.88, t = -0.29, df = 7; n.s.] presented as individual features. However, ES's memory recall for these same features integrated into objects was impaired [PE = 2.4, t = -2.39, df = 7; $p < 0.05$]. When ES's performance in the condition assessing memory for bound features was analyzed across set sizes, she was significantly poorer than controls at set size 1 [PE = 2.62, t = -2.33, df = 7; $p < 0.05$] but this difference did not reach significance for set size 2 [PE = 8.52, t = -1.53, df = 7; n.s.]. The discrepancy analysis showed that 9.42% of the population (t = -1.46, df = 7) would be expected to score lower than ES score when memory for the binding of objects with colours was compared to her average performance. In contrast, 62.99% (t = 0.35, df = 7) and 84.86% (t = 1.1, df =7) of the population would be expected to score lower than ES when performance in conditions assessing memory for shapes only and colours only respectively, were compared to her average performance.

When participants were instructed to use verbal codes to rehearse the combinations of shapes and colours ("with verbal aid"), ES's difficulties in recalling bound features disappeared [PE = 72.38, t = 0.64, df = 7; n.s.]. Analysis of the discrepancy of ES's performance in this block showed that 94.7% of the population (t = 1.90, df =7) would be expected to score lower than ES when her memory recall for bound features was compared to her average performance.

Figure 10 about here

Comments

The results of Experiment 6 support previous findings that ES displayed an inability to hold in STM bound information processed within the visual domain while her VSTM for individual features as well as her verbal STM for bound objects and individual features are preserved.

Assessing dissociations in ES

The results presented in this series of experiments revealed that ES exhibits two types of dissociations. One involves STM for visual bound versus verbal bound information and the other involves VSTM for unbound versus bound features. Together these dissociations suggest that ES's verbal STM is intact while her VSTM for object representations but not for individual features is impaired. In order to assess whether this pattern of performance meets criteria for classical dissociation, we implemented the methodology devised by Crawford and Garthwaite (2005). This methodology permits to verify whether this differential impairment in VSTM for complex objects reliably dissociates from the other forms of STM assessed.

To investigate these dissociations we selected performance in Experiments 3 and 4. These experiments differed in the retrieval stage only, as Experiment 3 used the recognition of words (in which the participants needed to translate the visual information into verbal codes), while Experiment 4 required recognition of visual objects. By comparing performance in conditions assessing memory for bound features in Experiments 3 and 4, it would be possible to investigate whether the selective impairment observed in ES's VSTM for bound information dissociates from her memory for verbal bound information. By comparing performance in the condition assessing memory for single objects or single colours with performance in the condition assessing memory for objects bound with colours of Experiment 4, it would be possible to assess whether the differential impairment observed in ES's memory for visual objects as compared to memory for visual features also meets the criteria for classical dissociation.

The method proposed by Crawford and Garthwaite (2005) requires that all inputs use the same metric. All the experiments presented here used percentage of correct responses as dependent variables. However, the chance level for these experiments differed. In Experiment 3 50% of the test displays showed items with the same object-colour pairs as the study display, whereas the other 50% of test displays showed objects from the study display that were re-paired with new colours (25% of trials) or new objects re-paired with colours from the study display (25% of trials). Therefore, chance performance in this condition was 50%. In Experiment 4 the participants' recognition was based on two new sets of colours and objects each double the number of objects presented in the study display. Participants were instructed to select each object with its corresponding colours. As 2 or 3 objects were presented in the condition assessing memory for bound features the probability of choosing the correct objects would be p = Σ n /(2 x no. of study objects - i * 2 x no. of study colours - i) (with n ranging from 1 to set size and i from 0 to set size -1). Therefore, when 2 objects were presented on the study display the probability of correct object recognition was:

p = 1/(4 * 4) + 1/(3 * 3) = 0.0625 + 0.11 = 0.1736 (17.36%)

When 3 objects were presented the probability for correct object recognition was:

p = 1/(6 * 6) + 1/(5 * 5) + 1/(4 * 4) = 0.027 + 0.04 + 0.0625 = 0.1295 (12.95%).

The total probability of correct recognition for the condition assessing memory for bound features was 30.31%. The percentage of correct responses above this probability (chance) was then used for calculation.

According to this analysis, ES's corrected STM performance (% above chance) for verbal features bound into objects (Experiment 3) was M = 45.37, and for visual features bound into objects (Experiment 4) was M = 28.01. Controls corrected STM performance for verbal features bound into objects (Experiment 3) was M = 44.79, SD = 3.76, and for visual features bound into objects (Experiment 4) was M = 45.04, SD = 2.97. These statistics were entered into the analysis (see Crawford & Garthwaite, 2005) and the results were significant [PE = 0.05, t = -5.406, df = 7; p < 0.001]. Therefore, when verbal and visual STM for integrated objects were analyzed in the comparison of ES with controls, the patient's pattern of performance fulfilled the criteria for a classical dissociation.

To test the dissociation between object and features the corrected STM performance obtained in the Experiment 4 was used. In this case we compared performance in conditions assessing memory for features (performance in colour and object only conditions was collapsed for such purpose) and memory for objects (i.e., the binding). We corrected performance for chance level which was 50% for single features and 30.31% for the binding of these features (as it was shown in the calculation above). According to this analysis, ES's corrected VSTM performance for features was M = 32.18 and for objects M = 28.01. Controls corrected VSTM performance for features was M = 33.79, SD = 3.96 and for objects was M = 45.04, SD = 2.97. These measures were entered into the analysis (Crawford & Garthwaite, 2005) and the results were highly significant [PE = 0.05, t = -5.406, df = 7; $p < 0.001$]. Therefore, when VSTM for features and objects were analyzed, ES's pattern of performance fulfilled the criteria for a classical dissociation.

Summarizing these results, ES presented with a selective impairment of VSTM for multi-feature objects while her VSTM for single features as well as her verbal STM were intact.

General Discussion

Implications of single case results for STM cognitive architecture

The selective impairment in VSTM for bound information demonstrated in this case study has not been reported in the literature to date. Specifically, there are three issues which emerge from ES's performance that may have implications for the functional organization of STM. Firstly, there is the selective impairment of VSTM for objects only with preserved verbal STM: the fact that ES showed preserved verbal STM for information presented in single and complex formats while she has impaired VSTM for bound information fits well into the two segregated components subserving the processing of verbal and visual information (Baddeley, 2007c; Baddeley & Hitch, 1974; Logie, 1995; Logie & van der Meulen, 2009). In relation to the central executive component of the WM model, ES showed little evidence of impairment on tests of executive functions. Furthermore, Allen et al. (2006) recently found that holding bound information in VSTM could be an automatic process which places little or no demand on the central executive (see also Allen, Hitch, & Baddeley, 2009).

The second issue relates to the functional interrelations of STM components. When ES was encouraged to transfer visual information into verbal codes (Experiment 2, 5, and block "with verbal aid" of Experiment 6), she showed no impairment in remembering bound features. Another case report which showed the opposite pattern is patient MJK (Best & Howard, 2005), who could use a visually based code to remember visually presented verbal items but could not re-code these items phonologically. The authors observed that MJK substituted visually similar items for one another, her performance was better with visual than auditory stimuli, and she was able for example to remember numbers better than written words. The pattern of performance observed in ES supports the view that STM components (i.e., verbal and visual) are relatively independent systems but with strong functional interrelations. These interrelations may provide the mechanism whereby compensatory strategies can be developed after selective damage and which may explain why ES had never been aware of this specific difficulty before.

The third issue is how to accommodate the finding of a selective VSTM binding deficit in a right handed patient with a focal damage to the left temporal lobe. The literature on memory and brain laterality has suggested that verbal memory functions mainly rely on the left hemisphere while visual memory functions mainly rely on the right hemisphere (Milner, 1971; Milner & Taylor, 1972). There is however alternative evidence against this left-verbal/right-nonverbal dichotomy. For example, Smith and Jonides (1995) reported activation on the left ventro-lateral frontal cortex during a task involving STM for abstract objects. In addition, MacLeod, Buckner, Miezin, Petersen, and Raichle (1998) found activation on the right frontal region

(BA10) using a semantic monitoring WM task. Della Sala et al. (1999) also reported dissociations within visual memory in patients with damage to the left and right brain hemispheres. Therefore, this evidence suggests that the functional laterality of the brain hemispheres largely supported by the literature may not be attributable to functions independently performed by each hemisphere but to networks to which both hemispheres provide different substrates.

Implications for current models of WM

The WM model proposed by Baddeley (Baddeley, 1992; 2007c; Baddeley & Hitch, 1974) may run into some difficulties in accounting for the pattern of performance observed in this case study. Specifically, the functional properties described for the Episodic Buffer (Baddeley, 2000; Baddeley, 2007a & b) may not account for ES's selective VSTM binding impairment. The Episodic Buffer was conceived as a multimodal binding buffer and not as a component that can be further fractionated into verbal and visual buffers. However, doubts have been cast about the actual functions of the Episodic Buffer and its insertion into the multi-component WM model (Allen et al., 2006; Allen et al., 2009; Baddeley, 2007a & b; Logie & van der Meulen, 2009). Recently, Baddeley (2007a & b) suggested that visual surface features (i.e., shapes and colours) may well be bound within the sketchpad, and from there they would be fed into the Episodic Buffer. Within the buffer, higher order representations (e.g., involving object and semantic information) will then be formed. ES's pattern of performance is consistent with this possibility. For example, ES could integrate visual features at perceptual level well (Experiment 2) and she could also bind object-based and semantic information (Experiments 3, 5, and 6 in the block "with verbal aid"). However, she could not retain integrated visual features on a temporary basis. This suggests that there should be functions other than perceptual grouping or multi-modal integration which are important in temporary memory for bindings. Some version of the visuo-spatial sketchpad (rather than an Episodic Buffer) could be the component responsible for this short-term binding function, but its characteristics would have to incorporate additional assumptions regarding how it supports temporary memory for integrated objects versus individual features (for a detailed discussion see Logie & van der Meulen, 2009).

Additional evidence from ES's performance supports this view. For example, when visual stimuli were transferred into verbal codes, her problem disappeared. This may have happened because ES was able to bridge these perceptual inputs to LTM before this information reached the visuo-spatial sketchpad. Through this information bypass, ES was able to compensate her temporary visual binding impairment. This also suggests that once visual inputs are transferred to verbal codes, they may enter the Episodic Buffer via the verbal component of WM (see Baddeley, 2003 for a model that may support this suggestion). In the buffer, information can be held as multimodal objects. Indeed, Logie's model (Logie, 2003; Logie & van der Meulen, 2009) of WM posits that linking perceptual inputs to LTM representations is a process that does not require WM, with the latter involved only when temporary memory for novel material or novel processing of familiar material (Logie, Brockmole, & Vandenbroucke, 2009) is required. Logie's workspace model could also help to explain why healthy participants' performance in tasks assessing verbal STM binding was more efficient than in tasks assessing VSTM binding. As was observed in Experiments 3, 5, and 6 (in the block "with verbal aid"), retaining bound features in verbal STM was apparently less demanding that retaining single features. However, in

Experiments 4 and 6 (in the block "without verbal aid"), in which the same stimuli were presented but they had to be held in VSTM, retaining bound features was more demanding than retaining individual features. One possible explanation for these results could be that in Experiments 3, 5, and 6 (in the block "with verbal aid"), perceptual inputs could access LTM representations via verbal coding, and this rendered the maintenance of this complex information in WM (i.e., the Episodic Buffer) more efficient and less demanding. This may also help to explain why arbitrary features retained in VSTM as integrated meaningless objects are very fragile and easily overwritten (Allen et al., 2006; Logie et al., 2009; Treisman, 2006). As these meaningless bindings are not linked to LTM representations they will only survive in WM until a new input displaces them (Logie et al., 2009). In sum, these arguments may help to settle some outstanding issues about the functions of WM and the Episodic Buffer. Firstly they support the assumption of Logie's model about the role of bridging perceptual inputs to LTM traces to ensure accurate and efficient WM representations. Secondly, they support the role of the Episodic Buffer as an interface between verbal WM and LTM (Baddeley, 2000; Baddeley, 2007a & b). Finally, they suggest that whenever verbal coding is available, WM representations would access LTM engrams. This is not consistent with Cowan's view about WM representations comprising activated areas of LTM (Cowan, 1988; 2008; Cowan & Chen, 2009), in that Cowan's view does not explicitly account for temporary retention of novel material (such as novel combinations of features) for which there are no pre-existing representations in LTM.

Implications for the current debate on the unit of capacity of VSTM

The memory deficit displayed by ES for bound visual features with intact memory for individual features suggests that VSTM for objects and features may be subserved by separate mechanisms. In their seminal paper, Vogel et al. (2001) suggested that the unit of capacity of VSTM seems to be determined by the number of objects rather than by the number of features, which are stored in VSTM within integrated objects representations. According to ES's performance, it seems unlikely that features are stored in VSTM within integrated objects as she could remember individual features without difficulty whereas she was less able to remember objects composed of the same number and types of features. It is worth noting that ES's problems in holding bound information in VSTM did not reflect a capacity limitation as she could remember individual features as well as controls during conditions assessing memory for single and bound information. Additionally, ES showed a normal visual span as assessed by the Visual Pattern Test (Della Sala et al., 1999). Her problem seems to reflect a limitation in holding in VSTM the relatedness between features. This suggests that the way features are integrated into objects, that is binding, represents an additional piece of information and that this information seems to be processed by mechanisms distinct from those responsible for feature processing and feature memory. This does not rule out that the final outcome of these processes may result in objects represented as a whole in VSTM. However, it does suggest that to reach this object-based representation, different parallel mechanisms should work in concert.

It is worth noting that Wojciulik and Kanwisher (1998) reported on patient RM who following a parietal lesion presented with intact implicit but compromised explicit perceptual binding mechanisms. According to this dichotomy, ES's memory binding deficits should be considered explicit although implicit processes have not been tested.

In summary, ES has a specific deficit in VSTM for visual objects defined by bound features while her memory for individual visual features as well as her verbal memory (for objects and features), and her visual perceptual binding remain intact. These findings are consistent with the suggestion that individual features and bindings are maintained by separate mechanisms.

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Table 1. Results of the neuropsychological assessment of ES.

	ES	**Cut-off scores from norms**
MMSE	28	< 23
ACE	91	< 85
Laterality Quotient (Handedness)	80	-100 left / 100 right
Logical Memory		
Immediate Recall	41	37 – 39 a
Delayed Recall	30	20 – 22 a
Percentage Retention	96.7	78 – 83 a
Visual Pattern Span	9.8	9.2 (2.25) b
Doors and People Test		
Overall Score	10	9.2(3.4) b
Verbal Recall	12	8.9(2.9) b
Verbal Recognition	8	9.7(3.4) b
Nonverbal Recall	9	10.1(4.5) b
Nonverbal Recognition	11	9.1(3.4) b
Visual-Verbal Discrepancy	10	10.2(2.2) b
Recall-Recognition Discrepancy	10	10.1(2.7) b
Rey-Osterrieth Complex Figure		
Copy	33	34.2 (10.8) b
Recall	14	18.6 (6) b
VOSP		
Ruff 2 & 7 Selective Attention test		
Speed Differences	3	7.08 – 9.30 a

Table 1. Contd.

Accuracy Difference	4	10.00 - 13.99 $_a$
Total Difference	1	5.43 – 7.70 $_a$
TMT-A	35	39.14 (11.84) $_b$
TMT-B	116	91.32 (28.89) $_b$
WCST		
Categories	3	≤ 2 $_a$
Perseverations	9*	≥ 6.41 $_a$
Hayling & Brixton Test		
Spatial Anticipation test	6	Average $_a$
Word Fluency Tests		
FAS – Total	40	29.6 (9.4) $_b$
Category Fluency – Animals	20	15 (4.3) $_b$
Incomplete Letters	19	< 16 $_a$
Object Decision	18	< 14 $_a$
Dot Counting	10	< 8 $_a$
Position Discrimination	20	< 18 $_a$

***** Tests in which ES scored abnormally; **a**: 50th percentile taken from standardised age matched normative data; **b**: mean and SD taken from standardised age matched normative data; MMSE = Minimental State Examination (Folstein, Folstein, & McHugh, 1975). The cut-off value presented is internationally accepted as the lowest score indicative of normal cognitive profile; ACE = Addenbrooke's Cognitive Examination. The cut-off score represents the control mean minus 2 SD for an age rage of 50-69 and education = 12.9 (Mioshi, Dawson, Mitchell, Arnold, & Hodges, 2006); Laterality Quotient as measured by the Edinburgh Handedness Inventory (Oldfield, 1971); Logical Memory, Wechsler Memory Scale-III (The Psychological Corporation, 1998); Doors and People Test (Baddeley, Emslie, & Emslie, 1994); Rey-Osterrieth Complex Figure (Osterrieth, 1944; Rey, 1941); Ruff 2 & 7 Selective Attention test (Ruff & Allen, 1996). Cut-off scores represent the confidence interval at 95% of the normal population (see also Messinis, Kosmidis, Tsakona, Georgiou, Aretouli, & Papathanasopoulos, 2007); TMT = Trail Making Test (Reitan, 1958); WCST = Wisconsin Card Sorting Test, modified version of Berg (1948) (48 cards); Hayling & Brixton Test: (see Burgess & Shallice, 1997); Word Fluency Tests form Control Oral Word Association Test - FAS (Sumerall, Timmons, James, Ewing, & Oehlert, 1997); Category Fluency – Animals; Visual Pattern Span (VPT) (Della, Gray, Baddeley, Allamano, & Wilson, 1999); Visual Object and Space Perception Battery - VOSP (Warrington & James, 1991).

Figure captions

Figure 1. ES's 3 month follow-up MRI scan showing the area of the surgical excision (arrows) within the left temporal lobe.

Figure 2. Experimental conditions and trial sequence used in Experiment 1.

Figure 3. **(A)** Percentage of correct responses above chance (50%) for ES and controls in Experiment 1. **(B)** Performance across array sizes for the condition assessing memory for the binding of shapes with colours (Error bars represent the standard error of the mean).

Figure 4. Experimental conditions and trial sequence used in Experiment 3 (the actual set sizes used in this experiment were 4 and 6 for colour and object only and 2 and 3 for object-colour binding).

Figure 5. Percentage of correct recognition in Experiment 3, (Error bars represent the standard error of the mean).

Figure 6. The experimental conditions and trial sequences used in Experiment 4 (these are examples as the actual set sizes were 4 and 6 for object and colour only and 2 and 3 for object-colour binding).

Figure 7. **(A)** Percentage of correct recognition in Experiment 4. **(B)** Performance split across array sizes for the condition assessing the binding of objects with colours (Error bars represent the standard error of the mean)

Figure 8. Percentage of correct recall for ES and controls in Experiment 5 (Error bars represent the standard error of the mean).

Figure 9. Experimental conditions and trial sequences used in Experiment 6.

Figure 10. **(A)** Percentage of correct recall in Experiment 6. **(B)** Performance split across array sizes for the condition assessing the binding of shapes and colours "without verbal aid" (Error bars represent the standard error of the mean).

Figure 1.

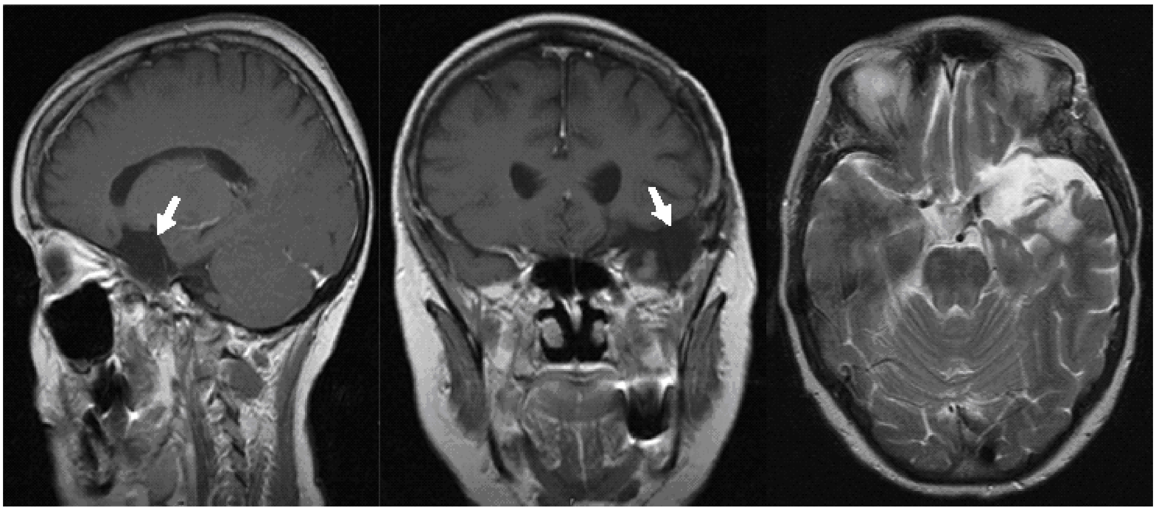

Figure 2.

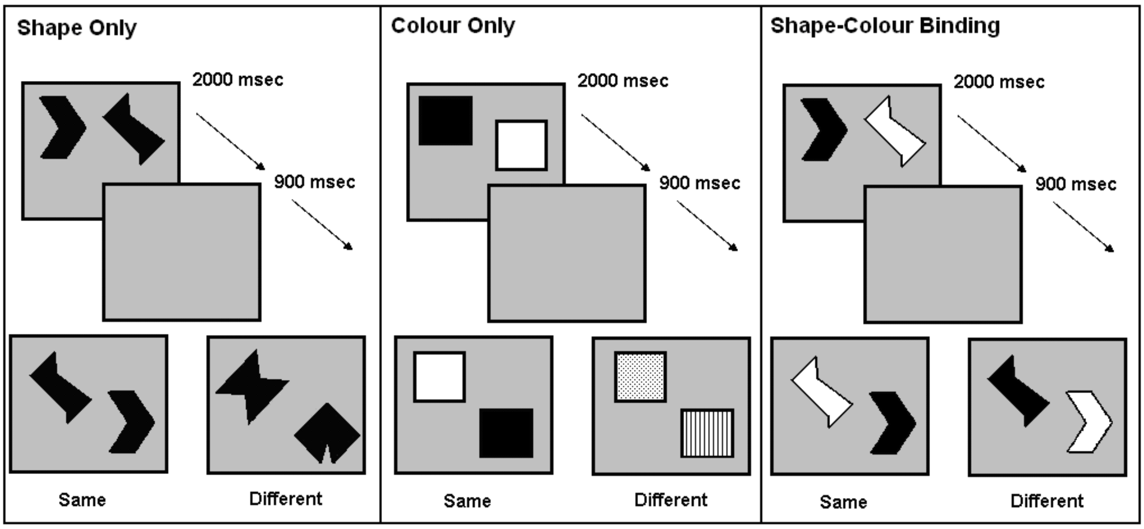
Shape Only
2000 msec
900 msec
Same
Different
Colour Only
2000 msec
900 msec
Same
Different
Shape-Colour Binding
2000 msec
900 msec
Same
Different

Figure 3.

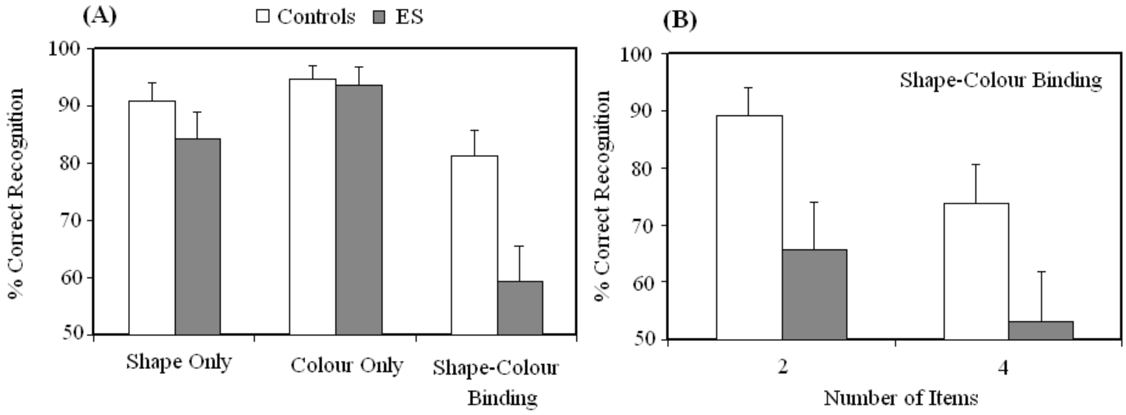
(A)
Controls
ES
100
90
80
70
60
50
% Correct Recognition
Shape Only
Colour Only
Shape-Colour Binding
(B)
Shape-Colour Binding
100
90
80
70
60
50
% Correct Recognition
2
4
Number of Items

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Figure 4.

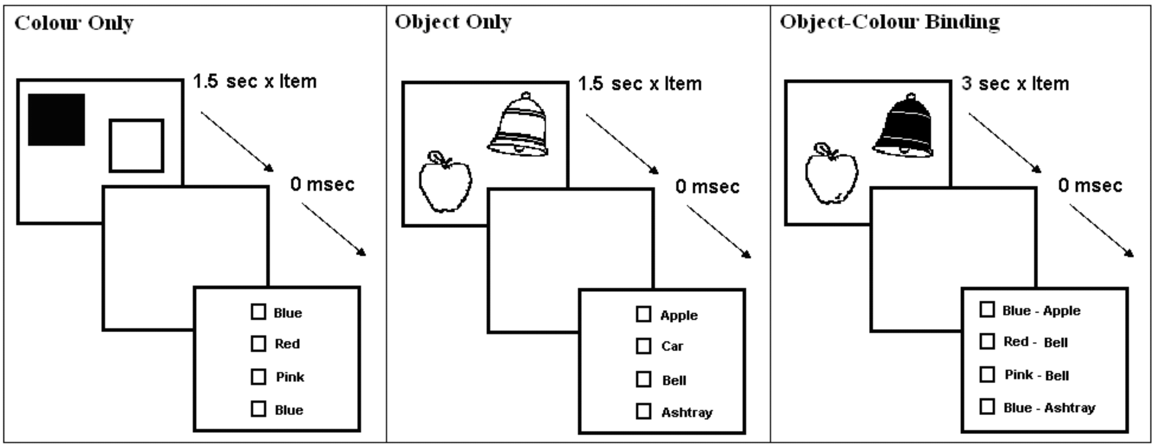


Figure 5.

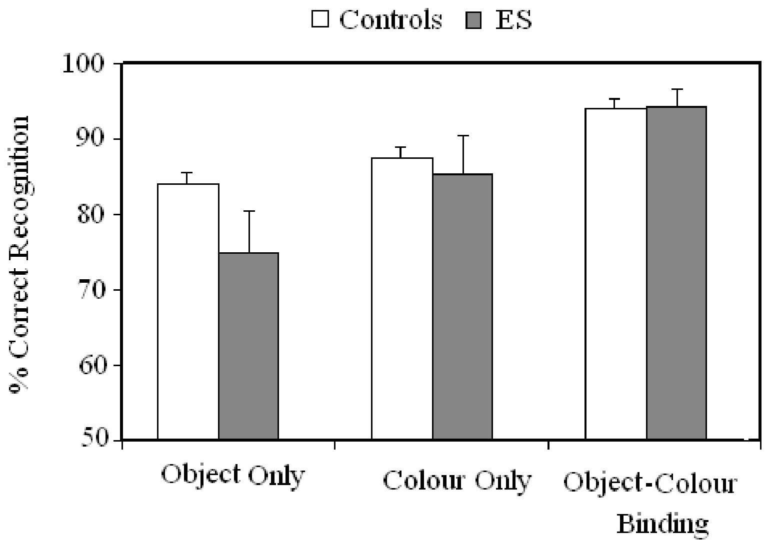

Controls
ES
100
90
80
70
60
50
% Correct Recognition
Object Only
Colour Only
Object-Colour Binding

Figure 6.

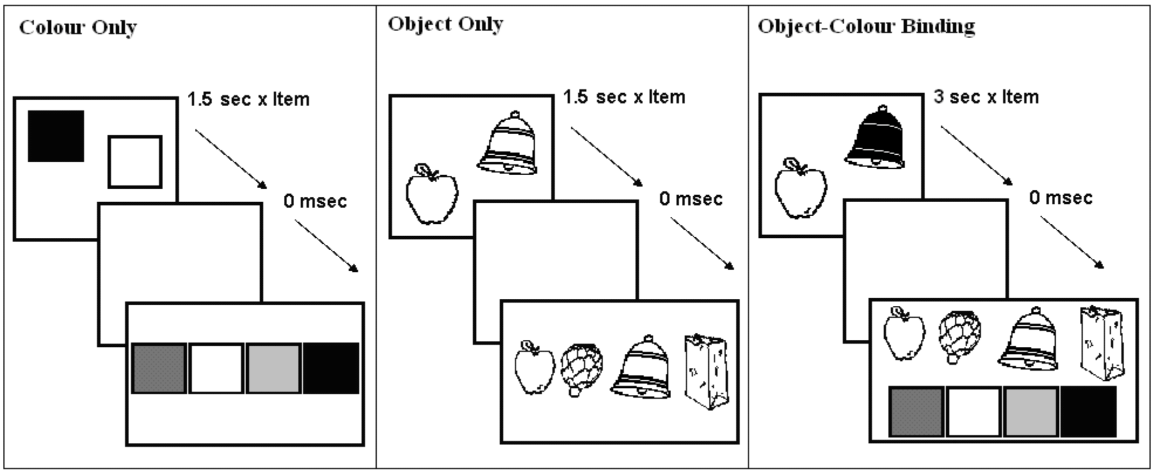
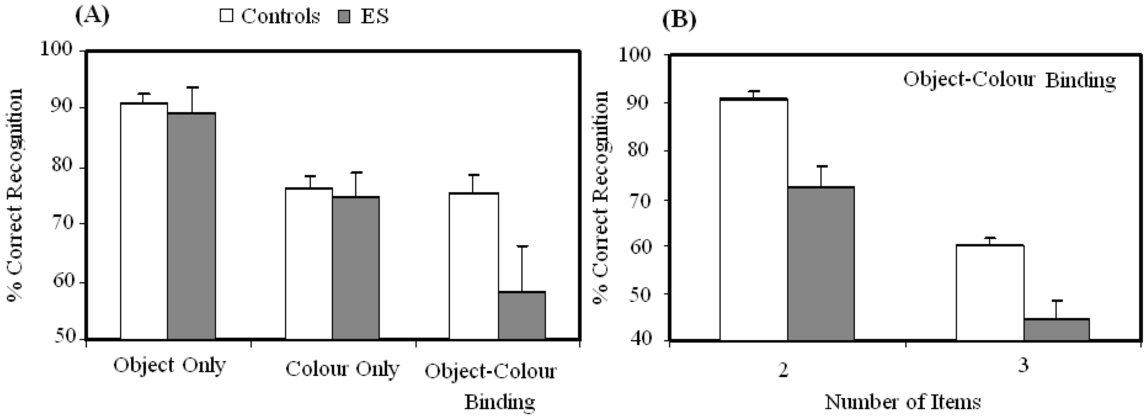

Colour Only
1.5 sec x Item
0 msec
Object Only
1.5 sec x Item
0 msec
Object-Colour Binding
3 sec x Item
0 msec

Figure 7.


(A)
Controls
ES
% Correct Recognition
100
90
80
70
60
50
Object Only
Colour Only
Object-Colour Binding
(B)
Object-Colour Binding
% Correct Recognition
100
90
80
70
60
50
40
2
3
Number of Items

© Parra, M., Della Sala, S., Logie, R. H., & Abrahams, S. (2009). Selective impairment in visual short-term memory binding. *Cognitive Neuropsychology*, *26*(7), 583-605. 10.1080/02643290903523286

Figure 8.

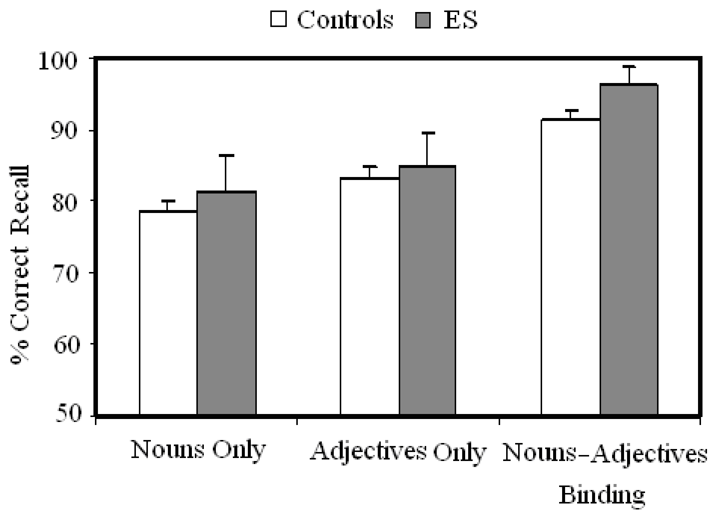


Figure 9.

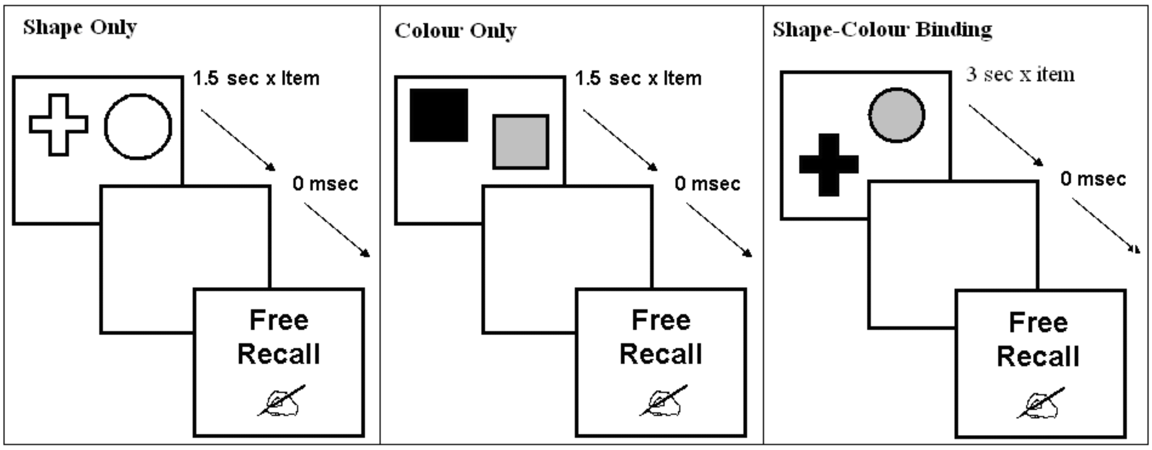
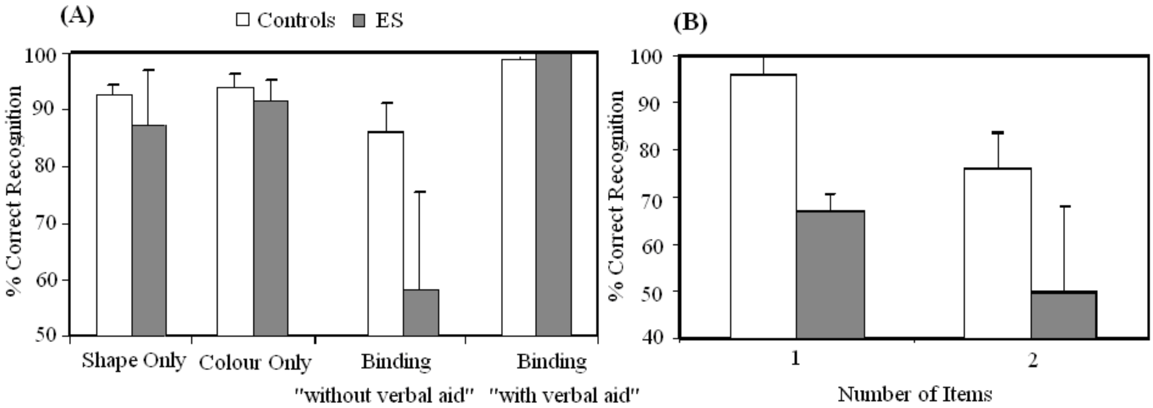

Shape Only
1.5 sec x Item
0 msec
Free Recall
Colour Only
1.5 sec x Item
0 msec
Free Recall
Shape-Colour Binding
3 sec x item
0 msec
Free Recall

Figure 10.


(A)
□ Controls ■ ES
% Correct Recognition
100
90
80
70
60
50
Shape Only
Colour Only
Binding "without verbal aid"
Binding "with verbal aid"
(B)
% Correct Recognition
100
90
80
70
60
50
40
1
2
Number of Items