Enhanced memory ability: Insights from synaesthesia

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3 authors:

Nicolas Rothen
Universität Bern

Beat Meier
Universität Bern

Jamie Ward
University of Sussex

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Review

Enhanced memory ability: Insights from synaesthesia

Nicolas Rothen[a,*], Beat Meier[b], Jamie Ward[a]

[a] *School of Psychology and Sackler Centre for Consciousness Science, University of Sussex, Falmer, Brighton, BN1 9QH, United Kingdom*
[b] *Department of Psychology and Center for Cognition, Learning and Memory, University of Bern, Bern, Switzerland*

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People with synaesthesia show an enhanced memory relative to demographically matched controls. The most obvious explanation for this is that the 'extra' perceptual experiences lead to richer encoding and retrieval opportunities of stimuli which induce synaesthesia (typically verbal stimuli). Although there is some evidence for this, it is unlikely to be the whole explanation. For instance, not all stimuli which trigger synaesthesia are better remembered (e.g., digit span) and some stimuli which do not trigger synaesthesia are better remembered. In fact, synaesthetes tend to have better visual memory than verbal memory. We suggest that enhanced memory in synaesthesia is linked to wider changes in cognitive systems at the interface of perception and memory and link this to recent findings in the neuroscience of memory.

Contents

* Corresponding author.
E-mail address: nicolas.rothen@gmail.com (N. Rothen).

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1. Introduction

"The ketones are yellow, because there is an o in it." (Bleuler and Lehmann, 1881, p. 1). This statement of the famous psychiatrist Eugen Bleuler (1857–1939) was published in his influential book on synaesthesia which he had written before turning to his more renowned work on schizophrenia. The statement originates from a situation in which he was not able to remember the appearance of ketones during a chemistry class and it is probably the first coincidence of synaesthesia and memory in a scientific publication. Synaesthesia is associated with unusual experiences, related to unusual patterns of neural activity, elicited in the presence of an appropriate inducing stimulus (e.g., Meier and Rothen, 2007; Ward and Mattingley, 2006; Ramachandran and Hubbard, 2001). For instance, in grapheme-colour synaesthesia a printed letter (e.g., O), or the sound of it ("o"), or even the thought of it may elicit a colour, such as yellow. Synaesthetic experiences are automatically triggered, highly specific, and consistent over time (Grossenbacher and Lovelace, 2001; but see Simner, 2011 for a current debate concerning the consistency criterion). Moreover, by almost all definitions, synaesthesia is defined by a percept-like phenomenology rather than being, say, a memory association. In most cases there are no known environmental correspondences that drive the associations. There is also very little correspondence to alphabet books, which are primarily designed for young children as a learning instrument and often include coloured letters (Rich et al., 2005). Nonetheless, there may be an intimate link between synaesthesia and memory. This may occur by virtue of the synaesthetic experiences themselves which provide a richer world of experience and, in many cases, an opportunity to better structure and organise memory. Alternatively, or in addition to this, synaesthesia itself may be linked to certain structural changes in the brain (e.g., unusual connectivity, changes in plasticity within visual regions) that are themselves beneficial to memory and are not a direct outcome of synaesthetic phenomenology (Meier and Rothen, in press). In this review, we consider evidence for enhanced memory function in synaesthesia and link this to various neurocognitive models of memory function.

To do so, we first present the reader – who might not be familiar with synaesthesia – with the phenomenon's key characteristics and its neural basis. Next, we give a brief summary about factors known to enhance memory performance in general. Thereafter, we review the literature on memory performance in synaesthesia, considering both case studies and group studies separately. Finally, we try to explain the memory advantage in synaesthesia on the basis of five different theoretical accounts, taking into consideration different processes, strategies, memory systems, and representations.

2. Key characteristics and neural basis of developmental synaesthesia

Before reviewing the literature on memory performance in synaesthesia, we want to briefly inform the reader who might not be familiar with the phenomenon of developmental synaesthesia about the terminology used, its key features, and its neural correlates. First of all, synaesthesia is not a disorder. It is not associated with general cognitive dysfunction and/or brain pathology (e.g., Ward and Mattingley, 2006). Conventionally, the stimulus triggering a synaesthetic experience is called the inducer and the elicited experience is called the concurrent (Grossenbacher and Lovelace, 2001). A specific form of synaesthesia is usually indicated by first naming the inducer hyphenated with its concurrent (e.g., grapheme-colour synaesthesia). Accordingly, synaesthetic experiences are usually reported to be unidirectional (e.g., letters trigger colours, but not vice versa). However, on an implicit basis concurrents (e.g., colour information) can affect inducer related tasks (i.e., implicit bidirectionality; Brugger et al., 2004; Cohen Kadosh and Henik, 2006; Meier and Rothen, 2007; Rothen et al., 2010). Synaesthesia has an early onset in life (Simner et al., 2009a). It runs in families and hence, seems to have a genetic basis (Barnett et al., 2008a; Asher et al., 2009). Generally, about five percent of the general population are affected by one or several forms of synaesthesia. To date, the best studied form is grapheme-colour synaesthesia which is found in about one percent of the general population (Simner et al., 2006). Another well studied form is sequence-space synaesthesia in which sequences as numbers, days of the week, and so on, are perceived in explicit and highly specific spatial arrangements. So far, memory studies on synaesthesia are limited to these two forms of synaesthesia (Fig. 1).

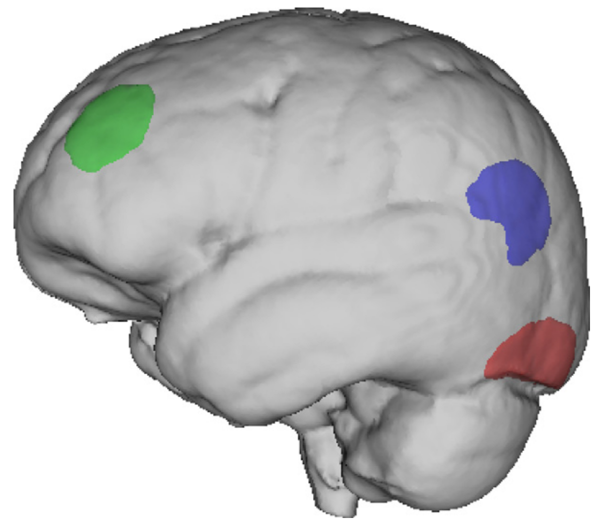

Fig. 1. Neural basis of grapheme-colour synaesthesia. (Green) Dorsolateral prefrontal; (blue) inferior parietal; (red) occipito-temporal brain areas. Due to reasons of simplicity, the dorsolateral prefrontal area is highlighted in the left hemisphere, although the same region in the right hemisphere was more frequently linked to grapheme-colour synaesthesia. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.) Q7

Today it is clear that synaesthesia is neither imagination nor is it metaphorical thinking, instead it has a neural basis. Functional (Nunn et al., 2002; Hubbard et al., 2005a; Weiss et al., 2005) and structural (Rouw and Scholte, 2007; Weiss and Fink, 2009)

6	5	8	1	2
1	4	3	0	6
5	8	7	9	5
7	3	0	6	7
2	9	8	4	2
5	7	4	2	5
6	2	5	8	7
7	4	1	3	4
8	6	0	2	9
7	2	4	5	1

Fig. 2. Exemplary digit matrix as it used in the digit matrix test. During the learning phase, the participant is presented with such or a similar matrix for memorization. During the testing phase, the participant is presented with an empty matrix for replication.

MRI studies consistently found evidence that occipito-temporal and parietal regions play an important role in grapheme-colour synaesthesia (although see Hupé et al., in press, for a critical discussion). In addition, three TMS studies have provided further evidence for the involvement of parieto-occipital areas (Esterman et al., 2006; Muggleton et al., 2007; Rothen et al., 2010). Neural activation related to synaesthesia was frequently also found in frontal brain regions – mostly dorsolateral prefrontal (Paulesu et al., 1995; Sperling et al., 2006; Laeng et al., 2011). For an in-depth review of functional and structural imaging studies of synaesthesia see Rouw et al. (2011).

For sequence-space synaesthesia it is assumed that parietal regions play an important role (Hubbard et al., 2005b). Consistent with this hypothesis an fMRI study found greater activation in the intraparietal sulcus in a task on number ordinality for number-form synaesthetes compared to non-synaesthetic controls (Tang et al., 2008). Moreover, it is hypothesised that temporal regions might play an important role in sequence-space synaesthesia (Pariyadath et al., 2008; Eagleman, 2009). Indirect support comes from an fMRI study; activity was found in the right middle temporal gyrus and right temporoparietal junction for overlearned sequences in 26 non-synaesthetes (Pariyadath et al., 2008).

3. What factors are known to enhance memory?

In this section we consider factors known to enhance memory in the general population. Later we attempt to link these general factors with synaesthesia. Note that the suggested factors and theoretical accounts are not mutually exclusive (Fig. 2). Q2

3.1. Imagery

Certain strategies, including the use of visual imagery, are known to benefit memory performance. Related to Paivio's dual coding theory, memory performance for verbal material is likely to be enhanced when additionally encoded as a mental image (Paivio, 1969). Findings that concreteness and imageability of word stimuli are beneficial to memory performance generally support the theory. These effects are found for paired associate learning, recognition memory, and free recall even when meaningfulness or other semantic or associative attributes were taken into account (e.g., Bowers, 1931; Gorman, 1961; Dukes and Bastian, 1966; Paivio et al., 1966, 1969). However, the influence of individual differences in imagery ability on memory performance is less clear cut (cf., Hänggi, 1989; Cohen and Saslona, 1990). The core of the theory is the notion of two different classes of mental representations. These are verbal representations and visual representations. Support for the notion of two different codes comes from studies related to selective interference. That is, performance is poorer when two different tasks are conducted which rely upon the same representational format (i.e., visual or spatial respectively) in comparison to tasks which engage different formats (e.g., Logie et al., 1990). In the context of memory performance and imagery, it is also important to consider eidetic memory. It can be described as the persistence of a visual image after the according stimulus has been removed (Allport, 1924). It is to be differentiated from non-visual memory and afterimages. In contrast to afterimages, eye movements during stimulus inspection do no prevent eidetic images from occurring, additionally they are positive in colouration and do not shift with eye movements (Giray et al., 1976; Haber, 1979). Eidetic imagery is predominantly, but rarely, found in children from 6 to 12 years and virtually absent in adult populations (Giray et al., 1976). It is important to mention that eidetic imagery is not photographic and hence does not generally benefit memory performance (cf., Haber, 1979).

3.2. Levels of processing (LOP)

Another factor related to memory performance is depth of encoding. The original theory generally proposed that a deeper level of encoding an event into the cognitive system is more beneficial for later recall than shallow encoding of the same event (Craik and Lockhart, 1972). The standard finding to mention here is, semantically encoded words lead to greater subsequent recognition than phonemically encoded words (Craik and Tulving, 1975). Mainly two possible mechanisms are discussed to underlie this levels-of-processing account. Firstly, it is suggested that more elaborated memory traces are more distinctive from other memory records. Greater distinctiveness in turn will lead to more effective recollection (Murdock, 1960; Craik, 2002). Secondly, it has been proposed that better integration with pre-existing memory structures might be the case for more elaborate memory traces. This in turn would help reconstructive processes during retrieval (Moscovitch and Craik, 1976; Craik, 2002). Although the LOP account is not free from criticisms (e.g., Baddeley, 1978; Kolers and Roediger, 1984), due to its predictive power and its broad applicability the notion that more elaborate encoding and hence deeper processing leads to better retention might be the most valuable Q3 general rule about human memory Fig. 3.

3.3. Transfer-appropriate processing (TAP)

While the LOP account in the first instance focuses on encoding processes, the transfer-appropriate-processing account emphasises the benefits of similarity between encoding and retrieval for memory performance. The notion of TAP was first proposed

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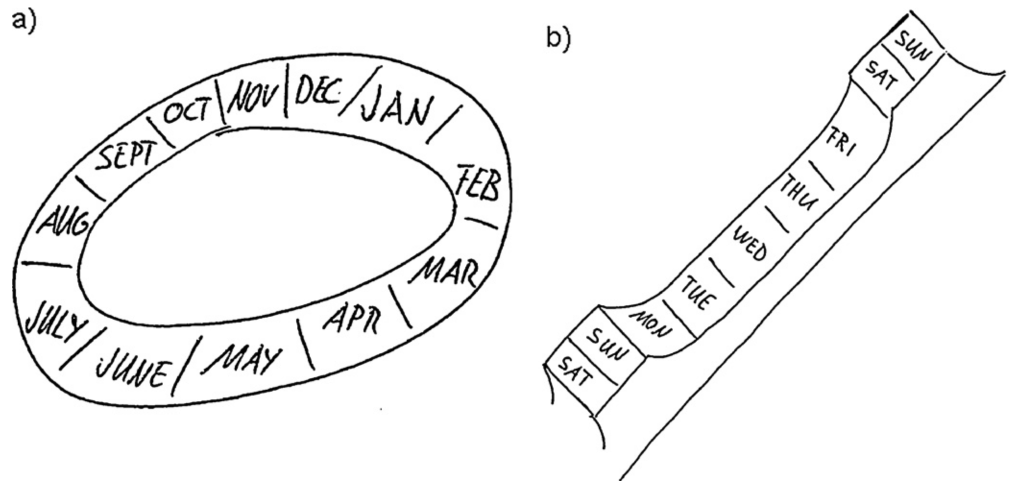

Fig. 3. Exemplary depiction of mental time-space calendars as they may occur for time-space synaesthetes. (a) Array for the months of the year and (b) days of the week.

by Morris et al. (1977). Using a semantic and rhyme encoding task, memory performance was shown to be better in a standard recognition test than in a rhyme recognition test after the semantic encoding but vice versa after rhyme encoding. According to TAP, retention is determined by how well the circumstances and requirements of processing at encoding match the conditions at retrieval. That is, other than LOP it does not assume that types of processing are inherently deep or shallow, it is rather suggested that later retrieval depends on the match between processing operations required during study and during test (cf., Kolers and Roediger, 1984; Meier and Graf, 2000). Note, both accounts – LOP and TAP – focus on memory processes rather than different memory systems.

3.4. Structure and organisation

Also structuring and organising is likely to enhance memory performance. That is, new material is strategically incorporated into previous knowledge structures. Probably the most effective and widest used memory strategy applied by mnemonists is the method of loci. This method relies on both visual imagery and deep encoding strategies and incorporates some instances of TAP. It basically consists of a mental walk along a predefined route during which the to-be-remembered-things are associated to fixed points of the route (cf., Parker et al., 2006). At retrieval, the mental walk is performed again and the fixed points serve as retrieval cues. With this method outstanding memory performance such as the memorization of digit matrices consisting of 50 digits or more could be achieved in only a few minutes time. A disadvantage of such memory strategies is their restriction to specific material. For example, they are not suitable to the memorization of abstract figures and thus do not normally lead to a general memory performance advantage. Furthermore, apart from a few exceptions, retention of information is restricted to relatively short time intervals if it is not rehearsed (Wilding and Valentine, 1997). Moreover, it has been suggested that extraordinary memory performance is achievable simply by training these techniques and that good memory abilities are not a necessary precondition (Ericsson and Chase, 1982; Ericsson, 2003). For human memory, another beneficial form of organization is chunking which refers to the process of combining several individual items into larger groups during encoding. For instance, recall performance of number sequences is improved when chunked into threes (Wickelgren, 1964; Ryan, 1969a,b). Similarly, stimuli which encourage chunking are likely to improve memory performance (Miller, 1956; Bor et al., 2003; Bor and Owen, 2007).

3.5. Domain expertise

Expertise can be defined as outstanding skills and/or knowledge in a domain deliberately acquired through training and experience. Unlike mnemonists, experts such as chess players or musicians do not usually focus on training their memories to be able to encode and retain immense amounts of any kind of information in short time. However, the practice involved in the domain of expertise gives rise to highly established knowledge structures, which in turn leads new information to be quickly understood and incorporated into previous knowledge structures and on the other hand boosts memory performance. Evidence comes from studies showing that knowledge providing meaning to a stimulus is critical for enhanced performance. That is, superior memory performance in experts is clearly related to their domain of expertise and chunking is one of the major factors to increase expertise (Chase and Simon, 1973; Chase and Ericsson, 1982; cf. also Bryan and Harter, 1899). Not surprisingly, chunking can therefore lead to outstanding memory performance (Ericsson et al., 1980). Occasionally, expert memory is also found in people with autism (cf. also Section 7.3). A reason might be their 'limited repertoire of interests' and propensity to 'systemise' (Baron-Cohen, 2002, 2009) rather than chunking. However, it is to be noted that rather than expertise, memory deficits are more common in autism which, in contrast to synaesthesia, is a developmental disorder (cf. Happé, 1999).

3.6. Structural brain differences

Evidence for a link between hippocampal size and memory in general population is weak and is often negatively correlated in a young sample (Van Petten, 2004). Interestingly, superior memory performance does not seem to be associated with structural brain differences in grey matter volume. Evidence comes from a study in which participants of World Memory Championships were compared with normal controls in various memory tasks (i.e., digits, faces, snow crystals). However, superior memory was associated with functional differences in brain areas usually involved in spatial processes and navigation. This might have been due to the use of strategies such as the method of loci which was applied by 90% of the superior memorisers (Maguire et al., 2003; cf. also Ericsson, 2003).

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4. Case studies of exceptional memory in synaesthetes

This section considers single case studies of people with synaesthesia for whom memory has been assessed, and for those with superior memory in which synaesthesia is reported.

Perhaps the most famous case of exceptional memory linked to synaesthesia is that of Solomon Shereshevskii, studied by Luria (1968). Shereshevskii was working for a Moscow newspaper when he came to the attention of his editor because he never took written notes of addresses, quotes or stories. He eventually became a professional memory expert giving stage performances. Over several decades he was studied by Luria who concluded that his memory "had no distinct limits... there was no limit either to the capacity of Shereshevskii's memory or the durability of the traces retained" (p. 11). For instance, he could recall long meaningless lists of nonsense syllables ("ma, sa, na, va, na, sa, na, ...") and written nonsense equations both immediately and after 4 and 8 years. He was able to remember matrices of 50 digits after only a few minutes inspection. Moreover, he was able to recall them when retested 15 or 16 years later. Shereshevskii had multiple forms of synaesthesia (e.g., sound-colour synaesthesia, phoneme-colour synaesthesia, phoneme-taste synaesthesia). However, the extent to which his memory ability was attributable to his synaesthesia is unclear. In the nonsense syllable list, described above, he notes that he could visualise them synaesthetically. He saw the syllables as a thin-greyish yellow line corresponding to the vowel "a" and he then saw "lumps, splashes, blurs, bunches, all of different colours, weights and thicknesses" appear on the line that corresponded to the different consonants. However, he also describes using deliberate mnemonic strategies to remember the list (e.g., "nava" is a Yiddish expression). Other researchers have queried whether superior performance by other memory experts on the digit matrix task is really akin to reading off a visual mental image (Ericsson and Chase, 1982; Wilding and Valentine, 1997; Ericsson, 2003). More recently, it has been suggested that Shereshevskii may also have had autism which together with his synaesthesia may have been the basis for his exceptional memory (Baron-Cohen et al., 2007; Bor et al., 2007).

A comparable but more recent case is Daniel Tammet, a mathematical and linguistic savant who has been diagnosed as having Asperger Syndrome (i.e., disorder of the autistic spectrum). In 2004, he became the European champion for reciting Pi from memory over more than 22,000 decimal places. Moreover, he has a particular aptitude for language learning: he speaks ten languages; learning conversational Icelandic in 1 week; and he has constructed his own language. In laboratory tests, he showed exceptional verbal short-term memory abilities. That is, when presented with digit-strings of increasing length he had a digit-span of 11.5 (i.e., the number of digits he was able to immediately repeat back in the order of presentation) in comparison to 6.5 in controls from a more general population. However, his spatial span for blocks which are arranged on a board and tapped in sequences of increasing length was 6.5 compared to 5.3 in controls (Baron-Cohen et al., 2007). A recognition memory test for faces yielded unremarkable performance. The memory benefit for numbers (and language learning) relative to faces may be attributable to his synaesthesia. Numbers up to an integer of 10,000 have unique shapes, colours, textures, and feels. A list of numbers creates the experience of a complex landscape (Tammet, 2006). Whereas controls show a benefit of chunking of verbal material in memory tasks, associated with increased activity in lateral prefrontal cortex (Bor et al., 2003; Bor and Owen, 2007), Tammet failed to show this chunking-effect either behaviourally or in terms of neural correlates (Bor et al., 2007). This is consistent with the idea that he is able to impose his own internal organisation on 'unchunked' sequences, thereby benefiting less from an externally imposed strategy.

Synaesthetic spatial forms of time (days, months, years) may also provide a 'natural' system to organise certain memories. AJ reported having synaesthetic mental calendars that she was able to use for virtually perfect autobiographical memory and a perfect memory for world events (Parker et al., 2006; Simner et al., 2009b). However, as with Shereshevskii and Tammet she appeared to train herself to use this system, in this case when she was traumatised by a move from the East to the West coast of the USA at the age of 8 years. Moreover, the superior recall was limited to events of interest to her which might suggest some autistic traits. Nevertheless, her memory was superior in general (on the WMS – Wechsler Memory Scale), although her IQ was normal (on the WAIS – Wechsler Adult Intelligence Scale) and other cognitive abilities (executive functioning, language and face recognition) were impaired.

Finally, we will consider three case studies of exceptional memory in grapheme-colour synaesthetes: C (Smilek et al., 2002), MLS (Mills et al., 2006) and JS (Brang and Ramachandran, 2010). The tests and findings are summarised in Table 1. C came to the attention of researchers due to her ability to recall lists almost perfectly during a psychology class. She was formally tested using a version of the 'digit matrix' test reported by Shereshevskii. However the test was adapted to include digits that were either coloured congruently or incongruently with her synaesthesia, or were achromatic. C showed an impaired ability to recall the incongruent matrix on the first trial, suggesting a direct impact of synaesthesia on her memory. Her ability to recollect the achromatic digits was enhanced relative to controls, but no such advantage was found in a separate test that used unfamiliar symbols that do not induce synaesthesia. The synaesthete MLS also showed a dissociation between memory for synaesthesia-inducing material versus other material (Mills et al., 2006). She was shown to have superior ability at recalling lists of names and words but performed normally on recall of abstract visual figures. However, a more recent case study reported memory abilities that are not readily attributable to the synaesthesia itself. JS claimed to have an extremely accurate visual memory and this was confirmed on two tests: one test involving memorising the location of objects in an array, and a test of change detection between two alternating complex visual scenes separated by a brief blank (Brang and Ramachandran, 2010). This may be a type of eidetic imagery, but in the absence of a more complete assessment of memory functioning this is uncertain. However, note that eidetic memory is generally not associated with enhanced memory performance (cf., Haber, 1979).

To summarise, the case studies discussed above all revealed enhanced if not exceptional memory abilities and, when assessed, these abilities were rarely found for all kinds of material but appears to be generally limited to synaesthesia-inducing material. Synaesthesia may provide an opportunity to structure information in memory (e.g., by creating coloured patterns, spatial layouts, or idiosyncratic chunks), although only certain individuals may be more inclined to make deliberate use of this as an explicit memory strategy. This may be particularly true for autistic individuals who have a particular interest in numbers and time. One suggestion is that the coincidental combination of synaesthesia with autism may lead to more savant skills than expected from either in isolation (Baron-Cohen et al., 2007; cf. also Simner et al., 2009b).

5. Group studies of memory ability in synaesthetes

The cases described above have been tested primarily because of their prodigious memory abilities (cf., Rothen and Meier, 2009; Meier and Rothen, in press). This raises the issue as to whether exceptional memory is the norm amongst synaesthetes in general. Several group studies have been conducted to test the generality, the magnitude, and the extent of the potential memory benefit

Table 1
Summary of case studies of grapheme-colour synaesthetes.

Memoranda	Test	Result	Notes	*N* (syn/con)	Study
Digit matrix (visual)	Cued recall, location–digit?	Enhanced/reduced	Black, congruent/incongruent	1	Smilek et al. (2002)
List of name pairs	Free recall, cued-recall	Enhanced		1/13	Mills et al. (2006)
Word lists (spoken)	Free recall	Enhanced	Rey Auditory-Verbal Learning Test	1/normative sample	Mills et al. (2006)
Complex visual figure	Free recall (drawing)	?; <+1 SD	Rey Figure	1/normative sample	Mills et al. (2006)
Complex visual figure	Free recall (drawing)	?; <+1 SD	Benton Visual Retention Test	1/normative sample	Mills et al. (2006)
Objects in an array	Cued recall	Enhanced	Where was a specific object	1/15	Brang and Ramachandran (2010)
Pairs of complex images	Cued recall	Enhanced	Spot the difference	1/11	Brang and Ramachandran (2010)

Table 2
Summary and effect sizes of verbal memory tests from group studies of grapheme-colour synaesthetes. Effect sizes were calculated according to Thalheimer and Cook (2002).

Memoranda	Test	Result	Cohen's *d*	Notes	*N* (syn/con)	Study
Word lists (spoken)	Free recall	Enhanced	.83	Rey Auditory-Verbal Learning Test	16/16	Yaro and Ward (2007)
Word lists (spoken)	Free and cued recall	Enhanced	.60/.68; .90/.53	California Verbal Learning Test: immediate free/cued; delayed free/cued	9/20	Gross et al. (2011)
Word lists (visual)	Free recall	Enhanced	1.58/2.01/1.43	Word lists: black/congruent/incongruent	10/48	Radvansky et al. (2011)
Word lists (visual)	Free recall	Enhanced	1.29/.45	Black words/isolated red word	10/48	Radvansky et al. (2011)
Word lists (visual)	Free recall	Enhanced	1.54/.73	Black words/semantically isolated word	10/48	Radvansky et al. (2011)
Word lists (visual)	Free recall	Enhanced/reduced	1.84/−1.18	Black words/semantically related intrusion	10/48	Radvansky et al. (2011)
Word lists (visual)	Recognition	Enhanced	1.52	Warrington-Recognition Memory Test – words	7/8	Gross et al. (2011)
Stories (spoken)	Free recall	Enhanced	0.33/0.37	WMS Logical Memory: immediate/delayed	44/normative sample	Rothen and Meier (2010)
Word pairs (spoken)	Cued recall, word1–word2?	Enhanced	1.07/.70	WMS Verbal Paired Associates: immediate/delayed	44/normative sample	Rothen and Meier (2010)
Word pairs (spoken)	Cued recall, word1–word2?	Enhanced	1.05	WMS Verbal Paired Associates: immediate trial 1	6/19	Gross et al. (2011)
Digit string (spoken)	Digit span	N.S.	−0.13/−0.06	WMS Digit Span: forward/backward	44/normative sample	Rothen and Meier (2010)
Digit string (spoken)	Digit span	N.S.	.38/.75	WMS Digit Span: forward/backward	6/20	Gross et al. (2011)
Digit matrix	Cued recall, location–digit?	N.S.	.37/.19	Congruent/incongruent	16/16	Yaro and Ward (2007)
Digit matrix	Cued recall, location–digit?	N.S.	−0.06/0.03	Black/incongruent	12/12	Rothen and Meier (2009)
Digit matrix	Cued recall, location–digit?	Reduced	−1.61	Congruent/incongruent (within comparison!)	6/6	Green and Goswami (2008)

Note: The normative sample in Rothen and Meier (2010) was assumed to match the sample size of the synaesthetes.

Table 3
Summary and effect sizes of visual memory tests from group studies of grapheme-colour synaesthetes. Effect sizes were calculated according to Thalheimer and Cook (2002).

Memoranda	Test	Result	Cohen's *d*	Notes	*N* (syn/con)	Study
Colour matrix	Cued recall, location–colour?	Enhanced	.31/.77	Immediate/delayed	16/16	Yaro and Ward (2007)
Colour swatch	Recognition (3AFC[a])	Enhanced	1.09	Farnsworth–Munsell memory	16/16	Yaro and Ward (2007)
Complex visual figure	Free recall (drawing)	N.S.	.26	Rey Figure	16/16	Yaro and Ward (2007)
Complex visual figure	Free recall (drawing)	N.S.	.94/−0.27/.98	Rey Figure: copy/immediate/delayed	7/8	Gross et al. (2011)
Simple visual figures	Free recall (drawing)	Enhanced	.51/.69	WMS Visual Reproduction: immediate/delayed	44/normative sample	Rothen and Meier (2010)
Shape–colour pairs	Cued recall, shape– colour?	Enhanced	1.50/.86	WMS Visual Paired Associates immediate/delayed	44/normative sample	Rothen and Meier (2010)
Shape–shape pairs	Cued recall, shape–shape?	N.S.	−0.27	WMS Visual Paired Associates (modified) immediate trial 1	4/8	Gross et al. (2011)
Simple visual figures	Recognition	Enhanced	.75	WMS Figural Memory	44/normative sample	Rothen and Meier (2010)
Faces (visual)	Recognition	N.S.	.62	Warrington-Recognition Memory Test – Faces	7/8	Gross et al. (2011)
Spatial sequence (visual)	Spatial span	N.S.	.08/.36	WMS Forward and Backward Spatial Span	44/normative sample	Rothen and Meier (2010)
Spatial sequence (visual)	Spatial span	N.S.	.11/.06	WMS Forward and Backward Spatial Span	6/20	Gross et al. (2011)

Note: The normative sample in Rothen and Meier (2010) was assumed to match the sample size of the synaesthetes.
[a] Three-alternative forced-choice.

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Table 4
Summary and effect sizes of non-declarative memory tests from group studies. Effect sizes were calculated according to Thalheimer and Cook (2002).

Memoranda	Test	Result	Cohen's *d*	Notes	*N* (syn/con)	Study
Conditioned response	Synaesthetic conditioning	Enhanced	.97	Generalised conditioned response (from colour to letter)	13/13	Meier and Rothen (2007)
Conditioned response	Synaesthetic conditioning	Reduced	−0.51/−0.63	TMS suppression LPO vs sham/RPO vs sham	3 × 12	Rothen et al. (2010)

in synaesthetes. In general, synaesthetes do self-report enhanced memory (Yaro and Ward, 2007) and this seems to be borne out by objective testing, although the effects tend to be more modest compared to some of the exceptional case reports noted earlier (typically within 1 standard deviation of a demographically matched control group; Yaro and Ward, 2007; Rothen and Meier, 2010). Tables 2 and 3 summarise the relevant evidence including effect sizes for verbal and visual memory tasks, respectively (Table 4).

In the sections below, we discuss these findings in the context of different memoranda: verbal material, visual material, and event-based knowledge. It is important to bear in mind that – depending on the specific form of synaesthesia – not all materials elicit synaesthetic experiences. Hence, three possibilities arise in which respect synaesthesia might be related to memory performance. First, synaesthesia affects memory performance restricted to the realm of the synaesthetic inducer (e.g., verbal stimuli in grapheme-colour synaesthesia). Second, potential benefits extend to the synaesthetic concurrent (e.g., coloured stimuli in grapheme-colour synaesthesia). Third, synaesthesia more generally affects memory performance (i.e., across all types of memoranda).

5.1. *Memory for verbal stimuli*

5.1.1. *Memory for words*

Several studies have used standardised assessments of verbal memory functioning that contrast grapheme-colour synaesthetes with demographically matched controls. It is to be noted that grapheme-colour synaesthetes typically report colours from words too (with the letters determining the overall colour/s of the word) and this can occur irrespective of whether they are spoken or written (although there may be individual differences which have tended not to be taken into consideration). Table 2 shows large effect sizes for long-term memory of words in synaesthetes relative to controls. This occurs across a range of different tests. The effect sizes tend to be greater when words are presented visually relative to orally, but in the absence of a direct comparison (i.e., using the same test on the same sample but varying oral/visual presentation modes) the trend is only suggestive.

The study of Radvansky et al. (2011) is noteworthy in that they varied the nature of the study material either perceptually or semantically and tested the impact on subsequent list recall. In the first experiment, words were either presented congruently or incongruently coloured to their synaesthesia, or achromatic. Synaesthetes outperform controls in all three conditions and do show a drop in performance for incongruently presented words (controls on the other hand show, if anything, a disruption of memory when stimuli are coloured). In three further experiments, Radvansky et al. (2011) manipulated the perceptual and semantic distinctiveness of items in the list. In one experiment, only a single word was coloured. In another experiment, a single word was semantically anomalous – the so-called von Restorff effect (e.g., the word "hour" in "diamond, ruby, emerald, sapphire. . ."; von Restorff, 1933). Finally, in the DRM paradigm (Deese–Roediger–McDermott: Deese, 1959; Roediger and McDermott, 1995) in which a list of semantically associated words is presented (e.g., "dream, bed, tired. . ."), but a strong semantic associate (e.g., "sleep") is not, synaesthetes showed overall better performance but, moreover, they showed no enhanced recall of the colour oddballs and less effect of semantic relatedness (i.e., no von Restorff effect, reduced DRM errors). Radvansky et al. (2011) suggested that a single coloured word in a black list might not affect grapheme-colour synaesthetes' performance because they see all words as coloured, and the reduced effect of semantic relatedness would appear to be consistent with a shallow encoding account (based on perceptual or orthographic features). However, there is a puzzle. Shallow encoding of words in non-synaesthetes tends to result in *worse* memory performance. If synaesthetes are relying on shallow encoding then why do they, as a group, perform better? We suggest later that synaesthetes have an enhanced ability to perceive and remember certain visual objects, including words. In summary, the studies above reveal a very consistent picture of enhanced memory.

5.1.2. *Digit span*

In contrast to the benefit for word lists there is no evidence for a memory advantage in grapheme-colour synaesthesia in a conventional measure of digit-span (Rothen and Meier, 2009; Gross et al., 2011). This contradicts the previous case study of Daniel Tammet, but note that he had a particular interest and expertise in numbers (Baron-Cohen et al., 2007; Bor et al., 2007). Crucially, digit span requires ordering of items rather than memory for item identity. It is also possible that word list free recall may benefit more than digit span from non-synaesthetic visual imagery, and future studies of word recall should compare memory advantages for concrete and abstract words to explore this possibility.

5.1.3. *Digit matrices*

Smilek et al. (2002) reported enhanced ability on this task in a case study and an effect of congruency. However, two studies have failed to replicate this at a group level (Yaro and Ward, 2007; Rothen and Meier, 2009). Moreover, Green and Goswami (2008) were not able to replicate a memory benefit for synaesthetic children. However, there was some evidence of interference from incongruent colours for those who experienced colours from written material (but not those reporting it from spoken material). Overall, there was no general performance advantage for the digit-matrix task in grapheme-colour synaesthetes and the effect of congruency was variable (perhaps being age-dependent).

Both digit span and digit matrices involve memory for contextual associations: associating digits to spatial positions (digit matrix) or positions in a sequence (digit span). The results stand in contrast to free recall of words in which enhanced memory is reliably observed and in which congruency effects are found at a group level (Radvansky et al., 2011).

5.1.4. *Summary*

A memory benefit in grapheme-colour synaesthesia is often found for the realm of the inducer. However, memorising verbal material does not always lead to a memory advantage even if that material generally elicits synaesthesia (as in digit span and digit matrices). Hence, it is likely that the synaesthetic experience itself is not entirely responsible for the memory advantage found in grapheme-colour synaesthesia. Instead it seems dependent on the nature of the task in addition to the nature of the synaesthesia.

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5.2. Memory for non-verbal stimuli

In this section, we will first focus on domain specific memory performance in grapheme-colour synaesthesia (i.e., colour). Thereafter, we will consider a more general memory advantage for stimulus material which is neither directly related to the realm of the inducer nor to the domain of the concurrent.

5.2.1. Memory for colour

A sample of 44 grapheme-colour synaesthetes performed particularly high on the visual paired associates test of the WMS-R (Rothen and Meier, 2010). This test involves associating a coloured square to a meaningless line-drawing. This memory test bears more than a passing resemblance to the phenomenon of grapheme-colour synaesthesia itself (i.e., linking colours to visual symbols). Several explanations might account for this result. Synaesthetes may develop synaesthetic like associations to the symbols, as has been reported elsewhere after training with novel graphemes (cf., Mroczko et al., 2009). However, the latter study made an explicit association to known graphemes whereas the visual paired associates test did not.

The benefit is found for colour memory itself and not just colour–shape associations. If shown a shade of red, a shade of brown, etc., and then given a recognition test with three shades of red (matched for luminance; one old, two new) then they are better able to remember the exact colour (Yaro and Ward, 2007). Similarly, if shown a grid with coloured squares in it (akin to the digit matrix task) then they are better able to recall the position of the colours (Yaro and Ward, 2007); even though the same synaesthetes showed no benefit when coloured digits were used (and the task was to recall the digits, not the colour). This implies a memory advantage for colour that is not directly attributable to synaesthetic associations (either explicit or implicit).

5.2.2. Memory for abstract figures

The visual memory sub-tests of the WMS-R all consist of abstract figures and patterns to recognise or recollect (there is no memory for, say, objects, faces or scenes). On each subtest, grapheme-colour synaesthetes were found to outperform controls (Rothen and Meier, 2010). Furthermore, these synaesthetes performed significantly better on the visual memory subtests (overall score) of the WMS-R than the verbal memory subtests (Rothen and Meier, 2010; Cohen's $d = .58$). This observation is crucial for the notion of a more general memory advantage in synaesthesia because the visual stimuli used in the tests did not evoke synaesthetic experiences.

There is, however, one test of abstract figural memory that has not consistently shown an enhancement of memory: the Rey Complex Figure Test. Yaro and Ward (2007) found no benefit on this task, and Gross et al. (2011) also failed to find a difference when applying the same scoring system (i.e., original scoring system which evaluates the presence/absence of the different components of the figure). In general, this is not a pure test of visual memory and the task also depends on constructional and organisational abilities (Shin et al., 2006) which might explain the absence of a memory advantage in synaesthetes. When evaluated with an alternative scoring system applying qualitative ratings on different dimensions of the figure, Gross et al. (2011) found a performance enhancement in configural accuracy (for the overall shape of the figure) but this was found for the copy condition in addition to recall conditions. Hence, it is unclear whether the benefits are related to memory per se.

5.2.3. Memory for objects, faces, and scenes

Given that many standard assessments of memory involve objects, faces or scenes (e.g., doors and people, Baddeley et al., 1994; Camden memory tests, Warrington, 1996), it is perhaps surprising that these have not been carried out on synaesthetes. Gross et al. (2011) tested seven grapheme-colour synaesthetes on a face recognition memory test and reported no enhancement, even though an enhancement was found for the equivalent test involving words.

5.2.4. Short-term visual and visuo-spatial memory

Rothen and Meier (2010) and Gross et al. (2011) conducted the spatial-span subtest of the WMS-R in grapheme-colour synaesthesia. In this task the experimenter taps a sequence of increasing length on board with blocks laid out in a grid and the participant taps the sequence back in either the same or the reversed order. There was no evidence of a benefit.

Spatial-visual short term memory in time-space synaesthetes was assessed with the visual patterns test (VPT). That is, checker board patterns consisting of black and white filled in squares on grids of varying sizes were to be memorised and followed by immediate recall. Synaesthetes ($N = 4$) were found to perform better than the education and age matched norming population (Simner et al., 2009b). However, little is known about the wider memory profile of this type of synaesthesia.

5.2.5. Summary

A memory performance advantage in grapheme-colour synaesthesia is not only found for the domain of the synaesthetic concurrent (i.e., colour). It rather seems to exist more generally for visual material consisting of simple abstract patterns. It is less clear whether this extends for meaningful visual stimuli such as faces and scenes.

5.3. Memory for events

Very little is known about autobiographical memory or memory for factual knowledge (i.e., part of semantic memory) in people with synaesthesia. The only study along these lines was conducted with six time-space synaesthetes (Simner et al., 2009b). They were given several memory tests including generating as many autobiographical events as they could (in a limited time) when presented with a year, dating of public events (death of Pope John Paul II) and cultural events (Oscar winners). The synaesthetes were more accurate at dating these events, without being slower to do so, and generated more autobiographical events given a probe year. This is consistent with the notion of a memory advantage related to the realm of the inducer. In this instance, the spatial form itself can be used as an internal 'place holder' to anchor events in time. However, the autobiographical reports were only verified in one synaesthete. Therefore, it is still possible that some of the other synaesthetes were conforming to demand characteristics.

5.4. Non-declarative memory

Only one study has tested the impact of grapheme-colour synaesthesia on non-declarative memory. Meier and Rothen (2007) used a modified version of a classical conditioning task introduced by Bechara et al. (1995). Across three phases (habituation, conditioning, and extinction) participants were presented with coloured squares. In the conditioning phase one specific colour (e.g., blue), the conditioned stimulus (CS), was followed immediately by a loud startling sound, which served as unconditioned stimulus (US). For each individual synaesthete and a matched control, the CS-colour (i.e., blue) was selected such that it corresponded to the synaesthete's specific concurrent colour experience of the particular grapheme. Throughout the experiment, these graphemes were presented occasionally in black on a white background, but they were never coupled with the US. For trials followed by a startling sound, as a consequence all participants showed a startle reaction for the CS as indicated by an increase in skin conductance response (SCR). For grapheme trials, there was a startle response for the synaesthetes, but not for the controls. The results suggest that associations with synaesthetic concurrents learned in a stimulus-response manner transfer immediately to the corresponding synaesthetic inducer. Interestingly, also controls who were excessively trained on grapheme-colour associations did not show this effect (Meier and Rothen, 2009). The mechanism of this transfer was more deeply assessed in a follow-up study and shown to rely on bilateral parieto-occipital processes associated with implicit bidirectional processes in synaesthesia (Rothen et al., 2010). These results suggest that synaesthesia creates learning opportunities which are not present in non-synaesthetes. Note, the learning advantage here is related to the domain of grapheme-colour synaesthesia and not restricted to the realm of the inducer.

6. Interim summary

The majority of research on memory in synaesthetes is related to grapheme-colour synaesthesia with the exception of two studies involving time-space synaesthetes (Parker et al., 2006; Simner et al., 2009b). There are a number of well-documented single cases of exceptional memory in synaesthetes, although in most of these cases the benefits may not be solely a product of their synaesthesia (e.g., reflecting strategies or numerical expertise). In group studies, synaesthetic individuals tend not to be exceptional (the enhancement of memory tends to lie within one standard deviation of the mean); but is statistically robust (as demonstrated by effect sizes). Synaesthesia may affect the way stimuli are encoded into memory. For example, if externally presented material can be easily incorporated into a synaesthetes pre-existing synaesthesia. However, not all memory tests involving synaesthesia-inducing material lead to a reliable memory advantage (e.g., digit matrix and digit span). In contrast, synaesthetes' performance on certain tests of visual memory not eliciting synaesthetic experiences can be as least as good as in tests involving synaesthesia-inducing material. Theoretical explanations in terms of models of memory, and factors known to enhance memory, are considered in the last main section.

7. Explaining the memory advantage in synaesthesia

7.1. A process account: encoding versus retention

Wilding and Valentine (1997) consider various ways in which memory could be said to be superior: either in terms of the amount of information learned (in a given time), or the time taken to learn information (of a given amount), or the ability to retain information over time (lack of forgetting). In the context of our discussion, do synaesthetes learn more or do they forget less? The single case studies of Smilek et al. (2002) and Mills et al. (2006) tended to perform normally on the initial learning phases but showed better long-term retention. However, many tests that lack a retention phase nevertheless show a benefit for initial learning in synaesthetes (e.g., Radvansky et al., 2011). The largest study to address this question found no difference in immediate recall versus delayed recall scores of synaesthetes on the WMS although both scores were higher in synaesthetes relative to controls (Rothen and Meier, 2010). That is, synaesthetes appear to both learn more and retain more relative to controls but learning and retention are proportional to each other.

7.2. A strategies account: visualizing versus verbalizing and shallow versus deep

Synaesthetic experiences may act similarly to visual mental images and thus, according to the dual coding theory of memory, benefit its performance. Dual coding is also possible for synaesthetic concurrents due to implicit bidirectionality (implicit co-activation of the inducer due to presence of the concurrent). Thus, one would expect a memory performance advantage in the domain of synaesthesia. However, this is not the case as there is also evidence for a more general memory advantage (e.g., for simple abstract figures in grapheme-colour synaesthesia) and not all tasks related to the realm of the inducer are associated with a memory benefit (Rothen and Meier, 2010). Hence, other mechanisms must be responsible for the memory advantage found in synaesthesia–at least for material beyond the domain of a particular form of synaesthesia.

Another strategy that is beneficial to memory is 'deep' encoding of stimuli (i.e., forming semantic associations) rather than 'shallow' encoding of stimuli (e.g., attending to the spelling pattern of a word). The evidence from Radvansky et al. (2011) suggests that synaesthetes may tend to encode words more shallowly than non-synaesthetes. As noted before, the paradox is why shallow encoding should produce worse memory performance in controls (relative to deep encoding) but better memory performance in synaesthetes (relative to controls). This could be explained if the visual appearance of a word is processed with greater efficiency in synaesthetes than in non-synaesthetes. Thus, verbal material may be encoded more as visual objects than semantic ones. Such a predominance of visual processes is also consistent with higher self-reported levels of visual imagery in synaesthesia (Barnett et al., 2008a; Price, 2009; for a more empirical account see Spiller and Jansari, 2008).

One particular domain in which synaesthesia may afford a specific strategy that leads to a more circumscribed memory advantage is for time-space synaesthetes. They seem perform better in tasks related to autobiographical and semantic memory for historic/popular events (Simner et al., 2009b). These synaesthetes seem to be able to use their visual 'time line' whereas others reconstruct the dates of events based on autobiographical knowledge (Fradera and Ward, 2006).

7.3. An expertise account: synaesthesia, savantism, and mnemonic strategies

Due to the strong propensity in people with autism to systemise and the memory enhancement found in synaesthetes, it was recently hypothesised that whenever autism co-occurs with synaesthesia the likelihood of savant skills is increased (Baron-Cohen et al., 2007). The cases of Tammet and Shereshevskii may suggest that this is indeed the case. It was also speculated as to whether a common neural basis might exist (Baron-Cohen et al., 2007). In this context, two characteristics which especially in combination may aid memory performance are identified. First, concretion of abstract mental concepts provides a mediating factor for extraordinary memory performance (cf., Murray, 2010). Strikingly, synaesthetic experiences are often – if not always (Nikolić et al., 2011) – induced by abstract mental concepts as for instance the meaning of letters and numbers. In that case, corresponding colour experiences render a given inducer more concrete. Regarding this notion, synaesthetic experiences may act as concrete labels. Similarly, there is anecdotal report for highly concrete representation of abstract concepts in savants (Murray, 2010). Second, there may be obsessive tendencies to think about certain concepts relating to prodigious memory performance (cf., Simner et al., 2009b). Such behaviour can be observed in most savants (Pring, 2005) and it was found in the above reported synaesthete AJ who "organised her memory" after she and her family moved from the East to the West coast (Parker et al., 2006). Similarly, mnemonists need to train their techniques in order to maintain their performance (Wilding and Valentine, 1997). It is certainly an important question whether or not, and under what circumstances, synaesthetes deliberately use their experiences in everyday life. Nevertheless, the expertise account fails to offer a general account of synaesthetic memory enhancement.

Moreover, it was also hypothesised that autism is characterised by a bias towards local rather than global information processing. That is, people with autism preferably process local information (Happé, 1999; Mottron et al., 2006). Although it is debated whether this is due to an imbalance between local and global processing (Happé, 1999; Happé and Booth, 2008) or due to a superiority of low-level perceptual functions (Mottron et al., 2006, 2009), the general idea of a *local bias* shares similarities with information processing in people with synaesthesia. As mentioned in the previous section, Radvansky et al. (2011) presented evidence for a bias towards item specific (local) processing in synaesthetes opposed to semantic processing in non-synaesthetes (cf. also Cohen Kadosh et al., 2011 for a similar account). Despite the similarities between synaesthesia and autism, it is important to mention that this link is controversial since there is, as yet, no evidence of a direct link between them (i.e., a higher prevalence of the two together than would be expected by chance). However, empirical research is needed to further establish a potential relationship and the exact underlying mechanism.

7.4. A stores account: the memory systems model

The memory systems model has been a very influential account of different aspects of memory functioning (Nyberg and Tulving, 1996). A broad division is made between short-term memory and long-term memory. Typically, short-term memory refers to the amount of information which can be actively held in mind for a short period of time. Classical short-term memory tests are digit-span and spatial-span. Moreover, it includes also working memory which additionally requires active manipulation and updating of information. Short-term memory and working memory are mainly associated with activity in frontal brain regions (cf., Cabeza and Nyberg, 2000). Long-term memory is divided into declarative and non-declarative memory (or explicit and implicit memory). Declarative memory is regarded as consciously accessible and consists of memories for events and facts (or episodic and semantic memory). Free recall, cued recall and recognition memory are all tests of declarative memory; that is, they require conscious access to a prior event, namely to an item in a study phase. Declarative memory is typically associated with structures in the medial temporal lobes, in and around the hippocampus (cf., Cabeza and Nyberg, 2000). In contrast, non-declarative memory is associated with memories that are not consciously accessible such as procedural knowledge (e.g., how to ride a bike, or play the piano), conditioned associations (e.g., the red square predicts a shock), and knowledge of the perceptual world (e.g., that "book" is a real word but "mook" is not). The latter is often divided into 'perceptual representation systems' which store knowledge of words, faces, objects and so on. Thus, whilst declarative memory is not typically divided into different memoranda (e.g., memory for words versus scenes) non-declarative memory *is*, within these perceptual representation systems. These systems are assumed to support measures of non-declarative memory such as perceptual priming in which previous exposure to a word makes it more accessible on subsequent encounters.

Within the memory systems model framework, long-term memory advantages of synaesthetes are hard to account for because they do not fall neatly into the predicted divisions of this model. To some extent one could say that the enhancements (when they are found) are more apparent in tests of long-term memory than short-term memory (although see Simner et al., 2009b for some contrary evidence regarding visual patterns).

Synaesthetes do not appear to have a general advantage for all declarative memory tasks. Grapheme-colour synaesthetes typically outperform age and education matched controls in tests involving words, colours, and simple abstract figures, but not for number matrices and more complex figures (and possibly memory for faces and scenes). Moreover, the advantage may extend to non-declarative memory involving colour (Meier and Rothen, 2007; Rothen et al., 2010).

7.5. A Representational account: the ventral stream as a perception–memory continuum

This account differs substantially from the multiple memory systems account in that there is no sharp division between declarative and non-declarative memory systems or, for that matter, between perception and memory (cf., Saksida, 2009). Instead, memory and perceptual processes are divisible according to the type of information they contain. Considering vision, there is an assumed hierarchy along the visual pathway from recognising features (colours, shapes, etc.) to conjunctions of features including recognition of objects, to recognising objects within scenes encountered on a particular occasion. In this scenario, recognition memory for, say, a colour could be achieved within the neural system for perceiving colour without necessarily recruiting the medial temporal lobes. In the memory systems view, all tests of recognition memory should depend upon the MTL whether it be for colours, words, etc. In the perception–memory continuum view, the MTL would still serve a function in terms of representing other kinds of associations; for instance, the perirhinal cortex is crucial for forming paired associates between objects and scenes, and other structures (such as the hippocampus) may be important for learning associations across sensory modalities or for linking items to semantic context. The implication of this is that a task such as shape–colour associations (the WMS visual paired associate task) may have a rather different neural substrate from digit–location associations (in the digit matrix task). The former is more akin to linking features within objects, whereas the latter associates an object (a digit in this case) to something else (a location on a grid). The former is also more closely akin to synaesthesia itself (the association of colours to particular shapes, such as graphemes) suggesting that the same neural mechanisms that give rise to the development of synaesthetic association may underpin recognition memory for colours and shapes (including graphemes and word shapes) and paired association memory for those features.

Crucially, the early visual system can be functionally and structurally divided in two interacting subsystems: magnocellular and parvocellular. The parvocellular pathway is related to processes involving high spatial frequency, high contrast, colour, and visual recognition (e.g., objects and words) whereas the magnocellular pathway is associated with processes involving low spatial frequency, low contrast, achromatic stimuli, and motion perception (e.g., spatial perception and attention) (Derrington and Lennie, 1984; Kaplan, 1991; Merigan and Maunsell, 1993). Interestingly, a recent EEG study presented evidence for differential effects in visual early potentials (VEP) related to magnocellular and parvocellular processes in grapheme-colour synaesthetes and non-synaesthetes (Barnett et al., 2008b). That is, synaesthetes showed an increase in responsiveness in parvocellular pathways and a decrease in magnocellular pathways. This is in line with recent findings of increased cortical volume within the posterior fusiform gyrus which is linked to processing colour information and a reduction in motion-selective regions of the visual cortex in grapheme-colour synaesthetes (Banissy et al., 2012). These findings might indicate that enhanced memory performance in synaesthesia is related to stimuli biased towards parvocellular but not magnocellular processing. This would be consistent with many findings on memory advantages in synaesthesia. Synaesthetes are particularly good at remembering colours, abstract shapes, and visual words (the latter being high contrast, high spatial frequency

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stimuli) (e.g., Yaro and Ward, 2007; Rothen and Meier, 2010); but perhaps show less memory advantage for faces and scenes, and for associating objects (such as digits) with spatial positions.

It is not yet clear, how the findings of enhanced parvocellular responsiveness in grapheme-colour synaesthesia are related to other forms of synaesthesia. Given that colour processing is related to parvocellular processing, it seems reasonable that grapheme-colour synaesthesia which involves the perception of (synaesthetic) colours is associated with enhanced parvocellular responsiveness. Conversely, it would not be surprising if time-space synaesthesia which involves the synaesthetic perception of spatial arrays is associated with enhanced magnocellular responsiveness, as spatial processing is linked to the magnocellular system. Accordingly, also the potential memory advantage for this form of synaesthesia would reflect the same pattern.

Moreover, autism spectrum disorders are also associated with changes (prolonged N1 component of VEP to chromatic gratings) in the parvocellular system (Fujita et al., 2011) and thus consistent with the suggested link between synaesthesia and savantism. Given that this link suggests a preference for local/item specific processing, it would be interesting to see whether time-space synaesthesia is related to global processing, as we hypothesised a link between magnocellular processing and time-space synaesthesia.

8. Conclusion

This review is a contribution on the current literature of how individual differences in perceiving and experiencing the world – in particular the healthy special case of synaesthetes – inform the study of memory. We conclude that a memory benefit in synaesthesia is not necessary directly related to the synaesthetic experience itself rather to wider changes in the synaesthetic brain (e.g., relating to structural and functional changes within their visual system). That is, enhanced memory performance can be found for materials that do not induce synaesthetic experiences and vice versa. Furthermore, this explanation allows for specific predictions about materials and tasks for which a memory advantage in synaesthesia is likely to be found and therefore, can be tested empirically in the future. We are looking forward to new and exciting findings in a growing research field.

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