Long term associations and serial recall

Using synaesthesia to probe memory for sequences

By

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Author's declaration

I declare that the work in this thesis has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. This project was approved by the Human Research Ethics Committee of Macquarie University (Reference Number: 5201200907).

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Summary

In our daily lives, we constantly have to remember sequences such as telephone numbers, license plates or pin codes. How do we hold and recall information that is presented in a sequential manner? Recent interest in the field of serial recall has highlighted that long-term memory seems to interact with our ability to accurately recall sequences. In this thesis, I examine this interaction using overlearnt sequences of digits and letters, and by testing an unusual group with extremely consistent long-term links between digits and colours: synaesthetes. For grapheme-colour synaesthetes, letters and digits elicit vivid perceptions of colours. As grapheme-colour pairings are different between synaesthetes but highly consistent for each individual, synaesthesia offers a unique opportunity to examine the effect of long- term associations on immediate serial recall. A recent study suggests that serial colour memory in synaesthetes is not generally enhanced but that synaesthetic associations can, under certain circumstances, be used strategically to improve colour memory. By further exploring this link, we may gain a more detailed insight into the time course of backward translation between colours and digits in synaesthetes and are at the same time able to examine the effect of long-term knowledge on Immediate Serial Recall (ISR) of colours.

CHAPTER 1

Immediate Serial Recall: Data, Models, and Methodology

Processing serial order information efficiently is vital to performing many higher level cognitive actions and has been referred to as central to most behaviour (Lashley, 1951). For example, non-verbal tasks such as motor movements and goal directed actions are heavily dependent on understanding serial order. Understanding sequences is also needed in verbal processes such as language acquisition, production, and perception. Thus, retaining serial information in memory is an essential mechanism shared by many higher level cognitive skills.

The field of serial memory is concerned with our ability to recall sequences of items in the correct order. Due to the long history of serial recall research, some key behavioural effects have been replicated many times across tasks and domains (for a recent review see Hurlstone, Hitch, & Baddeley, 2014). Many groups have developed computational models to incorporate the well-established behavioural findings into one construct in order to simulate the brain functions underlying these effects (Botvinick & Plaut, 2006; Brown, Neath, & Chater, 2007; Brown, Preece, & Hulme, 2000; Burgess & Hitch, 1992, 1999, 2006; Farrell & Lewandowsky, 2002; Grossberg & Pearson, 2008; Henson, 1998; Jones, Beaman, & Macken, 1996; Lewandowsky & Farrell, 2008; Lewandowsky & Murdock Jr, 1989; Murdock, 1993, 1995; Nairne, 1990; Neath, 1999; Page & Norris, 1998, 2009). These computational models are useful as specific behavioural paradigms can be constructed based on their predictions to further theoretical development. Additionally, behavioural findings might be the foundation for new models. For example, in response to behavioural data suggesting that background knowledge influences immediate serial recall (ISR) (Botvinick, 2005; Botvinick & Bylsma, 2005; Gathercole, 1995), Botvinick and Plaut (2006) developed a serial recall model that includes experience as a factor.

The interaction between long-term memory and ISR is of particular interest when trying to understand how expertise develops and how it might facilitate learning. Storkel (2001) points out how regularities in sequences are essential to learning language and, in fact, behavioural data suggests that familiarity of lexical structure interacts with ISR of non-words (e.g. Gathercole, 1995; Gathercole, Frankish, Pickering, & Peaker, 1999; Gathercole, Pickering, Hall, & Peaker, 2001; Thorn & Frankish, 2005). The aim of this thesis is twofold: The first goal is to examine the link between long-term memory and ISR by using overlearnt sequences of digits and letters. The second goal involves testing synaesthetes who have extremely consistent long-term links between digits and colours and examine whether they can use meaningful structure information of digit sequences to boost recall of colour sequences. For grapheme-colour synaesthetes, letters and digits elicit vivid perceptions of colours. Usually these associations are described as being unidirectional with graphemes evoking the conscious experience of colours but not *vice versa*. However, recent evidence demonstrates subtle backwards connections between colours and digits. Here, I will investigate whether synaesthetes can use this backward connection to enhance ISR performance. As grapheme-colour pairings are different between synaesthetes but highly consistent for each individual, synaesthesia offers a unique opportunity to examine the effect of long term associations on ISR while enhancing our understanding of the phenomenon synaesthesia. In this chapter, I will review previous ISR studies and ISR models. I will also discuss a method new to the ISR literature that could potentially improve the sensitivity of the ISR methodology.

1.1 Short-Term Memory for Sequences

Research in the field of serial recall has a long history (Page & Norris, 1998). Most studies of serial memory focus on tasks which involve recalling random or pseudo-random subsets of familiar items such as words, letters or digits. There are generally accepted key findings of serial recall studies which have been replicated in many empirical verbal short-term memory studies (e.g. Burgess & Hitch, 1999; Hurlstone et al., 2014). For example, the first and the last item of each sequence tend to be recalled with a higher accuracy than the items in the middle of the sequence (*primacy* and *recency effect*) and accuracy for items that are similar is lower than for items that are dissimilar (*item similarity effect*). If similar and dissimilar items are presented in an alternating fashion, accuracy is affected only for the similar items, creating a sawtooth pattern when accuracy is plotted against item position (Baddeley, 1968). Multiple theories and models have been developed trying to simulate mechanisms that can account for these types of patterns in ISR data. These simulations can integrate different aspects of ISR data into a whole and make predictions about underlying brain functions accounting for the pattern of the behavioural data.

The majority of contemporary models can be classified as context-specific models which can account for a wide range of the typical patterns in ISR data (Brown et al., 2007; Brown et al., 2000; Burgess & Hitch, 1992, 1999, 2006; Farrell, 2012; Farrell & Lewandowsky, 2002; Grossberg & Pearson, 2008; Henson, 1998; Lewandowsky & Farrell, 2008; Nairne, 1990; Neath, 1999;

Page & Norris, 1998, 2009). Context-specific models involve two separate mechanisms for serial recall: First, a temporary connection between items which is thought to be essential to encoding item identity and second, a time-locked context representation responsible for encoding item position (Hurlstone et al., 2014). The different context-specific models mainly vary in the type of context-representation. For example, Henson (1998) and Houghton (1990) model the context representations in terms of distance from the beginning and the end of the list whereas Brown et al. (2000) and Burgess and Hitch (1999) present context representations as sets of neural oscillations. Context-specific models have generally been successful in modelling the typical behavioural data obtained from ISR tasks (e.g. Hurlstone et al., 2014).

In comparison to context-specific models, earlier models of serial recall describe *associative chaining* as the key mechanism to recalling sequential information (Jones et al., 1996; Lewandowsky & Murdock Jr, 1989; Murdock, 1993, 1995; Wickelgren, 1965). Chaining accounts describe serial memory in terms of associations formed between items. Sequences are not recalled as a whole but are thought to be recalled one by one using a recalled item in a sequence (*n*) as a cue for the next item in the sequence (*n+1*). Most chaining models can be classified as activation-based models in which successfully recalling identity and serial order of items is dependent on sustained neural activation. The idea is that activation patterns are prolonged by continuously circulating activity amongst neurons which send and receive signals about the information being stored (e.g., Conrad, 1965). Although chaining is a very straightforward approach to explain serial memory, empirical findings show that chaining accounts fail to account for some typical patterns observed in serial recall data (Hurlstone et al., 2014). For example, associative chaining cannot account for the typical error patterns. Due to their shortcomings, activation-based models based on chaining are typically rejected as an adequate explanation (Brown et al., 2000; Burgess & Hitch, 1999; Henson, Norris, Page, & Baddeley, 1996; Houghton, 1990; Houghton & Hartley, 1995). However, Botvinick and Plaut (2006) argue that activation-based models do not necessarily have to involve chaining: Their activation-based, recurrent neural network model successfully models critical findings of ISR data that cannot be modelled relying on chaining mechanisms.

In most ISR models, there is no component accounting for background knowledge of regularities. In fact, Henson (1998) pointed out that a major shortcoming of the context-based framework is the missing link between short- and long-term memory. The model of Botvinick and Plaut (2006) is the only activation-based ISR model that is not based on associative chaining and that includes effects of background knowledge. Therefore, this model is superior to context-specific models in that it takes the influence of experience on ISR data into account.

Hartley and Houghton (1996) put forward another model that includes background knowledge of serial order. However, Botvinick and Plaut (2006) point out that this model is based on chaining and therefore makes different predictions. One of the main differences would be a case where two sequences are presented that have the same beginning but different endings, one ending which is very consistent with the beginning and one that is inconsistent with the beginning (consistency based on experience). If serial memory worked by chaining as predicted by Hartley and Houghton (1996), there should be no difference in recalling the beginning of the sequence, as forward chaining would not influence previous items. In contrast, the recurrent neural network model by Botvinick and Plaut (2006) assumes that the recall accuracy of the beginning of the sequence would be lower when the ending is not probable or consistent. Their simulation with an artificial grammar shows that recall for the beginning of the sequence is influenced by the match between the start and end of a sequence, suggesting the consistency based on experience does indeed affect the whole sequence.

1.1.1 The Influence of Experience on ISR

Behavioural data from many studies show that regularities in sequences influence ISR, suggesting that immediate recall for familiar sequences is enhanced (e.g. Baddeley, 1964; Baddeley, Conrad, & Hull, 1965; Kantowitz, Ornstein, & Schwartz, 1972; Miller & Selfridge, 1950). Specifically, studies comparing serial memory for non-words containing more permitted sound sequences of a language (high frequency bigrams) and non-words containing less permitted sound sequences (low-frequency bigrams) show that sound combinations that are encountered more often are recalled more easily than less frequent sound series (e.g. Gathercole, 1995; Gathercole et al., 1999). Gathercole et al. (1999) showed 7 and 8 year olds lists containing words and non-words and asked them to recall them. There were three types of non-words: non-words containing vowel-consonant structures that had a high, low and very low probability to occur in English. All children recalled words more accurately than non-words. Furthermore, recall accuracy was higher for non-words with a high probability in comparison to non-words with a low probability bigrams. When the group of children was split up into groups with high and low vocabulary scores, children with the high scores outperformed the children with the low scores in all types of word lists (i.e., words and all types of non-words), and both groups showed higher recall accuracies for non-words with high probability in comparison to low probability bigram non-words. This study suggests that the previous experience with the high probability bigram structures affected recall. However, the effect could also be due to children being more likely to be able to pronounce high-probability bigrams in comparison to low-probability bigrams. Thus, the effect might be influenced by higher chances of verbal encoding for the non-words with high-probability bigrams in comparison to non-words with low-probability bigrams. The addition of a group of children from a non-English speaking background for whom different vowel-consonant structures would be more common would strengthen the claim that background knowledge influences ISR.

Behavioural evidence for the effect of familiarity on ISR comes not only from lexical tasks but also from studies examining "grouping" or "chunking", which is a strategy of breaking information up into smaller subsets to enhance memory recall (Miller, 1956). Working memory capacity has been shown to be improved greatly by strategically grouping longer sequences into smaller and familiar sequences. For example, Ericcson, Chase, and Faloon (1980) tested a single participant daily and asked him to recall lists of digits which increased in length (digit span). They showed that their participant's digit span increased from 7 to 79 digits in only a couple of months by using more advanced chunking methods.

More recently, Bor, Duncan, Wiseman, and Owen (2003) showed that a structured spatial sequence is more easily recalled than a non-structured spatial sequence. They presented participants with a 4 by 4 grid of red squares. In the experiment, some of the squares briefly changed colour to blue, creating well-known shapes (e.g. squares, triangles) for one group and meaningless shapes for another group. Participants who saw the structured shapes were significantly better at recalling the spatial sequence of the squares that changed colour. Two additional groups were presented with spatial sequences that created two familiar shapes (e.g. a triangle and a parallelogram). For one group there was a temporal pause between the first and the second shape, meaning that the temporal interruption was congruent with the spatial sequence. For the other group the sequence contained a temporal break at an incongruent point of the sequence, for example, after the first line of the triangle was drawn. Participants showed a higher serial recall accuracy in the congruent condition compared to the incongruent condition. Taken together, these findings show that grouping spatial sequences into familiar shapes improves memory. Participants performed the same task during functional magnetic resonance imaging (fMRI) scanning. They again had higher recall accuracies in the spatially structured sequences compared to non-structured sequences. The fMRI data showed that there was greater lateral prefrontal activation during encoding of structured trials relative to unstructured trial. The authors interpret this as evidence that the higher recall by chunking or grouping of information requires more cognitive resources.

In the auditory-verbal domain, it has also been shown that structured auditory stimuli result in higher recall accuracy (Bor, Cumming, Scott, & Owen, 2004). Similarly to the previous study, participants were presented with meaningful structured sequences and non-meaningful unstructured sequences. This experiment used digit sequences presented auditorily. The meaningful sequences were mathematically structured sequences of numbers (e.g. ascending, descending, even or odd), whereas the meaningless sequences were random sequences of numbers. Again, participants'recall accuracies for the structured sequences were significantly higher than for non-structured sequences, and the fMRI results were consistent with the results of the visual-spatial study. There was greater lateral prefrontal activation during encoding structured sequences in comparison to unstructured sequences, suggesting that strategically facilitating memory by chunking places higher cognitive demands on the system and increases recruitment of the prefrontal areas.

A concern in both these studies is whether memory is actually improved or whether cued guessing is facilitated by known structure. Bor et al. (2004) tried to control for this by designing their structured sequences in a specific way: All their structured sequences consisted of eight digits in total with no more than five digits following a specific pattern (i.e., the entire sequence could not be made up of even numbers, even in the highest structure condition). This ensured that guessing which item would logically follow would be less likely to work because the pattern change could happen at any time. For example, the sequence “8-6-4-2-3-5-7-9” is made up of four even and four odd digits. If one purely relied on guessing here, an ascending sequence as the second part would have also been a possibility (i.e., “8-6-4-2-3-4-5-6”). By designing the sequences in this way, Bor et al. (2004) ensured that the sequences were hard to predict, making it unlikely that their finding of a memory benefit for structured sequences came from cued guessing. However, they did not analyse their data with respect to how often subjects used this strategy of cued guessing. Their design probably prevented subjects from guessing in a specific order but a false alarm analysis would have been useful to ensure that this strategy was not driving the effect.

The importance of structure has also been shown in rapid serial visual presentation (RSVP) tasks. In RSVP tasks, multiple items (usually around 10 per second) are presented to participants who have to recall specific target items. The presentation duration of the items and the time in between items is varied in order to explore temporal characteristics of attention. In one study that is of particular relevance here, Potter, Nieuwenstein, and Strohminger (2008) examined recall of complete sentences versus single words of these sentences in an RSVP task. They showed that in the whole sentence condition, ordered, meaningful sentences consisting of 10 words were recalled with a higher accuracy (86%) in comparison to the same words which did not form a meaningful sentence (56%). This suggests that structured, meaningful sentences are recalled more easily than unstructured, meaningless sentences.

Together, these results suggest that background knowledge does play a role in serial recall. Therefore, it is critical that models of serial recall include experience or prior knowledge as a factor.

1.1.2 Interim Summary: ISR and Background Knowledge

Recalling sequences of items in the correct order is an essential skill in everyday life. Despite a long tradition of serial memory research, there is no consensus regarding the processes of encoding and recalling serial information. Generally, most seem to agree that context-specific models are closest in simulating the clear ISR data obtained from empirical studies (e.g. Hurlstone et al., 2014). However, there are also groups arguing for activation-based models (e.g. Botvinick & Plaut, 2006; Hartley & Houghton, 1996). Some researchers have started to include background knowledge and learning into their serial memory models in response to research suggesting that grouping sequences into familiar sub-sequences is a good strategy to enhance memory performance (Bor et al., 2004; Bor et al., 2003; Ericcson et al., 1980; Miller, 1956).

1.2 Measuring Performance in ISR Tasks

Performance in ISR tasks is usually measured based on accuracy. One of the issues with accuracy scores in this context is that they are quite insensitive. For example, if a participant is required to recall a sequence of five items, the possible accuracy scores are 20, 40, 60, 80, and 100% correct. This means it is difficult to pick up on subtle, more fine-grained differences between conditions or groups. In psychophysics, staircase methods have proven to be very useful and sensitive in determining limits of performance. In staircase procedures, the task difficulty is varied depending on performance. The steps by which the difficulty is changed are reduced successively throughout the experimental run, which allows performance limits to be approached with high accuracy. Using a staircase method to test ISR might therefore provide a more sensitive measure of serial memory. In the following sections, I will summarise what staircase procedures are traditionally used for and discuss advantages of this method. I will then turn to the possibility of using staircase procedures in the context of ISR in order to improve the sensitivity of performance measurement.

1.2.1 Staircase Procedures in Psychophysics

Traditionally, staircases have been used in psychophysics to test perceptual limits more efficiently (e.g., Klein, 2001; Leek, 2001). There are different types of staircases but here I will focus on simple up-down staircases only, which were initially developed by Dixon and Mood (1948). In up-down staircases, stimuli are shown at a specific intensity or difficulty which is then changed in response to the participant's performance. The level of difficulty is changed according to simple rules: difficulty is increased when a participant responds accurately and it is decreased after an error. This is an example of a 1-up-1-down staircase in which difficulty is increased and decreased in response to performance on *one* previous trial. With this adaptive method, the intensity of the stimulus is changed until it reaches a particular level of interest. When the stimulus difficulty is plotted against the trials (psychometric function), the curve reaches a plateau at some point, which means that correct-incorrect responses come in an alternating fashion. This level of performance is called a *threshold*, which indicates the performance limit under the specific task conditions. In a 1-up-1-down staircase, the threshold corresponds to a performance of 50% accuracy as the correct and incorrect responses have to be alternating in order for the psychometric function to reach the plateau. The threshold level can be changed by using different types of up-down staircases such as the 1-up-2-down which targets a threshold accuracy of 70.71% (Wetherill & Levitt, 1965).

Staircases are used across tasks and stimuli but all have one goal in common: using the testing time to measure behaviour more efficiently. For example, when no staircase procedure is used, all possible stimulus intensities or difficulties have to be presented in different trials in order to determine when a participant is able to do the task and when he or she is not. An adaptive staircase includes trials that are close to the individual participant's threshold only and therefore results in much shorter testing time (e.g., Leek, 2001). On the down side, staircase procedures also mean that we lose a lot of data if we are only interested in the end threshold. Cornsweet (1962) points out that the starting point is a very important characteristic of the staircase method: if a participant is starting close to his or her actual threshold, a lot of trials are at or around threshold level and therefore contribute to the final threshold that is computed after all trials are completed. In addition to the starting point, Cornsweet (1962) comments on the importance of initial step sizes (the change in the stimulus) and their modification later in the experiment. Figure 1.1. shows a depiction of an example for a 1-up-1-down staircase. Here, the initial step size is 20 units of task intensity. That means if a participant performs successfully, the intensity is lowered, making the task more difficult. The initial step size determines how quickly the participant approaches their threshold level (Figure 1.1., red rectangle). This is critical because the longer a participant is performing the task at the threshold level, the more reliable is the computed final threshold value. In our example staircase, there will be an intensity level at which the participant is not able to perform successfully anymore and the intensity level has to be increased again to make the task easier. That means the curve changes direction, which is called a reversal (Figure 1.1., red circle). As one gets closer to threshold, the amount of change in the stimulus with each reversal is decreased. This is vital for approaching thresholds with more detail and obtaining values that are sensitive to subtle differences.

1.2.2 Staircase Procedures for ISR Tasks

There have been attempts to use staircase procedures in ISR tasks. Usually the length of the sequence is varied depending on performance: when sequences on the previous trial(s) are recalled accurately, the list length is increased by one item, and list length is decreased after inaccurate recall (e.g., Babcock & Salthouse, 1990; Li, Schweickert, & Gandour, 2000). Sequence length is also varied in the frequently-used digit span task of the Wechsler Memory Scale in which the experimenter reads non-ordered digit lists to the participant, who has to repeat the digits in the same order (*forward recall*) or in the opposite order (*backward recall*). The maximum length of items recalled correctly is recorded and used as dependent variable. Although this is a good way of exploring how many items specific groups of participants can recall in the correct order, it does not fix the sensitivity issue outlined earlier. When the sequence length is increased or decreased by one whole item there is not a lot of room to pick up on subtle differences between groups or stimuli types.

In the following two chapters, I will present experimental data I obtained using a novel ISR staircase approach. The number of items in each sequence was fixed but I used a 2-up-2-down staircase manipulating *presentation duration*. When two sequences in a row were recalled accurately, the duration for each item in the next trial was decreased to make the task more difficult. When two errors were made, presentation duration was increased, making the task

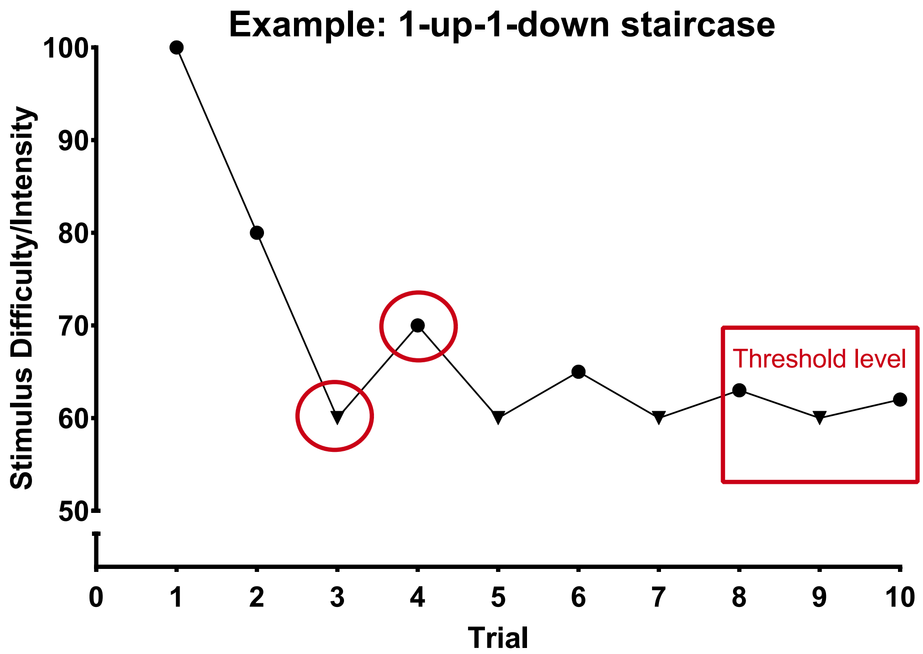

FIGURE 1.1. Example 1-up-1-down staircase. Dots indicate a correct response, triangles an incorrect response. Red circles show the first two reversals. The threshold is depicted in the red rectangle. At the threshold level, the curve flattens out. The exact number of trials that are used to determine the threshold level differs between experiments.

easier. That way the difficulty could be varied at a finer-grained level in comparison to using a staircase on sequence length. Our smallest step size was 8ms which allowed approaching the performance limit with very high accuracy, making even slight differences between conditions and groups visible. Note that by using this approach we are losing the possibility to analyse our data with traditional measurements of serial memory performance such as error patterns and item position effects (e.g., recency effect). However, we gain more sensitivity in measurement of ISR performance.

The aim of both experiments was to examine the effect of background knowledge on ISR. I compared how fast items could be shown in each condition in order for participants to recall the sequences correctly. In the first experiment, I focussed on ISR for colours and digits in synaesthetes and non-synaesthetes and in the second experiment I examined the effect of background knowledge on ISR with letter stimuli.

CHAPTER 2

SYNAESTHESIA AND THE EFFECT OF EXPERIENCE ON SERIAL RECALL

2.1 Introduction

Most serial recall models have focused on simulating recall of novel non-meaningful sequences in the correct order (Hurlstone et al., 2014). In reality, humans are learning sequences and encoding sequences to long-term memory given sufficient exposure (e.g. Botvinick, 2005; Botvinick & Bylsma, 2005; Botvinick & Plaut, 2006). Contemporary context-specific models cannot easily simulate this link between long-term memory and immediate serial recall because these models do not rely on item-to-item connections (Henson et al., 1996). However, a recent activation-based model does include background knowledge as a factor (Botvinick & Plaut, 2006). So far, evidence for the importance of background knowledge comes from (1) studies comparing recall accuracy for non-words containing high-frequency and low frequency bigrams (e.g. Gathercole, 1995; Gathercole et al., 1999), (2) studies examining the different effect of chunking for well-known sequences in comparison to novel sequences on recall accuracy (Bor et al., 2004; Bor et al., 2003), and (3) rapid serial visual presentation (RSVP) studies investigating the effect of structure on recall accuracy (e.g., Potter et al., 2008). However, it is very difficult to control for background knowledge in these experimental designs. Here, I argue that synaesthesia offers a unique opportunity to look at the effect of experience on immediate serial recall (ISR) for colours.

2.1.1 Synaesthesia and Serial Recall

Synaesthesia is a rare phenomenon in which specific stimuli evoke unusual additional experiences within the same or in another sensory modality relative to the inducer (Grossenbacher

& Lovelace, 2001; Ramachandran & Hubbard, 2001; Rich & Mattingley, 2002). The most common type of synaesthesia is grapheme-colour synaesthesia in which an additional colour is perceived upon presentation of letters, digits, or words (Barnett et al., 2008; Rich, Bradshaw, & Mattingley, 2005; Simner et al., 2006; Simner et al., 2005). The colour associations are idiosyncratic and highly consistent over time (Baron-Cohen, Burt, Smith-Laittan, Harrison, & Bolton, 1996). These two characteristics are relevant to ISR research: Each synaesthete has their own grapheme-colour associations and is essentially an “expert” who has had long-term exposure to a specific colour set. As pointed out previously, studies looking at the influence of background knowledge on ISR mainly use letters and words as stimuli. Research with grapheme-colour synaesthetes offers the opportunity to look at whether background knowledge and experience play a role when recalling different serial stimuli, such as colours, while exploring synaesthetes'memory abilities for sequential information.

2.1.2 Synaesthesia and Memory

Some studies suggest that synaesthetes have an enhanced memory in comparison to non-synaesthetes. There is disagreement as to whether this advantage is specific to stimuli that evoke synaesthesia (i.e., inducer), perceptions that are elicited due to synaesthesia (i.e., concurrent) or a general, overall superiority. In addition, there is still a debate about the extent to which synaesthetes' memories are better in comparison to the general population. Case-studies, in particular, seem to suggest that synaesthetes have extraordinary memories (Baron-Cohen et al., 2007; Luria, 1968; Mills, Innis, Westendorf, Owsianiecki, & McDonald, 2006; Smilek, Dixon, Cudahy, & Merikle, 2002). Baron-Cohen et al. (2007), Mills et al. (2006), and Smilek et al. (2002) present single-cases of synaesthetes who performed in the superior range in memory studies involving stimuli that induce synaesthesia (i.e., words and digits). Although case-studies provide hints of what might be going on in a population, we cannot generalise from those results to the entire group of synaesthetes. One of the reasons for caution is the selection bias: these specific synaesthetes might come to researcher's attention because of an enhanced memory. If they are then tested on memory abilities, the chances of these specific synaesthetes showing enhanced memory performance are high. Generalising from this biased sample to the population of synaesthetes is probably not valid.

In addition to case-studies, some group-studies seem to suggest that synaesthetes have an enhanced memory in comparison to non-synaesthetes (Gross, Neargarder, Caldwell-Harris, & Cronin-Golomb, 2011; Radvansky, Gibson, & McNerney, 2011; Rothen & Meier, 2009, 2010; Yaro & Ward, 2007). Evidence for a memory advantage for material that is related to the inducer is mixed. Some results show enhanced memories for word lists in synaesthetes (Gross et al., 2011; Radvansky et al., 2011; Yaro & Ward, 2007) but not for digits (Gross et al., 2011; Rothen & Meier, 2009, 2010; Teichmann, Nieuwenstein, & Rich, 2015; Yaro & Ward, 2007), although both words and digits evoke colours.

Generally, the advantage for synaesthetes in group studies is not as high as in single cases. Rothen and Meier (2010) administered the Wechsler Memory Scale to a large sample of synaesthetes (n = 44). In the short-term memory scales, synaesthetes did not show an advantage compared to controls but in the verbal and visual scales, synaesthetes performed slightly better than non-synaesthetes (within one standard deviation above the mean). Only in one of the tests (immediate visual paired associate learning) synaesthetes performed more than one standard deviation above the mean, which was defined as extraordinary. This test involves making associations between colours and line drawings. In the test phase, colours for the specific line drawings have to be recalled. Comparing the visual scale to the verbal scale showed that synaesthetes performed better in the visual in comparison to the verbal domain relative to controls. The superior memory performance in the visual paired associate learning task in the study of Rothen and Meier (2010) suggests that synaesthetes have an advantage for recalling information that is related to the concurrent. More evidence for that claim comes from a study by Yaro and Ward (2007) who showed that synaesthetes performed better in recognising colour chips and their positions on a colour matrix. However, there is also counterevidence, showing that synaesthetes do not perform better than matched controls when recalling pseudo-random colour sequences (Teichmann et al., 2015).

2.1.3 Synaesthesia and Bidirectionality

Usually synaesthesia is described as being unidirectional, meaning that a grapheme might evoke an involuntary perception of colour but a seeing a colour does not evoke perception of a grapheme. In recent studies, it has been shown that synaesthetes can be implicitly influenced by the backward link between colours and graphemes. Most studies claiming that a backward link exists rely on speeded judgments and reaction time differences (Brugger, Knoch, Mohr, & Gianotti, 2004; Cohen Kadosh et al., 2005; Knoch, Gianotti, Mohr, & Brugger, 2005). For example, Cohen Kadosh et al. (2005) showed that a modified size congruency paradigm works with colours for digit-colour synaesthetes. In their task, synaesthetes were presented with two coloured digits on the screen and had to indicate which of the two had a higher numerical value. If the colours corresponded to two digits with a larger numerical distance, synaesthetes were faster at detecting the number with the higher numerical value in comparison to when the colours matched the numerical value. Control participants intensively studied the digit-colour associations of their synaesthetic counterpart but still did not show this effect. This suggests that colours can facilitate numerical magnitude judgment if there is a close link between them. R. Cohen Kadosh, K. Cohen Kadosh, and Henik (2007) further showed that colours can influence size judgments of shapes. A single synaesthete and six naïve controls had to judge which of two triangles is larger. The triangles were coloured differently in each trial. In the congruent condition, the triangle that was larger in size was shown in a synaesthetic colour associated with a larger number, and *vice versa*. In the incongruent condition, the smaller triangle was shown in a synaesthetic colour associated with a larger number, and *vice versa*. The synaesthete, but not the controls, was slower in judging which triangle was physically smaller or larger in the incongruent compared to congruent trials. This suggests that synaesthetic colours could be evoking magnitude perceptions without numbers being present. Although this is intriguing, to know whether this is a general attribute of synaesthesia, we need to have data from more than one participant.

In another study, McCarthy, Barnes, Alvarez, and Caplovitz (2013) showed that in addition to the subtle influence of colours, a strategic use of the backward link between colours and digits is also possible. In their study, participants had to verify or reject solutions of simple mathematical problems (e.g., "2 + 3 = 5"). On some trials, synaesthetic colours that matched particular digits replaced parts of the equation. The results showed that digit-colour synaesthetes were able to calculate with colours only. However, performing this verification task with colours only came at a cost: an additional 250ms on average was necessary for each colour that had to be translated back to a digit.

In a recent study, we showed that digit-colour synaesthetes can translate colours back to digits to enhance their performance in a visual ISR task (Teichmann et al., 2015). We presented digit-colour synaesthetes and controls with five colours that were flashed one by one in the centre of the screen. The task was to recall the colours in the correct order. There were two different types of sequences: structured sequences which consisted of colours corresponding to ascending or descending digit sequences for the synaesthetes and unstructured sequences, which were pseudo-randomised in order. The structured sequences were again subdivided into three different categories: fully structured sequences had all five colours corresponding to an ascending or descending number sequence ("Structured5"), and partially structured sequences either consisting of four ("Structured4") or three ("Structured3") colours corresponding to ascending or descending digit sequences. The colours were presented for either 500ms (slow) or 200ms (fast) each.

In the slow, but not in the fast condition, synaesthetes recalled the colour series that were fully sequential (Structured 5) and partially sequential (Structured 4) more accurately than the pseudo-random colour series. Controls did not show any such effects (synaesthetes were not overall superior to controls statistically, although this may reflect a lack of power). These results suggest that the backward link between digits and colours can be used strategically to enhance serial memory, but this might only be possible when there is enough time for translation, corresponding to earlier results of McCarthy et al. (2013). However, the timing interpretation in this study was not completely straightforward. First, there were only two different durations (200ms and 500ms) from which we cannot conclude how much time was actually necessary for translation. Second, performance varied substantially from individual to individual, suggesting that some synaesthetes might need more time to do the strategic translation from colours to digits. Finally, we did not detect a three-way interaction. There are three possible explanations for the lack of an interaction. First, it is possible that this was an actual null effect. Alternatively, we might have not been able to detect a three-way interaction because there was insufficient power. Third, participants might have performed at ceiling level in the slow condition. Because the accuracy scale is compressed at the extremes (ceiling and floor) this makes it harder to detect an interaction. From our data we cannot determine which one of the reasons let to the lack of the three-way interaction. Our analyses of the different durations were exploratory; these showed there was only clear evidence of an effect in the slow (500ms) condition. This means no conclusion can be drawn about a potential benefit due to structure in the fast condition. We found evidence that synaesthetes were able to use structured information to boost colour recall relative to unstructured colour sequences, but they did not significantly outperform controls. In addition, there was insufficient sensitivity to determine whether the translation from colours to digits was slow and strategic or fast and involuntary.

2.1.4 The Present Study

In the current study, I developed a new, more sensitive methodology to answer three research questions. First, I examined whether synaesthetes have an enhanced memory for colour sequences relative to controls. Second, I investigated whether these groups perform better when digit and colour sequences contain items in well-known order in comparison to pseudo-randomised order. Third, I examined whether there is a difference for synaesthetes when recalling digits vs. colours corresponding to digits. If colours induced the perception of digits involuntarily we would expect to see a similar data pattern for digits and colours in synaesthetes.

In our previous study there were large individual differences between the participants. Some participants performed at ceiling at the slow (500ms) condition when all items were structured whereas it was challenging for others. These differences in performance might partially be due to age or to the individual colour sets: Some synaesthetes have more colours that are similar (e.g., three different shades of green) which makes serial recall harder. Therefore, I decided to take an approach that is more individually tailored. I moved away from setting fixed difficulty levels in terms of presentation duration and instead varied difficulty depending on performance. As pointed out in the previous chapter, measuring performance in terms of accuracy in the context of ISR is not very sensitive. My method is new to the field of ISR, involving interleaved staircases for the different conditions, increasing and decreasing the presentation duration. My hypothesis is that participants can recall structured sequences when presented for briefer times than non-structured sequences, and that synaesthetes can benefit from digit order implicit in coloured sequences, resulting in better colour memory than controls in structured conditions. The method used is a more sensitive way to test for a difference between synaesthetes and controls in overall serial memory for colours and in the effect of underlying structure within sequences.

2.2 Method

Participants. I tested a group of twelve digit-colour synaesthetes (all female, mean age = 29.58 years, SD = 11.39 years, all right-handed) and a group of thirteen control participants, matched for sex, age (mean age = 29.41 years, SD = 7.15 years), and handedness (see Appendix A for characteristics of the synaesthetes). One control was replaced because she was unable to do the task, leaving us with 12 matched synaesthete-control pairs. The groups did not differ significantly with regard to age (t = 0.046, n.s.). All participants reported normal or corrected-to-normal visual acuity and colour vision. All synaesthetes experienced colours in response to digits but did not report experiencing digits when looking at specific colours. Synaesthetes were highly consistent in the colour reported for each digit over time (Mean = 99.15%; SD= 0.03% ; test-retest range at least 4 months). All participants gave informed consent prior to the experiment and were reimbursed with $15/hour for participation.

Apparatus. A Dell Optiplex 9010 computer running MATLAB 7.5 with Psychtoolbox3 (Brainard & Pelli, 1997) was used for stimulus presentation and response collection. Stimuli were presented on a 27 inch Samsung LCD monitor with a refresh rate of 120Hz.

General procedure. Participants completed two memory tasks: the number and the colour task. The order of the tasks was counterbalanced across synaesthetes. All controls completed the tasks in the same order as their corresponding synaesthetes. The trials were self-paced, with a mouse click starting each trial. In the beginning of each trial, a fixation cross was displayed in the centre of the screen for 500ms. Then a sequence of five colour or digit stimuli was presented, for colour and number blocks respectively. I used an adaptive 2-up-2-down staircase procedure to vary the presentation duration of the stimuli. In the 2-up-2-down staircase, the presentation duration decreased when sequences of two previous trials of a particular condition were recalled with 100% accuracy and it increased when sequences of two previous trials of that condition were recalled with less than 100% accuracy. Pilot data showed that sequences are easier to recall when they are presented relatively slowly in comparison to when they are presented rapidly. However, if they are presented too slowly it is harder to recall them again, because the sequences have to be held in memory for a longer time. Therefore, I used an upper limit of 1000ms; the presentation duration for each item could not be slower than the upper limit. After each stimulus there was a 50ms inter-stimulus-interval (constant across stimulus durations). After presentation of all five stimuli, a response screen was shown with all nine possible stimuli in an invisible 3 x 3 grid. Participants had to select the items they saw in the correct order. I randomised the order of the stimuli on the response screen on a trial-to-trial basis to prevent selection based on learned motor sequences. When a stimulus was selected, a light grey square framed the item to confirm that the participant had clicked this item. In order to move on to the next trial, participants had to choose five stimuli, even if they could not recall what they were or were unsure of the correct order. After the last item had been clicked, feedback on accuracy was displayed for 500ms in the centre of the screen. When the participant recalled all five stimuli in the correct order the word “correct” was displayed, otherwise the word “incorrect” was shown (see Figure 2.1. for the depiction of a number (2A) and colour (2B) trial). In the following sections, I will first outline the procedure for the number task in detail and then describe the colour task.

Number task

Stimuli. In the number task, black digits in 95pt Calibri font were used as stimuli. Viewing distance was approximately 75cm, making the digits 2.56 degrees visual angle. Stimuli were shown on a grey background (RGB: 128, 128, 128). All nine digits from 1 to 9 were used. The 'Text Renderer'Matlab function was used to draw these digits as pixels on the screen to ensure high performance and accurate timing.

Procedure and Design. First, each participant completed five practice trials. The digit sequences for the practice trials were randomly generated and each digit was shown for 500ms. The data from these practice trials were not analysed.

After the practice trials, all participants completed a pre-test to determine the starting duration for the main test (see Figure 2.2. for sample pre-test data). In the pre-test, only randomly generated digit sequences were used. As described earlier, I used a 2-up-2-down staircase procedure to vary the presentation duration of the stimuli. In the first two trials, stimuli were presented for 500ms. The initial step size was set to 200ms and was modified after the first, third, and fifth reversal to 100ms, 50ms, and 25ms, respectively. A reversal was defined as a trial at which the step direction changed (e.g., when the presentation duration was increased in response to poor performance after it had been decreased before in response to strong performance). Each participant completed a maximum of 50 trials. In case the participant reached seven reversals before getting to the 50th trial, the pre-test was aborted. To obtain the starting duration for the main test, I averaged the stimulus presentation durations of the last five pre-test trials and added 50ms. This way, participants could start at a duration that was close to their performance limit for unstructured sequences, which made the staircase procedure in the main test more efficient and reliable.

In the main test, I tested the effect of structure on serial memory. There were four sequence types which differed in degree of structure. Degree of structure was defined by the number of items in ascending or descending order within a sequence. In each condition, there were ten different sequences (see Table 3.1..1.) and each sequence was shown five times on average throughout the experiment. In the fully structured (Structured5) condition, the sequences were completely ascending or descending (e.g., 4-5-6-7-8). To prevent participants from guessing in ascending or descending order, a condition with partially structured sequences was included. In the partially structured (Structured4) condition, four items of each sequence were in ascending or descending order (e.g., 1-5-6-7-8). The ordered part within each Structured4 sequence could either be positioned in the beginning or the end (e.g., 1-5-6-7-8 or 5-6-7-8-1). Thus, including this

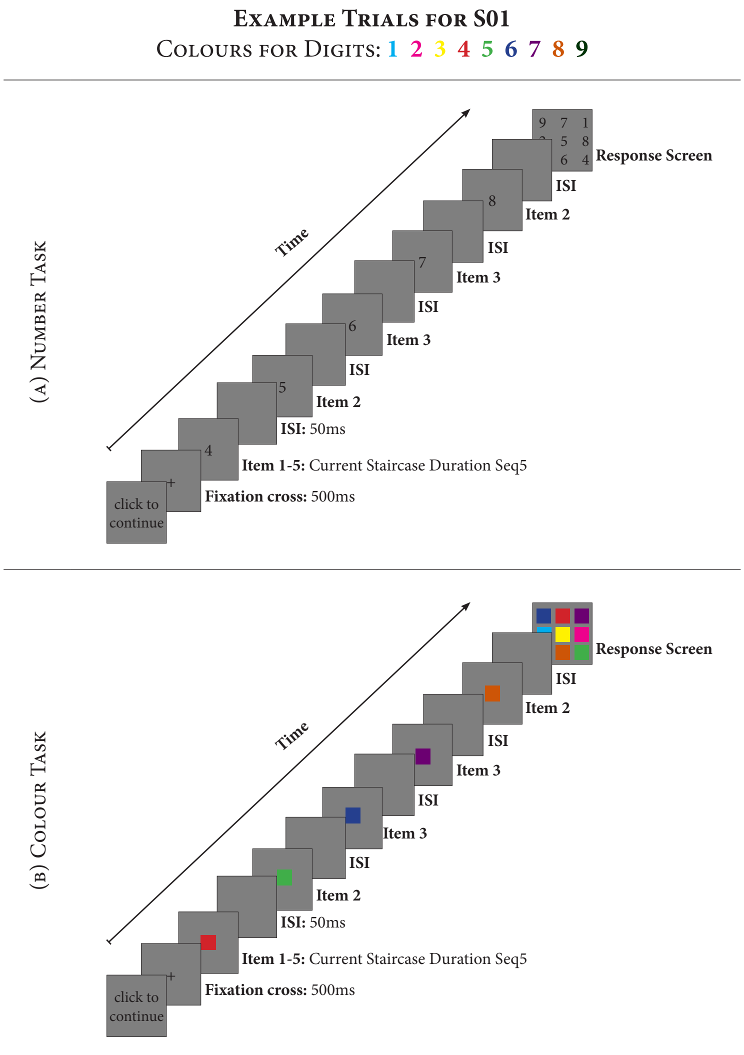

FIGURE 2.1. Example trials for S01. Five stimuli were shown consecutively in the centre of the screen. The task was to recall the items in the correct order. The presentation duration for each item varied on a trial-to-trial basis, depending on the condition and the current staircase duration. The ISI was 50ms. In the top row, the synaesthetic colours for digits 1-9 for S01 are shown. In panel (A), a Structured5 trial of the number task is depicted. In panel (B), the identical Structured5 sequence is shown in colours. Sequences of the two different tasks (i.e., numbers and colours) were shown in separate blocks. Sequence conditions (i.e., Structured5, Structured4, Non-Structured5, and Non-Structured4) were intermingled within a block.

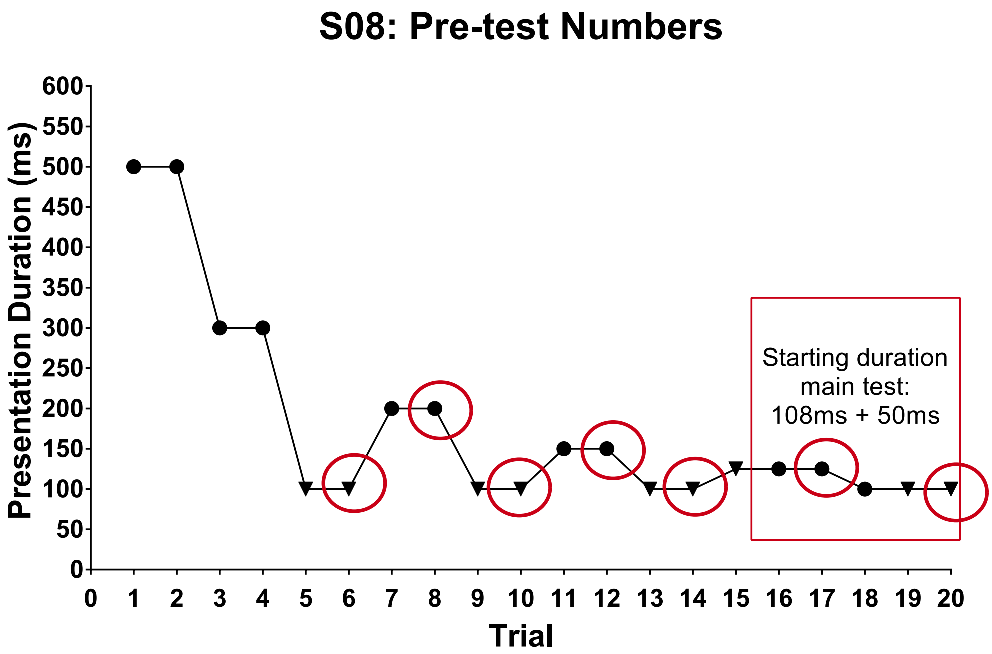

FIGURE 2.2. Example pre-test data from the number block for S08. Presentation duration is plotted against trial number. Dots symbolise a correct trial and triangles an incorrect trial. A 2-up-2-down staircase was used to change the presentation duration depending on performance. Red circles indicate reversals. Step sizes were reduced after the first (trial 6), third (trial 10), and fifth (trial 14) reversal. The pre-test for S08 finished after 20 trials because seven reversals were reached. The pre-test data was used to obtain the starting duration for the main test: The starting point was the presentation duration of the last five trials was averaged plus 50ms (red rectangle).

condition allowed us to measure how frequently participants guessed an ascending or descending order just based on the first items.

As structured sequences were defined as being ascending or descending only, the construction of them resulted in an unpreventable imbalance of pair frequencies. For instance, the combination of 3-4 occurred in six sequences but the combination 1-2 only occurred twice. To control for the imbalance in the structured trials, the non-structured sequences were constructed in a similar way to the structured sequences. The only difference was that all nine digits were randomised at first (e.g., 5-8-1-6-2-9-3-7-4) and then the non-structured sequences built in the identical way as the structured sequences. That means the two "non-structured" conditions (Non-Structured4 and Non-Structured5) were based on the randomised number set and contained different degrees of "pseudo-structure". In the Non-Structured5 condition, all five digits were in the ascending or descending pseudo-randomised order (e.g., <u>5-8-1-6-2</u> or <u>2-6-1-8-5</u>). The sequences in the Non-

Table 2.1: Number sequences used in all four conditions. Lines indicate (pseudo-) structured elements. Structured sequences were based on ascending number line of digits 1-9. Non-structured sequences were based on a pseudo-randomised number line.

Structured Conditions		**Non-Structured Conditions**	
Sequences based on: 1 2 3 4 5 6 7 8 9		Sequences based on: 5 8 1 6 2 9 3 7 4	
Structured5	**Structured4**	**Non-Structured5**	**Non-Structured4**
1 2 3 4 5	1 2 3 4 7	5 8 1 6 2	5 8 1 6 3
2 3 4 5 6	9 2 3 4 5	8 1 6 2 9	4 8 1 6 2
3 4 5 6 7	3 4 5 6 8	1 6 2 9 3	1 6 2 9 7
4 5 6 7 8	2 4 5 6 7	6 2 9 3 7	8 6 2 9 3
5 6 7 8 9	5 6 7 8 1	2 9 3 7 4	2 9 3 7 5
9 8 7 6 5	9 8 7 6 4	4 7 3 9 2	4 7 3 9 6
8 7 6 5 4	3 8 7 6 5	7 3 9 2 6	1 7 3 9 2
7 6 5 4 3	7 6 5 4 9	3 9 2 6 1	3 9 2 6 4
6 5 4 3 2	8 6 5 4 3	9 2 6 1 8	7 9 2 6 1
5 4 3 2 1	7 4 3 2 1	2 6 1 8 5	3 6 1 8 5

Structured4 condition contained four stimuli that were in pseudo-randomised order, again with the pseudo-random ordered part in the beginning or end of the sequence (e.g., 5-8-1-6-4 or 4-6-1-8-5). Note that neither the Non-Structured5 and Non-Structured4 condition contained any obvious mathematical structure. The careful matching of the conditions ensured an identical probability of digit pairs in all conditions. In the instructions, participants were informed that some of the trials would be fully or partially ascending and descending and therefore that it would be important to attend to the whole sequence. This way guessing in order was discouraged. Furthermore, analysing the errors within the Structured4 condition would give an indication how frequently participants still guessed in order.

All participants completed eight practice trials, two of each condition, to get used to the different types of sequences. In the practice trials, each digit was presented for each participant's individual starting duration obtained from the pre-test (pre-test threshold + 50ms). In the experimental trials, four adaptive staircases were interleaved, one for each condition, to obtain the serial memory duration threshold per condition (see Figure 2.3. for a sample data set). All participants completed 20 trials per staircase. A fixed number of trials was used to ensure that participants had the same exposure to the sequences of all conditions. The order of trials was randomly intermingled so that participants could not predict whether a structured or a non-structured trial was next. The first two trials of each staircase started with the individual

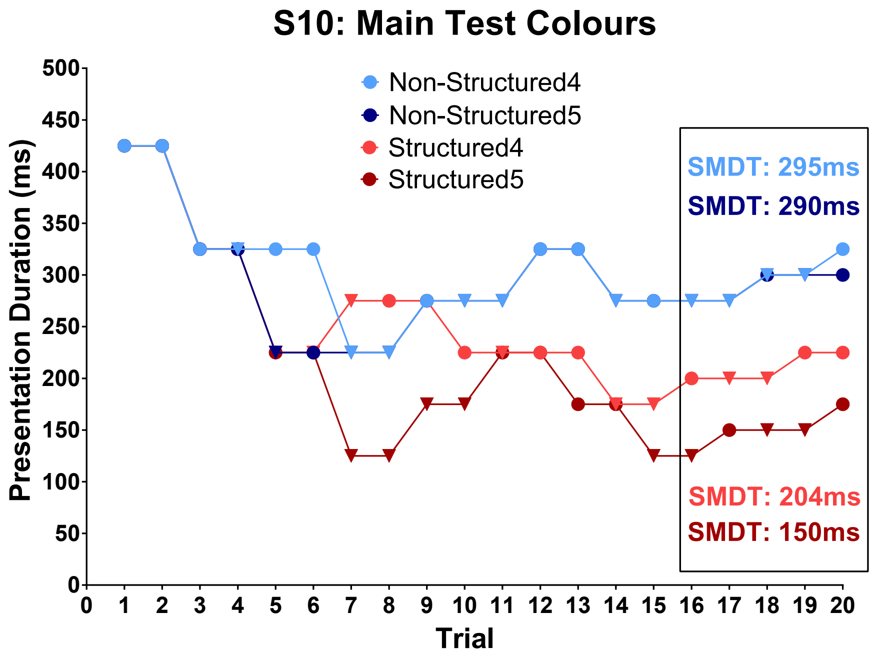

FIGURE 2.3. This is the data of one colour block of S10 as an example. There were four interleaved 2-up-2-down staircases, one for each sequence condition. The trial numbers within each staircase are shown on the x-axis. Dots symbolise accurate recall whereas triangles symbolise incorrect recall of the sequence. The starting duration for each participant was determined based on the pre-test performance. Step sizes were decreased after the 1st, 3rd and 5th reversal. The Serial Memory Duration Thresholds (SMDTs) were calculated by averaging the presentation durations of the last five trials in each staircase. The black rectangle frames the trials that were used to calculate the SMDTs.

starting duration of the pre-test. Then I used 2-up-2-down staircases to change the presentation duration depending on performance separately for each condition (i.e., 4 interleaved staircases). Small step sizes were used to approach fine differences with greater detail. The initial step size was set to 100ms which was reduced to 50, 25, and 8.333ms after the first, third, and fifth reversal, respectively. Again, I averaged the presentation durations of the last five trials of each staircase to obtain the Serial Memory Duration Thresholds (SMDT) of each condition. These SMDTs indicate how fast the digits could be presented in order for each participant to recall the sequences in the correct order with 100% accuracy in half of the trials. The 2-up-2-down staircase converges at 50% binary accuracy, meaning that of two sequences one would have been recalled with correctly (100%) and the other incorrectly (any accuracy below 100%). Each participant completed two blocks of experimental trials to counteract effects of practice and fatigue.

It is possible that participants may realise that the presentation duration is varied for each sequence type separately. If that was the case, they could guess according to their prediction and the structured trials would get faster than the non-structured trials. Such a bias would match our hypothesis that the SMDTs for fully structured sequences would be faster than for non-structured sequences. To avoid this, 20 catch trials per block were added. Catch trials were trials of each condition presented at the current staircase duration of another condition. For instance, a Structured5 catch trial would be a fully sequential trial shown at the current staircase duration of Non-Structured5. Half of the catch trials were structured trials, randomly selected from the Structured4 and Structured5 lists and shown at the duration of the Non-Structured4 and Non-Structured5 conditions, respectively. The other half were non-structured trials, randomly selected from the Non-Structured4 and Non-Structured5 lists, presented at the duration of the Structured4 and Structured5 condition, respectively. The catch trials were inserted at random positions after the 10th trial of each block. These trials were not part of any staircase, and therefore did not influence the presentation durations of a specific condition. However, they minimised the risk that participants predicted the condition even if they realised that some trials were faster than others.

Colour Task

Stimuli. In the colour task, five coloured squares (5cm x 5cm) were displayed in the centre of the screen. Viewing distance was approximately 75cm, making the squares 3.82 degrees of visual angle. The colours corresponded to each synaesthetes' colours associated with the digits 1-9.

Procedure and Design. The procedure and design of the colour block was almost identical to the number block, with a few exceptions. First, before the pre-test, I showed the participants the response screen with all possible colours so that they had an opportunity to label the colours and get used to slight differences between some of the colours (some synaesthetes had more difficult colour sets with multiple digits having similar colours, e.g., three different greens). Second, because pilot testing showed the colour task to be harder than the number task, I set the starting duration in the practice trials to 800ms instead of 500ms and participants completed 15 instead of five practice trials. Third, in the main test, there were again four conditions: Structured5, Structured4, Non-Structured5, and Non-Structured4. The sequences in these conditions were constructed in the same way as in the number block, but this time I presented the colours corresponding to these digits for each synaesthete and their matched control (see Figure 2.1.B for an example).

2.3 Results

The Serial Memory Duration Threshold (SMDT) was defined as the average presentation duration of the last five trials of each staircase condition. I calculated the SMDTs for each participant and condition separately. The staircases successfully converged at approximately 50% binary accuracy in all conditions and across groups (range: 42-61%). That means on average, participants recalled two to three sequences out of five with 100% accuracy when they reached the end of the staircase. Thus, the SMDT is an estimate of the duration at which a participant can recall approximately half of the sequences with 100% accuracy.

First, I compared the SMDTs of the two non-structured conditions (Non-Structured4 and Non-Structured5) to ensure that I could collapse across them to form a single baseline condition. The prediction was that there would be no difference between the two non-structured conditions. As inferential statistics do not allow interpretation of null effects, I calculated the Bayes Factor (Love et al., 2015) for repeated measures models including *Group* and *Pseudo-Structure* as factors, for each task separately. A Bayes Factor (BF) smaller than 1 indicates that there is more evidence for the null hypothesis than for the alternative (a BF $\approx$ 1 shows that there is insufficient sensitivity to decide for null or alternative hypothesis) (Dienes, 2011). For all possible models, data from both tasks revealed a Bayes Factor smaller than 1 (model including *Group*, *Structure*, and *Group x Structure* interaction for the number task: BF_{10}= 0.112, identical model for colour task: BF_{10}= 0.097). This indicates that there was no difference in SMDT for the Non-Structured4 and Non-Structured5 condition in the number and the colour task. Therefore, I collapsed across the SMDTs obtained from the Non-Structured4 and Non-Structured5 condition in the number task to form the baseline condition for the number task and from the Non-Structured4 and Non-Structured5 condition in the colour task to form the baseline condition for the colour task.

To assess the main hypotheses, I conducted a repeated-measures ANOVA with *Task* (numbers and colours) and *Structure* (Baseline, Structured4, and Structured5) as within-subject factors and *Group* (synaesthetes and controls) as a between-subjects factor. There was no significant main effect of *Group* ($F(1,22) = 1.991$, p = n.s.) but significant main effects of *Task* ($F(1,22) = 77.438$, $p < 0.0001$,$\eta_p^2 = 0.779$ and *Structure* ($F(1.526, 44) = 27.183$, $p < 0.0001$, $\eta_p^2 = 0.553$; Greenhouse-Geisser corrected for violation of sphericity). There were no two-way interactions between *Task* and *Group* ($F(1,22) = 2.219$, p = n.s.) and *Task* and *Structure* ($F(1.472, 32.383) = 2.233$, p = n.s.), but there was a significant interaction between *Structure* and *Group* ($F(1.526, 33{,}579) = 7.701$, $p = 0.004$, $\eta_p^2 = 0.259$). Most importantly, there was a significant three-way interaction between *Structure*, *Task*, and *Group* ($F(1.472, 32.383) = 8.666$, $p = 0.002$, $\eta_p^2 = 0.283$), which shows that the influence of structure on the two groups differed, but this influence differed between the tasks.

Post-hoc analyses were conducted to identify the source of the interaction, structured to answer my three research questions. First, I tested for differences between the groups by breaking the interaction down by *Task* and comparing the groups at each level of structure. For the number task, synaesthetes did not differ from controls (Figure 2.4.A) at any level (Baseline, Structured4, or Structured5; all ps > 0.583). For the colour task (Figure 2.4.B), synaesthetes and controls did not differ in the Baseline or Structured4 condition, but synaesthetes performed significantly better than controls in the Structured5 condition ($p = 0.014$). These results show that both groups benefit from structure when recalling numbers and that synaesthetes, when colour sequences have an implicit structure in the associated digits, have superior recall for colour sequences relative to controls.

To identify whether performance is significantly better in structured than in less structured trials, I then broke the interaction down by *Group*. For synaesthetes, in the number task there was a significantly shorter SMDT for the Structured5 than baseline, Structured5 than Structured4, and Structured4 than baseline condition (all ps < 0.0001). For controls, the same pattern was observed in the number task: the SMDT for the Structured5 condition was significantly faster compared to the Structured4 and the baseline condition and the SMDT for the Structured4 condition was significantly shorter than for the baseline condition (all ps < 0.0001). For the colour task, synaesthetes differed from controls. Controls showed no difference in SMDT between the Structured5 and baseline, Structured5 and Structured4, and the Structured4 and Baseline conditions (all ps > 0.39). However, synaesthetes showed a significantly shorter SMDT for the Structured5 than baseline ($p < 0.0001$) or Structured4 ($p = 0.006$) condition. Furthermore, they had a significant difference between the Structured4 and baseline condition ($p = 0.008$). These results suggest that both groups benefited from structure in the number condition but only synaesthetes were able to use the structure in the colour condition to boost their recall.

Finally, to test whether there was a difference between the colour and the digit task, I broke the interaction down by *Structure*. The results showed that there was a significant difference between the number and the colour task for both groups (Figure 2.4.). In the baseline condition, Structured4, and Structured5 condition controls had longer SMDTs in the colour task in comparison to the number task (all ps < 0.0001). Similarly, in the baseline, Structured4 and Structured5 condition, synaesthetes had longer SMDTs in the colour task than in the number ($p < 0.0001$, $p < 0.0001$, and $p = 0.001$, respectively). This suggests that both groups required more time to encode colour in comparison to number sequences across all structure conditions.

Together, these results show that both groups clearly benefit from structure in the number task. In the colour task, synaesthetes have an advantage over controls when recalling fully structured sequences. Furthermore, their performance in recalling fully or partially structured sequences is enhanced relative to baseline performance. In the baseline condition, in which the sequences were in pseudo-random order, synaesthetes did not perform better than controls. This suggests that synaesthetes' colour memory is not overall enhanced but that there is a specific benefit for them when the implicit digit information within the colours is in sequential order.

One possibility is that when the presentation rate gets fast, participants are guessing in order which would drive the staircase of the fully structured (Structured5) sequences to have a shorter SMDT in the end. If we look at the partially structured (Structured4) sequences we can determine how many times participants falsely completed a Structured4 sequence in fully sequential order (e.g., if the sequence was "4-5-6-7-2" and the participant reports "4-5-6-7-8"). I calculated the

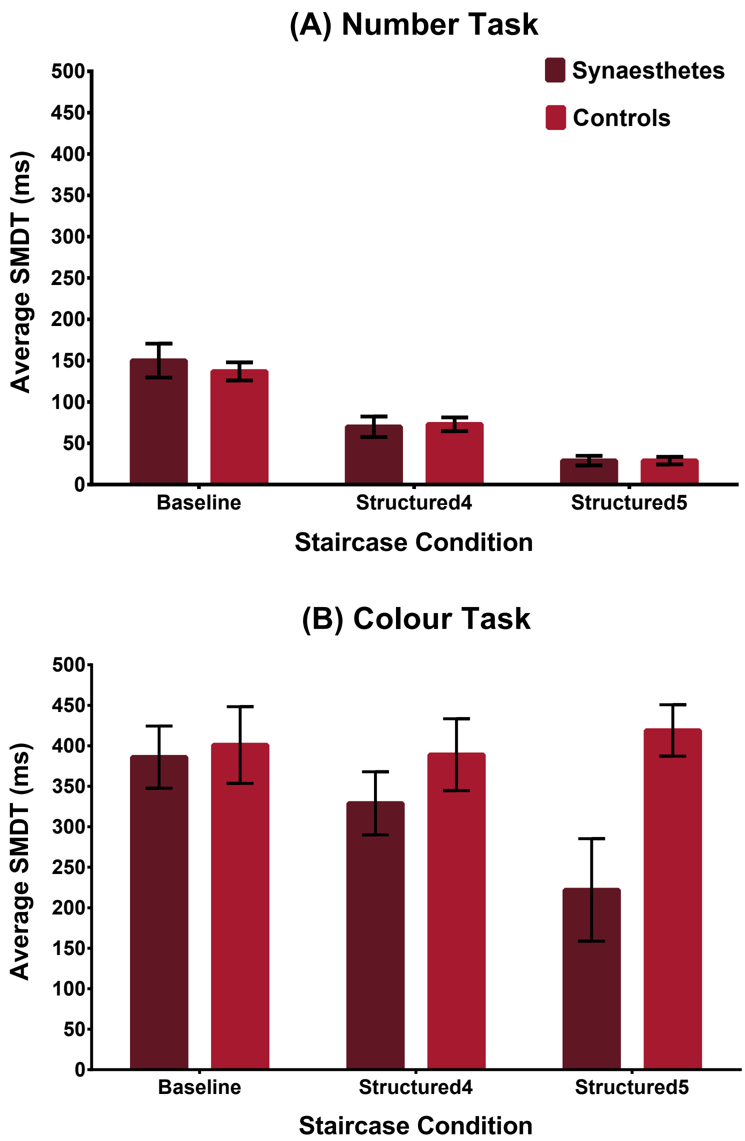

FIGURE 2.4. Serial Memory Duration Thresholds (SMDTs) in milliseconds for both groups. The SMDTs are the averaged presentation durations of the last five trials for each staircase. They represent the level at which ≈ 50% of the sequences were recalled with 100% accuracy. 5A shows the results of digit task and 5B of the colour task. The baseline condition corresponds to the mean performance of the two non-structured conditions. Error bars reflect standard error of the mean.

percentage of this type of false alarm out of all Structured4 trials, to examine whether our effect is driven by this type of guessing strategy. In the number task, synaesthetes reported 2.08% (SD = 0.21%) and controls 4.37% (SD = 0.32%) of Structured4 trials in completely ascending or descending order, falsely completing the partially structured sequence to be completely structured. In the colour task, synaesthetes had 3.3% (SD = 0.3%) and controls 0.21% (SD < 0.001%) of false alarms. This false alarm analysis demonstrates that on average, a maximum of 1.75 out of 40 Structured4 sequences were reported erroneously in ascending or descending order. Thus, the benefit in the Structured5 condition is unlikely to be driven purely by a guessing strategy. In the colour task, only synaesthetes erroneously report occasional colour sequences in ascending or descending order, which is not surprising as controls do not have the colour-digit associations. However, in the colour task synaesthetes report on average less than one sequence falsely in ascending or descending order which makes it unlikely that the effect is based on cued guessing. Importantly, the catch trials in our design also discouraged such a strategy.

2.4 Discussion

In this experiment, I examined whether the degree of numerical structure within a sequence enhances immediate serial recall (ISR) of digits and colours. I used a staircase approach to vary the level of difficulty by changing the presentation duration of each item. The dependent variable Serial Memory Duration Threshold (SMDT) represents the average duration of the end of a staircase. At the SMDT level, participants usually recalled sequences correctly and incorrectly in alternating fashion, as the staircase converged at 50% binary accuracy.

The data suggest that all participants benefitted from ascending and descending order in the number task: they had shorter SMDTs in the structured condition relative to the baseline. This shows that sequences stored in long-term memory can be encoded at a faster rate than novel sequences. This is in line with previous studies showing that the degree of background knowledge and structure enhances serial memory (e.g., Bor et al., 2004; Bor et al., 2003; Gathercole, 1995). In the colour task, this benefit of structure was observed for synaesthetes only: When the synaesthetic colour corresponded to ascending or descending digit sequences, synaesthetes showed a shorter SMDT in comparison to controls and to their own performance in the baseline condition. Overall, synaesthetes did not perform better than controls in the number condition and only outperformed them in the fully sequential (Structured5) colour condition. This suggests that there is no general advantage for synaesthetes in ISR of colours or digits but that they can use their unusual associations between colours and digits to boost memory performance for colours when the secondary digit information is more memorable. Additionally, the results show that recalling colours is more time-consuming than recalling digits: The SMDTs in the colour task were longer than in the number task across conditions and groups. In the following paragraphs, I discuss these results and relate them to previous findings.

For the number task, there was no difference between synaesthetes and controls in recalling digits in order. This is consistent with previous studies showing that synaesthetes have no advantage when recalling digit sequences in the standardised digit span task (Gross et al., 2011; Rothen

& Meier, 2010; Teichmann et al., 2015; Yaro & Ward, 2007). Both groups performed significantly better when the digit sequences contained four or five items in ascending or descending order in comparison to non-structured sequences. This is in line with findings of Bor et al. (2004) and Bor et al. (2003) who showed that memory is enhanced for sequences containing structure. In their first experiment, Bor et al. (2003) demonstrated that memory for spatial line sequences is enhanced when the lines form a well-known geometrical shape. Similar findings were obtained from their second study in which participants recalled digit sequences containing mathematical structure more accurately than non-structured sequences (Bor et al., 2004). According to Bor et al. (2004) recall for structured sequences is enhanced because multiple items can be grouped into a single item that is stored in memory. This grouping or chunking mechanism leads to a lower memory load, which they argue is reflected in a higher prefrontal cortex activation in structured trials in comparison to non-structured trials (Bor et al., 2004; Bor et al., 2003). Here, I examined accuracy indirectly by using a staircase procedure varying presentation durations depending on accuracy in two previous trials. The current results further show that structured digit sequences can be presented at a faster rate (SMDT 80ms per item including ISI) than non-structured sequences (SMDT 190ms per item) for the same level of recall accuracy. This is consistent with findings of Potter et al. (2008) who showed that recall of meaningful sentences in an RSVP task is superior in comparison to non-meaningful sentences when words are presented at a rate of 10 words per second. Thus, there is clear evidence that structured digit sequences can be recalled with high accuracy at a faster presentation rate than non-structured sequences, which suggests that structure results in a lower memory load.

The results of the colour task support the data of our previous study (Teichmann et al., 2015) in which an exploratory analysis pointed towards a benefit for synaesthetes when recalling fully structured (Structured5) and partially structured (Structured4) colour sequences in comparison to non-structured (Baseline) sequences. Our previous study did not have sufficient power or sensitivity to detect differences between synaesthetes and controls. Here, I show that synaesthetes can use the implicit structure information in the colour sequences to boost memory and benefit from more meaningful colour sequences. The current data clearly demonstrate an advantage for synaesthetes in comparison to controls when recalling fully structured colour sequences. This advantage for synaesthetes could not be observed in the Baseline or Structured4 condition, suggesting that synaesthetes do not have an overall enhanced memory for colours but can use synaesthetic associations strategically to facilitate memory. In a previous study, Yaro and Ward (2007) showed that synaesthetes had a benefit over controls when recalling spatial positions of colours. Similarly, Rothen and Meier (2010) found a benefit for synaesthetes in the visual paired associate learning task in which parings between abstract line drawings and colours have to be remembered. In contrast to these two studies, we did not find an advantage for synaesthetes when recalling non-structured colour sequences either in our previous study (Teichmann et al., 2015) or in the current study. This suggests that at least in the context of immediate serial recall, synaesthetes have no benefit when recalling material that is elicited by synaesthesia (e.g., colour), unless the secondary information (e.g., digit) is more memorable.

Previous studies suggest that magnitude information is activated implicitly when synaesthetes are presented with colours (e.g., Brugger et al., 2004; Cohen Kadosh et al., 2005; Knoch et al., 2005). For example, Cohen Kadosh et al. (2005) showed that synaesthetes are influenced by colours when making a speeded judgement about which one of two digits is numerically larger. The current data show that encoding colours is much more time-consuming than encoding digits for synaesthetes and controls across all conditions. Comparing synaesthetes' SMDTs of the fully sequential conditions in the number and colour task shows that numbers could be presented three times faster than colours. This suggests that digits are not evoked immediately (or perhaps automatically) by the presentation of synaesthetic colours, at least not to the level necessary to recognise sequential structure. The benefit for synaesthetes in the fully sequential condition suggests that synaesthetes are able to strategically activate a digit representation from a colour to boost serial colour memory – and this activation is relatively slow. This is in line with results of McCarthy et al. (2013) who showed that synaesthetes can translate colours to digits and perform an arithmetic verification task with colour patches but that the translation process takes $\approx 250ms$ per item. Similarly, here the process of recognising and benefiting of structure information implicit to the colour sequences is slow, suggesting that whatever immediate implicit activation exists is not sufficient to derive structure.

In conclusion, the results of the current study suggest that sequences containing well-known mathematical structure can be encoded at a faster rate than novel sequences. This highlights the importance of background knowledge in ISR: The current results clearly show that there is an interaction between long-term associations and short-term, serial memory. Furthermore, synaesthetes are able to translate synaesthetic colours to digits in order to boost memory, but this does not come close to the speed with which we can all use structured information of digits. Synaesthetes did not show an overall superiority of memory in the number or the colour task, but rather had a specific advantage in recalling colour sequences that contained a meaningful structure when translated back to digits. I will return to these results in Chapter 4 to discuss them in terms of theories explaining synaesthetes 'memory benefit.

Chapter 3

The Generalisability of the Effect of Structure

In the first experiment, I found a significant advantage for both synaesthetes and non-synaestehtes in recalling sequences that occur in a mathematical order. This could be due to an implicit activation of magnitude upon presentation of colour which has been show to influence speeded judgments (e.g., Brugger et al., 2004; Cohen Kadosh et al., 2005). Data by Brugger et al. (2004) show that synaesthetes are faster to respond to colour patches that correspond to relatively small digits with their left hand than with their right hand and *vice versa*. This is the same pattern as usually observed in non-synaesthetes when presented with digits, which has been interpreted as an automatic activation of magnitude on a mental continuum (Dehaene & Changeux, 1993). Hence, Brugger et al. (2004) concluded that for synaesthetes the magnitude information implicit in colours is activated upon perception of a colour. Here, the structure effect observed in Experiment 1 for both groups could be unique to numbers, perhaps reflecting some aspect of magnitude. Alternatively, the effect could reflect a benefit of an overlearnt sequence, regardless of the numeric content. This interpretation would be more consistent with Potter et al. (2008) who showed that meaningful sentences can be recalled more accurately than words that do not form a meaningful sentence. In this chapter, I will present data obtained from a non-synaesthete sample investigating whether there is an effect of structure on ISR of letter sequences. This allows a distinction between number-specific interpretations and more general structure effect in immediate serial recall.

3.1 Introduction

In Experiment 1, I examined the link between long term associations and immediate serial recall (ISR). The results clearly support previous findings showing that background knowledge influences short-term memory performance (e.g., Bor et al., 2004; Bor et al., 2003; Gathercole, 1995; Gathercole et al., 1999; Potter et al., 2008). Specifically, I showed that overlearnt mathematical order can boost ISR of digit sequences and that digit-colour synaesthetes can translate colours to digits to enhance memory for specific colour sequences. In this experiment, I will examine whether the effect of structure on ISR observed in Experiment 1 is unique to magnitudes or whether it is generalisable to letters.

In the field of numerical cognition, order information plays a key role. For example, magnitudes are thought to be represented in ordinal fashion on the "mental number line" (Moyer & Landauer, 1967), which describes an internal continuum with small magnitudes on the left and large magnitudes on the right hand side. A widely accepted model of numerical cognition, the Triple Code Model (Dehaene, 1992; Dehaene & Cohen, 1997; Dehaene, Piazza, Pinel, & Cohen, 2003), acknowledges the importance of the mental number line in numerical processing (for a review see Hubbard, Piazza, Pinel, & Dehaene, 2005). The mental number line has been repeatedly shown to correspond with spatial locations. For example, the Spatial Numerical Association of Response Codes (SNARC) effect (Dehaene, Bossini, & Giraux, 1993) refers to the observation that participants respond faster to relatively small numbers with their left hand than with their right hand and *vice versa* for large numbers. This finding is typically interpreted as an automatic activation of magnitudes in ascending order from left to right (Dehaene et al., 1993). Multiple studies have examined whether ordered sequences other than magnitudes are represented in a similar way. However, the evidence for non-numerical stimuli evoking a similar spatial activation is mixed. In the following paragraphs I will briefly discuss some of these findings.

Gevers, Reynvoet, and Fias (2003) showed that a SNARC-like effect occurs for non-numerical stimuli that are inherently ordered. They conducted two separate experiments, one examining the order of months and the other one investigating the order of letters. In each experiment, participants were presented with a month or a letter and had either an order-relevant or an order-irrelevant task. In the first experiment, the order-relevant task was to indicate as fast and accurately as possible whether the month presented on the screen was in the first half or the second half of the year. In the order-irrelevant task, participants had to judge whether the month presented on the screen ended with the letter "R" or not. Consistent with the SNARC effect in the numerical domain, Gevers et al. (2003) found that participants respond faster to months earlier in the year with their left hand than with right hand and *vice versa*. This effect was observed in both the order-relevant and irrelevant condition, but it was more pronounced in the order-relevant condition. The authors noted that the choice of months as stimuli might be problematic as months are often expressed in terms of numbers. Thus, they used letter stimuli for their second experiment. Letters are unlikely to be coded by numbers as translating letters to numerical positions in the alphabet takes $\approx 2000ms$ per item (Jou & Aldridge, 1999). In the letter task, Gevers et al. (2003) presented participants with a letter and asked them to indicate whether the letter comes before or after the letter "O" in the alphabet (order-relevant task), or whether the letter was a consonant or vowel (order-irrelevant task). Similar to number and months stimuli, they found that letters are coded in a sequential way, with participants responding faster with their left hand to letters early in the alphabet than later in the alphabet and *vice versa*. Consistent with these findings, Gevers, Reynvoet, and Fias (2004) found a SNARC effect for days of the week in a follow-up study. Together, these findings suggest that non-numerical items that have an inherent order are represented in a sequential way, with items in the beginning of the sequence on the left and at the end of the sequence on the right.

Quite different results have been reported by others comparing whether a SNARC effect occurs for numerical and non-numerical stimuli types (e.g., Dehaene et al., 1993; Gevers et al., 2003, 2004; Price & Mentzoni, 2008). One reason for these inconsistencies might be that the SNARC effect is not a suitable method to answer this question (Badets, Boutin, & Heuer, 2015). Initially, Badets et al. (2015) found a SNARC effect for numbers and letters but showed that with increased practice, the SNARC effect in the number task decreased and was not observable after multiple blocks. The SNARC effect in the letter task remained. Although this suggests that there are differences between numbers and letters in the strength of their ordinal representation, it also raises the possibility that inconsistencies in previous studies might have to do with a different number of trials.

Results of studies using different paradigms suggest that numerical and non-numerical sequences are processed in a fundamentally different way. For example, Fulbright, Manson, Skudlarski, Lacadie, and Gore (2003) examined whether a distance effect occurs for letters of the alphabet. The distance effect (Moyer & Landauer, 1967) refers to the observation that when faced with two numbers, participants are faster at determining which is numerically larger when the two digits are more distant on the mental number line in comparison to when they are relatively close. Fulbright et al. (2003) presented participants with sets of three letters, digits, or objects, in separate conditions. In two tasks (order relevant and irrelevant tasks), participants were asked to indicate whether (1) the set was in ascending or descending alphabetical, numerical, or size (e.g., small – medium – large) order, for the letter, digit, and object condition, respectively or (2) the letter “A”, digit “1”, or a triangle, was among the stimuli. The stimuli used in each set were divided in “far” and “close” stimuli depending on the distance between items (in terms of numerical order, alphabetical order, or area ratios for number, letter, and shape condition, respectively). They found a distance effect for numbers and shapes but not for letters. The authors interpreted this as indication for an existing mental continuum for numbers and shapes but not for letters. Although this is a potential explanation, it is important to note that participants performed less accurately in the letter task which suggests that the letter task was more difficult overall. This could partially have to do with the fact that Fulbright et al. (2003) used sets in ascending *and* descending order which might be more difficult for letters as backwards alphabetical order might not be as familiar. Examining only forward recall for the alphabet task would have been an option to facilitate the task and make the conclusion more powerful. Moreover, the authors point out that the sequences might not have been long enough to evoke the mental representation of order. However, taken together these results suggest that sequences of numerical and non-numerical stimuli are not represented in the same way.

The goal of the current experiment is to examine whether meaningful sequences can boost immediate serial recall (ISR) of non-numerical stimuli or whether the structure effect observed in Experiment 1 is unique to stimuli that have magnitude. I use letter sequences and investigate the effect of alphabetical structure on recall accuracy using the staircase method varying presentation duration.

3.2 Method

Participants and Apparatus. Twelve healthy young adults (7 female, 5 male, mean age = 27.42 years, SD = 4.68 years) participated in the experiment. All participants reported normal or corrected-to-normal visual acuity and gave informed consent prior to the experiment. Participants were reimbursed with $15/hour. The apparatus was the same as in Experiment 1.

Stimuli. Stimuli were black capital letters in 95pt Calibri font. Viewing distance was approximately 75cm, making the digits ≈ 2.56 degrees visual angle. Stimuli were shown on a grey background (RGB: 128, 128, 128). All 26 letters from A to Z were used. The 'Text Renderer' Matlab function was used to draw the stimuli as pixels on the screen to ensure high performance and accurate timing.

Procedure and Design. The main difference in comparison to the Number Task of Experiment 1 was that participants were asked to memorise a sequence of letters. The procedure was identical to the Number Task of Experiment 1 with the only exception that there were no options on the response screen to select but instead participants were asked to use the keyboard to type the sequence in the correct order (see Figure 3.1. for an example trial).

The design of the sequences was the same as in the Number Task of Experiment 1 with the following exceptions. Based on the differences in task difficulties between numbers and letters observed in the study by Fulbright et al. (2003), only forward alphabetical structure was used. Sequences in the Structured5 condition contained five letters in *forward* alphabetical order only (e.g., G-H-I-J-K). In the Structured4 condition, four out of five items were in *forward* alphabetical order. The structured part in the Structured4 condition was either in the beginning (e.g., G-H-I-J-U) or in the end (e.g., U-G-H-I-J) of the sequence. The non-structured (Non-Structured4 and Non-Structured5) conditions contained sequences that were based on a randomised letter order, containing a varying degree of *forward* pseudo-structure (for all possible sequences see Table 3.1.). Due to more items in the alphabet in comparison to single digits, more unique sequences could be built. There were 22 possible forward sequences in total so each staircase in the main test contained 22 trials, without any of the sequences repeating. The Serial Memory Duration Thresholds (SMDTs) were calculated from the last six trials of each staircase as there were

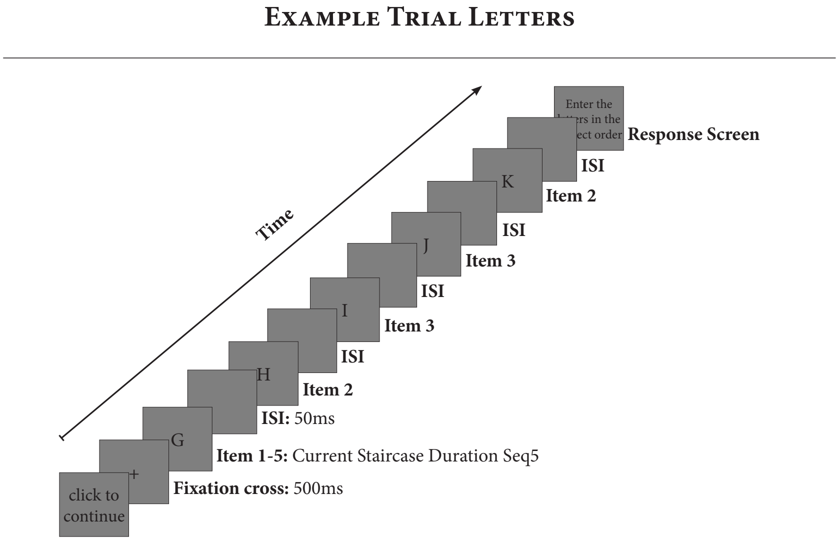

FIGURE 3.1. Example Structured5 letter trial. Five stimuli were shown consecutively in the centre of the screen. The task was to recall the items in the correct order. The presentation duration for each item varied on a trial-to-trial basis, depending on the current staircase duration. The ISI was 50ms. Sequence conditions (i.e., Structured5, Structured4, Non-Structured5, and Non-Structured4) were intermingled within a block.

more trials per staircase. 24 catch trials were added to prevent participants realising that the durations are dependent on sequence type. As in Experiment 1, catch trials were trials of each condition presented at the current staircase duration of another condition.

3.3 Results

To calculate the Serial Memory Duration Thresholds (SMDTs) for each participant and condition, the average presentation of the last six trials of each staircase condition were calculated. The staircases converged at approximately 50% (range: 45-50%) binary accuracy in all conditions. Thus, as in Experiment 1, the SMDTs represent the durations at which a participant can recall approximately half of the sequences with 100% accuracy.

I compared the SMDTs of the two non-structured conditions (Non-Structured4 and Non-Structured5) to ensure that I could collapse across them to form a single baseline condition. For the model including *Structure* as a factor, the analysis revealed a Bayes Factor smaller than 1 BF_{10}= 0.429), which indicates that there was no difference in SMDT for the Non-Structured4 and

Table 3.1: Letter sequences used in all four conditions. Lines indicate (pseudo-) structured elements. Structured sequences were based on forward alphabetical order. Non-structured sequences were based on a pseudo-randomised letter order.

Structured Conditions		**Non-Structured Conditions**	
Sequences based on: ABCDEFGHIJKLMNOPQRSTUVWXYZ		Sequences based on: VISWANXQDUFRTMZOKCYHJEBLGP	
Structured5	**Structured4**	**Non-Structured5**	**Non-Structured4**
A B C D E	A B C D H	V I S W A	V I S W Q
B C D E F	B C D E L	I S W A N	I S W A R
C D E F G	O D E F G	S W A N X	Z W A N X
D E F G H	Q E F G H	W A N X Q	K A N X Q
E F G H I	S F G H I	A N X Q D	Y N X Q D
F G H I J	F G H I C	N X Q D U	N X Q D S
G H I J K	G H I J R	X Q D U F	X Q D U C
H I J K L	H I J K P	Q D U F R	Q D U F O
I J K L M	I J K L V	D U F R T	D U F R E
J K L M N	J K L M T	U F R T M	U F R T H
K L M N O	U L M N O	F R T M Z	J R T M Z
L M N O P	B M N O P	R T M Z O	I T M Z O
M N O P Q	M N O P G	T M Z O K	T M Z O X
N O P Q R	F O P Q R	M Z O K C	N Z O K C
O P Q R S	O P Q R J	Z O K C Y	Z O K C U
P Q R S T	K Q R S T	O K C Y H	F K C Y H
Q R S T U	Q R S T N	K C Y H J	K C Y H M
R S T U V	R S T U A	C Y H J E	C Y H J V
S T U V W	M T U V W	Y H J E B	T H J E B
T U V W X	E U V W X	H J E B L	A J E B L
U V W X Y	I V W X Y	J E B L G	D E B L G
V W X Y Z	V W X Y D	E B L G P	E B L G W

Non-Structured5 condition in the letter task. Therefore, I collapsed across the SMDTs obtained from the non-structured conditions to form a baseline condition.

To test whether structure had an effect on SMDT, I conducted a repeated-measures ANOVA with *Structure* (Baseline, Structured4, and Structured5) as within-subject factor. There was a significant main effect of Structure ($F(2,22) = 74.27$, $p < 0.001$) showing that performance was

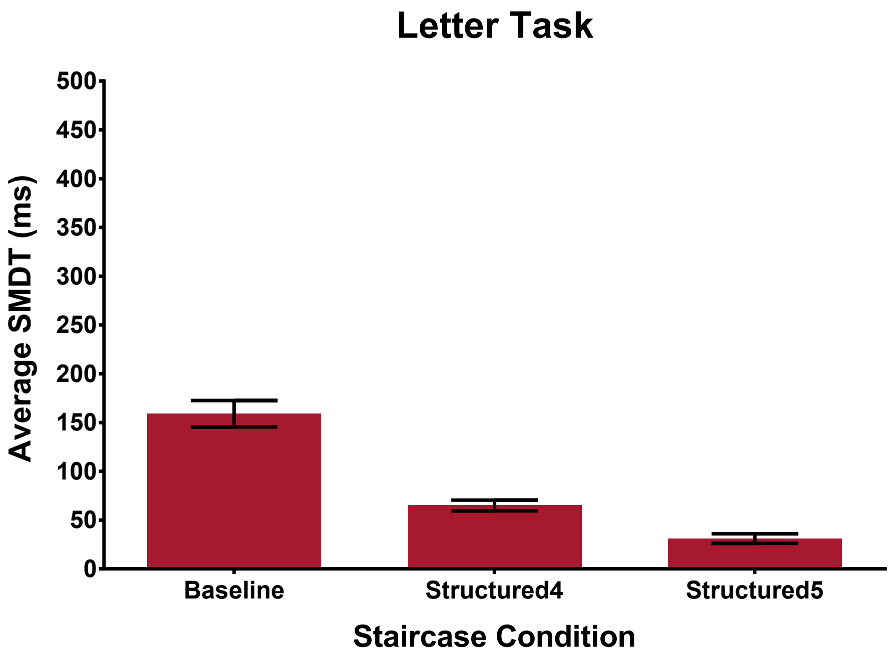

FIGURE 3.2. Serial Memory Duration Thresholds (SMDTs) in milliseconds for the letter task. The SMDTs are the averaged presentation durations of the last six trials for each staircase. They represent the level at which ≈ 50% of the sequences were recalled with 100% accuracy. The baseline condition corresponds to the mean performance of the two non-structured conditions. Error bars reflect standard error of the mean.

influenced by sequence structure (Figure 3.2.). Post-hoc analyses demonstrated that SMDTs were shorter in the Structured5 compared to the Baseline and Structured4 condition and in the Structured4 compared to the Baseline condition (all $ps < 0.001$).

To assess whether the structure benefit in the letter task could be due to sequential guessing, I calculated the percentage of false alarms for the Structured4 condition. Participants completed 4.9% (SD = 0.21%) of all Structured4 trials falsely in forward alphabetical order. That means approximately two sequences out of all 44 Structured4 trials was reported falsely in forward alphabetical order. This low rate of false alarms makes it unlikely that the structure benefit in the letter task is due to guessing in sequence.

3.4 Discussion

The goal of the current experiment was to investigate whether the structure effect observed in Experiment 1 is unique to numbers or whether it can be generalised to non-numerical sequences. The results show that the structure effect occurs for letter stimuli. This suggests that numerical and non-numerical overlearnt sequences boost short-term memory. Although no direct comparison between the two experiments has been conducted due to slight methodological differences (i.e., different number of trials per staircase, only forward alphabetical in comparison to ascending and descending number structure), the time course of encoding letter and digit stimuli across conditions is very similar. These results are in line with previous studies showing that meaningful sentences can be recalled when presented at a fast rate (Potter et al., 2008). Similarly, the current results support the notion that background knowledge does influence ISR (e.g., Botvinick & Bylsma, 2005; Gathercole, 1995).

Previous studies have examined whether numerical and non-numerical sequences are represented in a similar way (Badets et al., 2015; Dehaene et al., 1993; Fulbright et al., 2003; Gevers et al., 2003, 2004; Price & Mentzoni, 2008; Zorzi, Priftis, Meneghello, Marenzi, & Umiltà, 2006). As discussed in the introduction, the SNARC effect has been interpreted as an automatic activation of magnitudes which are represented on a mental continuum in sequential, ascending order with a left-to-right orientation. The results for non-numerical sequences of stimuli are mixed with some showing a similar effect for months, letters, and days of the week (Gevers et al., 2003, 2004) and others not finding any such effect (Dehaene & Changeux, 1993; Fulbright et al., 2003). Here, I showed that the inherent sequential order in both letters and digit sequences can be used to boost memory. These data do not speak to the left-right spatial organisation of sequential information, but they do demonstrate that encoding of highly structured sequences is enhanced for both numerical and non-numerical stimuli, suggesting that the structure effect is not unique to magnitudes.

In the current experiment, I tested non-synaesthetes to examine whether the structure effect observed in Experiment 1 is specific to stimuli with magnitudes or whether a similar effect can be observed in non-numerical overlearnt sequences. In the following general discussion, I draw together the results of my two experiments and interpret them in the context of the broader literature on serial memory and synaesthesia.

CHAPTER 4

General Discussion: Long Term Associations and Serial Recall

The aims of this thesis were (1) to examine the link between long-term memory and immediate serial recall (ISR) by comparing recall performance of ordered and non-ordered digit and letter sequences and (2) to investigate whether digit-colour synaesthetes can translate synaesthetic colours to digits in order to boost their serial memory for colours. The results show that well-known, structured sequences of digits (ascending or descending in order) can be encoded at a faster rate than novel, non-structured (pseudo-randomised) sequences. There was no difference between synaesthetes and controls when recalling digit sequences. This effect of structure was not unique to digits and was also found in non-synaesthetes when they were asked to recall alphabetically ordered letter sequences. This suggests that overlearnt order of sequential information leads to this benefit and not necessarily magnitude information, which is inherently ordinal. Digit-colour synaesthetes can also use the implicit digit information in colour patches to enhance their serial memory for structured colour sequences (ascending or descending in order when translated back to digits). In the fully structured condition, they had a clear memory benefit for colour sequences in comparison to controls despite a similar overall performance in the non-structured colour conditions. However, colours had to be presented at a much slower rate than digits suggesting that any implicit activation of magnitude suggested by other research on bidirectionality in synaesthetes (e.g., Brugger et al., 2004; Cohen Kadosh et al., 2005) is not sufficient for the structure effect to occur. The process of consciously accessing digits upon presentation of colour is slow and strategic. Together, these results suggest that long-term memory influences ISR and that synaesthetes can translate colours to digits strategically to enhance their memory for colour sequences. In this chapter, I will discuss the current findings with regard to previous literature and contemporary theories.

4.1 The Effect of Sequence Structure on ISR in Non-Synaesthetes

Recalling sequences in the correct order is essential in many everyday life situations. Many stimuli such as numbers, letters, months, and days form ordered categories that are important when organising modern life. The field of immediate serial recall (ISR) examines how we remember sequences in the correct order. Many computational models have been developed in order to simulate ISR. Most of these models do not include a factor accounting for background knowledge and experience (see Henson, 1998; Hurlstone et al., 2014). Based on the current results, I argue that long-term associations represent an important part of ISR. The data obtained from the two experiments presented in this thesis show that digit and letter sequences stored in long-term memory can be encoded at a faster rate than novel sequences. The Serial Memory Duration Thresholds (SMDTs) of sequences that were fully structured were much shorter than pseudo-randomised sequences. This is consistent with a study by Potter et al. (2008) who showed that recall of meaningful sentences is enhanced in comparison to words that do not form a sentence when presented at a rate of 10 words per second. Moreover, a similar benefit for structured information has also been shown by Bor et al. (2003) for spatial sequences forming well-known shapes vs. meaningless shapes and by Bor et al. (2004) for mathematically structured (ascending, descending, odd, even) vs. non-structured digit sequences.

The current data show that for synaesthetes *and* non-synaesthetes encoding colours was slower than encoding digits. This is particularly evident for the non-structured sequences as neither group can use structure information in these sequences to boost memory. There are at least two possible explanations for the difference between digits and colours. First, it is possible that verbal encoding is necessary to perform the current task and that we are faster at naming digits than colours. Naming colours might be particularly slow for colour sets which contain multiple shades of one colour (e.g., light blue, dark blue) (Guest & Van Laar, 2000). If digits can be named faster than colours, the digit sequences could then be encoded at a faster rate in comparison to colour sequences. A second alternative explanation for the difference in encoding speed of digits and colours is that we might be used to remembering digit sequences but not to remembering colour sequences. In everyday life we are required to recall birthdays, telephone numbers, and licence plate numbers but rarely have to remember particular colour sequences. Due to more practice, we might have developed a strategy of encoding digits faster.

Usually, the differences in performance in ISR tasks are measured in terms of recall accuracy. Here, I presented data obtained with a method new to the field of serial recall, a staircase procedure varying presentation duration depending on performance. I used different staircases for the sequences with different degrees of structure, showing that the final presentation duration for fully structured sequences was shorter than for non-structured sequences. The only use of staircase procedures previously in ISR studies has been through varying sequence length to adjust task difficulty. Although this method is suitable to examine, for example, differences between multiple types of stimuli (e.g., Li et al., 2000), it is not a very sensitive measure to detect subtle differences. Similar to accuracy measures, this type of staircase can only add whole items to the sequence and can measure whether, for example, 6 or 7 items can be recalled accurately. However, in some cases it might be necessary to detect smaller differences. Here, I showed that detecting subtle differences is possible by using a staircase procedure on presentation duration. The presentation durations of items could change in steps as small as 8ms approaching the performance limits in a fine-grained manner. The SMDTs seem to be a robust measure across groups (synaesthetes and controls in the number task, Experiment 1) and tasks (number and letter task, Experiment 1 & 2). They represent the duration at which participants recall half the trials correctly (100% accuracy) and half the trials incorrectly (less than 100% accuracy).

The effect of structure I found occurred for both digit and letter sequences, suggesting that the benefit of background knowledge is not unique to numbers. In previous studies, some researchers have argued that magnitudes, but not letters, are represented in an ascending order on a mental continuum (e.g., Dehaene et al., 1993). Others have found that different types of sequences such as months, letters, and days of the week (Gevers et al., 2003, 2004) are represented in a similar fashion. Results of a functional magnetic resonance imaging (fMRI) study show that the sequential aspects of numerical and non-numerical sequences are represented in the intraparietal sulcus (hIPS) (Fias, Lammertyn, Caessens, & Orban, 2007). In this study, Fias et al. (2007) presented participants with two letters and asked them to compare the stimuli in terms of position in the alphabet. They measured the blood oxygenation level-dependent (BOLD) response when participants completed this task and examined whether similar brain activity could be observed in a similar task with number stimuli. The letter and the number task were each compared against a dimming task in which participants were asked to indicate which one of the two items was dimmed. This task involved the identical stimuli and required participants to give the same motor response. Moreover, they included a control task in which two squares had to be compared in terms of saturation. Fias et al. (2007) found that the letter and the number condition in the comparison task activated a very similar neural network. Many areas in this network were also activated by the saturation comparison task but the hIPS activation was specific to the sequential position comparison for both numbers and letters. This suggests that the hIPS, which has been shown to be active in numerical processing (Dehaene et al., 2003), is involved in processing order information of numerical *and* non-numerical sequences. As with all behavioural data, the results of the current study are not direct evidence for underlying brain processes. However, our data suggest that the benefit of structure in ISR tasks using number and letter stimuli is very similar. If the structure effect is related to the representation of sequences, it seems like the sequential nature of overlearnt sequences such as letters is represented in a similar way to numbers.

The current results clearly demonstrate that overlearnt sequences which are stored in long-term memory are encoded faster in an ISR task. However, in most ISR models, there is no component accounting for background knowledge of regularities. Henson (1998) pointed out that this is a major shortcoming of contemporary context-based ISR models. Activation based models that are based on chaining (i.e., linking each item in the sequence to the previous one) are more successful at simulating the effect of experience on ISR than context-based models. However, as outlined in Chapter 1, models based on chaining have mainly been abandoned due to other shortcomings. The model of Botvinick and Plaut (2006) is the only activation-based ISR model that is not based on associative chaining and that includes effects of background knowledge. Their recurrent neural network model for serial memory has five core features which I will describe briefly in the following paragraphs.

First, the model by Botvinick and Plaut (2006) is an artificial neural network model that is based on the connections between three different groups of processing units: the input group which represents the to-be-remembered sequence, the output group which represents the recalled sequence, and the hidden group which links the input and output group together. In contrast to context-based models, the input group is encoding position *and* identity information simultaneously. In addition, the list elements are represented independently which means processing of one element is not influenced by the presence of the other elements. There are, however, relations due to similarity: pairs of elements have a different correlation depending on at which position they are presented, how similar the items are, and how much distance is between them. The correlation for the highly similar (i.e., confusable) items presented at the same position is highest. Correlation decreases with less similarity of the items and a larger distance between the positions.

Second, the activation is repeated constantly which results in a continuous feedback flow. For example, feedback between the items in the hidden layer can vary at each point in time, influencing the next item in the sequence after recall. The hidden layer has two tasks: representing all items of the input group and making only one of those items visible to the output group.

Third, according to this model, domain-specific experience plays a role in the mechanism for serial recall. In the learning phase, the connection weights are attuned in response to potential consistencies in sequences. The authors point out that human participants do not need to practice the task directly, but rather that there are differences in weights because of previous experiences. In the model, the weights only change during the training and not during the test phase. The process of making only one item of the hidden units visible for the output group partially depends on the weights. If the activation vector correlates highly with the weights vector, it is more likely to be visible for the output group and thus more likely to be recalled.

Fourth, encoding is thought to be activation-based and not weight based. That means that encoding occurs because of patterns that depend on the constantly repeated activation. The weights remain constant in the test phase and hence they cannot be the driving force behind encoding.

Fifth, there is random noise introduced to the hidden layer and to the training phase. This is thought to be the main source of errors. The model works generally in a probabilistic way: When confronted with an unclear input, the model picks the sequence with the highest probability.

Multiple simulations (Botvinick & Plaut, 2006) show that this recurrent neural network model can account for the main empirical findings of serial recall. For example, the model is capable of simulating the effect of list length on accuracy, the shape of the serial position curve, effects of item repetition, and the item similarity effect. Importantly, this is the only model that does not rely on chaining but is nevertheless able to simulate the regularity of item pairs in the sequence. This is critical when modelling serial memory, as humans encounter regularities in sequences based on experience. The current data highlights the importance of background knowledge as a factor in ISR models by showing that sequences stored in long-term memory enhance encoding in ISR. The model by Botvinick and Plaut (2006) can account for this pattern of data: structured and non-structured sequences potentially have different weights based on previous experience and thus recall for structured sequences is enhanced. To explore this link further, I also tested digit-colour synaesthetes. Due to their highly consistent long-term associations between digits and colours, synaesthetes have background knowledge in the colour domain that is different from individual to individual. In the following section, I will discuss the synaesthete data in detail.

4.2 Synaesthesia: A Benefit for Immediate Serial Recall?

The aim of testing synaesthetes in the first experiment was to examine whether the benefit of structure observed in the digit task can be indirectly observed in colour sequences corresponding to digits. This is a unique opportunity to control for the degree of background knowledge, as each synaesthete has individual digit-colour pairings and for non-synaesthetes, digits do not evoke colours. At the same time, this study gave new insight into the ongoing debate about whether or not, or to what extent, synaesthetes' memories are enhanced in comparison to non-synaesthetes. Results of most group studies suggest that synaesthetes show specific memory benefits and not generally enhanced memory performance compared to non-synaesthetes (Gross et al., 2011; Radvansky et al., 2011; Rothen & Meier, 2009, 2010; Yaro & Ward, 2007). Some studies have shown that synaesthetes perform better when memorising material that evokes synaesthesia such as word lists (Gross et al., 2011; Radvansky et al., 2011; Yaro & Ward, 2007) but failed to find an advantage when recalling digit sequences, even though digits evoke colours as well (Gross et al., 2011; Rothen & Meier, 2009, 2010; Yaro & Ward, 2007). Other results show that synaesthetes perform better than non-synaesthetes when memorising colours (Rothen & Meier, 2010; Yaro & Ward, 2007). One possible explanation for such findings is that synaesthetes benefit from the additional information attached to items that have to be memorised.

The idea that additional information boosts memory was first suggested by Paivio (1969) in the context of mental imagery. In a number of studies, Paivio showed that verbal memory can be enhanced by mental imagery (for a review see Paivio, 1991). These results were incorporated into a theory known as the dual coding theory of memory. For grapheme-colour synaesthetes, even abstract material such as letters or digits evokes a mental representation of a colour. According to the dual coding theory, the additional colour information should thus enhance their memory for stimuli that evoke synaesthesia. The current results do not show evidence of an advantage for synaesthetes over controls in serial recall of digits. This could mean that the additional colour information did not enhance recall; alternatively, it could reflect the fact that both groups performed, at least in the fully structured digit condition, nearly at ceiling. Synaesthetes and controls had a SMDT of approximately 30ms in the fully structured digit condition. As the smallest step size was approximately 8ms, the potential ceiling effect is not due to a technical limitation. Rather it seems like approximately 30ms of unmasked presentation duration plus a 50ms blank interval might be the perceptual limit for both groups. Thus, a potential benefit associated with synaesthesia might not have been visible in the fully sequential condition due to both groups reaching their limit to perceive five consecutive digits. In the baseline condition, however, synaesthetes and controls showed similar performance that was not at ceiling level, which is evidence that there is no benefit of synaesthesia associated with recalling *non-structured* sequences. This is consistent with previous studies showing that synaesthetes do not perform better in the standardised digit span task in which random digit sequences of varying length have to be recalled (Gross et al., 2011; Radvansky et al., 2011; Rothen & Meier, 2009, 2010; Teichmann et al., 2015). Thus, based on the results from the digit task, the dual coding theory seems not to hold for the case of synaesthetes.

Synaesthetes had a benefit compared to controls when recalling colour sequences. This advantage was not observed across conditions but was specific to the fully structured sequences. In our previous study, we showed that synaesthetes performed significantly better in the fully structured colour condition when compared to their own baseline, but we found no evidence for a benefit of synaesthetes over controls, which might have been due to a lack of power. In the current study, I developed an improved, more sensitive method to measure accuracy indirectly in terms of encoding rate. The results clearly demonstrate that synaesthetes can activate digits in response to colours and encode colour sequences that are meaningful at a faster rate than controls. In the baseline condition, synaesthetes did not perform better than controls, which shows that serial memory for colours is not overall enhanced. A modified version of the dual coding account could explain these findings: if, for synaesthetes, the secondary information (i.e., digits in the colour task) of stimuli is more memorable or meaningful than the primary information (i.e., colours in the colour task), serial recall can be enhanced by strategically memorising sequences in terms of the secondary information. A future study could further investigate this question by presenting letter or digit sequences in which the secondary, *colour* information evoked by this sequence is more memorable than the graphemes themselves. For example, synaesthetes could be presented with digits that correspond to overlearnt colour sequences such as the colours of the rainbow. If secondary information boosts their memory, synaesthetes but not controls should show a benefit for digit sequences that are more meaningful in terms of colours than in terms of digits.

For synaesthetes, consciously accessing digit information upon presentation of colours seems to be a relatively slow process as the results show that across all conditions the encoding rate for colours was much slower than for digits. This is in line with findings by McCarthy et al. (2013) who showed that it takes synaesthetes approximately 250ms to translate a colour back to a digit. A potential reason for the relatively slow process of translating colours to digits might be that a particular colour could be associated with more than one stimulus. Although the digit "2" might consistently activate a perception of yellow, it does not mean that "2" is the only inducer for the colour yellow. Here, I only tested synaesthetes who had clearly distinguishable colour associations for the digits 1 to 9. However, the same colours might be induced by other stimuli such as letters or words. In the context of the experiment, it was clear that each colour in the sequence represents a number, however, the colour-to-stimuli mapping could still be a one-to-many relationship. This goes beyond synaesthesia to object colour knowledge more broadly. Yellow might not only be associated with "2" or "Tuesday" but in the context of fruit it might also be associated with "banana". This is fundamentally different to the experiences of the forward associations of synaesthesia in which abstract stimuli such as digits consistently evoke specific colour perceptions. Thus, the difference in encoding speed in the number and colour task for synaesthetes potentially reflects the effortful process of interpreting the colours in terms of numbers and translating them back. The process of translating colours to numbers could be comparable to encoding a word in another language: the attachment of meaning and translation of words in a foreign language involves higher-level brain areas and is similar to brain activation in non-automatised tasks such as the Stroop test (Dehaene, 1999). Attention and prior knowledge have to be employed to translate the colours back to the digits, which is time consuming.

Experiment 2 showed that for non-synaesthetes the structure effect is not unique to numbers. As synaesthetes and controls showed a similar performance in the digit task in Experiment 1 and synaesthetes only had an advanced memory for one specific condition in the colour task, we can assume that the benefit for recalling structured colour sequences does not necessarily depend on magnitude information. However, there is a possibility that for synaesthetes, backward translation for numerical and non-numerical stimuli differs. Previous studies have mainly looked at implicit activation of magnitude by colour because paradigms such as the modified size congruency paradigm used by Cohen Kadosh et al. (2005) rely on magnitude information. The current method would allow future studies to test whether other synaesthetic inducers such as letters can be consciously activated by colours to enhance memory.

In sum, the data show that synaesthetes and controls are able to benefit from structure in the digit task and can thus encode fully sequential digit sequences at a faster rate than non-structured sequences. Only synaesthetes show a similar benefit for the colour sequences, and perform significantly better in the fully structured colour sequences compared to controls and compared to their own baseline performance. However, colour stimuli across conditions had to be presented at a slower rate than digit stimuli, suggesting that colours had to be translated to digits to boost memory. This process seems to be relatively slow. Overall, synaesthetes are not better at recalling digit sequences and non-structured colour sequences in comparison to controls. This means only a modified version of the dual coding theory would be suitable here: Memory is only enhanced by secondary information if this information is more memorable.

4.3 Limitations

In comparison to the methodology of our previous study in which we used a traditional type ISR task (Teichmann et al., 2015), the method I used in the current study was more sensitive. In our previous study, we did not have enough power to detect differences between synaesthetes and controls but the current data obtained with the staircase method varying presentation duration detects more fine-grained differences. For the purpose of the current study the method was beneficial, however, this design has some consequences for the measures that can be derived.

Manipulating the presentation duration in a staircase procedure allowed my paradigm to have a much greater degree of sensitivity than previous ISR studies. However, this comes at the cost of being unable to analyse accuracy in the traditional manner. In the current design, only binary accuracies were relevant for presentation durations to change. The drawback of binary accuracies is that in incorrect trials, we do not take into account how many items in a sequence were reported correctly. A binary accuracy of 0 in a given trial could mean 0, 20, 40, or 80% of items were recalled accurately. This means that we are not able to analyse the data to examine accuracy depending on serial position, for example. Despite losing the possibility to measure accuracy in a traditional sense, this experimental design makes up for it with increased sensitivity.

In all studies that examine the effect of background knowledge, controlling for cued guessing is vital to see whether the effect is a true benefit or just occurs because of a bias in guessing. In the current design, I counteracted a guessing strategy based on expectancy in two ways. First, I added catch trials, which were trials of all conditions that were not part of any staircase but were shown at the presentation duration of another staircase (e.g., a Non-Structured5 trial would be presented at the current duration of the Structured5 staircase condition). These trials were included to prevent participants from guessing sequences in fully structured order just because the presentation duration was brief. Second, I included partially structured sequences to again reduce strategic guessing and also to allow analysis of how many sequences were guessed falsely in order, giving some indication as to whether the participants were guessing in fully sequential order when unsure. The problem with this analysis is that we only know for sure how many trials were falsely guessed in ascending and descending order at the duration of the *Structured4* trials. We use this false alarm rate to infer that there is unlikely to be a problem for Structured5 trials. Ideally, however, we would identify in how many trials at the Structured5 rate participants guessed sequences in ascending or descending order – as both the "guesses" and the correct responses give the same answer, this is obviously not possible. Analysing performance on catch trials would be a solution, but the presentation durations for the catch trials would have to be the same as the presentation durations of the Structured5 level, at least at the end of the staircase. However, pre-specifying durations of catch trials is not possible as each individual staircase runs through different durations. Thus, the only option would be to include as many catch trials as Structured5 trials that mirror the durations of the Structured5 staircase. In the current design we included 20% of such catch trials to ensure that participants had experiences of all conditions at the different durations, reducing the likelihood of guessing a sequence just because the duration was brief. However, these were inserted at random positions, meaning that analysing the catch trials we have is not meaningful. To get enough catch trials at each duration would require many more trials, increasing an already long testing session. Fatigue effects can lead to random responding, which would prevent a staircase design from being effective. Finding a balance between completely controlling for guessing and not wasting too much data is difficult. Here, I included a smaller amount of catch trials and analysed the false alarms in the Structured4 condition, which suggested my effect is not simply reflecting a guessing strategy.

Another area of potential limitation is the design of the non-structured sequences. I matched the conditions very carefully to prevent participants from seeing specific digit, colour, or letter combinations more often in one condition than another. As a consequence, the pseudo-randomised, "non-structured" conditions actually did have a structure - the structure in these trials was just not meaningful. Over time, participants might have learnt that some patterns occurred more often than others over the course of the experiment (e.g., red follows blue more often than red follows green). In previous ISR studies, this type of long-term learning of sequences over the course of an experiment has been observed (Hurlstone et al., 2014). The *Hebb repetition effect* describes enhanced recall of sequences that are repeated throughout the course of testing (Hebb, 1961). It is possible that this sort of long-term learning of the pseudo-structure occurred in the current experiment and boosted performance in the baseline condition. Importantly, however, the difference between structured and non-structured sequences was large enough in all three tasks to show that there is a benefit of meaningful structure over pseudo-random structure. The effect size might potentially have been larger if truly random sequences were used instead of pseudo-random sequences, but then we would have had the confound of differences in predictability between our key conditions. Thus, for the current research question, it was more important to allow clear interpretation of the condition differences rather than get an absolute measure of the threshold for recalling random sentences.

A related issue concerns the sequences within each condition. In psychophysics, staircases are used with stimuli that have the same level of difficulty. This is important when interpreting, for example, the threshold duration: If all stimuli have the same difficulty the threshold value obtained is valid for all stimuli presented. Here, I grouped ascending or descending sequences together and compared them to pseudo-randomised sequences. I assumed that the difficulty within each condition is the same but there is a possibility that difficulty varied within a condition. For example, it may be that ascending sequences are easier to encode than descending sequences. From the current data we cannot be certain that there were no differences between such sequences within a condition. Depending on which sequences were shown at the end of the staircase, it is possible that the serial memory duration threshold (SMDT) is not valid for all sequences within this condition. However, as we randomised the order of the sequences across participants, we can be confident that there is no consistent error in our SMDT measurement across participants.

Overall, the staircase method developed here was more sensitive than traditional ISR paradigms for detecting subtle differences between groups and conditions and is a robust measure of performance levels. Despite the inevitable trade-offs discussed above, this novel method has potential to be very useful for examining ISR. In the following section, I will suggest some avenues for future work based on the current results.

4.4 Future Directions

The results of the current study clearly show that overlearnt digit and letter sequences can be encoded at a faster rate than novel sequences. This highlights the importance of background knowledge in immediate serial recall (ISR) tasks. Furthermore, I showed that synaesthetes can activate digit order to boost their performance for structured colour sequences relative to controls. In the following paragraphs, I will discuss some possible future directions.

We saw that sequence structure boosts ISR. An open question is at which stage of processing the structure information helped participants: encoding or recall. In a previous study, Nieuwenstein and Potter (2006) showed that recall accuracy of items presented at a fast rate successively decreases with serial position. The authors interpret this drop in performance as an accumulating cost of encoding earlier items into working memory, which reduces the capacity for accurately encoding items in later serial positions. Here, a similar explanation is conceivable: It is possible that the benefit in the structured conditions is due to a reduced memory load that enhanced encoding speed. Alternatively, the structure information may only be beneficial at recall, after the whole sequence has been presented. From the current data it is not possible to disentangle whether structure benefits participants at encoding or recall. It would be interesting to address this question in future studies and to investigate whether there is a difference between the tasks in which the structure was explicit to the items (i.e., digits and letters) and the colour task in which only the secondary, associated digit information was ordered. Potentially, the difference in encoding rate between the digit and the colour task in synaesthetes could be explained by the processing stage at which structure was beneficial. Another possibility is that verbal encoding was necessary for the colour task but not for the digit or letter task. A future study could examine whether the structure effect in the colour condition for synaesthetes remains when they have to complete a secondary verbal interference task.

From the current behavioural data we cannot draw any conclusions about brain activations underlying the effect of structure on ISR. A lot of research has been conducted to address the question of how numerical and non-numerical order is represented in the brain. Some studies suggest that the horizontal intraparietal sulcus (hIPS) is vital for representing numerical and non-numerical ordered information (e.g., Fias et al., 2007). This is controversial as it has been claimed that the IPS is specialised for numerical processing (e.g., Dehaene, Dehaene-Lambertz, & Cohen, 1998). Using the current paradigm, we could test whether the hIPS is vital for the structure effect to occur in the number, letter, and colour task by combining the behavioural measure with transcranial magnetic stimulation (TMS). TMS is a non-invasive technique that briefly disrupts cognitive processes in the brain by inducing a “virtual lesion” to a specific area of the cortex (e.g., Siebner, Hartwigsen, Kassuba, & Rothwell, 2009). This way we can examine whether a particular area in the cortex is essential to perform a task. Here, a TMS study could give further insights into the importance of the hIPS for the structure effect we observed. In addition to investigating how order is represented in the brain, it would be interesting to examine which brain circuits are involved in synaesthetes translating colours to digits and how this would fit into contemporary models of synaesthesia.

4.5 Conclusion

In sum, the current findings clearly show that overlearnt structure information enhance immediate serial recall (ISR), and this is not dependent on magnitude information. This demonstrates that background knowledge is an essential factor when modelling ISR. With the sensitive staircase method varying presentation duration, I showed that synaesthetes do not have an overall enhanced memory for sequences but that they can use their synaesthesia strategically to translate colours to digits in order to boost sequential memory for colours. Future studies will have to examine at which level of processing the structure information benefits participants and which brain circuits are involved in the process of synaesthetes translating colours to digits to enhance serial memory.

Appendix A

Characteristics of the synaesthetes tested

Participant	Gender	Age	Handedness	Types of Synaesthesia
S01	Female	22	Right	Grapheme-Colour, Auditory-Visual, Sequence-Form
S02	Female	44	Right	Grapheme-Colour
S03	Female	19	Right	Grapheme-Colour
S04	Female	28	Right	Grapheme-Colour, Auditory-Visual
S05	Female	31	Right	Grapheme-Colour, Auditory-Visual
S06	Female	23	Right	Grapheme-Colour
S07	Female	22	Right	Grapheme-Colour
S08	Female	32	Right	Grapheme-Colour, Auditory-Visual
S09	Female	21	Right	Grapheme-Colour
S10	Female	29	Right	Grapheme-Colour, Auditory-Visual, Olfactory-Visual
S11	Female	40	Right	Grapheme-Colour
S12	Female	44	Right	Grapheme-Colour

APPENDIX B

Digit-colour associations for all synaesthetes tested. Top row shows the digits 1-9, each row corresponds to one synaesthete and shows the RGB values associated with the colour for each digit.

	1	2	3	4	5	6	7	8	9
S01	255 255 255	20 25 208	255 255 0	255 62 174	134 89 44	212 0 0	7 149 13	122 15 193	81 54 27
S02	38 38 38	22 131 250	245 113 154	17 17 53	255 255 0	246 38 22	0 34 4	69 1 20	95 30 1
S03	0 0 0	248 255 22	37 197 20	51 7 102	251 10 7	19 21 177	41 123 0	233 133 15	96 100 45
S04	255 255 255	0 31 145	133 204 58	231 157 48	215 20 31	15 139 93	255 220 70	73 60 153	158 120 137
S05	0 0 0	255 244 99	148 16 21	33 113 27	240 86 0	1 0 42	138 181 238	96 0 0	35 12 2
S06	0 0 0	254 201 34	255 67 158	211 33 45	255 63 12	211 209 34	31 148 15	14 85 227	148 21 154
S07	255 243 120	174 0 0	243 116 1	41 42 82	221 173 0	216 32 122	0 191 96	140 255 177	245 211 236
S08	0 0 0	192 0 0	238 169 76	0 126 57	214 107 0	253 207 227	79 79 79	255 155 9	255 255 255
S09	255 255 153	255 0 102	28 152 28	249 123 180	184 9 27	153 204 255	255 72 29	0 51 153	153 255 51
S10	0 0 0	72 46 36	0 204 0	128 0 128	252 124 28	255 102 204	51 51 153	255 255 255	141 106 71
S11	255 255 255	0 51 204	3 128 3	194 96 23	0 0 0	178 139 255	240 228 0	115 11 11	61 6 6
S12	51 51 51	255 255 204	210 210 254	255 0 0	255 255 0	255 255 251	46 146 48	51 51 0	112 56 0

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