

## Synesthesia improves sensory memory, when perceptual awareness is high

Article (Accepted Version)

Rothen, Nicolas, Seth, Anil K and Ward, Jamie (2018) Synesthesia improves sensory memory, when perceptual awareness is high. *Vision Research*, 153. pp. 1-6. ISSN 0042-6989

This version is available from Sussex Research Online: <http://sro.sussex.ac.uk/id/eprint/78615/>

This document is made available in accordance with publisher policies and may differ from the published version or from the version of record. If you wish to cite this item you are advised to consult the publisher's version. Please see the URL above for details on accessing the published version.

### **Copyright and reuse:**

Sussex Research Online is a digital repository of the research output of the University.

Copyright and all moral rights to the version of the paper presented here belong to the individual author(s) and/or other copyright owners. To the extent reasonable and practicable, the material made available in SRO has been checked for eligibility before being made available.

Copies of full text items generally can be reproduced, displayed or performed and given to third parties in any format or medium for personal research or study, educational, or not-for-profit purposes without prior permission or charge, provided that the authors, title and full bibliographic details are credited, a hyperlink and/or URL is given for the original metadata page and the content is not changed in any way.

**Synesthesia improves sensory memory, when perceptual awareness is high**

Nicolas Rothen<sup>1,2</sup>, Anil K. Seth<sup>2,3</sup>, and Jamie Ward<sup>2,4</sup>

<sup>1</sup>Institute of Psychology, University of Bern, Switzerland

and Swiss Distance Learning University

<sup>2</sup>Sackler Centre for Consciousness Science, University of Sussex, Brighton, UK

<sup>3</sup>School of Engineering and Informatics, University of Sussex, Brighton, UK

<sup>4</sup>School of Psychology, University of Sussex, Brighton, UK

Manuscript submitted to *Vision Research*: 05, February 2018

Revision submitted to *Vision Research*: 05, September 2018

Accepted for publication in *Vision Research*: 08, September 2018

Author Note

Correspondence concerning this article should be addressed to Nicolas Rothen, Institute of Psychology, Center for Learning Memory and Cognition, University of Bern, Fabrikstrasse 8, 3012 Bern, Switzerland. E-mail: [nicolas.rothen@gmail.com](mailto:nicolas.rothen@gmail.com)

Acknowledgements: This work was supported by the Swiss National Science Foundation (Grant Number: PZ00P1\_154954). AKS is grateful to the Dr. Mortimer and Theresa Sackler Foundation, which supports the Sackler Centre for Consciousness Science.

### **Abstract**

Empirical evidence suggests that synesthesia is associated with enhanced sensory processing. A separate body of empirical literature suggests that synesthesia is linked to a specific profile of enhanced episodic and working memory performance. However, whether sensory (iconic) memory performance is also affected by synesthesia remains unknown. Therefore, we tested 22 grapheme-color synesthetes and compared their performance in a partial-report paradigm with 22 individually matched non-synesthete controls. Participants were briefly presented with a circular-letter array and required to report the identity of the letter at a probed target location after various delays. Furthermore, they were required to indicate the subjective clarity of the target letter after every trial. The results suggest that sensory memory performance is enhanced in synesthesia, but only when subjective clarity of the target letter is high. Additional exploratory analyses revealed that synesthetic consistency, which is widely used to confirm the genuineness of synesthesia, correlated significantly with performance in the partial report paradigm. We conclude that synesthesia does not generally enhance sensory memory performance, but that synesthetic experiences may enhance sensory memory performance when perceptual awareness of the target is high. Furthermore, the stability of synesthetic associations may be linked to sensory memory performance.

Keywords: grapheme-color, perception, memory, partial report, iconic memory, sensory memory, perceptual awareness, subjective clarity, meta-cognition

**Synesthesia improves sensory memory, when perceptual awareness is high**

Synesthesia is associated with additional percept-like experiences which are consistently and automatically triggered by the presence of a specific inducer (Ward, 2013). In grapheme-color synesthesia (henceforth synesthesia if not otherwise specified), the letter A printed in black may elicit a red color experience. There is empirical evidence that synesthesia leads to a specific profile of enhanced memory performance (e.g., Rothen & Meier, 2010; Yaro & Ward, 2007). Moreover, there is empirical evidence that synesthesia is associated with enhanced sensory processing (e.g., Banissy et al., 2013; Barnett et al., 2008). It has previously been suggested that enhanced sensory processing could underlie the memory advantages observed in synesthesia (Rothen, Meier, & Ward, 2012). Thus, it seems reasonable to assume that synesthesia leads to a performance benefit also in sensory memory. However, this has never been formally tested. We conducted the present study to close this gap and to further characterize the profile of memory performance in synesthesia.

In previous research, synesthetes have been shown to outperform non-synesthetes in direct tests of memory. In direct memory tests, participants are explicitly asked to remember a previous episode (e.g., learning phase). For instance, episodic memory benefits for synesthetes have been reported for free-recall of word lists and simple abstract figures (Gibson, Radvansky, Johnson, & McNerney, 2012; Radvansky, Gibson, & McNerney, 2011; Rothen & Meier, 2010; Yaro & Ward, 2007), recognition memory for words, fractal patterns, and outdoor scenes (Ward, Hovard, Jones, & Rothen, 2013), associative memory for words and color information (Bankieris & Aslin, 2016a; Pritchard, Rothen, Coolbear, & Ward, 2013; Rothen & Meier, 2010; Yaro & Ward, 2007). By contrast, synesthesia does not seem to enhance episodic memory performance for the location of digits in a matrix (Rothen & Meier, 2009; Yaro & Ward, 2007) and does not

seem to scale to more complex levels of information, such as the situation level model (Radvansky, Gibson, & McNerney, 2014). Synesthesia can also benefit working memory performance. For instance, measures of complex verbal working memory spans (Radvansky et al., 2014) and visual working memory for color, but not grapheme, information were found to be enhanced in synesthesia (Terhune, Wudarczyk, Kochuparampil, & Cohen Kadosh, 2013).

A memory advantage in synesthesia has also been reported for indirect tests of memory. Indirect tests of memory do not explicitly ask participants to remember previous episodes, but assess memory indirectly (e.g., faster reaction times due to prior exposure). Here, synesthesia has been shown to create additional learning opportunities in classical conditioning (Meier & Rothen, 2007; Rothen, Nyffeler, von Wartburg, Müri, & Meier, 2010), to enhance learning of artificial grammars for synesthesia eliciting material (Rothen, Scott, et al., 2013), and to enhance learning of shape-color associations (Bankieris & Aslin, 2016b).

Summarizing, memory is affected by synesthesia. However, the memory advantage does not consistently occur for material which elicits synesthetic experiences (e.g., digits in a matrix, where the specific locations must be remembered; Rothen & Meier, 2009; Yaro & Ward, 2007), and furthermore, can also be found for material which does not elicit synesthesia (e.g., free recall of simple abstract patterns and recognition of complex fractal patterns; Rothen & Meier, 2010; Ward et al., 2013). Overall, memory advantages in synesthesia seem to be associated with stimulus characteristics biased towards processing in the ventral visual pathway of the human brain (e.g., color, high contrast, and high spatial frequency), but not with stimulus characteristics biased towards processing in the dorsal visual pathway (e.g., low contrast, low spatial frequency, and motion) (cf. Rothen et al., 2012 for a review; cf. also Meier & Rothen, 2013).

In line with this, it has been shown that synesthesia is associated with enhanced sensory processing for stimulus characteristics biased towards processing in the ventral visual stream, but not for stimulus characteristics biased towards processing in the dorsal visual stream. For example, there is empirical evidence that synesthesia is linked to increased visual evoked potentials in response to high contrast, but not low contrast, checkerboard patterns (Barnett et al., 2008). Moreover, synesthesia is associated with enhanced color discrimination (Banissy et al., 2013; Yaro & Ward, 2007), but also with impaired motion detection (Banissy et al., 2013). Accordingly, there is evidence for increased cortical volume within the posterior fusiform gyrus which is linked to processing color information and a reduction in motion-selective regions of the visual cortex in synesthetes (Banissy et al., 2012).

Sensory memory (equivalently, iconic memory) refers to the brief transient sensory response of the multiple stimuli processed in parallel by the sensory systems (Neisser, 1967; Sperling, 1960; cf. also Graziano & Sigman, 2008). Sensory memory has a high information capacity and decays rapidly within about one second after stimulus duration (Averbach & Sperling, 1961; Graziano & Sigman, 2008). Given enhanced sensory processing and enhanced memory performance in synesthesia, we aimed to test whether synesthesia is associated with enhanced sensory memory performance (i.e., reduced decay of sensory information).

## Method

### Participants

We tested 22 grapheme-color synesthetes and 22 non-synesthetic controls, individually matched by gender and age (syn *mean* = 31.95 years, *SD* = 10.54, *min* = 20, *max* = 57 vs. con *mean* = 30.18 years, *SD* = 9.97, *min* = 18, *max* = 55). Participants' first language was English and matched in all but two cases in which a Dutch synesthete was matched with a German

control, and a Slovak synesthete with an Italian control. Handedness was matched in all but 5 cases. Synesthetes were confirmed by means of an internet-based test of consistency which is widely used to assess synesthetic consistency within a single session (Eagleman, Kagan, Nelson, Sagaram, & Sarma, 2007). The test was completed online before the laboratory session. Consistency was calculated in CIE  $L^* u^* v^*$  color space which is perceptually uniform (i.e., perceived distances correspond to measured distances). Average consistency was 67.93 ( $SE = 4.11$ ,  $min = 41.76$ ,  $max = 106.38$ ). All synesthetes were below the recommended cutoff of 135, sufficient to diagnose grapheme-color synesthesia in CIE  $L^* u^* v^*$  (Rothen, Seth, Witzel, & Ward, 2013). Potential non-synesthete controls were given a description of synesthesia and a few examples of different types of synesthesia. They were only invited to participate in the study if they confirmed that they did not have synesthetic phenomenology or synesthetic associations. This was again confirmed at the beginning of the testing session by means of an interview. None of the controls reported synesthetic phenomenology or synesthetic associations. Controls were not required to complete the test of consistency. The study was approved by the local ethics committee of the University of Sussex and carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

### **Stimuli and Procedure**

We adapted the partial report method of Graziano and Sigman (2008). Stimuli were presented on a 19-inch CRT monitor at a refresh rate of 60 Hz and resolution of 1024 x 768 pixels. A chin- and forehead rest was used to keep the distance between the participants' eyes and the center of the monitor at 73 cm for the entire duration of the experiment. Eight different black uppercase letters were used as stimuli (B, D, F, K, L, P, R, T). The letters were created using the Times New Roman font with a size of 1.2 degrees of visual angle. The eight letters were

arranged on a circle, around the fixation point at an eccentricity of 5.2 degrees of visual angle. A red asterisk of 0.1 degree of visual angle was used as target-cue and black asterisks as place holders. Grey was used as background color.

Participants were individually tested. After consenting to participate, their synesthetic status was again confirmed by means of a brief interview. Next, the lights were turned off with the computer monitor as the only light source in laboratory and participants were instructed for the sensory memory task: to verbally report the letter at the position indicated by the red asterisk.

Participants first completed a practice block of eight trials and were given the opportunity to ask questions about the procedure. After any such questions were responded to, participants completed a total of 336 trials across seven blocks of 48 trials. In every block, each stimulus location out of eight was cued equally often as the target location in randomized order. Each target location was once paired with each of six different inter-stimulus-intervals (ISI) in randomized order. Letters were always randomly assigned to the positions on the stimulus array.

Stimulus presentation was controlled with E-Prime 2.0. Each trial started with a central fixation (1000 ms), followed by the eight letter circular stimulus array (100 ms corresponding to 6 frames) and ISI of variable duration (0, 50, 100, 250, 500, or 1000 ms). Thereafter, the red asterisk appeared at one of the letter positions while the black asterisks appeared at the other letter positions as place holders. Asterisks remained on the screen until the experimenter entered the participant's verbal response about the letter identity. Next, to assess perceptual awareness, participants were required to state a number to indicate the subjective clarity of the target letter (see Ramsøy & Overgaard, 2004; Sandberg, Timmermans, Overgaard, & Cleeremans, 2010): 1) *No experience of the letter at all. Guessing.* 2) *Brief glimpse of the letter. But, the letter cannot be specified further.* 3) *Almost clear experience of the letter. Feeling of knowing the letter.* 4)

*Clear experience of the letter. Non-ambiguous.* After the experimenter entered the participants response, a blank screen followed for 50 ms before the next trial started. The central fixation remained on the screen for the entire trial, except for the last blank to indicate the start of a new trial (Figure 1A).

### **Analysis and Results**

We followed the data analysis strategy of Graziano and Sigman (2008) including the additional factor group. We focused on overall performance differences between the groups (synesthetes vs. controls), before separately evaluating the following four different experimental manipulations as function of group: ISI (0, 50, 100, 250, 500, 1000), Letter (B, D, F, K, L, P, R, T), Position (1-8), and Clarity (clear experience, almost clear experience, brief glimpse, guessing).

The alpha level was set to .05 for all statistical analyses. We applied the Greenhouse-Geisser correction where the assumption of sphericity was violated on tests involving repeated-measures factors with more than two levels. For analyses of variance (ANOVAs), effect sizes are indicated as partial eta squared ( $\eta_p^2$ ) and mean square errors (MSEs) are reported to help any researcher who might want to conduct a meta-analysis (cf. Fritz, Morris, & Richler, 2012).

#### **Effect of Group**

The average proportion of correctly identified target letters was .44 ( $SE = .025$ ) for the synesthetes and .42 ( $SE = .025$ ) for the controls. Performance did not differ significantly between the groups,  $F(1,42) = 0.39$ ,  $MSE = .014$ ,  $p = .538$ ,  $\eta_p^2 = .01$ .

#### **Effect of ISI**

Descriptive statistics are shown in Figure 1B. A two-factorial ANOVA consisting of the within subjects factor ISI and between subjects factor Group revealed a significant effect of ISI

on the proportion of correctly identified target letters,  $F(5,210) = 61.72$ ,  $MSE = .006$ ,  $p < .001$ ,  $\eta_p^2 = .60$ . This was due to decreasing performance with longer ISIs. The effect of Group and the interaction Group x ISI did not reach statistical significance,  $F(1,42) = 0.39$ ,  $MSE = .082$ ,  $p = .538$ ,  $\eta_p^2 = .01$  and  $F(5,210) = 0.37$ ,  $MSE = .006$ ,  $p = .751$ ,  $\eta_p^2 = .01$ , respectively.

### **Effect of Letter**

Descriptive statistics are shown in Figure 1C. A two-factorial ANOVA consisting of the within subjects factor Letter and between subjects factor Group revealed a significant effect of Letter on the proportion of correctly identified target letters,  $F(7,294) = 27.76$ ,  $MSE = .011$ ,  $p < .001$ ,  $\eta_p^2 = .40$ . This was due to better task performance with some target letters than others. The effect of Group and the interaction Group x Letter did not reach statistical significance,  $F(1,42) = 0.38$ ,  $MSE = .110$ ,  $p = .540$ ,  $\eta_p^2 = .01$  and  $F(7,294) = 0.89$ ,  $MSE = .011$ ,  $p = .518$ ,  $\eta_p^2 = .02$ , respectively. We further explored if participants were “guessing” strategically (i.e., if they were always reporting the same letter when guessing). For each individual letter, we calculated the ratio of reporting a specific letter when it was not presented. A value of one would indicate perfectly random guessing, a value of eight always reporting the same letter. The average ratio was 1 ( $SE = .015$ ,  $median = 1$ ,  $min = .22$ ,  $max = 1.79$ ). Thus, we can rule out strategic guessing.

### **Effect of Position**

Descriptive statistics are shown in Figure 1D and 1E. A two-factorial ANOVA consisting of the within subjects factor Position and between subjects factor Group revealed a significant effect of Position on the proportion of correctly identified target letters,  $F(7,294) = 18.04$ ,  $MSE = .021$ ,  $p < .001$ ,  $\eta_p^2 = .30$ . This was due to better task performance if the target letters appeared in the upper-right part of the stimulus arrangement in comparison to the lower-left part. The effect of Group and the interaction Group x Position did not reach statistical significance,

$F(1,42) = 0.39$ ,  $MSE = .109$ ,  $p = .538$ ,  $\eta_p^2 = .01$  and  $F(7,294) = 1.24$ ,  $MSE = .021$ ,  $p = .297$ ,  $\eta_p^2 = .03$ , respectively.

### **Effect of Subjective Clarity**

Descriptive statistics are shown in Figure 1F. Several participants never used the highest possible subjective clarity rating (i.e., clear experience). One non-synesthete provided only clarity ratings in the two lowest categories (i.e., brief glimpse and guessing). Due to the missing values, we opted for a mixed-effects logistic regression approach. This type of analysis uses the information present at the trial level rather than discarding it by averaging, and accounts for different  $N$ s across factor levels. We combined the previous tests and the factor Clarity into a single mixed-effects logistic regression, thereby controlling for the effects of all experimental manipulations at the same time and attempting to replicate the previously reported results with a different statistical procedure. The model included the main factors Group, ISI, Letter, Position, Clarity and the interactions Group x ISI, Group x Letter, Group x Position, Group x Clarity as fixed effects. Participant ID was included as random effect. Accounting for varied scale use across participants, we standardized the rating scores by participants. The model replicated the significant main effects of ISI, Letter, Position of the previous analyses (all  $F$ s > 26.69) and further revealed a main effect of Clarity ( $F = 2103.13$ ): higher clarity ratings were associated with better task performance. The main effect Group was not significant ( $F = 0.09$ ), but the Group x Clarity interaction was significant ( $F = 9.86$ ). Specifically, synesthetes had a performance advantage when clarity was high but there was no advantage at mid and low clarity levels. No other interactions reached statistical significance (all  $F$ s < 1.34).<sup>1</sup>

We further analyzed if the groups differed in terms of clarity ratings for correctly identified target letters (i.e., metacognition). Average subjective clarity for correct responses was

0.55 ( $SE = .033$ ) for the synesthetes and 0.54 ( $SE = .029$ ) for the controls. The groups did not differ significantly in terms of their clarity ratings for correctly identified target letters,  $F(1,42) = 0.08$ ,  $MSE = .021$ ,  $p = .777$ ,  $\eta_p^2 < .01$ .<sup>2</sup>

### **Exploratory Analyses**

The following analysis is not based on a-priori hypothesizing and therefore, must be treated as purely exploratory. Given the limited evidence for a sensory memory advantage in synesthesia, we further probed whether sensory memory performance in the synesthete group was associated with their performance in the test of consistency (Rothen, Seth, et al., 2013). The assumption seems legitimate since consistency tests are used to confirm the genuineness of synesthesia (Baron-Cohen, Wyke, & Binnie, 1987). Thus, if synesthesia is associated with enhanced sensory memory performance, synesthetes who are more consistent should exhibit the larger memory benefit. This was indeed the case, consistency was significantly correlated with overall task performance  $r = -.43$ ,  $p = .047$  (Figure 1G). Synesthetes who were more consistent (i.e., lower consistency scores) showed better performance in the sensory memory task. Notably, correlations of .50 are conventionally interpreted as large effects (Cohen, 1988).

### **Discussion**

In the present study, we used a partial report paradigm to test whether synesthesia benefits sensory memory performance. We compared grapheme-color synesthetes and matched controls while manipulating three different factors: the ISI, target letter, and target position. Furthermore, we assessed whether synesthetes and controls differed in performance as a function of subjective clarity ratings. We found that all four factors had an impact on sensory memory performance, in both the synesthete and control samples. Sensory memory was not generally enhanced in the sample of synesthetes relative to the sample of controls, but synesthetes showed

enhanced performance when subjective clarity of the target was high. Moreover, we observed a relatively strong association between performance in the test of consistency and sensory memory performance within the synesthete sample. This association does suggest that synesthesia is linked to sensory memory performance. Thus, despite limited evidence that sensory memory is enhanced in synesthesia, there seems to be an association between synesthesia and sensory memory performance more generally.

Why did we not observe a general sensory memory benefit of synesthesia? Crucially, a performance advantage was only observed when perceptual awareness (i.e., subjective clarity) for the target was high. A likely explanation is that enhanced perceptual processing abilities in synesthesia do not occur pre-attentively and not across a large portion of the visual field, but within a circumscribed locus of attention. That is, processing benefits in synesthesia start to emerge only when perceptual awareness for a given stimulus is high. This is consistent with the notion that the performance advantage of synesthetes in visual search tasks, where embedded shapes consisting of  $\mathcal{Z}$  had to be found among distractors of  $\mathcal{S}$ , is related to the proportion of graphemes that were noted to be colored (Ward, Jonas, Dienes, & Seth, 2010). It is also consistent with the reports that unconscious priming eliminates automatic binding between synesthetic colors and grapheme shape (Mattingley, Rich, Yelland, & Bradshaw, 2001). Furthermore, it does not contradict the observation of enhanced sensory processing in synesthesia which was demonstrated to occur around 100 ms after stimulus onset in a visual evoked potential study (Barnett et al., 2008), as the stimuli were presented centrally in the full focus of attention and because it is reasonable to assume that some processing time is required for these early differences to affect overt behavior. From a neuronal perspective, the lack of a general advantage may be related to the circular arrangement of the stimulus array which

requires spatial attention and judgements on the location of potential target stimuli. However, spatial attention biases processing towards the dorsal visual stream in the human cortex which is less likely to be associated with a processing advantage in synesthesia and may have counteracted the processing advantage for the high contrast grapheme stimuli which bias processing towards the ventral visual stream (e.g., Rothen et al., 2012; cf. also Banissy et al., 2013). Thus, we demonstrated in line with previous research that synesthesia can enhance sensory memory.

Despite the absence of a general group difference, the within-group association between synesthetic consistency and sensory memory performance is notable. The consistency test, which is the gold standard to diagnose synesthesia, involves selecting colors from a large color palette on several occasions and measuring consistency of the colors selected. (e.g., Baron-Cohen et al., 1987; Asher, Aitken, Farooqi, Kurmani, & Baron-Cohen, 2006; Eagleman et al., 2007; cf. also Simner, 2011). Following our previous studies, consistency in the present experiment was measured in a perceptually uniform color space (CIE  $L^* u^* v^*$ ), where perceived color differences correspond to measured distances in color space (cf. Rothen, Seth, et al., 2013). Hence, our data suggest that the test of consistency, at least as used in the present study, is able to quantify the perceptual / sensory quality of synesthetic experiences.

This link between synesthetic consistency and sensory memory performance has several implications for future studies, as well as for synesthesia more generally. Studies comparing synesthetes and controls on sensory and cognitive tasks should attempt to link task performance with performance in the test used to diagnose synesthesia. Whenever possible, measures of synesthetic consistency should be based on perceptually uniform color spaces (cf. Rothen, Seth, et al., 2013). The measure used to confirm synesthesia should be carefully described in the

participants section (i.e., not only an averaged value but also a measure of variability as well as the minimum and maximum value). Ideally, the distribution of such measures should be provided (as can be seen in Figure 1G, consistency scores in our study approximated a normal distribution over the whole synesthetic range). In fact, we would have found a *general* memory performance advantage in the partial report paradigm for the synesthetes relative to the controls had we only sampled highly consistent synesthetes. Hence, differences in synesthetic consistency across different studies may be an explanation for conflicting results in the synesthesia literature more generally (e.g., regarding visual search performance Ramachandran & Hubbard, 2001; Hubbard, Arman, Ramachandran, & Boynton, 2005; Rothen & Meier, 2009; Ward et al., 2010; or regarding the neural basis of synesthesia Esterman, Verstynen, Ivry, & Robertson, 2006; Muggleton, Tsakanikos, Walsh, & Ward, 2007; Rothen et al., 2010; for a critical review cf. also Hupé & Dojat, 2015). Therefore, we recommend that future studies which do not report task performance on an individual level should include sufficiently sized samples in order to avoid false positive findings.

An interesting hypothesis is that we would be able to observe a similar correlation in the control sample if there existed an analogue to synesthetic consistency. In fact, we might even observe a correlation for the consistency test in controls. However, control responses might be too noisy. For instance, while the letter A might be associated with different shades of the color red in the consistency test for a synesthete, it might be associated with different colors altogether for a control. Related to this notion, it has been suggested that sensory processing in synesthesia may carry into memory processes too (Rothen et al., 2012). More precisely, group differences in sensory processing and memory performance between synesthetes and non-synesthetes have been found for stimulus characteristics biased towards processing in the ventral visual stream,

but not for stimulus characteristics biased towards processing in the dorsal visual stream. Obviously, this does not mean that sensory processing abilities are entirely unrelated to memory performance when dorsal processes are involved, such as spatial attention. Thus, if sensory processing is key to enhanced memory in synesthesia, it is reasonable to assume that sensory processing abilities in a more general population are also related to memory performance, except in the trivial case in which not being able to discriminate between colors leads to worse memory for color stimuli. This view is also in line with the notion that memory representations are stored throughout the hierarchy of the visual processing stream (Ahissar & Hochstein, 2004; Brady, Konkle, Alvarez, & Oliva, 2008; Wheeler, Petersen, & Buckner, 2000).

Based on the within-group association between synesthetic consistency and sensory memory performance, and despite the absence of a general group difference, we conclude that sensory memory performance can be enhanced in synesthesia when perceptual awareness for the target is high and that performance is linked to qualitative perceptual abilities. This complements the existing literature on memory performance in synesthesia according to which increased sensory responsiveness transposes into a memory advantage.

## References

- Ahissar, M., & Hochstein, S. (2004). The reverse hierarchy theory of visual perceptual learning. *Trends in Cognitive Sciences*, 8(10), 457–464. <https://doi.org/10.1016/j.tics.2004.08.011>
- Asher, J. E., Aitken, M. R. F., Farooqi, N., Kurmani, S., & Baron-Cohen, S. (2006). Diagnosing and phenotyping visual synaesthesia: A preliminary evaluation of the Revised Test of Genuineness (TOG-R). *Cortex*, 42(2), 137–146. [https://doi.org/10.1016/S0010-9452\(08\)70337-X](https://doi.org/10.1016/S0010-9452(08)70337-X)
- Averbach, E., & Sperling, G. (1961). Short term storage of information in vision. In C. Cherry (Ed.), *Information theory* (pp. 196–211). Washington, DC: Butterworth & Co.
- Banissy, M. J., Stewart, L., Muggleton, N. G., Griffiths, T. D., Walsh, V. Y., Ward, J., & Kanai, R. (2012). Grapheme-color and tone-color synesthesia is associated with structural brain changes in visual regions implicated in color, form, and motion. *Cognitive Neuroscience*, 3(1), 29–35. <https://doi.org/10.1080/17588928.2011.594499>
- Banissy, M. J., Tester, V., Muggleton, N. G., Janik, A. B., Davenport, A., Franklin, A., ... Ward, J. (2013). Synesthesia for color is linked to improved color perception but reduced motion perception. *Psychological Science*, 24(12), 2390–2397. <https://doi.org/10.1177/0956797613492424>
- Bankieris, K. R., & Aslin, R. N. (2016a). Explicit Associative Learning and Memory in Synesthetes and Nonsynesthetes. *I-Perception*, 7(5), 2041669516658488. <https://doi.org/10.1177/2041669516658488>
- Bankieris, K. R., & Aslin, R. N. (2016b). Implicit associative learning in synesthetes and nonsynesthetes. *Psychonomic Bulletin & Review*, 1–9. <https://doi.org/10.3758/s13423-016-1162-y>

- Barnett, K. J., Foxe, J. J., Molholm, S., Kelly, S. P., Shalgi, S., Mitchell, K. J., & Newell, F. N. (2008). Differences in early sensory-perceptual processing in synesthesia: A visual evoked potential study. *NeuroImage*, *43*(3), 605–613.  
<https://doi.org/10.1016/j.neuroimage.2008.07.028>
- Baron-Cohen, S., Wyke, M. A., & Binnie, C. (1987). Hearing words and seeing colours: An experimental investigation of a case of synaesthesia. *Perception*, *16*(6), 761–767.  
<https://doi.org/10.1068/p160761>
- Brady, T. F., Konkle, T., Alvarez, G. A., & Oliva, A. (2008). Visual long-term memory has a massive storage capacity for object details. *Proceedings of the National Academy of Sciences*, *105*(38), 14325–14329. <https://doi.org/10.1073/pnas.0803390105>
- Cohen, J. (1988). *Statistical Power Analysis for the Behavioral Sciences* (2 edition). Hillsdale, N.J: Routledge.
- Eagleman, D. M., Kagan, A. D., Nelson, S. S., Sagaram, D., & Sarma, A. K. (2007). A standardized test battery for the study of synesthesia. *Journal of Neuroscience Methods*, *159*(1), 139–145. <https://doi.org/10.1016/j.jneumeth.2006.07.012>
- Esterman, M., Verstynen, T., Ivry, R. B., & Robertson, L. C. (2006). Coming unbound: Disrupting automatic integration of synesthetic color and graphemes by transcranial magnetic stimulation of the right parietal lobe. *Journal of Cognitive Neuroscience*, *18*(9), 1570–1576. <https://doi.org/10.1162/jocn.2006.18.9.1570>
- Fritz, C. O., Morris, P. E., & Richler, J. J. (2012). Effect size estimates: Current use, calculations, and interpretation. *Journal of Experimental Psychology: General*, *141*(1), 2–18.  
<https://doi.org/10.1037/a0024338>

- Gibson, B., Radvansky, G., Johnson, A., & McNerney, M. (2012). Grapheme–color synesthesia can enhance immediate memory without disrupting the encoding of relational cues. *Psychonomic Bulletin & Review*, *19*(6), 1172–1177. <https://doi.org/10.3758/s13423-012-0306-y>
- Graziano, M., & Sigman, M. (2008). The dynamics of sensory buffers: Geometric, spatial, and experience-dependent shaping of iconic memory. *Journal of Vision*, *8*(5), 1–13. <https://doi.org/10.1167/8.5.9>
- Hubbard, E. M., Arman, A. C., Ramachandran, V. S., & Boynton, G. M. (2005). Individual differences among grapheme-color synesthetes: Brain-behavior correlations. *Neuron*, *45*(6), 975–985. <https://doi.org/10.1016/j.neuron.2005.02.008>
- Hupé, J.-M., & Dojat, M. (2015). A critical review of the neuroimaging literature on synesthesia. *Frontiers in Human Neuroscience*, *9*, 103. <https://doi.org/10.3389/fnhum.2015.00103>
- Mattingley, J. B., Rich, A. N., Yelland, G., & Bradshaw, J. L. (2001). Unconscious priming eliminates automatic binding of colour and alphanumeric form in synaesthesia. *Nature*, *410*(6828), 580–582. <https://doi.org/10.1038/35069062>
- Meier, B., & Rothen, N. (2007). When conditioned responses “fire back”: Bidirectional cross-activation creates learning opportunities in synesthesia. *Neuroscience*, *147*(3), 569–572. <https://doi.org/10.1016/j.neuroscience.2007.04.008>
- Meier, B., & Rothen, N. (2013). Synaesthesia and memory. In J. Simner & E. M. Hubbard (Eds.), *Oxford Handbook of Synaesthesia* (pp. 692–706). Oxford, UK: Oxford University Press.

- Muggleton, N., Tsakanikos, E., Walsh, V., & Ward, J. (2007). Disruption of synaesthesia following TMS of the right posterior parietal cortex. *Neuropsychologia*, *45*(7), 1582–1585. <https://doi.org/10.1016/j.neuropsychologia.2006.11.021>
- Neisser, U. (1967). *Cognitive Psychology*. New York: Appleton-Century-Crofts.
- Pritchard, J., Rothen, N., Coolbear, D., & Ward, J. (2013). Enhanced associative memory for colour (but not shape or location) in synaesthesia. *Cognition*, *127*(2), 230–234. <https://doi.org/10.1016/j.cognition.2012.12.012>
- Radvansky, G. A., Gibson, B. S., & McNERNEY, M. W. (2011). Synesthesia and memory: Color congruency, von Restorff, and false memory effects. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *37*(1), 219–229. <https://doi.org/10.1037/a0021329>
- Radvansky, G. A., Gibson, B. S., & McNERNEY, M. W. (2014). Working memory, situation models, and synesthesia. *The American Journal of Psychology*, *127*(3), 325–342.
- Ramachandran, V. S., & Hubbard, E. M. (2001). Psychophysical investigations into the neural basis of synaesthesia. *Proceedings of the Royal Society B: Biological Sciences*, *268*(1470), 979–983. <https://doi.org/10.1098/rspb.2001.1576>
- Ramsøy, T. Z., & Overgaard, M. (2004). Introspection and subliminal perception. *Phenomenology and the Cognitive Sciences*, *3*(1), 1–23. <https://doi.org/10.1023/B:PHEN.0000041900.30172.e8>
- Rothen, N., & Meier, B. (2009). Do synesthetes have a general advantage in visual search and episodic memory? A case for group studies. *PLoS ONE*, *4*(4), e5037. <https://doi.org/10.1371/journal.pone.0005037>

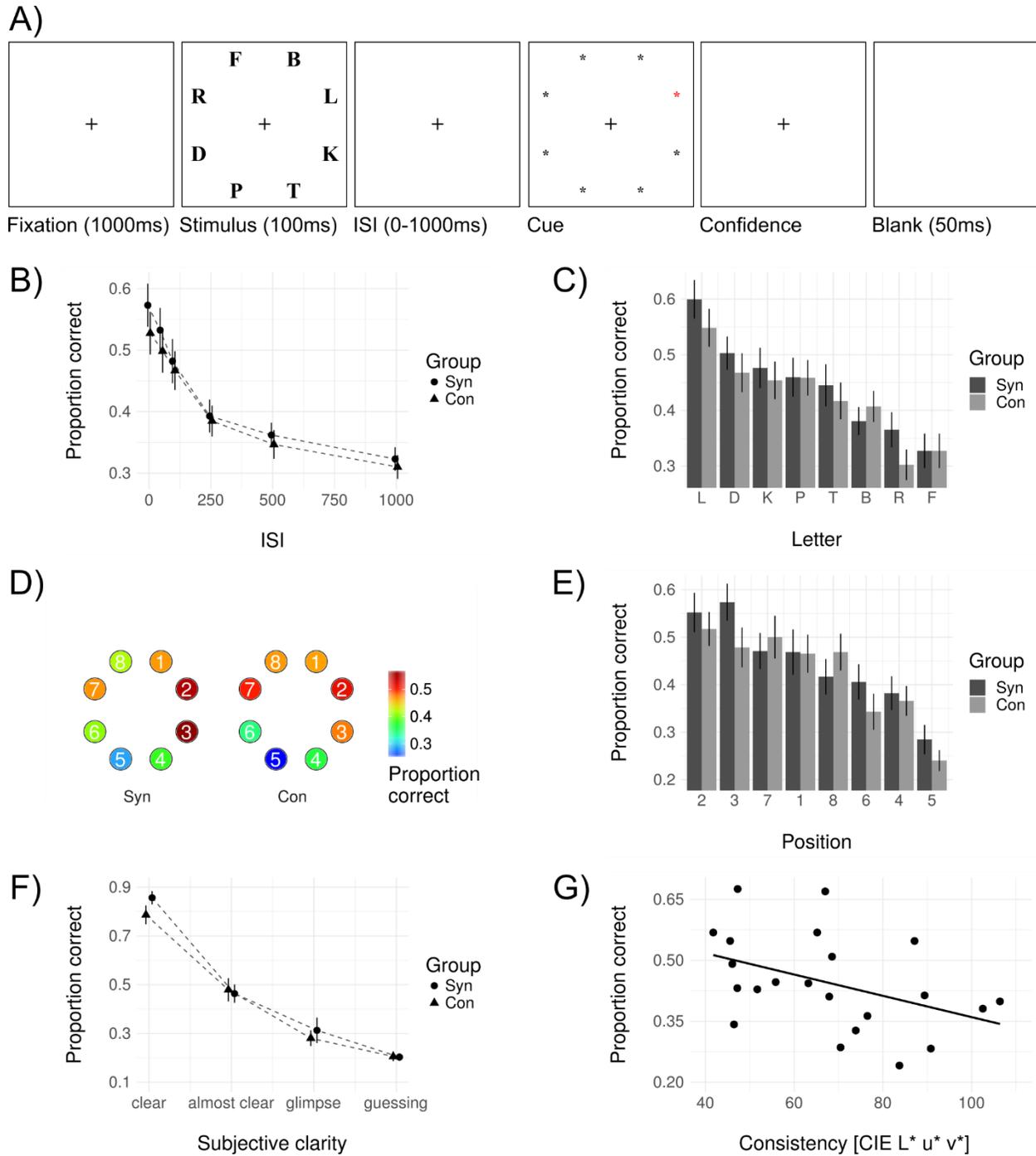
- Rothen, N., & Meier, B. (2010). Grapheme–colour synaesthesia yields an ordinary rather than extraordinary memory advantage: Evidence from a group study. *Memory*, *18*(3), 258–264. <https://doi.org/10.1080/09658210903527308>
- Rothen, N., Meier, B., & Ward, J. (2012). Enhanced memory ability: Insights from synaesthesia. *Neuroscience & Biobehavioral Reviews*, *36*(8), 1952–1963. <https://doi.org/10.1016/j.neubiorev.2012.05.004>
- Rothen, N., Nyffeler, T., von Wartburg, R., Müri, R., & Meier, B. (2010). Parieto-occipital suppression eliminates implicit bidirectionality in grapheme-colour synaesthesia. *Neuropsychologia*, *48*(12), 3482–3487. <https://doi.org/10.1016/j.neuropsychologia.2010.07.032>
- Rothen, N., Scott, R. B., Meador, A. D., Coolbear, D. J., Burckhardt, V., & Ward, J. (2013). Synesthetic experiences enhance unconscious learning. *Cognitive Neuroscience*, *4*(3–4), 231–238. <https://doi.org/10.1080/17588928.2013.847077>
- Rothen, N., Seth, A. K., Witzel, C., & Ward, J. (2013). Diagnosing synaesthesia with online colour pickers: Maximising sensitivity and specificity. *Journal of Neuroscience Methods*, *215*(1), 156–160. <https://doi.org/10.1016/j.jneumeth.2013.02.009>
- Sandberg, K., Timmermans, B., Overgaard, M., & Cleeremans, A. (2010). Measuring consciousness: Is one measure better than the other? *Consciousness and Cognition*, *19*(4), 1069–1078. <https://doi.org/10.1016/j.concog.2009.12.013>
- Simner, J. (2011). Defining synaesthesia. *British Journal of Psychology*, *103*(1), 1–15. <https://doi.org/10.1348/000712610X528305>
- Sperling, G. (1960). The information available in brief visual presentation. *Psychological Monographs: General and Applied*, *74*(11), 1–29.

- Terhune, D. B., Wudarczyk, O. A., Kochuparampil, P., & Cohen Kadosh, R. (2013). Enhanced dimension-specific visual working memory in grapheme–color synesthesia. *Cognition*, *129*(1), 123–137. <https://doi.org/10.1016/j.cognition.2013.06.009>
- Ward, J. (2013). Synesthesia. *Annual Review of Psychology*, *64*(1), 49–75. <https://doi.org/10.1146/annurev-psych-113011-143840>
- Ward, J., Hovard, P., Jones, A., & Rothen, N. (2013). Enhanced recognition memory in grapheme-color synaesthesia for different categories of visual stimuli. *Frontiers in Psychology*, *4*, 762. <https://doi.org/10.3389/fpsyg.2013.00762>
- Ward, J., Jonas, C., Dienes, Z., & Seth, A. (2010). Grapheme-colour synaesthesia improves detection of embedded shapes, but without pre-attentive “pop-out” of synaesthetic colour. *Proceedings of the Royal Society B. Biological Sciences*, *277*(1684), 1021–1026. <https://doi.org/10.1098/rspb.2009.1765>
- Wheeler, M. E., Petersen, S. E., & Buckner, R. L. (2000). Memory’s echo: Vivid remembering reactivates sensory-specific cortex. *Proceedings of the National Academy of Sciences*, *97*(20), 11125–11129. <https://doi.org/10.1073/pnas.97.20.11125>
- Yaro, C., & Ward, J. (2007). Searching for Shereshevskii: What is superior about the memory of synaesthetes? *The Quarterly Journal of Experimental Psychology*, *60*(5), 681–695. <https://doi.org/10.1080/17470210600785208>

## Footnotes

1 Repeating the analysis without standardized rating scores revealed an identical pattern of results. The main effects ISI, Letter, Position, and Clarity were significant (all  $F$ s > 26.98). The main effect Group was not significant ( $F = 0.09$ ). The Group x Clarity interaction was trending towards significance ( $F = 2.73$ ). No other interactions reached statistical significance (all  $F$ s < 1.20).

2 Repeating the analysis without standardized rating scores revealed an identical pattern of results. Average subjective clarity for correct responses was 2.41 ( $SE = .104$ ) for the synesthetes and 2.30 ( $SE = .118$ ) for the controls. The groups did not differ significantly in terms of their clarity ratings for correctly identified target letters,  $F(1,42) = 0.45$ ,  $MSE = .273$ ,  $p = .506$ ,  $\eta_p^2 = .01$ .



**Figure 1:** **A)** Exemplary trial of the partial report paradigm. **B)** Sensory memory performance (i.e., proportion of correctly identified target letters) as a function of group and ISI, **C)** group and letter, **D + E)** group and position, **F)** group and clarity. Error bars represent standard errors. **G)** Relationship between synesthetic consistency and sensory memory performance ( $r = -.43$ ).