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Enhanced perception and memory: insights from synesthesia and expertise

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Abstract

Memory research has identified many strategies to enhance memory. However, natural foundations of enhanced memory are vastly underexplored. Interestingly, numerous studies show that synesthesia is associated with enhanced memory performance. Although it has been hypothesized for years that wider changes in visual perception are closely linked with enhanced memory functions in synesthesia, the hypothesis has never been directly put to the test. Here, we investigated whether visual perceptual abilities in synesthesia are linked with higher memory performance by comparing synesthetes who experience colors for letters with non-synesthetic color experts and non-synesthetic individuals from the more general population. Our results showed that synesthesia and expertise share a common profile of enhanced visual perceptual ability and memory in contrast to non-synesthetic individuals from the more general population. Overall, our findings suggest that visual perception and visual memory are more closely connected than previously thought.

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Enhanced perception and memory: insights from synesthesia and expertise

Research on human memory has identified many powerful strategies to enhance memory (e.g., Craik & Lockhart, 1972; Morris, Bransford, & Franks, 1977; Paivio, Yuille, & Rogers, 1969). Additionally, a lot of research has been dedicated to memory deficits, mostly due to brain damage or neurological disorders (e.g., Scoville & Milner, 2000). Thus, theories and models of memory are mostly informed by strategic manipulations or studies on memory deficits. By contrast, natural (i.e., strategy-free) foundations of enhanced memory are vastly underexplored. Interestingly, a decade of group studies on memory in synesthesia (i.e., a perceptual condition in otherwise healthy individuals) is providing increasing evidence for a specific profile of enhanced memory which cannot be explained by means of conventional memory strategies (Rothen, Meier, & Ward, 2012). However, the currently favored integrative working hypothesis to explain the memory benefit in grapheme-color synesthesia – the enhanced processing account according to which visual perceptual ability and memory are closely related – has never been empirically tested. We ran the current study to confirm the enhanced processing account, comparing a synesthetic sample and a more general non-synesthetic sample with similar visual perceptual abilities against a randomly sampled non-synesthetic control group.

In grapheme-color synesthesia, which is the best studied form of synesthesia, letters and numbers trigger color experiences. For instance, the letter "C" printed in black on a white background may elicit a yellow color experience. Grapheme-color synesthesia is associated with a memory advantage which is not restricted to stimulus material eliciting synesthetic experiences (e.g., simple abstract figures; Rothen & Meier, 2010) and not all stimuli which trigger synesthesia are better remembered (e.g., recalling the location of digits in a matrix; Rothen & Meier, 2009; Yaro & Ward, 2007). Thus, the memory advantage in synesthesia cannot be explained by means of a dual coding strategy (cf. also Paivio, 1969), where synesthetic experiences are used as additional retrieval cues. In fact, synesthetes tend to have better visual memory (e.g., for color and abstract fractal patterns) than verbal memory (Ward, Hovard, Jones, & Rothen, 2013). There is also some evidence that grapheme-color synesthetes tend to think more visually and seem to rely less on semantic connotations (Radvansky, Gibson, & McNerney, 2011). Moreover, the advantage does not fall into the divisions of the classical memory systems (Bankieris & Aslin, 2017; Rothen, Nyffeler, von Wartburg, Müri, & Meier, 2010; Rothen, Scott, et al., 2013; Rothen, Seth, & Ward, 2018; Teichmann, Nieuwenstein, & Rich, 2017; Terhune, Wudarczyk, Kochuparampil, & Cohen Kadosh, 2013; for declarative vs. non-declarative cf. Squire, 1992). The alternative explanation is that wider changes in the visual system of grapheme-color synesthetes transpose into a memory advantage (Rothen et al., 2012).

Current evidence suggests that the memory advantage in grapheme-color synesthesia reflects the structural and functional divisions of the human visual system (e.g., Barnett et al., 2008). The human visual system can be divided in two different pathways: the ventral visual pathway (also "what" pathway) and the dorsal visual pathway (also "where" pathway). Although processing in both pathways interacts, processing in the ventral visual pathway is biased by stimulus material involving high spatial frequency information, high contrast information, color information and visual recognition (e.g., words, objects, patterns). By contrast, processing in the dorsal visual pathway is biased by stimulus material involving low spatial frequency information, low contrast information, achromatic information and motion perception (e.g., spatial attention Derrington & Lennie, 1984; Kaplan, 1991). Interestingly, the memory advantage in grapheme-color synesthesia is associated with stimulus material biasing processing towards the ventral visual pathway, but not the dorsal visual pathway. For instance, memory benefits in grapheme-color synesthesia have been found for words (which elicit synesthetic color experiences but also consist of high contrast and high spatial frequency information; e.g., Gross, Neargarder, Caldwell-Harris, & Cronin-Golomb, 2011; Ward et al., 2013), color information (which does not elicit synesthetic experiences; e.g., Lunke & Meier, 2018; Pritchard, Rothen, Coolbear, & Ward, 2013; Rothen & Meier, 2010; Terhune et al., 2013; Yaro & Ward, 2007), simple abstract figures and more complex abstract fractal patterns (which consist of high spatial frequency information but do not elicit synesthetic experiences and are not in the synesthetic domain of color; Rothen & Meier, 2010; Ward et al., 2013). By contrast, no memory benefit has been found in grapheme-color synesthesia, for instance, for the position of numbers in a matrix (which elicit color experiences but also require spatial attention; Rothen & Meier, 2010; Yaro & Ward, 2007) and in tasks concerned with the location of abstract forms (which also requires spatial attention; Pritchard et al., 2013).

The memory advantage in grapheme-color synesthesia lends first empirical support to the emergent memory account (Graham, Barense, & Lee, 2010) from an enhanced memory performance perspective (Rothen et al., 2012). The emergent memory account, which so far was almost exclusively informed by studies on animals and brain-damaged patients, is based on a representational view of memory and perception along the ventral visual pathway (Graham et al., 2010; Saksida, 2009). The account does not rely on distinctions between different memory systems but emphasizes the characteristics of the represented information, from simple features (e.g., color) in early visual areas to feature conjunctions (e.g., individual objects) to conjunctions of feature conjunctions (i.e., complex visual scenes) in the hippocampus. Accordingly, visual perceptual ability and visual memory should be closely related.

In line with this, grapheme-color synesthesia is associated with enhanced visual perceptual sensitivity for stimulus material biasing processing towards the ventral visual pathway, but not for stimulus material biasing processing towards the dorsal visual pathway. For instance, grapheme-color synesthesia is associated with enhanced visual perceptual sensitivity for high contrast, high spatial frequency, color information, but not for low contrast, motion, achromatic information (Banissy et al., 2013; Barnett et al., 2008; Ward, Rothen, Chang, & Kanai, 2017). Interestingly, enhanced visual perceptual sensitivity is also observed when synesthetic phenomenology is acquired by means of prolonged letter-color association training (Bor, Rothen, Schwartzman, Clayton, & Seth, 2014; Rothen, Schwartzman, Bor, & Seth, 2018; cf. also Colizoli, Murre, & Rouw, 2012; Colizoli, Murre, Scholte, & Rouw, 2017) and might even transpose into a memory advantage (Ovalle Fresa & Rothen, 2019a).

Crucially, it has never been investigated in a single study with comparable methods across tasks whether enhanced visual perceptual ability is associated with enhanced visual memory in grapheme-color synesthesia. Moreover, it remains to be elucidated if this view also applies to the more general population of healthy non-synesthetic individuals. Thus, we tested a group of grapheme-color synesthetes, a group of non-synesthetic color experts and a group of non-synesthetic controls without color expertise with a continuous response space paradigm to assess visual perceptual ability, visual working memory and visual long-term memory for color information. We further conducted a contrast sensitivity task to obtain basic parameters of visual perceptual ability. We predicted a similar profile of enhanced visual perceptual ability in grapheme-color synesthetes and color experts in comparison to controls. In line with the representation view of perception and memory, we predicted a corresponding memory benefit in synesthetes and experts in comparison to controls.

Methods

Sample size determination and stopping criterion

The minimum required sample was based on the following heuristics. Sample size determination is based on effect sizes for the memory benefits in grapheme-color synesthesia which are predominantly in the range of medium effects (Cohen's $d = .65$; cf. Cohen, 1988, for the interpretation of effect sizes), for a review see Rothen et al. (2012) and for a meta-analysis Ward, Field, and Chin (2019). The power analyses were conducted with G*Power 3 (Faul, Erdfelder, Lang, Buchner, 2007) and followed a within-subject design between two conditions (presence vs. absence of synesthesia) due to the careful control of factors that might influence memory between groups (i.e. narrow age range and yoking for age and education). The power analysis revealed that a minimum of 21 synesthetes and 21 controls are required to achieve a 80% probability of detecting a true difference between synesthetes and controls. Thus, we aimed for a minimum sample of 21 participants per group, but continued to test as many participants as possible until the end of the funding period of the current project (cf. acknowledgements for grant number), to increase the reliability of our findings.

Participants

We recruited a total of 81 participants ($N = 27$ grapheme-color synesthetes, $N = 27$ color experts, $N = 27$ controls). Synesthetes were recruited based on phenomenological reports. Color experts were defined as someone who dealt intensively with color due to their job, education or hobby. They were recruited based on self-reports. Controls were interviewed to guarantee that they did not experience synesthesia and had no color expertise. To confirm the presence / absence of synesthesia, all participants completed a test of consistency (cf. Ovalle Fresa & Rothen, 2019a; Rothen, Seth, Witzel, & Ward, 2013). Inclusion criteria were an age range between 18 to 40 years, no colorblindness, and normal or corrected-to-normal vision. Participants were excluded if they self-reported grapheme-color synesthesia and color expertise. Participants in the synesthesia group had an average age of 25.56 ($SD = 4.91$) years, 25 were female, 2 were male, 25 were right-handed, 2 were left-handed. Participants in the expert group had an average age of 26.11 ($SD = 4.48$) years, 24 were female, 3 were male, 23 were right-handed, 4 were left-handed. Participants in the control group had an average age of 25.48 ($SD = 4.26$), 25 were female, 2 were male, 24 were right-handed, 3 were left-handed. Participants were yoked for age (+/- three years) and similar levels of education across the different groups. Moreover, they were matched across groups as closely as possible for gender and handedness. The study was approved by the local ethics committee of the University of Bern.

Apparatus and materials

Visual acuity and color-blindness test. We assessed participant's visual acuity with a printable version of the Landolt rings test (www.sov.ch, retrieved on 5th of December 2019). To assess color vision, we applied an online version of the Farnsworth Dichotomous Test (D-15; www.color-blindness.com/color-arrangement-test, retrieved on 5th of December 2019).

Consistency test. Participants synesthetic status was confirmed with an online version of a consistency test (cf. Ovalle Fresa & Rothen, 2019a; Rothen, Seth, et al., 2013). The task was programmed in HTML/PHP and JavaScript. It included questions to potential synesthetic experiences. Stimuli consisted of the following potential synesthetic inducers: the letters of the alphabet (A – Z), digits (0 – 9), days of the week (Monday – Sunday), months of the year (January – December). Stimuli were further accompanied by a continuous color palette (disk) and a vertical scale from white to black on its right. The color palette included a circle that could be moved with the computer mouse to select a color. The vertical scale included a rectangle that could be moved to adjust the luminance of the color palette. Color palette and luminance bar represented all colors that could possible be presented on a computer screen. Two buttons were positioned below the color palette. The left button included the word "OK", the right button included the word "keine Farbe" (no color in German). By contrast to standard version of this test, which exclusively include potential synesthetic inducers, our stimuli additionally included five different color squares, which were not relevant for the current study and hence, are not further discussed.

Experimental tasks. Stimuli of the experimental tasks, as described in the following sections, were rendered in MATLAB using Psychophysics Toolbox 3 (Brainard, Pelli, & Robson, 2002; Pelli, 1997). Stimuli were presented on a flat 21-inch Sony Trinitron cathode ray tube monitor (85 Hz refresh rate) driven by a NVIDIA GeForce GTX970 graphics card (NVIDIA Corporation, Santa Clara, California) with a spatial resolution of 1280 × 1024 pixels and a color resolution of 8 bits per channel. The CIE1931 chromaticity coordinates and luminance of the monitor primaries were R = (0.624; 0.341; 17.698), G = (0.286; 0.609; 51.816), and B = (0.150; 0.073; 5.615). A chin- and forehead rest was used to keep the viewing distance of 100 cm constant for the duration of the experiment. A black cardboard tunnel led directly from the monitor to the chin- and forehead rest and overlapped it by 20 cm at the top and both sides in order to shield peripheral vision and guarantee that the participants' visual system adapted to the computer monitor.

Visual memory tasks. Stimuli were created as in Ovalle Fresa and Rothen (2019b). Stimuli of the visual short-term task and visual long-term memory task consisted of 185 distinct and identifiable objects from the Bank of Standardized Stimuli (Brodeur, Dionne-Dostie, Montreuil, & Lepage, 2010), which were randomly assigned to five lists of different objects for the memory tasks: a practice list consisting of five objects and four testing lists consisting of 45 objects each. Forty-five colors representing every eight degree on an isoluminant color circle were assigned to each of the different stimulus lists. An additional five colors that were equally distributed over the color circle were assigned to the practice list.

The original objects were converted to gray scale and adjusted to red (RGB = 125, 0, 0) in Irfanview (version: 4.42, ©2016 by Irfan Skiljan). During the experiment, stimuli were resized to 5° × 5° of visual angle, converted to CIELUV color space, and gray scaled by means of adjusting chromaticity to zero and retaining lightness. Gamma corrections were applied based on the measured gamma curves of the monitor primaries. Next, the lightness of each object was compressed by setting the L* of each pixel to 25% of its original value. Then, the objects were shifted along the L*-axis that the averaged luminance of the object was isoluminant with the background of the monitor. Thereafter, one of the different test colors which were equidistantly sampled along an isoluminant hue circle in CIELUV space (L* = 76, u* = 0, v* = 0, radius of 28) was randomly assigned to each of the objects without replacement, resulting in unique object-color associations for each participant. Compression was necessary to make sure colors were rendered within the gamut of the monitor. Pixels with values > 98 on the L*-axis were masked with the background color to remove untidy borderlines.

The luminance of the background was y = 40.7 cd/m^2. The background was used as the white point for the conversion into CIELUV space. Hence the lightness of the background was L* = 76. This definition of the white point avoids L*-values above 100, when parts of the stimuli were lighter than the background (cf. Witzel & Franklin, 2014). For important implications of careful color rendering the reader is referred to the following research articles (Allred & Olkkonen, 2015; Bae, Olkkonen, Allred, & Flombaum, 2015; Bae, Olkkonen, Allred, Wilson, & Flombaum, 2014).

Visual perception task. The stimulus material of the visual perception task consisted of a disk object and the same colors, as in the visual memory tasks. All other aspects of the task were identical with those of the visual memory tasks, described in the previous two paragraphs.

Spatial contrast sensitivity task. The method was adapted from Lesmes, Lu, Baek, and Albright (2010), who used a Bayesian adaptive estimation of the spatial contrast sensitivity function. Stimuli consisted of Gaussian-windowed (SD = .87° of visual angle) sinusoidal gratings (5.6° x 5.6° of visual angle) of varying contrast, oriented +/-45° from the vertical. Stimuli were based on 16 potential spatial frequency levels from .6 cycles per degree to 20 cycles per degree and 60 potential contrast levels ranging from .001% to 100%. The spatial contrast sensitivity function, which describes reciprocal contrast threshold as a function of spatial frequency, can be expressed by four parameters. Initial parameter settings (priors) for the function were set as peak gain (γ_{max}) of 100, peak spatial frequency (f_{max}) of 2.5 cycles per degree, bandwidth (full-width at half-maximum; β) of 3 octaves, and truncation at low spatial frequency (δ) of 0.5 log units. The formulae for adjusting parameters on the basis of performance are given by Hou et al. (2010); Lesmes et al. (2010). The background of the monitor was a gamma corrected mid-level gray, with gamma corrections based on the measured gamma curves of the monitor primaries. The task also included a black fixation cross which subtended .16° of visual angle. The task contained a fixed number of 20 practice trials and 300 test trials. The estimated parameters after the final trial are analyzed.

Procedure

Participants were individually tested. First, they were informed that they could withdraw at any time during the experiment and written consent was obtained. Next, visual acuity (i.e., Landolt rings) was tested before the lights in the testing room were turned-off, with he computer monitor as the only remaining light source. Participants were seated in front of the computer monitor with a black viewing tunnel and instructed to rest their chin and forehead on the respective parts of the chin- and forehead rest for the duration of the experiment. Next, they completed a demographics questionnaire and a color blindness test (i.e., Farnsworth Dichotomous Test, D–15), before they completed the experimental tasks and finished with the test of consistency. The experimental tasks consisted of a continuous report paradigm to test visual long-term memory, visual short-term memory, visual perception (cf. Brady, Konkle, Gill, Oliva, & Alvarez, 2013) and the spatial contrast sensitivity task to measure contrast sensitivity at different spatial frequencies (cf. Lesmes et al., 2010), in the outlined order. Each experimental task and task condition started with a practice block, during which potential questions were answered by the experimenter. Thereafter, the experimenter left the room and waited in the anteroom for the participant to complete each task. Between tasks participants had the opportunity to take short breaks. On average testing lasted 120 minutes. Participants received 50 Swiss franks or two hours towards their course credit requirements for their participation.

Visual long-term memory task. The task consisted of two phases, a study phase and a test phase. Participant were instructed that they will be presented with distinct objects in different colors, that they should memorize the object-color associations, to be able to retrieve the exact colors of the objects in a subsequent retrieval phase. First, participants completed a practice block (study and test) consisting of five trials, immediately before the main part of the experiment (study and test) consisting of 45 trials. Each trial of the study phase started with a central fixation for 1 s that was followed by a colored object for 3 s (surrounded by a black circle with a radius of 3° of visual angle), before the next trial started. During the test phase, all objects from the study phase were presented again. Each trial started with a central fixation for 1 s, followed by the object in gray scale, surrounded by a black circle with a radius of 3° of visual angle. The black circle represented an underlying color wheel. Participants had to adjust the color of the gray object to the target color (original color of the object in the study phase), by moving a black dot on the circle by means of the computer mouse. Upon the first mouse movement the gray object changed the color according to the underlying color wheel. A chosen color had to be submitted by mouse click, which also initiated the next trial. The starting point of the color wheel underlying the black circle was randomized for each trial to avoid position effects. The focus lay on accuracy, response time was not restricted. Participants received the feedback ”Good!” if their response was within 10° of the original color on the underlying color wheel. Object-color associations and order of object presentation were randomized within the different stimulus lists for each participant.

Visual short-term memory task. The task was identical to the visual long-term memory task, except for the following specifications. Again participants were instructed that they will be presented with distinct objects in different colors, that they should memorize the objects and their colors, to be able to retrieve the exact color when subsequently probed with the specific objects. The task started with a practice trial, immediately before the main part of the experiment consisting of 45 trials. Each trial started with a central fixation for 1 s, followed by a centrally presented colored object for 3 s (surrounded by the black circle), followed by a blank for 1 s, and the same object in gray scale surrounded by the black circle representing the underlying color wheel. Participants had to adjust the color of the gray object to the target color (original color of the object presented before). Submitting the color by mouse-click initiated the next trial. Thereafter, participants completed the same task again with different object-color pairings (i.e., novel objects) and a memory load of three. That is, during encoding three objects were presented simultaneously on a circular array ($r = 5.5°$) around a central fixation for 3 s, followed by a blank of 1 s duration, before the objects were probed individually at the center of the monitor. Each color submission was followed by a blank of 1 s before the next object of the encoding array was probed. Also this condition included a practice trial, before the main part of the experiment. The 45 object-color associations of the main part of the experiment were distributed across a total of 15 trials. Next, participants completed an analogous block with a memory load of five objects.

Visual perception task. The visual perception task followed the same logic as the memory tasks. The task was identical to the memory tasks, except for the following specifications. The task consisted of five practice trials and 45 trials in the main part of the experiment. Each trial started with a central fixation presented for 1 s, before two identical images of a disk appeared simultaneously on either side of the fixation. The distance from the central fixation to the center of each of the disks was 5° of visual angle. The disk on the left had a distinct color and the disk on the right was gray scaled. Each disk was surrounded by a black circle, but only the circle of the response object was representing a color wheel. Participants were instructed to adjust the color of the right disk to match the color of the left disk as closely as possible.

Spatial contrast sensitivity task. The task was used to test participants' sensitivity to spatial frequency and contrast (Hou et al., 2010; Lesmes et al., 2010; Ward et al., 2017). Participants were instructed to indicate the direction of a grating stimulus. If the orientation of a presented grating was from the upper left to the lower right participants had to press ”y” on the keyboard, and if the orientation of the grid is from the upper right to the lower left ”n” had to be pressed. Each trial started with a central fixation with a duration of 500 ms, followed by a grating with a duration of 130 ms. The task consisted of a practice block including 20 trials and six main blocks of 50 trials each. The orientation of the grating was randomized across the task, both conditions appeared equally often often the course of the 6 experimental blocks. Spatial frequency and contrast of each trial were determined by a Bayesian adaptive estimation procedure (cf. section apparatus and materials). The estimation procedure was restarted after the practice trials and continuously applied over the six main blocks of the task.

Consistency test. First participants were asked which of the following potential inducers triggered synesthetic experiences: digits, letters, words, days of the week, months of the year or none of the aforementioned. Depending on their responses, participants' consistency was only assessed for digits and letters or additionally also for days and / or months. That is, synesthetic inducers were presented one-by-one in randomized order on the left of a continuous color palette with the luminance bar. Participants were instructed to use the color palette and luminance bar to select the color that matched best with the presented inducer. Participants from the expert and control group were additionally instructed to memorize the selected color for each of the inducers and to reproduce it in an immediately following second round of the test. Moreover, they were also instructed not to use the ”no color” option. After all inducers had been presented, a short note appeared that the first round of the test had been completed, before all synesthetic inducers were presented again in randomized order (second round).

Analysis

Based on the theoretical motivation of this study, we followed the conservative approach to always compute the following two planned contrasts: 1) [synesthetes + experts] vs. controls and 2) synesthetes vs. experts. The analysis of the consistency was the only exception to this approach, because we explicitly recruited non-synesthetic color experts. Thus, the following two contrasts were computed: 1) synesthetes vs. [experts + controls] and 2) experts vs. controls. All tests were two-tailed. Cohen's *d* and their 95% confidence intervals (CIs) are reported as measures of effect size. The following conventions apply: values smaller than .2 are interpreted as negligible effects, values between .2 and .5 are interpreted as small effects, values between .5 and .8 are interpreted as medium effects, values between .8 and 1.1 are interpreted as large effects and values greater than 1.1 are interpreted as very large effects (cf. Cohen, 1988). An alpha level of .05 was used for all statistical tests. Outliers that differed more than +/- 2.5 SD from the mean of a given task condition were excluded from that condition.

Results

Consistency test

Consistency (smaller values correspond to more consistent responses) was for grapheme-color synesthetes $M = 21.5$ ($SE = 2.1$), for color experts $M = 61.2$ ($SE = 4.89$) and for controls $M = 67.0$ ($SE = 5.90$). Due to technical errors, the data of two synesthetes and one control were lost. Comparing synesthetes against experts and controls (non-synesthetes), an independent samples *t*-test revealed that synesthetes differed significantly from experts and controls, $t(76) = 7.40$, $p < .001$, $d = 1.80$ [1.23, 2.36]. That is, synesthetes were more consistent than non-synesthetes. Comparing experts against controls, an independent *t*-test revealed that the groups did not differ significantly, $t(51) = 0.75$, $p = .454$, $d = 0.21$ [-0.76, 0.35]. For the purpose of comparing relatively pure groups (experts and controls who do not have synesthesia and synesthetes who do not fall in a potentially non-synesthetic spectrum) in the following analyses, we excluded an equal number of participants per group with overlapping consistency values, while retaining as many as possible (cf. Figure 1). This resulted in 18 participants per group.[1]

Visual perception

Descriptives for the visual perception task are depicted in Figure 2a. Three participants (one of each group) had to be excluded as outliers. Comparing synesthetes and experts against controls, an independent samples *t*-test revealed that synesthetes and experts differed significantly from controls, $t(49) = 3.59$, $p = .001$, $d = 1.07$ [0.43, 1.70]. That is, synesthetes and experts had on average smaller deviations from the original color in

[1]Notably, the pattern of the results is virtually identical with slightly weaker effects when this exclusion criterion is not applied. One exception to this observation concerns the γ parameter of the spatial sensitivity task (cf. relevant results section below).

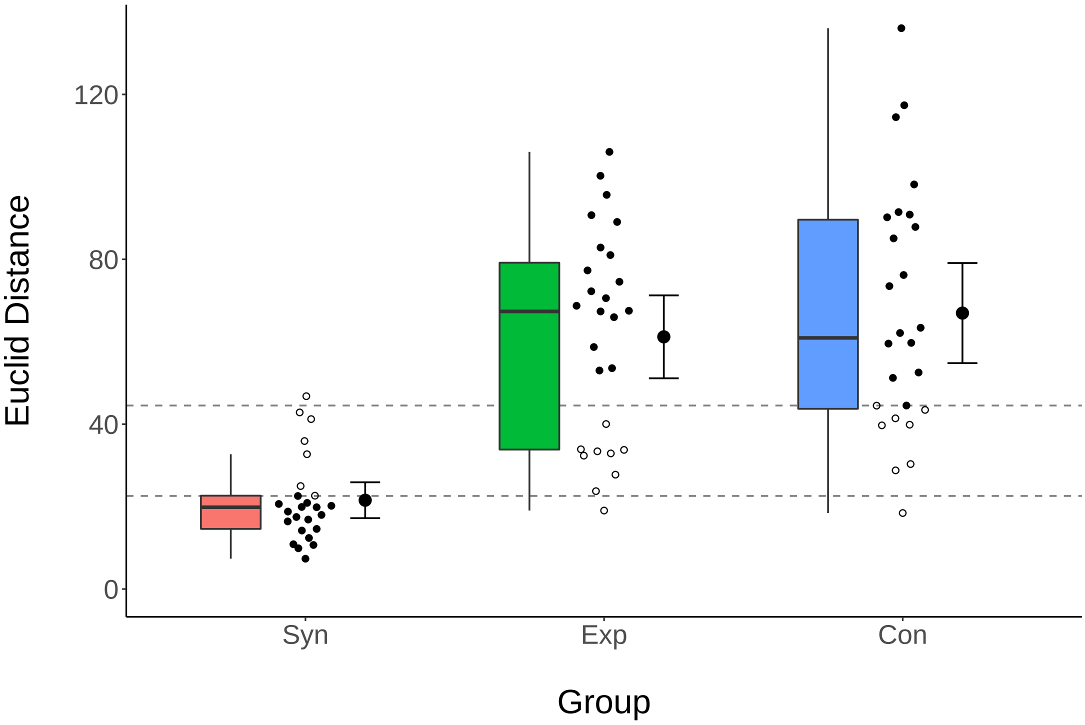


Figure 1. Synesthetic consistency (Euclid distance in CIELUV color space) as a function of group. Depicted are boxplots, individual participant data and group average, including 95% confidence intervals. Filled circles represent participants whose consistency values were regarded as non-ambiguous. Unfilled circles represent participants whose consistency values were regarded as ambiguous. Note, smaller values reflect more consistent responses.

comparison to controls. The point estimate of the effect size indicated a large effect. Comparing synesthetes against experts, an independent samples t-test revealed that synesthetes did not significantly differ from experts, $t(32) = 0.13$, $p = .894$, $d = 0.05$ [-0.65, 0.74]. The point estimate of the effect size indicated a negligible effect.

Visual short-term memory

Descriptives for the visual short-term memory task are depicted in Figure 2b. A synesthete had to be excluded as outlier from the condition with a memory load of one. Comparing synesthetes and experts against controls in the condition with a memory load one, an independent samples t-test revealed that synesthetes and experts differed significantly from controls, $t(51) = 2.87$, $p = .006$, $d = 0.83$ [0.23, 1.44]. That is, synesthetes and experts had on average smaller deviations from the original color in comparison to controls. The point estimate of the effect size indicated a large effect. Comparing synesthetes against experts, an independent samples t-test revealed that synesthetes did not significantly differ from experts, $t(33) = 1.77$, $p = .085$, $d = 0.60$ [-.10, 1.30]. However, the point estimate of the effect size indicated a medium effect in favor of the synesthetes, possibly suggesting a statistical power problem for this comparison.

An expert had to be excluded as outlier from the condition with a memory load of

(a) Visual perception (b) Visual short-term memory

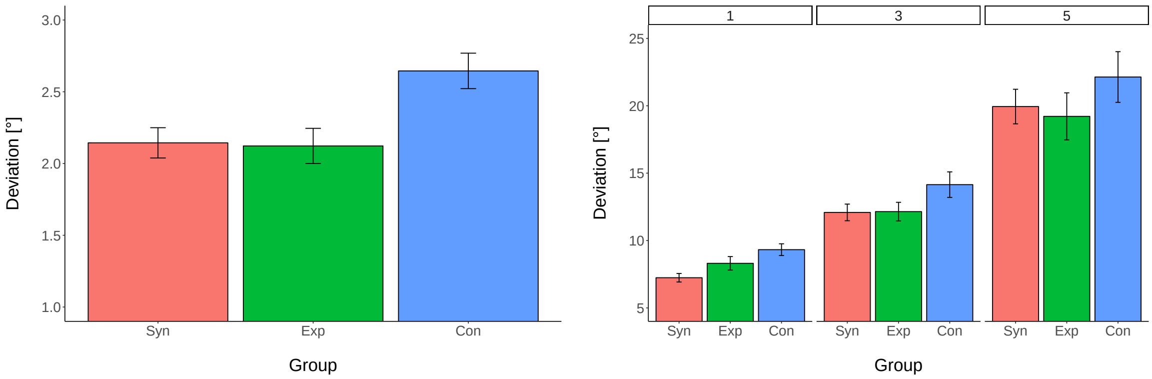


Figure 2. Different subfigures show average task performance as a function of group for (2a) the visual perception task and (2b) the visual short-term memory task with different load conditions. Smaller values represent better performance. Error bars represent standard errors. The figures highlight the similarity between grapheme-color synesthetes (Syn) and color experts (Exp) in comparison to controls (Con). In both tasks, grapheme-color synesthetes and color experts outperform controls.

three. Comparing synesthetes and experts against controls in the condition with a memory load of three, an independent samples t-test revealed that synesthetes and experts differed significantly from controls, $t(51) = 2.19$, $p = .033$, $d = 0.64$ [0.04, 1.23]. That is, synesthetes and experts had on average smaller deviations from the original color in comparison to controls. The point estimate of the effect size indicated a medium effect. Comparing synesthetes against experts, an independent samples t-test revealed that synesthetes did not significantly differ from experts, $t(33) = 0.06$, $p = .949$, $d = 0.02$ [-0.67, 0.71]. The point estimate of the effect size indicated a negligible effect.

The same expert as for the condition with a memory load of three and a synesthete had to be excluded as outliers from the condition with a memory load of five. Comparing synesthetes and experts against controls in the condition with a memory load of five, an independent samples t-test revealed that synesthetes and experts did not significantly differ from controls, $t(50) = 1.28$, $p = .208$, $d = 0.37$ [-0.22, 0.96]. However, the point estimate of the effect size indicated a small effect in favor of the synesthetes and controls, possibly suggesting a power problem for this comparison. Comparing synesthetes against experts, an independent samples t-test revealed that synesthetes did not significantly differ from experts, $t(32) = 0.34$, $p = .739$, $d = 0.12$ [-0.58, 0.81]. The point estimate of the effect size indicated a negligible effect.

Visual long-term memory

Average deviation was $M = 39.8$ ($SE = 4.95$) for grapheme-color synesthetes, $M = 39.3$ ($SE = 4.79$) for color experts and $M = 39.8$ ($SE = 5.14$) for controls. There were no outliers. Comparing synesthetes and experts against controls, an independent samples t-test revealed that synesthetes and experts did not significantly differ from controls, $t(52)$

= 0.05, p = .961, d = 0.01 [-0.57, 0.59]. The point estimate of the effect size indicated a negligible effect. Comparing synesthetes against experts, an independent samples t-test revealed that synesthetes did not significantly differ from experts, $t(34) = 0.07$, p = .944, d = 0.02 [-0.65, 0.70]. The point estimate of the effect size indicated a negligible effect.

Spatial contrast sensitivity

Descriptives for the spatial contrast sensitivity task can be found in Figure 3. A total of 3 participants (one in each group) had to be excluded because they mixed up the response keys, resulting in the model to fail. No outliers had to be excluded for δ, f and β. A total of three outliers had to be excluded for γ (one in each group). Parameters were individually analyzed.

Descriptives for the δ-parameter are depicted in Figure 3a. Comparing synesthetes and experts against controls, an independent samples t-test revealed a trend for synesthetes and experts to differ from controls, $t(49) = 1.99$, p = .052, d = 0.59 [-0.02, 1.20]. That is, synesthetes and experts tended to have less negative δ-values in comparison to controls. The point estimate of the effect size indicated a medium effect. Comparing synesthetes against experts, an independent samples t-test revealed that synesthetes did not significantly differ from experts, $t(32) = 0.81$, p = .422, d = 0.28 [-0.42, 0.98]. The point estimate of the effect size indicated a small effect.

Descriptives for the f-parameter are depicted in Figure 3b. Comparing synesthetes and experts against controls, an independent samples t-test revealed that synesthetes and experts did not significantly from controls, $t(49) = 1.42$, p = .161, d = 0.42 [-0.18, 1.03]. However, the point estimate of the effect size indicated a small effect, suggesting a potential statistical power problem. Comparing synesthetes against experts, an independent samples t-test revealed that synesthetes did not significantly differ from experts, $t(32) = 0.23$, p = .823, d = 0.08 [-0.62, 0.78]. The point estimate of the effect size indicated a negligible effect.

Descriptives for the γ-parameter are depicted in Figure 3c. Comparing synesthetes and experts against controls, an independent samples t-test revealed that synesthetes and experts did not significantly differ from controls, $t(46) = 0.69$, p = .494, d = 0.21 [-0.41, 0.83]. The point estimate of the effect size indicated a small effect. Comparing synesthetes against experts, an independent samples t-test revealed that synesthetes did not significantly differ from experts, $t(30) = 0.50$, p = .617, d = 0.18 [-0.54, 0.90]. The point estimate of the effect size indicated a negligible effect.

Including all participants irrespective of their consistency performance, γ was for grapheme-color synesthetes $M = 2.06$ ($SE = 0.0098$), for color experts $M = 2.05$ ($SE = 0.0106$) and for controls $M = 2.02$ ($SE = 0.0133$). In this case, a total of five participants ($N_{\text{Syn}} = 2$, $N_{\text{Exp}} = 1$, $N_{\text{Con}} = 2$) had to be excluded because they mixed up the response keys, resulting in the model to fail. Moreover, five participants had to be additionally excluded as outliers ($N_{\text{Syn}} = 2$, $N_{\text{Exp}} = 2$, $N_{\text{Con}} = 1$). Comparing synesthetes and experts against controls, an independent samples t-test revealed that synesthetes and experts differed significantly from controls, $t(69) = 2.55$, p = .013, d = 0.64 [0.13, 1.15]. That is, synesthetes and experts had higher γ-values than controls. The point estimate of the effect size indicated a medium effect. Comparing synesthetes against experts, an independent samples t-test revealed that synesthetes did not significantly differ from experts, $t(45)$ =

0.44, p = .662, d = 0.13 [-0.46, 0.72]. The point estimate of the effect size indicated a negligible effect.

Descriptives for the β-parameter are depicted in Figure 3d. Comparing synesthetes and experts against controls, an independent samples t-test revealed that synesthetes and experts differed significantly from controls, $t(49) = 2.22$, $p = .031$, $d = 0.66$ [0.05, 1.27]. That is, synesthets and experts had higher β-values than controls. The point estimate of the effect size indicated a medium effect. Comparing synesthetes against experts, an independent samples t-test revealed that synesthetes did not significantly differ from experts, $t(32)$ = 0.53, p = .600, d = 0.18 [-0.52, 0.88]. The point estimate of the effect size indicated a negligible effect.

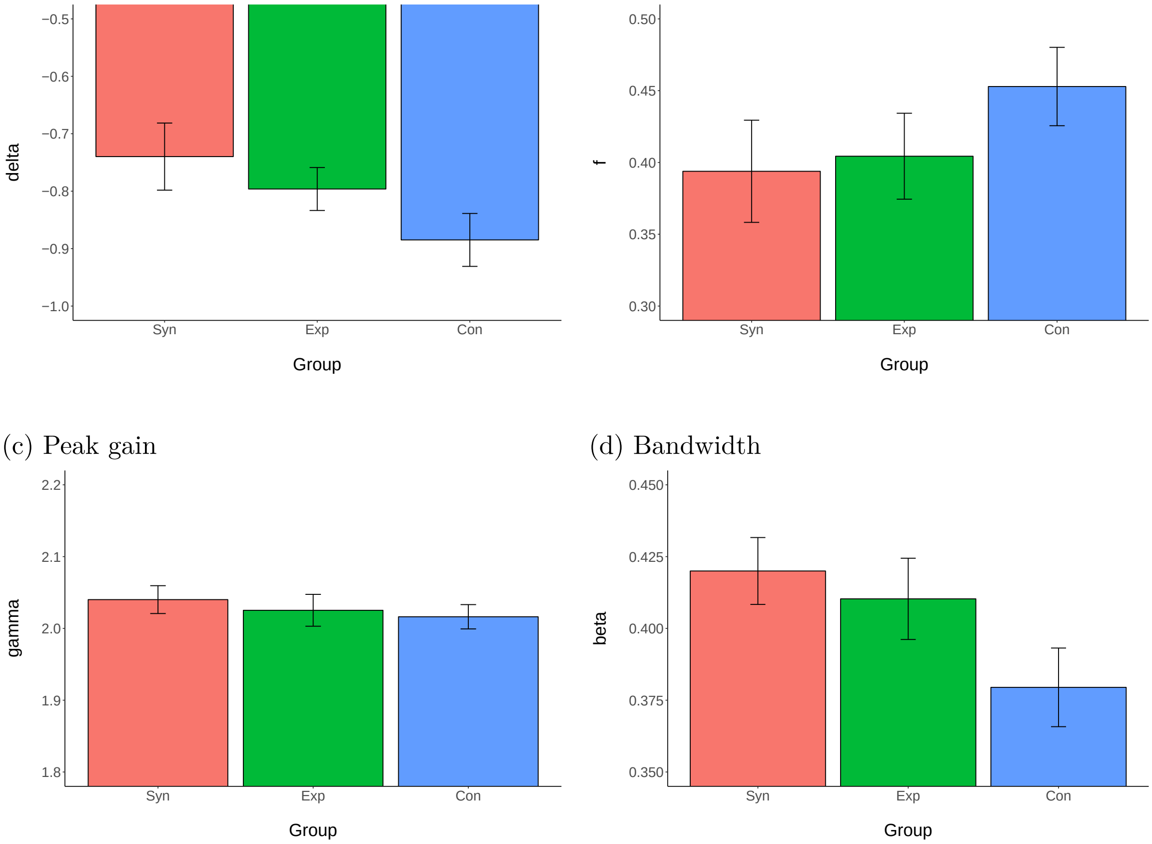
Discussion

Comparing two distinct healthy normal-sighted special populations against a more general normal-sighted sample, we found that enhanced visual perceptual ability is associated with a memory advantage. Specifically, grapheme-color synesthetes and non-synesthetic color experts exhibited an extremely similar profile of enhanced visual perceptual ability (i.e., color and spatial contrast) and a corresponding memory profile (i.e., color). Thus, visual perceptual ability and visual memory are more closely related than previously thought.

Our findings are in line with the general pattern of results in the field of synesthesia research on memory. That is, memory in grapheme-color synesthesia was found to be enhanced in studies including stimulus material biasing processing towards the ventral visual pathway. However, memory was not found to be enhanced in other studies including stimulus material biasing processing towards the dorsal visual pathway. For instance, memory benefits have been found for words (which elicit synesthetic color experiences but also consist of high contrast and high spatial frequency information; e.g., Gross et al., 2011; Ward et al., 2013), color information (which does not elicit synesthetic experiences; e.g., Lunke & Meier, 2018; Pritchard et al., 2013; Rothen & Meier, 2010; Terhune et al., 2013; Yaro & Ward, 2007), simple abstract figures and more complex abstract fractal patterns (which consist of high spatial frequency information but do not elicit synesthetic experiences and are not in the synesthetic domain of color; Rothen & Meier, 2010; Ward et al., 2013). By contrast, no memory benefit has been found for the position of numbers in a matrix (which elicit color experiences but also require spatial attention; Rothen & Meier, 2010; Yaro & Ward, 2007) and in tasks concerned with the location of abstract forms (which also requires spatial attention; Pritchard et al., 2013).

Crucially, our findings are also in line with the general pattern of results in the field of synesthesia on perception. That is visual perceptual ability in grapheme-color synesthesia was found to be enhanced for basic visual perceptual stimuli biasing processing towards the ventral visual pathway, but not for stimuli biasing processing towards the dorsal visual pathway (Banissy et al., 2013; Barnett et al., 2008).

Thus, our study provides first direct empirical evidence for the enhanced processing account of synesthesia. That is, we observed enhanced visual perceptual ability in grapheme-color synesthesia and a corresponding memory benefit. Furthermore, we were able to show that the enhanced processing account also applies to the more general population (i.e., non-synesthetic individuals with comparable visual perceptual abilities and again



(a) Low spatial frequency truncation

(b) Peak spatial frequency

(c) Peak gain

(d) Bandwidth

Figure 3. Different subfigures show average parameter estimations as a function of group for the spatial contrast sensitivity task: (3a) δ = low spatial frequency truncation, (3b) f = peak spatial frequency, (3c) γ = peak gain, (3d) β = bandwidth. Error bars represent standard errors. The figures highlight the similarity between grapheme-color synesthetes (Syn) and color experts (Exp) in comparison to controls (Con). Grapheme-color synesthetes and color experts outperform controls especially with regards to bandwidth (i.e., full-width at half-maximum) and low spatial frequency truncation.

a corresponding memory benefit). The enhanced processing account is based on a representational view of perception and memory, a biological account which is mostly informed by animal studies (Saksida, 2009) and studies with brain damaged patients (cf. emergent memory account, Graham et al., 2010). Thus, our findings provide also first empirical evidence for a representational view of perception and memory from a healthy human perspective.

The implications of a close relationship between perceptual ability and memory are far-reaching. Considering the fact that perceptual expertise can be acquired, as well as synesthetic phenomenology including its behavioral and neurophysiological markers (Bor et al., 2014; Rothen, Schwartzman, et al., 2018), visual perceptual ability training regimes can be designed to enhance memory performance. Preliminary evidence for such a related approach has been recently reported (Ovalle Fresa & Rothen, 2019a). This is noteworthy, given the strong preconceptions that working memory is the bottle-neck for other higher cognitive functions. Unsurprisingly, different forms of working memory training have been praised as means to enhance higher cognitive functioning (e.g., Jaeggi, Buschkuehl, Jonides, & Shah, 2011). However, working memory training is not always possible, because working memory training itself is cognitively demanding. By contrast, perceptual ability training can be conducted even when cognitive abilities are limited. Thus, perceptual ability training provides a relatively straightforward practical basis to enhance higher cognitive functioning. The extend and limitations of this approach will need to be addressed in future studies.

Our findings further have the potential to settle a long standing debate in cognitive science. That is, the direction of travel between perception and memory is contested within the respective fields of research (cf. Fallon, Zokaei, & Husain, 2016). Some researchers argue that the neural basis of visual short-term memory closely resemble perception (Albers, Kok, Toni, Dijkerman, & de Lange, 2013). Others claim that visual working-term memory and visual long-term memory can operate with the same constraints (Brady et al., 2013). Crucially, these opposing views are not mutually exclusive. By contrast, they might just reflect that visual perception and visual long-term memory are more interconnected than previously thought (cf. also representational view of perception and memory Saksida, 2009).

To summarize, we provide first empirical evidence from a healthy human perspective that visual perception and visual memory are more closely connected than previously thought. The finding has broad practical implications (e.g., with regards to restorative training regimes after brain damage). Moreover, the findings has also theoretical implications which might help to settle long standing debates in cognitive science (e.g., the direction of travel between visual perception and visual long-term memory). Collectively, this line of research has the potential to fundamentally transform the way that researchers have viewed the relationship between perception and memory.

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