RUNNING HEAD: Colour Perception in Grapheme-Colour Synaesthesia

The time course of synaesthetic colour perception

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Contributions:

All authors developed the study concept and design. LL performed the testing and data collection. All authors analysed and interpreted the data. DBT and LL drafted the manuscript and all authors approved the final version of the manuscript for submission.

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Abstract

Grapheme-colour synaesthesia is a neurodevelopmental condition wherein perception of numbers and letters consistently and involuntarily elicits concurrent experiences of colour photisms. Accumulating evidence suggests that heterogeneity in the visuospatial phenomenology of synaesthesia is attributable to the operation of top-down processes underlying photisms experienced as representations in associator synaesthetes and bottom-up processes subserving photisms experienced as spatially localized in projector synaesthetes. An untested corollary of this hypothesis is that bottom-up mechanisms will actuate earlier photism perception in projector than associator synaesthetes. We tested this prediction in a pre-registered study wherein associators and projectors completed adaptive temporal order judgment tasks for graphemes, colours, and photisms. In corroboration of the hypothesis of differential photism access across subtypes, projectors displayed lower photism colour thresholds than associators whereas the two subtypes did not significantly differ in veridical colour thresholds. Synesthetes did not differ in grapheme or colour thresholds relative to non-synesthete controls. These results are consistent with the proposal of differential neural mechanisms underlying photism perception in subtypes of grapheme-colour synaesthesia and warrant renewed attention to heterogeneity in the mechanisms and phenomenology of this condition.

Keywords: colour; synaesthesia; heterogeneity; photism; psychophysics; temporal order judgment

Introduction

Grapheme-colour synaesthesia is a neurodevelopmental condition in which letters and numbers automatically and consistently induce the experience of a colour photism. This condition occurs in ~2% of the population (Ward & Simner, 2020) with emerging consensus for a genetic basis (Tilot et al., 2020; Ward & Simner, 2005). Understanding this atypical condition has implications for visual awareness, learning, memory, and multisensory integration (Cohen Kadosh & Henik, 2007; Rothen et al., 2012; Witthoft & Winawer, 2013).

Attempts to elucidate the neural basis of synaesthesia are challenged by perceptual heterogeneity within this condition (Dixon et al., 2004; Ward et al., 2007). In particular, synaesthetes vary in the perceived visuospatial location of their colour photisms with some experiencing photisms "in their mind's eye" (*associators*) and others as spatially co-localized with the inducing grapheme (*projectors*) (Dixon et al., 2004; Simner, 2013; Ward et al., 2007). Multiple lines of evidence have corroborated this distinction using cognitive and perceptual tasks and suggest that projectors are impacted to a greater extent by colour photisms during selective attention tasks (Dixon et al., 2004) and can use photisms to aid visual search to a greater extent than associators (Ward et al., 2007). Further research has documented other neurophysiological and perceptual differences between these subtypes (Brang et al., 2011; Hamada et al., 2017).

One interpretation of these phenomenological differences is that they arise as a result of distinct neural mechanisms (Cohen et al., 2015; van Leeuwen et al., 2011; Terhune et al., 2015a). Applying dynamic causal modelling to fMRI data, van Leeuwen et al. (2011) observed that grapheme processing was characterized by a bottom-up pathway from the letter-shape area (LSA) in fusiform gyrus to V4 in projectors but a top-down pathway between these regions that was mediated by activation of superior parietal lobe (SPL) in associators. Other studies have provided additional data consistent with this model (Brang et al., 2010; Amsel et al., 2017). One as of yet untested corollary of this evidence for differential neural mechanisms in synaesthesia subtypes is that projectors should experience colour photisms earlier than associators.

This pre-registered study investigated the time course of synaesthetic colour (photism) perception using adaptive psychophysics (https://osf.io/59gwd/). Associators and projectors completed a temporal order judgment (TOJ) task wherein they estimated whether colour photisms preceded or proceeded a reference stimulus. In order to clarify the perceptual specificity of any observed effects, and control for potential general responses biases, synaesthesia subtypes and controls also completed the TOJ task with graphemes and veridical colours. Our central prediction was that if projectors experience colour photisms earlier than associators, they would display selectively lower thresholds than associators in the photism, but not grapheme or colour, conditions. In order to evaluate the temporal locus of superior colour processing in synaesthesia (Arnold et al., 2012; Banissy et al., 2009; Banissy et al., 2013; Hamada et al., in press), we further tested the prediction that synaesthetes would display lower thresholds in the colour, but not grapheme, conditions when compared to controls. Further exploratory analyses examined associations between thresholds and psychometric measures of synaesthesia phenomenology (Rothen, Tsakanikos, et al., 2013b; Skelton et al., 2009).

Methods

We report how we determined our sample size, all data exclusions (if any), all data inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

Participants

46 participants (24 synesthetes and 22 controls) took part in the study. Controls and synaesthetes were comparable in age (synaesthetes: range: 19-37, *M*=26.75, *SD*=5.93; controls: range: 19-39; *M*=26.14, *SD*=5.50), gender distributions (synaesthetes: 21 females [87.5%], 3 males [12.5%]; controls: 20 females [91%], 2 males [9%]), and years of post-secondary education (synaesthetes: range: 0-9; *M*=3.63, *SD*=2.58; controls: range: 0-8, *M*=4.45, *SD*=2.15). Participants had normal or corrected-to-normal vision and no history of psychiatric or neurological disorders. Sample size was estimated via an *a priori* power analysis

in Gpower (Erdfelder et al., 1996). A pilot study with a similar design yielded an effect size of d=1.87 for the contrast of photism thresholds in associators and projectors. Using this effect size and the following parameters (1-B=.90, α=.05, two-tailed, sample size ratio of 2:1), the analysis required a sample of 11 associators and 5 projectors. We intended to recruit past this number (16 associators, 8 projectors [24 synaesthetes] and 24 yoked controls) to account for attrition. However, due to the COVID-19 pandemic outbreak, the study was terminated earlier, resulting in slight deviation of our control sample (15 associators, 9 projectors, 22 controls). Participants were recruited on the basis of having synaesthesia or not without any reference to their synaesthesia subtype, which was only determined at the end of the experiment to ensure that the experimenter was blind (see below). This also resulted in a slight deviation of the anticipated proportion of each subtype in the final sample size. Psychophysical data were not inspected or analysed until after data collection had ceased in order to prevent optional stopping. All participants provided informed consent in accordance with local ethical approval.

Materials

Grapheme-colour consistency

Consistency of grapheme-colour associations (Eagleman et al., 2007; Rothen, Seth, et al., 2013a), was assessed with the Texsyn toolbox in MATLAB (v. 2018b; MathWorks, Natick, USA) available from www.synesthete.org (Eagleman et al., 2007). The task involves the random presentation of 36 graphemes (letters from A to Z and numbers from 0 to 9) alongside an RGB colour palette consisting of 255 x 255 x 255 possible colours. Graphemes are presented randomly and synaesthetes are instructed to use the colour palette to select the colour that most closely approximates their photism for the respective grapheme. A "no colour" option is available for non-inducing graphemes. Controls were instructed to select the first colour that came to mind for each grapheme, without trying to remember their previous choices.

Associator/projector phenomenology

Visuospatial phenomenology of synaesthesia was measured using two self-report psychometric measures.

The *Coloured Letters and Numbers* (CLaN) questionnaire (Rothen, Tsakanikos, et al., 2013b) is a 16-item self-report measure regarding different features of synaesthesia that has strong reliability and construct validity. Participants rated each item on a 5-point Likert-scale (1: strongly disagree; to 5: strongly agree). Scores were computed for four subscales: localisation (6 items; Cronbach's α=.94), deliberate use (5 items; α = .80), automaticity/attention (3 items; α =.82), and longitudinal changes (3 items; α =.75).

The *Illustrated Synaesthetic Experiences Questionnaire* (ISEQ) is a five-item questionnaire that queries synaesthetes regarding the visuospatial location of synaesthetic colour photisms (Skelton et al., 2009). Each item consists of an illustrated synaesthetic experience accompanied by a phenomenological description. Two items refer to projector experiences whereas three refer to associator experiences. Synaesthetes rate the extent to which each illustrated example accurately reflects their experience of photisms using a 7-point Likert scale (1: inaccurate to 7: accurate). After reverse-scoring the two projector items, the total scale displayed poor internal consistency (α =.46), potentially because associator and projector phenomenology can coexist (Anderson & Ward, 2015). However, the two projector items used in our subtype classification (see below) displayed greater consistency (α =.61).

Temporal order judgment task

In this visual task, participants judged whether a target stimulus (grapheme, colour, or photism [synaesthetes only]) or a reference stimulus (cross) appeared first (see **Figure 1**). Against a grey background, each trial consisted of a blank inter-trial interval (600ms), a black fixation point (200ms), a jittered interstimulus interval (400-600ms), a target stimulus (black grapheme or coloured oval) and a concurrent reference stimulus (cross) (200ms from onset of second stimulus), an oval noise mask (200ms), a blank interval (200ms), and an untimed binary response prompt. At the prompt, participants used the mouse to select which of two visually depicted options (target and reference stimuli) had appeared first. Target and reference stimuli were presented asynchronously with the stimulus onset asynchrony (SOA) varying on a trial-by-trial basis in an adaptive manner dependent on performance, according to the adaptive PSI method (Kingdom & Prins, 2009; see also Procedure).

The task included three conditions involving different perceptual judgments. In the grapheme condition, the target stimulus consisted of achromatic graphemes and participants judged whether they perceived the grapheme or cross first. The photism condition involved the same (grapheme) target and reference stimuli but participants judged whether they perceived the colour photism or cross first. Finally, in the colour condition, the target stimulus consisted of an oval colour patch and participants judged whether they saw the colour or the cross first. Each condition involved four different target stimuli that were presented in random order within each block.

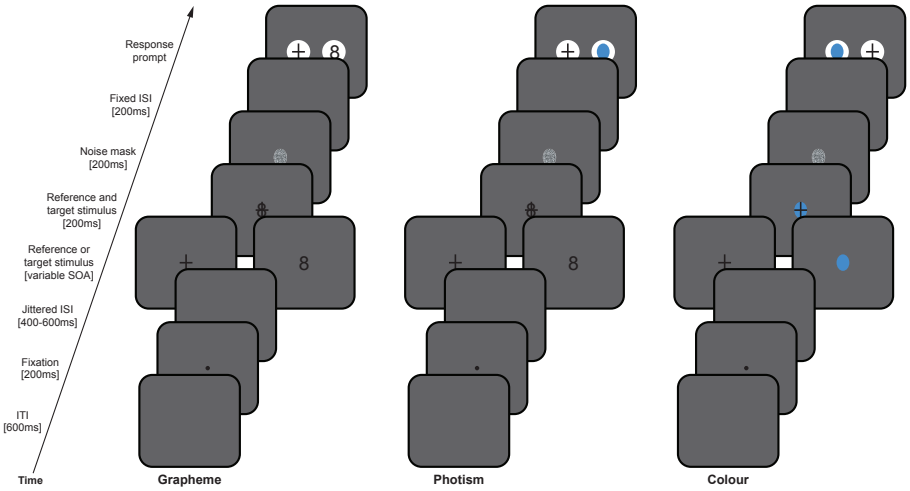

Figure 1. Temporal Order Judgement (TOJ) task. Temporal sequence of example trials in each of the three conditions (grapheme, photism, colour). Each trial involved the presentation of two stimuli (a reference [cross] stimulus and the target [grapheme or colour patch] stimulus) with a stimulus onset asynchrony (SOA) followed by a noise mask. Participants subsequently judged which of the two stimuli appeared first with the position of response options randomized across trials. Synaesthetes completed all three conditions whereas controls completed only the grapheme and colour conditions.

Procedure

After providing informed written consent, all participants completed the Eagleman battery (grapheme-colour associations) involving 3 blocks of 36 randomly-presented graphemes. Using these data, the

experimenter selected four numbers (and their associated RGB colour values) for use in the respective synaesthetes' TOJ task (see Statistical Analyses). Numbers were used for all synaesthetes because they tend to have more homogeneous structural characteristics. The four pairs were selected with consideration of the subjective vividness of photisms, grapheme-colour consistency, and inclusion of colours that were sufficiently distinguishable. Yoked controls were allocated a grapheme-colour set for the TOJ task based on demographic match (age, gender, and years of education) to a specific synaesthete.

Participants subsequently completed either three conditions (synaesthetes) or two conditions (controls) of the TOJ task. Each condition consisted of one practice block of 20 trials followed by four experimental blocks of 50 trials, amounting to 200 trials per condition. Condition order was counterbalanced across participants and matched for synaesthete-control pairs. Prior to each block, participants were instructed to focus on the black fixation circle at the start of the trial, then pay close attention to the target and reference (cross) stimuli and then judge to the best of their ability which appeared first on the monitor. Trial-by-trial variations in the SOA between target and reference stimuli were implemented using the PSI method (Kingdom & Prins, 2009). After each trial, this method updates a Bayesian posterior distribution across a range of possible values for the threshold and slope parameters of the psychometric function. Based on this posterior distribution, the method determines for each of the possible SOAs the probabilities of observing the two different responses (target or reference) and the corresponding entropy in the posterior distribution for each response. The SOA that minimizes expected entropy in the posterior distribution is subsequently applied in the next trial.

Each condition included four adaptive sequences, corresponding to each of the four unique stimuli. These sequences were randomly interleaved to minimize participants' ability to detect response pattern structures. Stimuli and visual prompts (1.3 (h) x 0.8 (w) cm) were presented at a distance of 65cm, subtending a visual angle of 1.1° x 0.7°. Stimulus presentation and data recording were implemented using Psychtoolbox (Brainard, 1997, Kleiner et al., 2007) and the adaptive PSI method was implemented using the Palamedes toolbox (Prins & Kingdom, 2018), both in MATLAB. The task was presented on a 19inch iMac screen with a 60Hz refresh rate.

After completing the task, synaesthetes completed the CLaN and ISEQ to determine their associator/projector status. This was done at the end of the experiment in order to ensure that the experimenter was blind to synaesthesia subtype throughout the experiment. Participants were subsequently debriefed regarding the purpose of the study.

Analysis

Grapheme-colour consistency

Colour variation for each grapheme across the three trials was recorded using the geometric distance in RGB colour space and the data was normalized between 0 and 1. Grapheme-consistency scores were calculated using the method of Rothen et al. (2013a). RGB values were converted to CIELUV values and the Euclidean distances in CIELUV colour space for the three trials of each individual grapheme were calculated. Consistency was then computed as the mean Euclidean distance across the entire grapheme set, with lower scores reflecting greater consistency. As per previous research (Rothen et al., 2013a), scores lower than 135 were taken to denote synaesthesia.

Associator/projector subtype status

Due to the challenges of determining associator-projector status (Simner, 2013) and limitations of individual measures, including the common tendency to incorrectly assume that projectors do not experience associator phenomenology, we drew upon multiple projector items from two different measures to determine associator-projector status. In particular, we disregarded the widespread assumption implicit in many measures that projectors cannot, or do not, experience associator-like synaesthetic phenomenology, on the basis of empirical research suggesting that associator and projector phenomenology reflect distinct dimensions of synaesthesia rather than converse positions on a continuum (Anderson & Ward, 2015). In turn, synaesthesia subtype was determined solely on the basis of projector-specific CLaN and ISEQ items; we used items from these two scales in order to avoid potential limitations or ambiguities inherent to either measure. Synaesthetes were classified as projectors if they scored at least a 4 out of 7 for one of the two

ISEQ projector items (1 and 2), and at least a 4 out of 5 for two of the five CLaN projector items (2, 4, 7, 8, and 10). Synaesthetes that did not meet these criteria were classified as associators. These criteria were agreed upon by the authors prior to the start of data collection (see OSF pre-registration). After reverse-scoring one negatively-worded CLaN item, the seven items together displayed excellent internal consistency (α =.93).

TOJ parameters

In each TOJ condition, the median threshold and median slope were computed from the final thresholds and slopes for the four adaptive sequences involving different target stimuli. In addition, the median RT across the 200 trials in each stimulus condition was also computed.

Statistical analyses

This was a pre-registered study (https://osf.io/59gwd/) and the data and task script are publicly available (https://osf.io/j4eau/). All analyses were performed in MATLAB and JASP (v. 0.12.2; JASP Team, Amsterdam, Netherlands). 10 univariate outliers ($M \pm 2.5$ *SD*s) across the 11 dependent variables (3%) were corrected to the corresponding outlier threshold; this included 2 grapheme thresholds (1 projector, 1 control), 2 grapheme slopes (1 projector, 1 control), 2 grapheme RTs (controls), 1 colour threshold (associator), 1 slope threshold (projector) and 2 colour RT (controls). There were no outliers among the three dependent measures in the photism condition or in the threshold difference measures.

The primary analyses consisted of hypothesis-focused independent Welch *t*-tests comparing associators and projectors on the central dependent variable of interest (photism thresholds), control *t*-tests comparing these two subtypes on grapheme and colour thresholds and condition difference (photism-grapheme and photism-colour) thresholds, and finally a hypothesis-driven *t*-test comparing synaesthetes and controls on colour thresholds. Effect sizes consisted of Hedges's gs and Bootstrap 95% CIs (10,000 samples, bias-corrected and accelerated method; Efron, 1987). In order to test two central null hypotheses of interest, namely that associators and projectors would not differ in grapheme and colour thresholds, we computed

Bayes factors for these differences using the corresponding difference between subtypes in photism thresholds as a prior. Bayes factors were computed in MATLAB using half-normal distributions ($BF_{0,SD}$) where *SD* corresponds to the prior (Dienes, 2014). BFs provide an estimate of the relative likelihood of one hypothesis relative to another; following convention (Dienes, 2011; Jeffreys, 1961), we interpret BFs less than 0.33 or greater than 3 as reflecting moderate evidence for the null and alternative hypotheses, respectively, and in-between values as reflecting insensitive evidence.

For completeness, analyses of thresholds were repeated using a series of mixed-model ANOVAs with different between-groups independent variables (Subtype: associator vs. projector; Group: associator vs. projector vs. control), and within-groups independent variables (grapheme vs. colour vs. photism [synaesthetes only]). Greenhouse-Geisser corrections were applied when data violated the assumption of sphericity. Secondary and exploratory analyses are described in the **Supplementary Materials**.

Results

Grapheme-colour consistency

Grapheme-colour consistency is widely used as a method to corroborate synaesthesia (Eagleman et al., 2007; Rothen et al., 2013a). All synaesthetes displayed averaged distances in CIELUV colour space below the threshold for synaesthesia (Rothen et al., 2013a), M=64, SD=27, whereas none of the controls did, M=306, SD=52. Synaesthetes' scores were significantly lower than those of controls, $t(30.93)=19.35$, $p<.001$, g=5.76 [4.72, 7.85], whereas associators, M=63, SD=26, did not significantly differ from projectors, M=66, SD=31, $t(14.56)=0.24$, $p=.81$, g=0.10 [-0.75, 1.02]. These results corroborate the presence of synaesthesia in these synaesthetes.

Pre-registered analyses

Pre-registered analyses consisted of primary analyses directly pertaining to the effects of interest including photism threshold differences across synaesthesia subtypes and secondary analyses of slopes and RTs.

Primary analyses

Photism thresholds

As predicted, projectors, *M*=84ms, *SD*=106, displayed significantly lower photism thresholds than associators, *M*=217ms, *SD*=163, *t*(21.74)=2.41, *p*=.025, corresponding to a large effect, *g*=0.88 [0.25, 1.58] (see **Figure 2**). The magnitude of this effect was only slightly attenuated or similar when using difference threshold scores, accounting for grapheme thresholds (photism-grapheme), *t*(21.63)=1.76, *p*=.093, *g*=0.65 [-0.06, 1.32], and colour thresholds (photism-colour), *t*(21.90)=2.57, *p*=.018, *g*=0.93 [0.31, 1.61].

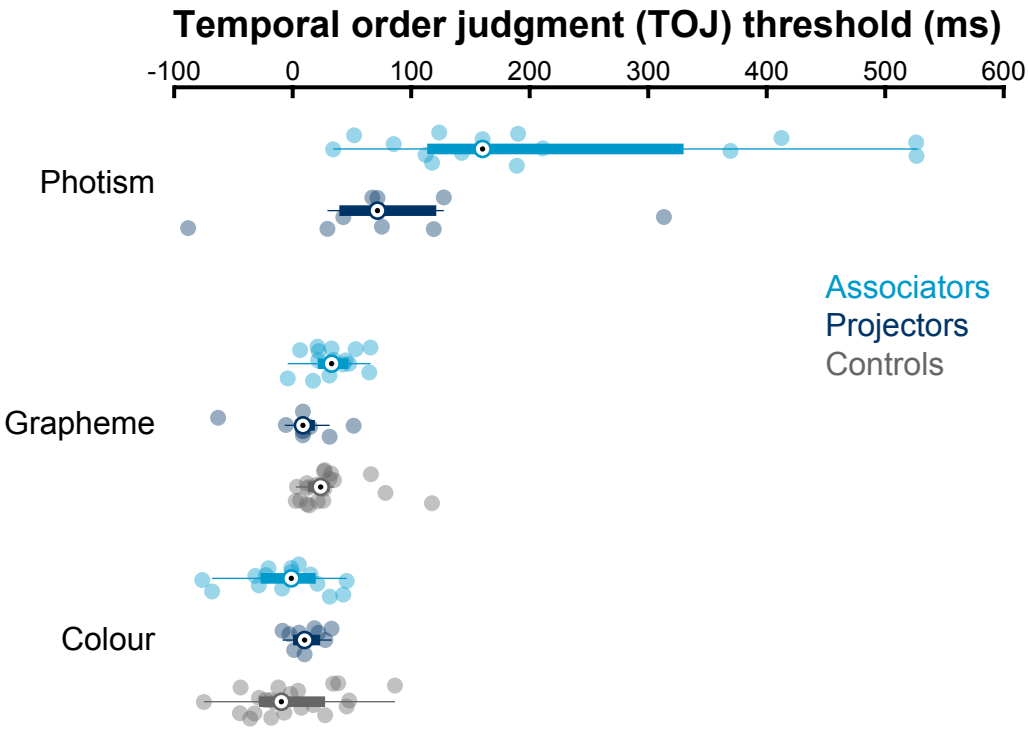

Figure 2. Box plots and individual values for TOJ thresholds as a function of Condition and Group. Controls did not complete the photism condition. Positive thresholds indicate that the target stimulus (photism, grapheme, or colour) was perceived later than the reference stimulus (cross) whereas negative thresholds indicate that the target stimulus was perceived earlier than the reference stimulus.

Grapheme thresholds

We expected that the three groups would not differ in grapheme thresholds. As predicted, controls, *M*=29, *SD*=27, had comparable thresholds relative to synaesthetes, *M*=25, *SD*=32, and did not significantly differ, $t(43.77)=0.42$, $p=.67$, $g=0.12$ [-0.49, .64]. Unexpectedly, projectors displayed lower grapheme thresholds, *M*=7, *SD*=32, than associators, *M*=36, *SD*=27, $t(14.68)=2.32$, $p=.035$, $g=0.99$ [0.35, 1.79]. Using the associator-projector difference in photism thresholds as a prior, *M*=133, we found evidence that the subtype difference in grapheme thresholds, *M*=29, *SE*=12, was consistent with the hypothesis, that the two subtypes differ, $BF_{0,133}=3.23$. However, it is notable that projectors did not significantly differ from controls, $t(12.92)=1.83$, $p=.091$, $g=0.76$ [0.07, 1.47]; similarly associators and controls did not significantly differ, $t(30.35)=0.82$, $p=.42$, $g=0.27$ [-0.32, 1.09].

Colour thresholds

We did not expect associators and projectors to differ in colour thresholds although we suspected that synaesthetes would exhibit earlier colour thresholds than controls. In contrast with the photism threshold results, projectors tended to display higher colour thresholds, *M*=12, *SD*=14, than associators, *M*=-1, *SD*=36, although this did not achieve significance, $t(19.96)=1.75$, $p=.096$, $g=0.59$ [0.05, 1.33]. As above, we used the associator-projector difference in photism thresholds as a prior, *M*=133, and found that there was evidence that the subtype difference in colour thresholds, *M*=-13, *SE*=9, was consistent with the null hypothesis that the two subtypes do not differ, $BF_{0,133}=0.027$. In addition, the expected colour advantage in synaesthetes did not hold, as controls, *M*=-2, SD=38, exhibited similar colour thresholds relative to synaesthetes, *M*=0, *SD*=30, $t(40.35)=0.80$, $p=.91$, $g=0.08$ [-0.48, 0.73].

Factorial analyses of variance

For completeness, we repeated these analyses using three mixed-model ANOVAs with Condition as a repeated-measures variable and subtype (associator vs. projector) and group (control vs. synaesthete and control vs. associator vs. projector) as between-groups factors.

The 3 (Condition) x 2 (Synaesthesia subtype) mixed-model ANOVA on thresholds yielded a significant effect of Condition, $F(1.09, 23.88)=17.66$, $p<.001$, $\eta^2_p=.45$, a significant Subtype effect, $F(1,22)=6.29$, $p=.020$, $\eta^2_p=.22$, which were moderated by a marginal Condition x Subtype interaction, $F(1.09,23.88)=4.05$, $p=.053$, $\eta^2_p=.16$. *Post hoc* Tukey tests revealed that this interaction was driven by significantly lower thresholds among projectors than associators in the photism condition, $M=133$, $SE=37$, $t=3.62$, $p=.007$, but not in the grapheme, $M=29$, $SE=37$, $t=0.80$, $p=.97$, or the colour condition, $M=-18$, $SE=37$, $t=0.49$, $p=1.00$ (for all contrasts, see **Supplementary Materials, Table 2**).

The 2 (Condition) x 3 (Group) mixed-model ANOVA on thresholds yielded a significant Condition effect, $F(1,43)=13.31$, $p<.001$, $\eta^2_p=.24$, a non-significant Group effect with a miniscule effect size, $F(2,43)=0.16$, $p=.85$, $\eta^2_p<.01$, which were moderated by a Condition x Group interaction, $F(2,43)=4.15$, $p=.022$, $\eta^2_p=.16$. *Post hoc* Tukey tests revealed that this interaction was driven by significantly higher thresholds in the grapheme than the colour conditions in both controls, $M=31$, $SE=8$, $t=3.70$, $p=.005$, and associators, $M=42$, $SE=10$, $t=4.14$, $p=.002$. By contrast, projectors displayed relatively similar thresholds in the two conditions, $M=5$, $SE=13$, $t=0.38$, $p=0.99$ (for all contrasts and analyses collapsing across synaesthesia subtypes, see **Supplementary Materials, Table 3**).

Secondary and exploratory analyses

Secondary analyses were performed on psychometric function slopes and RTs in the different conditions in controls and synaesthetes. These analyses did not reveal any significant differences between groups or synaesthesia subtypes. They further suggested that synaesthetes displayed lower (i.e., flatter) slopes and slower RTs in the photism condition relative to the grapheme and colour conditions (see **Supplementary Results**).

Exploratory correlations assessed associations between TOJ thresholds in the three conditions and psychometric measures pertaining to synaesthesia phenomenology using Spearman skipped correlations (Pernet et al., 2012). Across synaesthetes, photism thresholds were weakly, albeit non-significantly, correlated with self-reported synaesthesia phenomenology (see **Supplementary Results**).

Discussion

By coupling a temporal-order judgment (TOJ) task with adaptive psychophysics, our results corroborate the hypothesis that projector synaesthetes experience colour photisms earlier than associator synaesthetes (Ruiz et al., 2015; van Leeuwen et al., 2011). Further analyses suggest that this effect was independent of TOJ thresholds for graphemes and colours and thus this difference between subtypes seems to be specific to photism perception and not reflective of a general colour processing benefit or response bias in projectors (Ruiz et al., 2015). These results are consistent with the view that synaesthesia subtypes experience colour photisms through distinct neurophysiological mechanisms (Amsel et al., 2017; van Leeuwen et al., 2011) and have implications for the neural basis of synaesthesia (Ward, 2013).

Our central prediction, that projectors would display selectively lower photism thresholds than associators, was supported. This result indicates that photisms have greater temporal perceptual salience in projectors and are consistent with our broader hypothesis that photism perception occurs earlier in this subtype of synaesthesia. Our results further suggest that differential temporal priority in these two subtypes is specific to photism perception and not robustly observed in colour and grapheme perception. Earlier photism perception in projectors relative to associators complements the previous observation that projector synaesthesia seems to occur through a bottom-up (direct) neural pathway – from LSA to V4 – whereas associator synaesthesia involves a top-down (indirect) pathway involving intermediary processing by SPL before V4 activation (van Leeuwen et al., 2011). Our results suggest the latter route produces an average delay of ~133ms although this difference was variable in our sample. The relatively early time course of photism perception in projectors is conceptually congruent with a magnetoencephalography study of projectors showing V4 activation ~114ms after grapheme presentation (Brang et al., 2010). The greater temporal perceptual salience of photisms in projectors also aligns with an ERP study showing that projector phenomenology among synaesthetes was associated with reduced P1 and larger N170 amplitudes in response to graphemes, which the authors suggested could reflect V4 cross-activation among projectors during grapheme processing (Amsel et al., 2017). The present results build on these prior studies by

dissociating grapheme and photism processing through different attentional conditions and by harnessing adaptive psychophysics to provide an estimation of differential photism awareness in synaesthesia subtypes. By contrast, we expect that results suggestive of top-down mechanisms in synaesthesia (e.g., Brauchli et al., 2018) are attributable to an under-representation of projectors. The differential time course of photism awareness in synaesthesia subtypes remains undetermined but could be addressed more rigorously using other methods such as continuous flash suppression (Tsuchiya & Koch, 2005) and by coupling neurophysiological methods with strong temporal resolution (Amsal et al., 2017; Brang et al., 2010) with precise psychophysical methods. These various effects may be subserved by enhanced parietal cortex power in the alpha band frequency and/or enhanced primary visual cortex excitability in projectors relative to associators (Cohen et al., 2015; Terhune et al., 2015a; Terhune et al., 2015b), or superior imagery abilities in projectors (Amsel et al., 2017; Simner, 2013). Insofar as the two subtypes did not differ in colour thresholds - with Bayesian evidence in favor of the null hypothesis of no difference - it appears that these differential pathways between associators and projectors are specific to colour photisms and not reflective of broader differences in colour processing between these subtypes.

The observation of earlier photism perception in projectors can help to understand various unique characteristics in this subgroup. Previous research studying the "pop-out effect" indicated that projector synaesthetes experience colours more reliably relative to associators and that projectors are more likely to be aware of their photisms during brief presentations (Ward et al., 2010; Palmeri et al., 2002; Smilek et al., 2003). Accordingly, projector synaesthetes displaying lower photism thresholds in the present study would be expected to display earlier photism awareness in such paradigms. Similarly, the previous observations that projectors exhibit faster photism colour naming and greater Stroop interference from photisms during veridical colour naming than associators (Dixon et al., 2004) are plausibly attributable to earlier photism awareness in this subgroup. An outstanding question is whether associators and projectors are best understood as discrete subtypes or as overlapping expressions of a heterogeneous phenomenon. A strict interpretation of van Leeuwen et al.'s (2011) neurophysiological model implies no overlap in photism TOJ thresholds in the two subtypes, but this is not borne out in our data. However, overlap in photism thresholds

between subtypes in our data is plausibly attributable to ancillary inter- and intra-individual differences in factors independent of synaesthesia such as response biases, selective attention, colour processing, and random errors. In addition, classification of associators and projectors based on subjective psychometric measures is partly limited by idiosyncratic responses. For instance, two of the three asociators with the lowest photism thresholds met our projector criteria on the CLaN, but not on the ISEQ, whilst the single projector who had a borderline-outlying high photism threshold only marginally met the CLaN criteria. These issues warrant greater attention to the reliability and validity of associator-projector classification methods.

An alternative interpretation of these results is that projectors displayed lower thresholds than associators because of a response bias. TOJ thresholds are indeed influenced by response biases (Grabot & Wassenhove, 2017; Yates & Nicholls, 2011). For example, participants might have a bias toward a specific category (e.g., colour stimuli relative to the reference stimulus) that would manifest as a tendency to estimate colour stimuli as being presented earlier than the reference stimulus and yield an artifactually lower threshold in the colour condition of this paradigm. Insofar as the observed threshold difference across subtypes was specific to photism thresholds and condition thresholds did not significantly correlate, the present data are at odds with a general response bias for non-reference stimuli or percepts in projectors as well as a specific bias for colours. Thus, if the present results are interpreted as a bias they are reflective of a photism-specific bias among projectors. Although this interpretation cannot be excluded completely, we maintain that earlier photism perception among projectors provides a more parsimonious explanation of the results. First, the results are consistent with previous studies using different behavioural, electrophysiological, and neuroimaging methods showing differential processing of photisms in early perceptual stages in paradigms that are unlikely to be confounded by response biases (Amsel et al., 2017; Brang et al., 2010; van Leeuwen et al., 2011; see also Cohen et al., 2015; Terhune et al., 2015a). This collective body of results aligns with the interpretation that projectors display earlier photism access. Moreover, the estimated lag of photism, relative to grapheme, perception (i.e., photism threshold - grapheme threshold: projectors: 77ms, associators: 181ms) aligns with what would be expected if TOJ

thresholds provide an approximation of the time course of photism perception whereas it is unclear how these lags can be explained by a response bias. Similarly, interpreting this subtype difference as a response bias is conceptually challenging given that projectors did not display any evidence for a similar bias for the same colours in the veridical colour condition. In addition, the results cannot be attributed to a simple motor response bias or a spatial attention effect given that response options were randomised on a trial-by-trial basis and all stimuli were presented centrally, respectively. The potential for a selective bias in projectors is further reduced because insofar as the experimenter was blind to synaesthesia subtype, it is highly unlikely that she could have implicitly or explicitly influenced synaesthetes to differentially bias their responses in a specific way. Finally, research has shown that psychophysical methods that have been argued to circumvent responses biases in TOJ paradigms, such as simultaneity judgment tasks, yield similar results (Yates & Nicholls, 2011); thus a response bias is unlikely to explain the observed photism threshold difference between synaesthesia subtypes (113ms). Nevertheless, this issue could potentially be explored further through the inclusion of a control group of non-synaesthetes who are trained in grapheme-colour associations (e.g., Rothen et al., 2018; Saiki et al., 2011). We would expect that trained controls would display higher photism thresholds than projectors, and potentially, associators although trained controls that display projector-type phenomenology (e.g., Rothen et al., 2018) might potentially display lower thresholds similar to our projectors, and lower than trained controls that do not display these phenomenological effects, thereby replicating the observed association between variability in synaesthetic phenomenology and photism thresholds.

An unexpected result was that projectors displayed slightly lower (~29ms) grapheme thresholds than associators. Although this effect was significant when performing direct comparisons, it did not survive a *post hoc* Tukey correction. Additionally, neither associators' nor projectors' grapheme thresholds significantly differed from those of controls indicating that projectors do not seem to display atypical grapheme processing. Nevertheless, if this effect is genuine it may relate to other evidence suggesting atypical early grapheme processing in projectors relative to associators (Amsel et al., 2017). At first glance, it could be taken as evidence that synaesthetic photisms facilitate grapheme processing, similar to putative

pre-attentive pop-out effects in synaesthesia (Ward et al., 2010). However, this seems highly unlikely given that grapheme and photism thresholds did not significantly correlate (see **Supplementary Materials**) and the photism threshold difference between subtypes remained strong in magnitude (g=0.65) after adjusting for grapheme thresholds. Taken together, these results suggest that the difference between associators and projectors in grapheme thresholds is not robust. This is in line with its notably smaller magnitude relative to the differential photism threshold effect in synaesthesia subtypes (~133ms), although Bayesian statistics showed that the former was consistent with the latter. These results suggest that lower grapheme and photism thresholds among projectors reflect independent effects. Further research is required to replicate the unpredicted difference in grapheme thresholds between synaesthesia subtypes.

Controls and synaesthetes did not reliably differ in grapheme or stimulus colour processing with uniformly small effect sizes. This suggests that synaesthetes do not exhibit atypical conscious access of graphemes relative to controls. The lack of a group difference in the stimulus colour condition is potentially surprising given the multitude of studies highlighting superior colour discriminationin in synaesthetes (e.g., Banissy et al., 2013; Hamada et al., in press; Ovalle-Fresa et al., in press). This apparent discrepancy is potentially because we assessed temporal order characteristics of colour processing, which was not done in previous studies, to our knowledge. That is, most previous studies compared participants in the capacity to distinguish between different colours whereas our study assessed the capacity to determine whether a colour stimulus or achromatic stimulus appeared first. Moreover, insofar as both controls and synaesthetes displayed near-zero colour thresholds, we might have observed a ceiling effect in temporal order judgements in this condition; that is, this task might be insufficient to index atypical colour processing in synaesthesia. Although we could not confirm differences in processing speed for veridical colours between synaesthesia subtypes or between synaesthetes and controls, this does not exclude the possibility that synaesthesia confers an advantage in colour discrimination. For example, our results could be reconciled with the extant literature by conjecturing that synaesthetes have superior colour discrimination than controls but that the two groups do not differ in the temporal perceptual salience of colours. There was a weak, albeit non-significant, trend for projectors to display higher colour thresholds than associators, which is

potentially consistent with research suggesting that associators are more sensitive to synaesthetic relative to non-synaesthetic colours than projectors (Hamada et al., in press). However, it should be acknowledged that projectors did not significantly differ from controls and all projectors' colour thresholds fell within the colour threshold distributions of both associators and controls. Although this unexpected effect warrants further attention, it should be treated with caution.

In summary, our results suggest that projector synaesthetes experience colour photisms earlier than associator synaesthetes, thereby corroborating the hypothesis that projectors process synaesthetic colours through a direct, bottom-up pathway whereas associators process synaesthetic colours more indirectly through a top-down pathway (Amsal et al., 2017; Brang et al., 2010; van Leeuwen et al., 2011). These results help to explain the impact of differential visuospatial phenomenology of colour photisms on a range of cognitive-perceptual tasks in synaesthetes (Ward et al., 2010) and reinforce the importance of elucidating the characteristics and mechanisms underlying heterogeneity in this condition.

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