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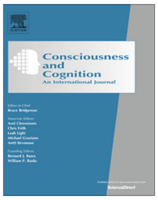

Cross-modal, bidirectional priming in grapheme-color synesthesia

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ABSTRACT

Grapheme-color synesthetes perceive achromatic graphemes to be inherently colored. In this study grapheme-color synesthetes and non-synesthetes discriminated (1) the color of visual targets presented along with aurally presented digit primes, and (2) the identity of aurally presented digit targets presented with visual color primes. Reaction times to visual color targets were longer when the color of the target was incongruent with the synesthetic percept reported for the prime. Likewise, discriminating aurally presented digit targets took longer when the color of the prime was incongruent with the synesthetic percept for the target. These priming effects were absent in non-synesthetes. We conclude that binding between digits and colors in grapheme-color synesthetes can occur bidirectionally *across* senses. The results are in line with the idea that synesthesia is the result of linking inducing stimuli (e.g. digits) to synesthetic percepts (colors) at an abstract – supra-modal – conceptual level of processing.

1. Introduction

For grapheme-color synesthetes, letters or digits appear to be inherently colored (for a recent review on synesthesia in general, see Ward, 2013). At first sight, the phenomenology in this type of synesthesia suggests a unidirectional relation between inducer (the stimulus inducing the synesthetic experience) and its concurrent (the resulting synesthetic experience).[1] For a typical grapheme-color synesthete, an achromatic digit (e.g. the digit ‘2’) will for example be perceived as having a specific color (e.g. red), but presenting that specific color to the synesthete will generally not lead to the perception of the digit ‘2’. Interestingly though, a case of explicit bi-directional synesthesia has been reported (Cohen Kadosh, Cohen Kadosh, & Henik, 2007; Cohen Kadosh & Henik, 2006), in which a digit-color synesthete reported perceiving digits when presented with specific colors. In a speeded reaction time task, this synesthete compared the length of lines of different colors. When the smaller line had the synesthetic color of a numerically larger number compared to that of the larger line, reaction times increased. Next to this case of *explicit* bidirectionality, there is evidence suggesting that bidirectionality is present at the behavioral level even in synesthetes for whom the *explicit* phenomenomenal relation between inducer and concurrent is unidirectional (Brugger, Knoch, Mohr, & Gianotti, 2004; Cohen Kadosh et al., 2005; Gebuis, Nijboer, & van der Smagt, 2009a, 2009b; Gevers, Imbo, Cohen Kadosh, Fias, & Hartsuiker, 2010; Johnson, Jepma, & De Jong, 2007; Knoch, Gianotti, Mohr, & Brugger, 2005; McCarthy, Barnes, Alvarez, & Caploviz, 2013; Richer, Beaufils, & Poirier, 2011; Weiss, Kalckert, & Fink, 2009). In the priming studies by

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[1] The terms ‘inducer’ and ‘concurrent’ were introduced by Grossenbacher and Lovelace (2001).

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Gebuis et al. (2009a, 2009b), for example, shorter RTs for identifying a target were found not only when the inducer was preceded by the concurrent, but also the other way round. Next to bidirectional priming effects, synesthetes can even use synesthetic colors to complete cognitive tasks, such as using colors (associated with a specific number) to evaluate simple math problems (McCarthy et al., 2013), demonstrating that these synesthetes have access to numerical information through color.

A recent hypothesis regarding synesthesia is that cross-modal interactions are exaggerated compared to non-synesthetes (Afra et al., 2012; Brang, Williams, & Ramachandran, 2011; Cohen Kadosh & Henik, 2007; Hubbard, 2007; Mulvenna & Walsh, 2006; Robertson, 2003; Ward, Huckstep, & Tsakanikos, 2006; Zamm, Schlaug, Eagleman, & Loui, 2013). Brang et al. (2011), for example, showed that the *non-synesthetic* auditory-visual double flash illusion (the illusory perception of a visual flash induced by an auditory event, (Shams, Kamitani, & Shimojo, 2000)) was stronger in synesthetes compared to non-synesthetes. Importantly, this audio-visual illusion was studied in synesthetes with unimodal grapheme color (e.g. visual-visual) synesthesia. This hypothesis of exaggerated cross-modal interactions is related to the argument that some forms of synesthesia are caused by the recruitment of cross-modal mechanisms, that are also present in the non-synesthete brain (Chiou, Stelter, & Rich, 2013; Ward et al., 2006). For example, Ward et al. (2006), using a group of music-color synesthetes, showed that detection of a peripheral target could be facilitated by a congruent (synesthetic) sound-color coupling, an effect that is reminiscent of exogenous cross-modal cuing. The results of this and other studies demonstrating recruitment of (exaggerated) cross-modal interactions in synesthetes are generally interpreted as being the result of 'hyperbinding' between two sensory modalities, at the level of parietal areas (Hubbard, 2007).

The aim of the present study is the following: if synesthesia is the result of the recruitment of cross-modal interactions, and if the coupling between inducer and concurrent is bidirectional, it is to be expected that bidirectionality is observed even when inducer and concurrent are presented to different sensory modalities. In order to test this idea, we recruited grapheme-color synesthetes who reported perceiving color not only when presented with graphemes, but also with aurally presented digits. Bidirectionality was assessed in a simple priming paradigm (similar to Gebuis et al., 2009a, 2009b) where prime and target were presented to different sensory modalities. If bidirectional priming is observed across different sensory modalities, it will provide evidence that grapheme-color synesthesia is caused by bidirectional, supra-modal binding between letters or digits on the one hand and colors on the other. Such a result would also be in support of the idea that synesthesia is the result of conceptual links between inducers and concurrents (Chiou & Rich, 2014, Simner, 2012). In this conceptualization of synesthesia, the link between inducer (grapheme) and concurrent (color) occurs at a level that transcends the level of early sensory processing: it occurs at a level where abstract representations of concepts are linked to concrete features of these concepts. We will evaluate the results in the context of this model in Section 4.

2. Method

We assessed the bidirectionality of cross-modal digit-color associations of synesthetes and compared it to a group of non-synesthetes for which *explicit* associations were absent. The experiment consisted of four blocks: two containing auditory primes and visual targets and two containing visual primes and auditory targets. Visual target blocks were of two kinds, depending on the nature of the prime. In a digit prime–color target block, participants responded to a visual target color, which was presented along with an auditory digit prime. In a color prime–digit target block, an auditory digit was the target and a visual color the prime. In both blocks, trials were of two kinds: the prime-target coupling was either congruent or incongruent to the mappings of synesthetes (see below). Two other blocks served as controls: in neutral prime–color target blocks, the visual target was presented along with a neutral auditory prime; in neutral prime–digit target blocks an auditory target was presented with a neutral visual prime. In these blocks primes were presented that did not elicit a synesthetic association.

2.1. Participants

Eleven synesthetes and eight[2] age- and gender-matched non-synesthetes, all naïve as to the purpose of the study, took part in the experiments. Only synesthetes with the presence of grapheme–color associations, but with no history of substance abuse and neurological disorders, were included. Participants gave informed consent to participate in the study according to the Declaration of Helsinki.

2.2. Assessing synesthesia

We made sure that the synesthetes in the study had an explicit unidirectional coupling between inducer and concurrent by asking them about the nature of their synesthesia. To map inducer-concurrent relations, each synesthete listened to recorded sounds of spoken numbers and had to select a color that matched as closely as possible the synesthetic color elicited by the digit using a modified version of the Texsyn ToolBox (Eagleman, Kagan, Nelson, Sagaram, & Sarma, 2007) for Matlab. This procedure was repeated three times, after which color variation was calculated for each number. Finally, total color variation for all numbers was computed for each participant, according to the procedure of (Eagleman et al.,

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[2] Only eight non-synesthetes were needed since the data of three synesthetes was excluded from data analysis (see Section 3).

2007). Average total color variation for the synesthetes was $M = 0.41$ (range: min = 0.18, max = 0.67), which is classified as synesthetic (total variation < 1; Eagleman et al., 2007). Next, four numbers for which the color percept was most vivid were chosen by each synesthete. These four numbers and their associated colors were used in the experiment (Fig. 2).

2.3. Apparatus

The visual stimuli were presented using an Apple Mac Pro on a 22' LaCie Electron Blue III monitor with a refresh rate of 120 Hz. The auditory stimuli were presented via Harman Kardon speakers placed on both sides adjacent to the monitor. The screen was placed on a distance of 114.5 cm from the participant. The visual and auditory stimuli were prepared and presented using MATLAB in conjunction with the Psychophysics Toolbox (Brainard, 1997).

2.4. Stimuli

Stimuli are presented in Fig. 1. A prime (auditory in visual target blocks; visual in auditory target blocks) was presented along with a target (visual in visual target blocks; auditory in auditory target blocks) in all four blocks. The visual stimulus (whether prime or target) was a square consisting of a single color (for both visual target blocks and for the auditory target-color prime block) or a square where one of four colors was assigned randomly to each pixel (neutral prime-auditory target). The squares were 2 by 2 deg VA and were presented at the center of the screen. The auditory primes (and targets) were digits spoken in Dutch by a male voice and recorded via PRAAT software (Boersma & Weenink, n.d.). For creating the neutral auditory prime, we first computed the average Fourier power spectrum and phase of each synesthete's four digits. Next, we computed the inverse transform of the average power spectrum with a scrambled phase. Both auditory and visual neutral primes did not lead to explicit synesthetic percepts. The colors used for the visual stimuli were the matched synesthetic percepts for these four digits (see assessing synesthesia). Each synesthete and a matched non-synesthete were presented with a unique set of prime-target combinations (see Fig. 2).

2.5. Procedure

Participants performed a reaction time experiment. They were instructed to keep fixating a fixation cross throughout a trial, and to identify as fast and accurately as possible – by choosing between four options – which color was presented in visual target blocks, or which digit was presented in auditory target blocks via one of four buttons on a response box. Each participant used the same buttons for each digit and color throughout the entire experiment.

A single trial started with the presentation of a gray fixation cross at the center of the screen. The fixation cross changed to white 750 ms later, to alert the participant that prime and target were to appear soon. After this, the target would appear 750–1000 ms later. In visual target blocks, the target was a colored square; in auditory target blocks, the target was a digit, presented aurally. In visual target blocks, an auditory prime was presented with a latency of −400, 0 and 200 ms with respect to the onset of the visual target. In auditory target blocks, a visual prime was presented with a latency of −200, 0 and 100 ms with respect to the onset of the auditory target.

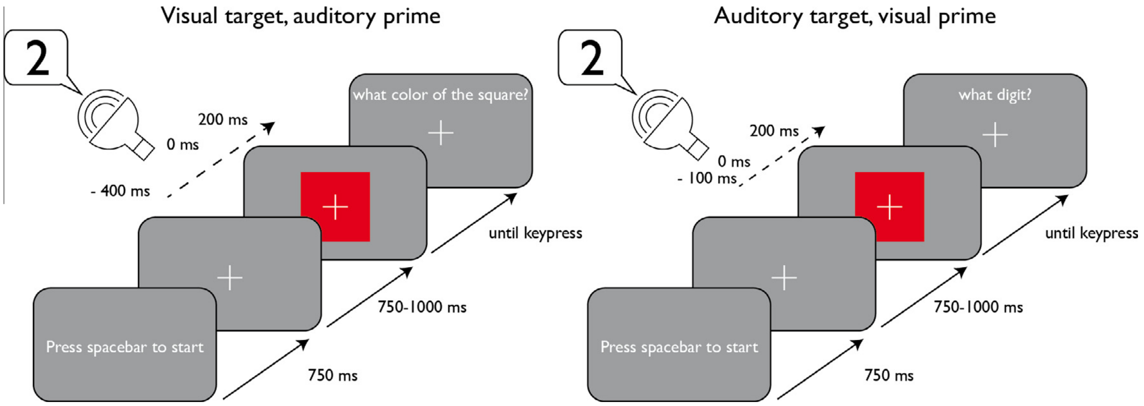

Fig. 1. Stimulus & procedure. Schematic representation of the sequence of a trial in blocks containing visual targets and auditory primes (left panel) versus blocks containing auditory targets and visual primes (right panel). In both blocks, the participant initiated a trial by pressing the space bar. 750 ms later a white fixation cross appeared. Between 750 and 1000 ms later a colored square appeared at fixation. In auditory prime–visual target blocks, an auditory prime was presented with a latency of −400, 0 or 200 ms with respect to the onset of the colored target. Here, participants reported the color of the square as soon and accurately as possible. In visual prime–auditory taget blocks, the colored square served as the prime and was presented with a latency of −200, 0 and 100 ms with respect to the auditory target (note that different latencies are presented in the figure, this is because for display purposes, the latency is computed with respect to the *visual* stimulus). In these blocks, participants identified as fast and accurately as possible which digit was presented. (The reader of the non-colored print version of this article is referred to the web version for interpretation of the references to color in the figure legend.)

2	3	4	6
3	4	5	8
2	3	5	8
2	3	4	8
1	4	5	10
2	3	5	11
2	3	4	5
2	4	6	8

Fig. 2. Synesthetic digit-color pairs. Each row represents four digit-color pairs (one in each column) for a single synesthete and his or her control. Each digit and color pair was determined as described in the method section. (The reader of the non-colored print version of this article is referred to the web version for interpretation of the references to color in the figure legend.)

In digit prime–visual target blocks, four target colors were used along with four auditory digits at the three different latencies. Each digit was either congruent (i.e. matching the synesthetic inducer-concurrent relation) or incongruent to one of the four targets. This resulted in a $4 * 2 * 3$ design (target $*$ congruency $*$ latency). Color prime–auditory target blocks had the same design, except that the nature of prime and target was reversed. For congruent prime-target combinations, each prime was coupled with a single target (the auditory ‘two’ with a green visual square in row 1 of Fig. 2); for incongruent combinations, each prime was coupled with one of three possible targets (the ‘two’ could be coupled with a blue, yellow or purple square). To keep an equal amount of congruent and incongruent trials (50% each), specific congruent prime-target combinations (e.g. ‘two’ and green) occurred more often than specific incongruent combinations (e.g. ‘two’ and blue). In neutral prime blocks, four targets were combined with a single (neutral) prime with three different latencies, leading to a $4 * 3$ (target $*$ latency) design.

3. Results

3.1. Analyses

Three synesthetes were excluded from analysis since they performed less than 70% correct on one of the four blocks. Closer inspection of the errors revealed that these synesthetes performed particularly poor on incongruent trials in which the target was visual, which potentially indicates that their synesthetic percept induced by the digit was interfering with labeling the color of the target to such an extent that they made many errors. Although this observation is interesting, we excluded their data from the analysis since a prerequisite for inclusion was that they were performing the task (as fast and accurately as possible reporting the color of the target), which they clearly did not. The remaining participants (eight synesthetes and eight non-synesthetes) performed 90% correct or higher on all blocks. In statistical analyses (repeated measures ANOVAs) and in the results presented in Fig. 3 we analyzed the median RTs for correct trials, averaged across observers. The results are discussed in the following order: first we report the effect of an auditory prime on visual targets that are congruent or incongruent with (synesthetic) visual targets, and compare this effect between both groups (synesthetes and non-synesthetes). To zoom in on the effect of primes on targets, we next analyzed the effect of congruency separately for each

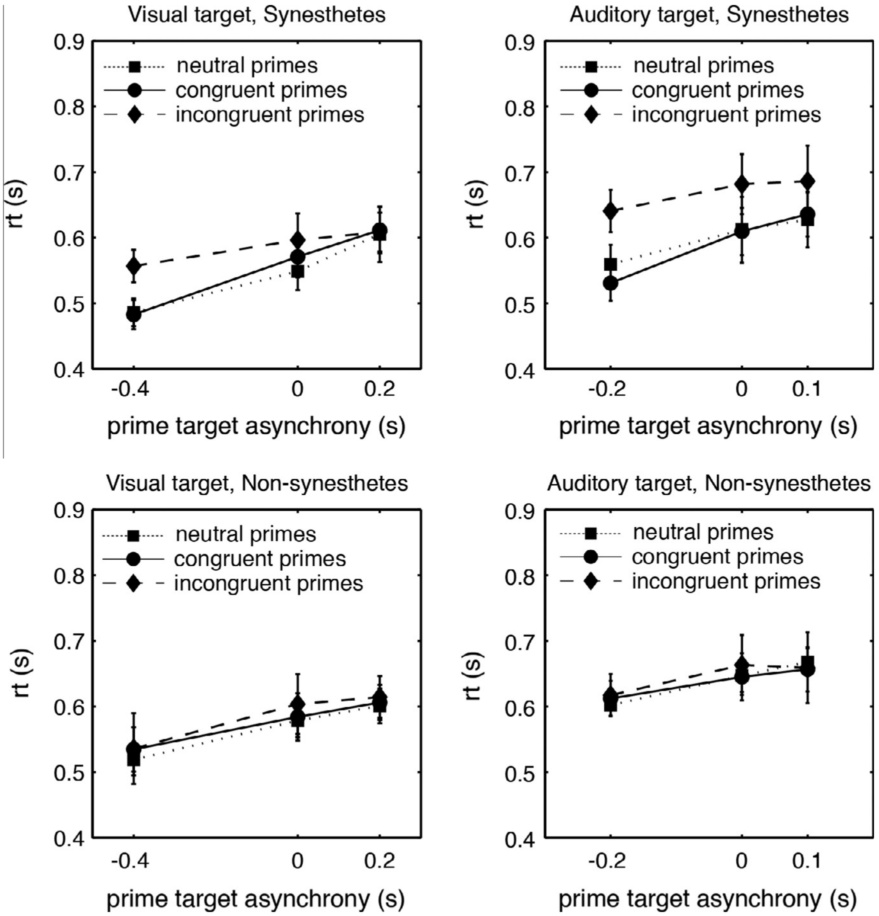

Fig. 3. Results. The data are plotted according to the nature of the prime-target relation: the left column represents averages of median reaction times for correct trials when the prime was auditory and the target visual; the right column represents the data when the prime was visual and the target auditory. The top row represents data for synesthetes; the bottom row for non-synesthetes. Dotted lines and squares represent reaction times for targets presented with neutral primes; solid lines and circles for targets congruent to (synesthetic) color associations; dashed lines and diamonds for targets incongruent to (synesthetic) color associations. Errorbars represent standard errors of the mean. Note, negative values on the abscissa denote conditions where the prime preceded target onset, positive values where target onset preceded prime onset. For auditory primes and visual targets, reaction times were longer for visual targets when their colors did not match with the synesthetic color associated with the auditory prime for synesthetes, but not for non-synesthetes, at the first and second SOA. For visual primes and auditory targets, reaction times were longer for auditory targets when the color of the prime was incongruent with the color associated with the auditory target. This effect occurred at all three SOAs, but only for synesthetes. See text for details.

group. We performed the same analysis for the block where the nature of prime and target were reversed (visual prime, auditory target). Next, we analyzed differences between groups for the blocks where a neutral prime (auditory or visual) was presented along with a visual or auditory target respectively. Our final analysis concerns the nature of a potential effect of congruency: we address whether primes facilitate and interfere with responding to congruent and incongruent targets respectively. Each analysis of reaction time is preceded by an analysis of performance (for example, to check whether differences in RT can be accounted for by speed-accuracy trade-offs).

3.2. Auditory prime and visual target

Analysis of *performance* (percentage correct) revealed a main effect of congruency only ($F(1,14) = 13.21$, $p = .003$, $\eta^2 = 0.49$), with a higher performance on congruent trials ($M = 97.3\%$ correct) compared to incongruent trials ($M = 95.7\%$ correct). No main effects of group (F1,14) = 0.90, $p = .36$, $\eta^2 = 0.06$), latency ($F(2,28) = 2.68$ $p = .086$, $\eta^2 = 0.16$), nor interactions between them or with congruency ($F < 1.54$, $p > .23$, $\eta^2 < 0.10$), were observed.

The analysis of *reaction times* revealed a significant three-way interaction between group, congruency and latency ($F(2,28) = 6.5$, $p = .005$, $\eta^2 = 0.32$), significant interactions between group and congruency ($F(1,14) = 5.2$, $p = .038$, $\eta^2 = 0.27$) and between congruency and latency ($F(2,28) = 4.1$, $p = .028$, $\eta^2 = 0.23$). In addition, main effects were revealed for both congruency ($F(1,14) = 18.0$, $p = .001$, $\eta^2 = 0.56$) and latency ($F(2,28) = 46.6$ $p < .0001$, $\eta^2 = 0.77$), but – importantly – not for group (F1,14) = 0.05, $p = .8$, $\eta^2 = 0.004$). To understand these results (especially the three-way interaction), and since we expected a congruency effect in synesthetes, but not in non-synesthetes, we performed separate analyses for each group. For synesthetes, we observed significant interactions between congruency and latency ($F(2,14) = 9.8$, $p = .002$, $\eta^2 = 0.58$), as well as significant main effects for each of them (congruency: $F(1,7) = 11.9$, $p = .011$, $\eta^2 = 0.63$; latency: $F(2,14) = 24.4$, $p < .0001$, $\eta^2 = 0.78$). The interaction between congruency and latency was caused by RTs in congruent trials being significantly shorter than RTs in incongruent trials for primes preceding the target by 400 ms ($t(7) = 6.2$, $p < .0001$, $d = 4.7$), and for simultaneous onset ($t(7) = 2.0$, $p = .044$, $d = 1.5$) but not significant for primes trailing the target by 200 ms ($t(7) = 0.2$, $p = .43$, $d = 0.15$)[3]. For non-synesthetes, there was (surprisingly) a main effect of congruency ($F(1,7) = 9.2$, $p = .02$, $\eta^2 = 0.57$), and also for latency ($F(2,14) = 22.3$, $p < .0001$, $\eta^2 = 0.77$), although the interaction between them was not significant ($F(2,14) = 0.58$, $p = .57$, $\eta^2 = 0.08$). Even though there was a main effect of congruency, no pairwise comparisons revealed significantly shorter reaction times for congruent trials for any of the latencies separately ($t(7) < 1.4$, $p > .11$, $d < 1.06$).

Finally, we analyzed whether *congruency-effects* were larger for synesthetes compared to non-synesthetes, for each latency. For this analysis, we subtracted reaction times on congruent trials from those on incongruent trials. Next, we performed a repeated measures ANOVA on this data with latency as within subjects factor and group as between groups factors. The results revealed a significant interaction between latency and group ($F(2,28) = 6.45$, $p = .005$, $\eta^2 = 0.32$), as well as significant main effects of group ($F(1,14) = 5.21$, $p = .038$, $\eta^2 = 0.27$) and latency ($F(2,28) = 4.03$, $p = .029$, $\eta^2 = 0.22$). The interaction was caused by the fact that congruency effects were larger for synesthetes for the first latency (primes preceding the target 400 ms, $t(14) = 5.23$, $p < .001$, $d = 2.80$), but not for the other latencies ($t(14) > 0.17$, $p > .38$, $d < 0.34$[4]).

To summarize the results: we observed a significant congruency effect both in synesthetes and non-synesthetes. The congruency effect in non-synesthetes is surprising and is likely to be found in the design of the study: each congruent prime target coupling was unique (e.g. the digit 3 and the synesthetic color red), whereas incongruent prime target coupling was not (e.g. the digit 3 was either coupled with blue, green or magenta). We aimed at presenting an equal amount of congruent and incongruent trials, resulting in the situation that a given digit was followed by given color in 50% of the cases (congruent) and one of three other colors in the other 50% of the cases (incongruent). As a result, observers might have built up (consciously or not) an expectation of the target following a given prime, leading to slightly shorter reaction times on congruent trials. In addition, as observers (synesthetes as well as non-synesthetes) used the same buttons for each digit and color (for example, a specific button for both ‘1’ and ‘red’), implicit associations between digits and color might have been developed, also in non-synesthetes. For synesthetes, however, reaction times were clearly shorter on congruent trials for latencies of -400 and 0 ms, while shorter reaction times for congruent trials were not observed for non-synesthete observers when analyzed separately for each latency. Moreover, the congruency effect for synesthetes was larger than for non-synesthetes at the first latency. Thus, although there is evidence for a congruency effect in non-synesthetes, the effect is absent when analyzed for each latency separately, and certainly smaller compared to synesthetes. Importantly, shorter reaction times on congruent trials compared to incongruent trials were not caused by a speed-accuracy trade-off: performance on congruent trials (which were fast) was *better* compared to that on incongruent trials (which were slower).

3.3. Visual prime and auditory target

Analysis of performance revealed a significant interaction between group, congruency and latency ($F(2,28) = 3.81$, $p = .034$, $\eta^2 = 0.21$), between group and congruency ($F(1,14) = 13.49$, $p = .003$, $\eta^2 = 0.49$), between latency and group ($F(2,28) = 3.51$, $p = .044$, $\eta^2 = 0.20$), as well as main a main effect of congruency ($F(1,14) = 10.82$, $p = .005$, $\eta^2 = 0.44$). The main effect of group was not significant ($F(1,14) = 2.30$, $p = .15$, $\eta^2 = 0.14$). To find the source of the interactions with the factor group, we analyzed performance for each group separately. For synesthetes, we observed a significant interaction between congruency and latency ($F(2,14) = 8.23$, $p = .004$, $\eta^2 = 0.54$), a significant main effect of congruency ($F(1,7) = 14.13$, $p = .007$, $\eta^2 = 0.67$), but no main effect of latency ($F(2,14) = 2.89$, $p = .09$, $\eta^2 = 0.29$). The interaction was caused by the fact that performance in congruent compared to incongruent trials was better for the latency for which the target preceded the prime ($t(7) = 1.97$, $p = .045$, $d = 1.49$), but not for the other two latencies ($t(7) < 1.87$, $p > .05$, $d < 1.41$). For controls, no main effects of congruency or latency, nor an interaction between them was observed ($F < 1.00$, $p > .38$, $\eta^2 < 0.12$).

For reaction times to auditory targets, the three-way interaction between group, congruency and latency was significant at trend level ($F(2,28) = 3.3$, $p = .051$, $\eta^2 = 0.19$), while the interactions between congruency and group ($F(1,14) = 8.5$, $p = .011$, $\eta^2 = 0.38$) and between congruency and latency ($F(2,28), = 3.4$, $p = .048$, $\eta^2 = 0.20$) were significant. Main effects were observed for congruency ($F(1,14), = 13.2$, $p = .003$, $\eta^2 = 0.49$) and latency ($F(2,28) = 24.1$, $p < .0001$, $\eta^2 = 0.63$), but not for group ($F(1,14) = 0.08$, $p = .79$, $\eta^2 = 0.005$). In addition, the interaction between group and latency was not significant either ($F(2,28) = 1.6$, $p = .22$, $\eta^2 = 0.10$). The analysis per group revealed significant interactions between congruency and latency ($F(2,14) = 5.8$, $p = .015$, $\eta^2 = 0.45$), as well as significant main effects for each of them (congruency: $F(1,7) = 15.6$, $p = .006$, $\eta^2 = 0.69$; latency: $F(2,14) = 14.0$, $p < .0001$, $\eta^2 = 0.67$) for synesthetes. The interaction was caused by the fact that there was significant congruency effect for all latencies (prime preceding the target by 200 ms: $t(7) = 5.5$, $p < .001$, $d = 4.16$; prime onset together with that of the target: $t(7) = 3.3$, $p = .007$, $d = 2.49$; prime trailing the target by 100 ms: $t(7) = 2.1$, $p = .04$, $d = 1.59$). For non-synesthetes, the main effect of latency was significant ($F(2,14) = 10.5$, $p = .002$,

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[3] We applied one-tailed t-tests since our hypothesis was that congruent primes would lead to shorter RTs compared to incongruent primes.

[4] One-tailed independent t-tests.

$\eta^2 = 0.60$), whereas the main effect of congruency was not ($F(1,7) = 0.42$, $p = .54$, $\eta^2 = 0.06$), nor was the interaction between them significant ($F(2,14) = 0.53$, $p = .60$, $\eta^2 = 0.07$).

To summarize the results for auditory targets and visual primes: for synesthetes, reaction times to auditory targets were shorter for visual primes that were congruent compared to incongruent with the synesthetic color of the visual prime for all latencies. In non-synesthetes, no such effect was observed. Again, differences in reaction times were not caused by a speed-accuracy trade-off since shorter reaction times on congruent trials compared to incongruent trials were accompanied by *better* performance on congruent trials.

3.3.1. Neutral primes

For both visual and auditory targets, we observed neither a significant main effect of group or latency, nor a significant interaction between both factors when analyzing performance ($F < 1.57$, $p > .23$, $\eta^2 < 0.10$).

For reaction times for neutral auditory primes with visual targets, we observed a main effect of latency ($F(2,28) = 30.5$, $p < .0001$, $\eta^2 = 0.69$), but no main effect of group ($F(1,14) = 0.31$, $p = .59$, $\eta^2 = 0.02$), nor any significant interaction between them ($F(2,28) = 1.25$, $p = .30$, $\eta^2 = 0.08$). Post-hoc comparisons further revealed that the difference between each latency was significant ($p < .016$ for all comparisons) indicating that reaction times increased with latency. A similar result was observed for auditory targets with visual primes: there was a main effect of latency ($F(2,28) = 26.6$, $p < .0001$, $\eta^2 = 0.66$), no main effect of group ($F(1,14) = 0.88$, $p = .37$, $\eta^2 = 0.06$), and no significant interaction between them ($F(2,28) = 0.08$, $p = .93$, $\eta^2 = 0.01$). Again, RTs were significantly different between each of the three latencies ($p < .044$ for all comparisons) indicating that reaction times increased with latency. The results of these two blocks again show that there was no general difference in reaction times between synesthetes and non-synesthetes.

3.4. Facilitation and interference

Although the trials with neutral primes were run in different blocks, comparing them with non-neutral (i.e. congruent and incongruent) primes allows us to see whether reaction times were shorter for congruent primes compared to neutral primes and whether they were longer following incongruent primes. To see whether congruent primes shortened reaction times compared to neutral primes in synesthetes for visual targets, we performed one-tailed, pairwise t-tests between reaction times to congruent and neutral primes. Reaction times for congruent primes were not shorter at any of the three latencies ($t(7) < 1.2$, $p > .14$, $d < 0.90$)[5]. However, reaction times were significantly longer for incongruent primes presented 400 ms before the target ($t(7) = 4.8$, $p = .001$, $d = 3.6$), while not significantly different for the simultaneously presented primes ($t(7) = 1.57$, $p = .08$, $d = 1.19$) nor for primes presented after target onset ($t(7) = 0.1$, $p = .47$, $d = 0.08$). Importantly, accuracy did not differ between incongruent versus neutral trials for primes preceding the target ($t(7) = 1.31$, $p = .23$, $d = 0.99$), again excluding the possibility that incongruent trials were slower due to a speed-accuracy trade-off. Repeating the same analysis for non-synesthete observers revealed no significant difference in reaction time to visual targets for any of the three auditory prime latencies ($t(7) < 1.64$, $p > .08$, $d < 1.24$).

For visual primes and auditory targets, reaction times to targets with congruent primes were not significantly shorter than to targets with neutral primes for any of the prime latencies for synesthetes ($t(7) < 1.6$, $p > .075$, $d < 1.23$). However, reaction times were significantly longer to targets with incongruent primes for all three prime latencies ($t(7) > 4.0$, $p < .0025$, $d > 2.99$). Performance on incongruent trials was not better on incongruent compared to neutral trials (in fact, performance was worse for primes presented before or simultaneously with target onset; $t(7) > 2.08$, $p < .04$, $d > 1.57$), again excluding a speed-accuracy trade-off. For non-synesthetes, no significant differences were observed for both congruent and incongruent primes when comparing each of the them with reaction times on neutral trials ($t(7) < 0.93$, $p > .19$, $d < 0.70$).

The results of this analysis indicate that the effect of a prime on responding to a target was mainly reflected by longer reaction times to primes that were incongruent to the synesthetic mapping between concurrent and inducer. That is, when an auditory digit preceded a color that was incongruent to the synesthetic color of that digit, reaction times were longer. Moreover, when a visual prime (a color) was presented along with an auditory target (a digit), reaction times were longer when the color was incongruent with the synesthetic color associated with that particular digit.

4. General discussion

This study was designed to test whether bidirectional priming across different modalities can be observed for grapheme-color synesthetes whose synesthesia is explicitly unidirectional. The results reveal that (1) priming occurred in two directions (digits affecting reaction times to colors and colors affecting reaction times to digits) and (2) priming occurred across different sensory modalities (audition affected vision and vision affected audition). Moreover, interference with responding to targets occurred for synesthetes when the color of the visual stimulus did not match the synesthetic color of the auditory stimulus: reaction times were longer for incongruent primes, whereas reaction times to congruent primes were not shorter compared to neutral primes. This interference by incongruent primes is in line with effects observed by Mattingley, Rich, Yelland, and Bradshaw (2001).

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[5] We used a critical alpha of 0.008 (0.05 divided by 6), since we performed six comparisons for each block.

A notable result of the present study is that priming in synesthetes was bidirectional, while the phenomenology of their digit-color association was unidirectional. That is, our synesthetes experienced colors following digits, but did not report experiencing digits when seeing a color. In spite of this, responding to digits was affected by colors presented along with the digits. Thus, even though their synesthesia was explicitly unidirectional, the results show that – in contrast to non-synesthetes – the coupling between inducer and concurrent was implicitly bidirectional. This result is in line with those of Brugger et al., 2004; Cohen Kadosh et al., 2005; Gebuis et al., 2009a; Gebuis et al., 2009b; Gevers et al., 2010; Johnson et al., 2007; Knoch et al., 2005; McCarthy et al., 2013; Richer et al., 2011; Weiss et al., 2009 and refutes the idea that grapheme-color synesthesia is caused by a one-way, feed-forward coupling between inducer and concurrent.

In this study, we included synesthetes who reported experiencing a color when hearing a digit. In this sense, the nature of their synesthesia was already supra-modal. An interesting question is at what level of processing the unusual coupling between inducer and concurrent occurs. A perspective on this question is dissociating whether the coupling between inducer and concurrent is direct or indirect (Bargary & Mitchell, 2008). Direct coupling (also labeled cross-wiring (Hubbard, Brang, & Ramachandran, 2011; Ramachandran & Hubbard, 2001)) between inducer and concurrent would require connections between (visual) grapheme areas and color areas. Indirect coupling (more consistent with hyperbinding (Hubbard, 2007)) would *not* require direct wiring between areas processing the inducer and activating the concurrent. Interestingly, the unidirectional nature of synesthesia has been used to argue for the direct, feedforward account of synesthesia (Bargary & Mitchell, 2008). Absence of a direct link between brain areas processing inducer and concurrent is also proposed in the recent 'hub' and 'spoke' model by Chiou and Rich (2014). In this model on synesthesia, synesthetic experiences result from conceptual links between inducers and concurrents. Analogous to conceptualizing that a banana has certain features: it is yellow and has a certain shape, synesthetes add additional features to inducers, for example when the concept 'A' – next to its shape and sound – also has a color. Our results are in line with this model on synesthesia, as the bidirectional (synesthetic) interaction between digits and colors occurred at a level transcending that of modality-specific processing: the 'hub' and 'spoke' model would explain our data by arguing that the interaction between auditory digits and visual colors occurred an abstract conceptual level. Interestingly, the model aptly explains why an auditory inducer affects a visual concurrent (as the inducer would activate the abstract concept of the digit, as well as its (synesthetic) features). However, in our experiments concurrents (colors) also affected processing of inducers (digits), at least at an implicit level. This aspect of our results (and of implicit bi-directionality in synesthesia in general) might indicate that the synesthetic associations are strong enough to activate abstract concepts such as digits. Thus, as encountering a certain shape (a curved object) might activate the concept of a banana, encountering a certain color might activate abstract concepts of digits and letters in grapheme-color synesthetes.

To conclude, the current study is the first to show that bidirectional priming in grapheme-color synesthetes occurs across sensory modalities. The results imply that the interaction between concurrent and inducer occurred at an abstract level of processing that is independent of the 'notation' (visual or auditory) of the digit and its synesthetic color.

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