

COGNITIVE NEUROSCIENCE

Multiple dimensions in bi-directional synesthesia



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Keywords: associators, congruency, ERP, priming, projectors, unitarity

Abstract

Grapheme-color synesthetes report seeing a specific color when a number is perceived. The reverse, the synesthetic experience of a specific grapheme after the percept of a color is extremely rare. However, recent studies have revealed these interactions at both behavioral and neurophysiological levels. We investigated whether similar neuronal processes (i.e. perceptual and/or attentional) may underlie this bi-directional interaction by measuring event-related potentials (ERPs) during both a number-color and color-number priming task. In addition, we investigated the unitarity of synesthesia by comparing two distinct subtypes of synesthetes, projectors and associators, and assessed whether consistencies between measures (i.e. behavioral and electrophysiological) were present across synesthetes. Our results show longer reaction times for incongruent compared with congruent trials in both tasks. This priming effect is also present in the P3b latency (parietal electrode site) and P3a amplitude (frontal electrode site) of the ERP data. Interestingly, projector and associator synesthetes did not reveal distinct behavioral or electrophysiological patterns. Instead, a dissociation was found when synesthetes were divided in two groups on the basis of their behavioral data. Synesthetes with a large behavioral priming effect revealed ERP modulation at the frontal and parietal electrode sites, whereas synesthetes with a small priming effect revealed a frontal effect only. Together, these results show, for the first time, that similar neural mechanisms underlie bi-directional synesthesia in synesthetes that do not report a synesthetic experience of a grapheme when a color is perceived. In addition, they add support for the notion of the existence of both 'lower' and 'higher' synesthetes.

Introduction

Bi-directional synesthesia

Synesthesia is the phenomenon in which one sensory modality automatically activates an experience in another sensory modality. For instance, grapheme-color synesthetes experience a color when a number or a letter is perceived. The reverse, the experience of a number when a color is perceived, is extremely rare; only a single case has been reported ('explicit' bi-directional synesthesia; Cohen Kadosh *et al.*, 2007). Recently, it has been suggested that colors can activate number processes in synesthetes, even though a synesthetic number experience is absent at the phenomenological level ('implicit' bi-directional synesthesia; Knoch *et al.*, 2005). This bi-directionality in synesthesia was more comprehensively investigated by Cohen Kadosh and colleagues (Cohen Kadosh & Henik, 2006; Cohen Kadosh *et al.*, 2007). Their results revealed an influence of color on task performance even when different magnitudes, such as line lengths and triangle sizes, were used instead of numbers. The elegance of the above studies lies in that they eliminated the possibility of number processes being triggered by the mere presence of number stimuli. Another way to overcome this confound is to present numbers and colors at different moments in time as is common in, for instance, priming studies. In a recent priming study, a bi-directional interaction (i.e. from number to color as well as

from color to number) of equal magnitude for both directions was revealed with grapheme-color synesthetes (Gebuis *et al.*, in press). This result is surprising given the clear distinction present at the phenomenological level (i.e. the lack of reporting the presence of a number experience when a color is perceived) and hints at a similar mechanism underlying both directions of information flow.

To date, only a single study investigated the underlying processes of bi-directional interactions in synesthesia using imaging techniques (Cohen Kadosh *et al.*, 2007). In this study, distinct activation patterns and time courses were found for both directions of information flow (grapheme to color and the reverse), suggesting the recruitment of different mechanisms. It is important to note, however, that the synesthete participating in that study experienced colors when numbers were presented but the reverse as well: the experience of numbers when colors were perceived. This is (to the best of our knowledge) the only reported case, and thus extremely rare. Therefore, we will investigate (using both behavioral and ERP measures) whether synesthetes who do not experience this explicit bi-directionality (thus showing the more common form of grapheme-color synesthesia) also have distinct neurophysiological patterns when performing in a bi-directional synesthetic priming experiment.

Bi-directionality and homogeneity within synesthesia

Synesthetes have been classified in two groups based on their subjective experience and response patterns (Dixon *et al.*, 2004):

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Received 24 November 2008, revised 4 February 2009, accepted 5 February 2009

synesthetes who see their synesthetic color experience projected onto the grapheme (called 'projectors'); and synesthetes who see the synesthetic color experience in their 'mind's eye' (called 'associators'). Differences between projectors and associators have been reported on behavioral (Dixon *et al.*, 2004) and physiological levels (Rouw & Scholte, 2007). A different classification of synesthetes was proposed by Ramachandran & Hubbard (2001), who classified synesthetes into 'higher synesthetes', for whom the number 'concept' is critical, vs. 'lower' synesthetes, for whom the 'percept' of the physical grapheme is necessary to elicit the synesthetic experience. This distinction recently gained support from a behavioral and imaging study (Hubbard *et al.*, 2005). Although Dixon & Smilek (2005) have suggested that these classifications overlap to a large extent, this claim is yet to be substantiated. Therefore, we will also investigate whether these classifications of synesthetes (projector vs. associator – higher vs. lower) are equivalent or dissociable using behavioral and neurophysiological techniques.

The above-raised issues are addressed using a number-color (Mattingley *et al.*, 2001) as well as a color-number priming task (Gebuis *et al.*, in press). Faster responses are expected for congruently compared with incongruently primed targets as a result of correctly activated processes prior to target presentation. Event-related potentials (ERPs) were used as a neurophysiological measure, because the accuracy in the temporal domain gives an insight in the timing of the distinct processes involved. The P3b latency is generally thought to be related to the processing time needed to evaluate a stimulus (e.g. perceptual processes; Luck, 2005), therefore longer P3b latencies are expected for the incongruent compared with the congruent trials. Based on the results of previous studies, effects of early perceptual or orthographic processing (N170 component) at the parietal-occipital electrodes (Cohen Kadosh *et al.*, 2007; Sagiv & Ward, 2006) and possibly inhibitory frontal effects (Schiltz *et al.*, 1999) are expected as well. Whether distinct time courses for both priming tasks (as found with an 'explicit' synesthete; Cohen Kadosh *et al.*, 2007) will be obtained in (subtypes of) 'implicit' synesthetes remains a matter of scrutiny.

Materials and methods

Participants

Eighteen grapheme-color synesthetes participated in the experiment. Before participation synesthetes who applied to attend the study received a questionnaire that included a large variety of questions about their synesthetic experiences as well as their history of neurological disorders or substance abuse. Only synesthetes with no history of substance abuse, neurological disorders and the presence of grapheme-color associations were included. Furthermore, the specific color associations that were tested prior to and after the experiment (see below) should be consistent between them as well as with the colors reported in the questionnaire. Due to artifacts in the electroencephalogram (EEG) data, only 14 synesthetes (aged between 18 and 53 years; $M = 33.9$, $SD = 3.24$; 13 female; 12 right-handed) were included in the analyses. Out of the 14 synesthetes, six reported to perceive the synesthetic color projected onto the grapheme (projectors) and eight reported to perceive the synesthetic color in their 'mind's eye' (associators). Fifteen controls that did not report any grapheme-color or other synesthetic associations participated in the experiment, of which 14 (aged between 19 and 35 years; $M = 23.7$, $SD = 1.36$; 13 female; 13 right-handed) were included in the analyses. All participants were native Dutch speakers and had normal or corrected-to-normal visual

acuity. They reported no color blindness or a history of neurological disorders. Written informed consent was obtained according to the Declaration of Helsinki and as approved by the Ethical Committee of the University of Utrecht.

Apparatus, stimuli and procedure

In each trial, the prime and target were displayed on a 22-inch CRT monitor using the Presentation software (Neurobehavioral Systems, Albany, CA, USA). The paradigm was a slightly adapted version of our previous study (Gebuis *et al.*, in press; Fig. 1). Prior to and after the experiment, all synesthetes had to color the numbers 1–9 in the specific hues they experience when seeing the number. The colors were chosen from the custom color palette available in Microsoft Office 2000 (32 bit color-depth; hue, saturation and brightness could be set independently). All synesthetes colored the numbers almost identical in both instances, indicating that good color/hue matches could be obtained. Pair-matched controls used the color-number pairs of each synesthete.

The stimuli consisted of black Arabic numbers ranging from 3 to 6 and color patches in the synesthetic colors that were related to the numbers 3–6 (width = 1.6° visual angle, height = 2° visual angle). None of the synesthetes participating in the experiment had similar synesthetic colors for the distinct numbers, therefore cross-priming can be excluded as a factor causing congruency effects. Fourteen prime-target combinations were used (3–3, 3–4, 3–5, 4–3, 4–4, 4–5, 4–6, 5–3, 5–4, 5–5, 5–6, 6–4, 6–5, 6–6). The stimuli were presented centrally on a gray background and the viewing distance was approximately 57 cm. The study consisted of two tasks (384 trials each), each consisting of both congruent and incongruent trials (192 trials each).

The two tasks were: (i) a number-color priming task in which participants had to press the button of a response box that corresponded to the color target presented on the screen (Fig. 1A); and (ii) a color-number priming task in which participants had to press the button of the response box that corresponded to the number target presented on the screen (Fig. 1B). The order of the two priming tasks was counterbalanced between participants. Each trial began with a fixation cross (500 ms), followed by the prime (500 ms), an interstimulus interval (500 ms), the target (500 ms) and a random intertrial interval (1250–1500 ms). Participants responded with the left middle finger to the number 3, the left index finger to the number 4, the right index finger to the number 5 and the right middle finger to the number 6 (or the synesthetic color corresponding to that particular number). Prior to each experiment, 20 practice trials were completed. In addition, the buttons on the response box were marked with the colors or numbers they corresponded to.

Reaction time analyses

All participants reached our criterion of 80% correct responses. For each participant, median reaction times for these correct responses were calculated per congruency condition. All statistical analyses were performed on these median reaction times.

Electrophysiological recordings

EEG and electrooculogram (EOG) activity were recorded using an Electrocap with 58 tin electrodes, referenced to the right mastoid.

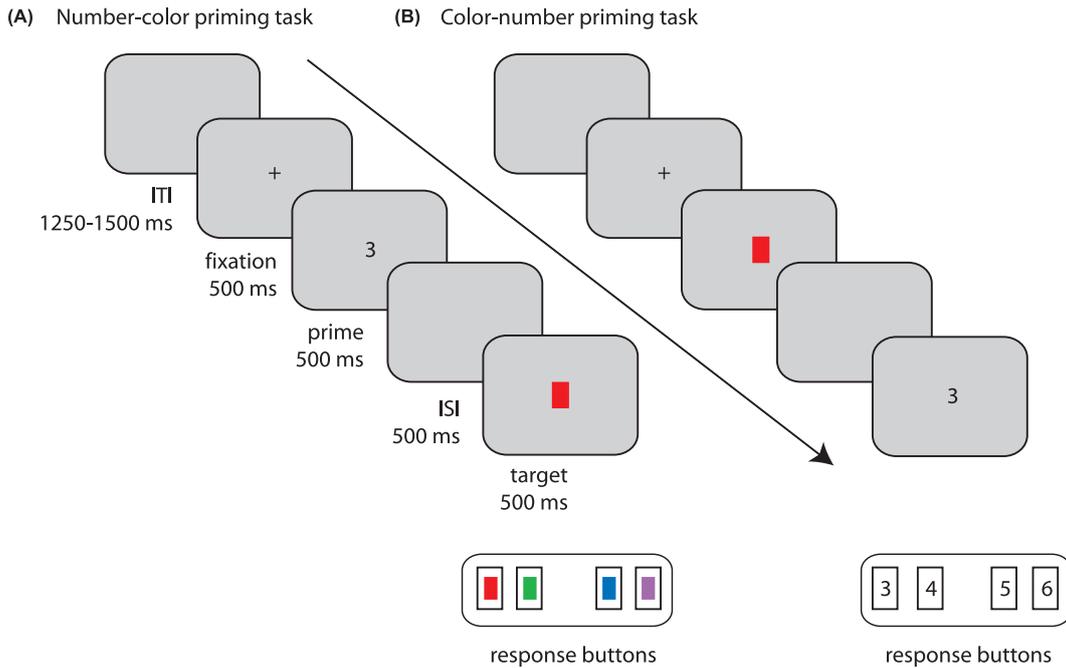


FIG. 1. Schematic representation of a trial of the number-color priming task (A) and the color-number priming task (B) where subjects had to manually respond to the target stimulus by pressing the corresponding button.

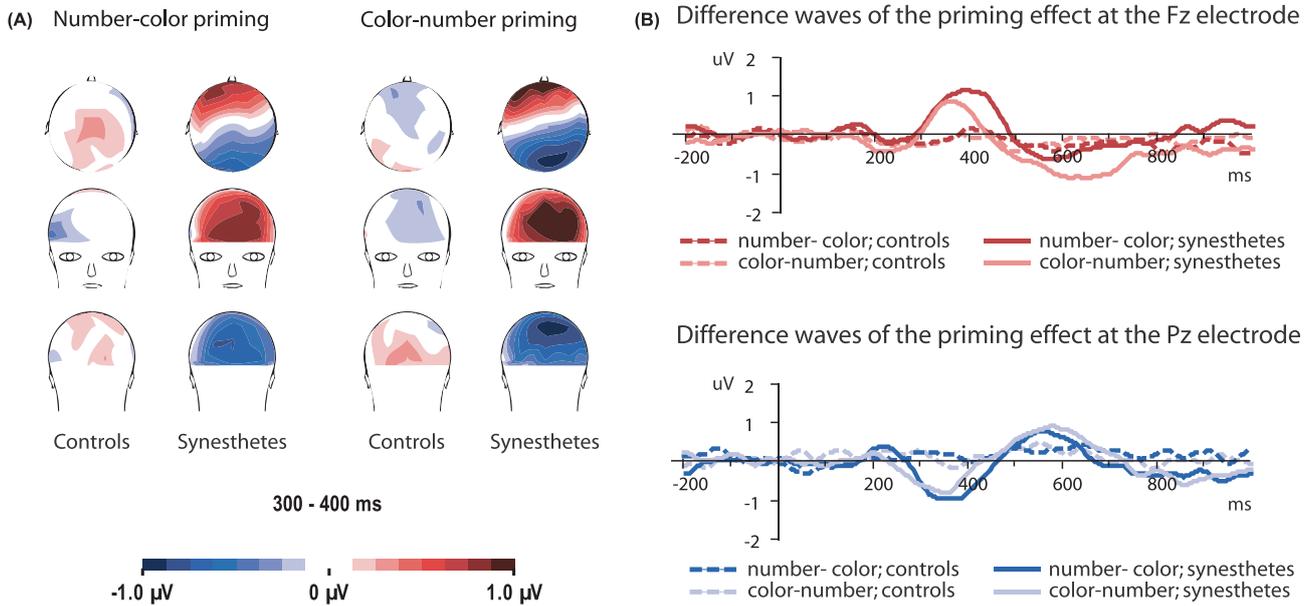


FIG. 2. Scalp maps portraying the priming effects (incongruent-congruent) for both controls and synesthetes and both priming tasks (A). Difference waves portraying the priming effect (incongruent-congruent) of both controls (dashed lines) and synesthetes (solid lines), and both priming tasks at the electrode Fz (upper figure, red lines) and electrode Pz (lower figure, blue lines) (B).

The ground electrode was placed within the cap between Fpz and Fz. Vertical EOG was recorded from electrodes attached above and below the left eye, and the horizontal EOG from the outer canthi of both eyes. Electrode impedance was kept below 5k Ω EEG and EOG were amplified with a Brain-Amp amplifier (Brain Products GmbH, Germany) with a bandwidth of 0.04–100 Hz. The sampling rate was 500 Hz.

ERP analyses

Participants were discarded from both the ERP and the behavioral analyses when more than 25% of the trials contained artifacts. This resulted in the exclusion of four synesthetes and one control participant. EEG and EOG data were analysed using Brain Vision Analyser software (1.05). Data from noisy or flat electrodes were

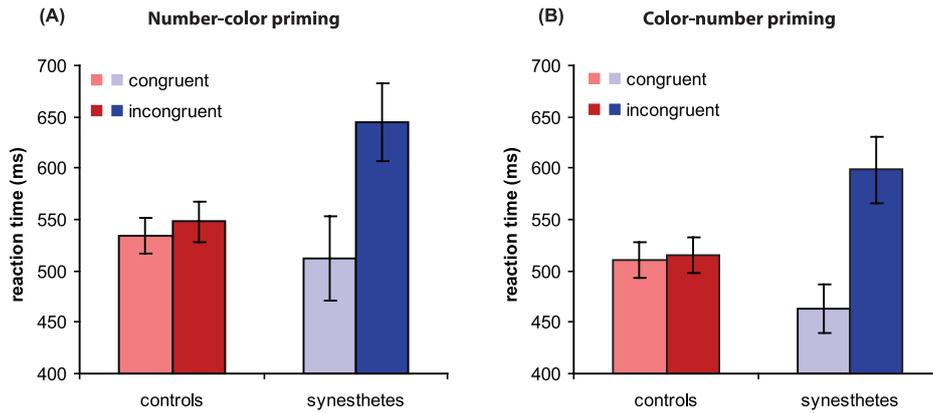


FIG. 3. In contrast to the results of the controls (red), the results of the synesthetes (blue) reveal a congruency effect with faster responses for the congruent (color and number matched) compared with the incongruent (color and number did not match) condition in both the priming tasks, indicating an effect of number on color processes (A), as well as of color on number processes (B).

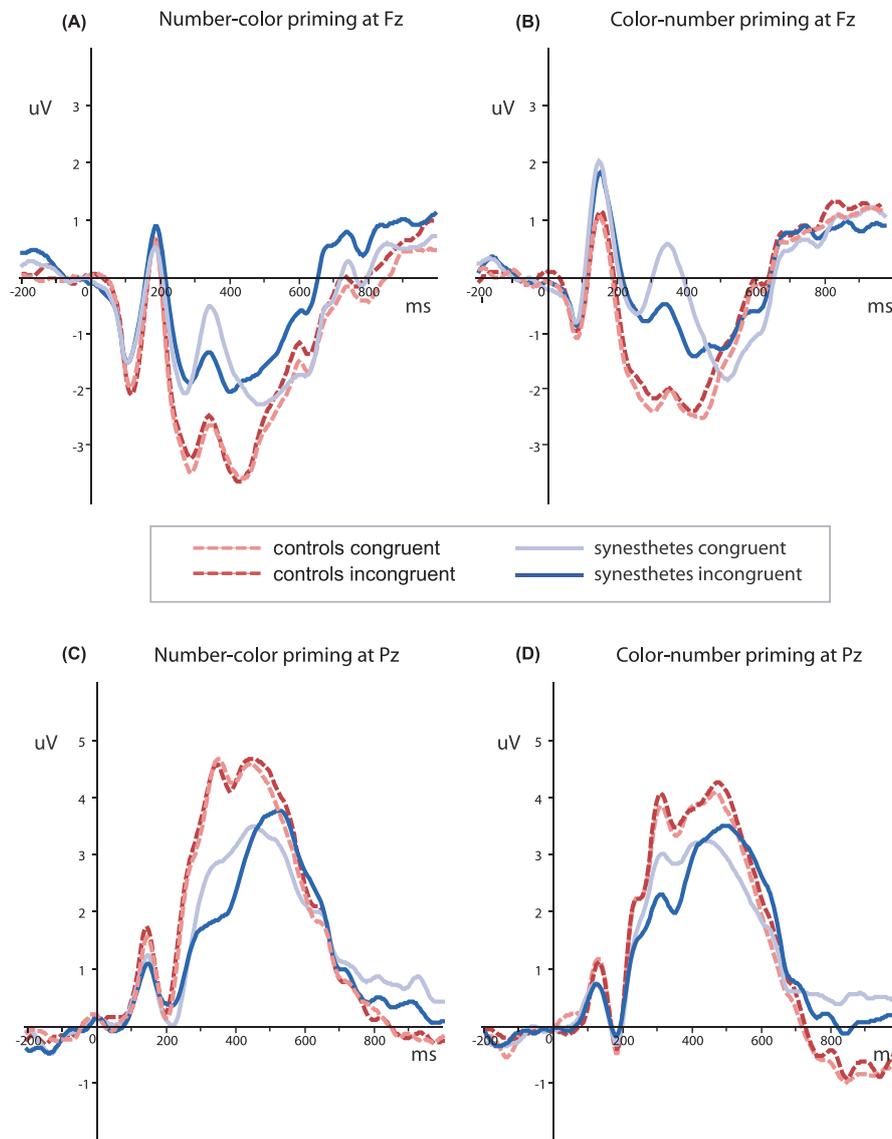


FIG. 4. The ERPs revealing the congruent and incongruent priming condition of the controls (dashed lines) and the synesthetes (solid lines) in the number-color priming task (A and C) and the color-number priming task (B and D) at the Fz (upper row) and the Pz electrode (lower row).

TABLE 1. The behavioral and neurophysiological priming effects

	Reaction time (ms)	P3a amplitude (μ V)	P3b latency (ms)
Number-color priming task			
Synesthetes (small behavioral priming effect)	49.1 \pm 12.2	0.3 \pm 0.7	18.0 \pm 14.7
Synesthetes (large behavioral priming effect)	216.1 \pm 60.2	1.0 \pm 0.5	73.7 \pm 29.9
Controls	12.7 \pm 4.8	0.0 \pm 0.2	11.4 \pm 13.4
Color-number priming task			
Synesthetes (small behavioral priming effect)	26.4 \pm 14.9	0.6 \pm 0.3	27.4 \pm 16.0
Synesthetes (large behavioral priming effect)	245.0 \pm 37.1	1.5 \pm 0.6	94.0 \pm 27.4
Controls	5.0 \pm 3.3	-0.1 \pm 0.1	3.6 \pm 10.6

The data are presented as means \pm SD. The two groups of synesthetes were distinguished on the basis of their behavioral priming effect (incongruent-congruent).

discarded (this never concerned more than two electrodes per subject); the electrodes included in the rest of the analyses were not among them. EEG signals were off-line re-referenced to the average of all electrodes. The continuous EEG data were segmented into epochs from 300 ms prior to the prime until 1000 ms after the presentation of the target (in total an epoch comprised 2000 ms). An artifact of any kind during the prime might severely influence the response to the target. Including the prime in the epoch allowed rejecting the segment when an artifact was present during the presentation of the prime. Epochs were filtered with a bandpass filter (0.05 Hz, 12 dB octave; 40 Hz, 24 dB/octave) and corrected for eye movements according to the Gratton *et al.* (1983) algorithm. Trials with artifacts (difference criterion of 100 μ V within an epoch; low activity criterion of 0.5 μ V within a 100-ms time window) or an incorrect response were rejected from further analyses. The baseline for the ERPs was defined as the mean of the 100-ms period before the onset of the target stimulus. Grand average ERPs were created for each congruency condition. These were filtered at 8 Hz low pass, 12 dB/octave for visualization purposes only.

On the basis of scalp maps of the synesthetes reflecting the difference waves (incongruent-congruent), a frontal positivity and a parietal negativity were obtained (Fig. 2A and B). Inspection of the grand average waveforms revealed that the frontal positivity reflects a difference in amplitude (Fig. 4A and B), whereas the parietal negativity reflects a latency difference (Fig. 4C and D). The frontal-central priming effect started about 280–450 ms post-stimulus, which corresponds to the component commonly referred to as the P3a. The parietal priming effect started about 300–500 ms post-stimulus and corresponds to the component commonly referred to as the P3b. Peak amplitudes were estimated for each subject separately at the Fz electrode in the 280–450-ms time window and peak latencies at the Pz electrode in the 300–600-ms time window. We also estimated the peak latencies of the P1 (80–180 ms) and N2 (150–220 ms) components at the Pz electrode to investigate whether the peak latency effect was already apparent at an earlier stage. Moreover, even though no early perceptual effects were apparent from the difference waves, the N170 component (a component related to orthographic processing) was estimated at the occipital and parietal-occipital electrodes as well. Specifically, it was estimated as the largest negative deflection at 150–200 ms at the electrode sites Oz, PO7 and PO8. This allowed us to ascertain whether early perceptual effects are present in subtypes of synesthetes that are not apparent at the group level.

Results

Behavioral results

To test whether priming effects were present in the number-color and the color-number priming task of the synesthetes and controls independent of the direction of information flow, we performed a repeated-measures ANOVA with Task (number-color and color-number priming) \times Congruency (congruent and incongruent) as within-subjects factors, and Group (controls and synesthetes) as a between-subjects factor. A significant main effect of Group ($F_{2,26} = 16.128$, $P < 0.001$) as well as an interaction between Congruency and Group was present ($F_{2,26} = 12.380$, $P = 0.002$), indicating that a significantly larger congruency effect was present for synesthetes compared with controls in the number-color (132.6 ms vs. 12.7 ms) and color-number priming task (135.7 ms vs. 5 ms; Fig. 3). *Post hoc t*-tests revealed a significant congruency effect within the group of synesthetes with increased reaction times for the incongruent compared with the congruent condition for both the number-color priming ($t_{13} = -3.782$, $P = 0.002$) and the color-number priming ($t_{13} = -3.537$, $P = 0.004$) task. *Post hoc* paired samples *t*-tests for the control group showed a significant congruency effect of the color-number priming task only ($t_{13} = -2.625$, $P = 0.021$). Even though the congruency effect of the controls was significant, it was only 5 ms and was, as described above, significantly smaller compared with the synesthetic priming effect (135.7 ms; ~ 41 standard deviations away from that of the controls). Moreover, even when the group of synesthetes was split, based on the strength of the priming effect (see below), the group with the smallest priming effect revealed a priming effect that was more than five times larger than that of the controls (26.4 ms; ~ 8 standard deviations from that of the controls; see Table 1). Therefore, we consider this outcome coincidental.

Having established that a congruency effect was present for synesthetes in both the number-color and color-number priming task, we subsequently analysed whether these synesthetic congruency effects were of similar magnitude. To this end we performed paired *t*-tests on the relative and absolute congruency effects of the synesthetes, which were calculated by dividing the incongruent by the congruent condition or subtracting the congruent from the incongruent condition, respectively. Both relative ($t_{13} = 0.164$, $P = 0.872$) and absolute ($t_{13} = 0.032$, $P = 0.975$) congruency effects did not differ significantly, suggesting that colors primed numbers equally well as numbers primed colors.

In addition, we compared the results of projector and associator synesthetes to test for potential differences between subtypes. A second repeated-measures ANOVA was performed with Task (number-color and color-number priming) \times Congruency (congruent and incongruent) as within-subjects factors, and Subtype (projectors and associators) as a between-subjects factor. No significant main effect or interaction was present.

ERP results

Bi-directionality

Difference waves (incongruent-congruent) for both tasks are shown in Fig. 2B, from which a substantial effect of priming in both directions is apparent, but only for synesthetes. As stated in the Materials and methods, the frontal positivity reflects a difference in amplitude, whereas the parietal negativity reflects a latency difference (Fig. 4). To test the frontal amplitude and the parietal latency effects we performed a repeated-measures ANOVA with Task (number-color and color-number priming) \times Congruency (congruent and incongruent) as

within-subjects factors, and Group (controls and synesthetes) as a between-subject factor for both the P3a amplitude at Fz as well as the P3b latency at Pz. [No statistical main or interaction effects were found for P3a latency at Fz or P3b amplitude at Pz.]

For P3a peak amplitude, a significant effect of Congruency was present ($F_{2,26} = 6.35$, $P = 0.018$), as well as an interaction between Congruency and Group ($F_{2,26} = 7.81$, $P = 0.010$), which suggests that the congruency main effect was modulated by Group. *Post hoc* paired samples *t*-tests revealed a significant congruency effect (larger amplitudes for incongruent compared with congruent trials) for the number–color ($t_{13} = -3.064$, $P = 0.009$) as well as the color–number ($t_{13} = -3.206$, $P = 0.007$) priming task (Fig. 4A and B), but only for the synesthetes. *Post hoc* paired *t*-tests of the congruency effect of the P3a amplitude (incongruent–congruent) revealed that the effect was of similar magnitude in both priming tasks ($t_{13} = 0.691$, $P = 0.502$), which concurs with the behavioral data (see above).

For P3b peak latency, the results revealed a significant congruency effect ($F_{2,26} = 12.426$, $P = 0.002$) with longer latencies for incongruent compared with congruent trials. This congruency effect interacted with Group ($F_{2,26} = 7.05$, $P = 0.013$), indicating a significantly larger congruency effect for synesthetes (45 ms for the number–color and 61 ms for the color–number priming task) compared with controls (11 ms for the number–color and 4 ms for the color–number priming task). Paired samples *t*-tests underlined these results: a significant congruency effect on the number–color priming ($t_{13} = -3.408$, $P = 0.005$) as well as color–number priming task ($t_{13} = -2.578$, $P = 0.023$) was present for synesthetes only (Fig. 4C and D). *Post hoc* paired *t*-tests of the congruency effect of the P3b latency (incongruent–congruent) revealed that the congruency effect was of similar magnitude in both priming tasks ($t_{13} = 0.769$, $P = 0.456$), as was the case for the behavioral and P3a amplitude data (see above).

A latency effect of the P3b component is the result of processes leading up to stimulus evaluation (i.e. processes that happen before the P3b peak; Luck, 2005). To test whether these P3b latency effects can be explained by processes starting before P3b onset, we performed a repeated-measures ANOVA with Task (number–color and color–number priming) \times Congruency (congruent and incongruent) as within-subjects factors, and Group (controls and synesthetes) as a between-subject factor for the earlier components at Pz (P1 and N2) and ERP measures (latency and amplitude). No significant Congruency or interaction of Congruency and Group was obtained, suggesting that the latency effect of the P3b could not directly be related to effects present at earlier components (P1 and N2) at Pz.

Projector–associator vs. lower–higher synesthetes

As the inclusion of distinct subtypes of synesthetes might have obscured synesthetic subtype-specific effects, we performed a repeated-measurements analysis with Task (number–color and color–number priming) \times Congruency (congruent and incongruent) as within-subjects factors, and subtype (projectors and associators) as a between-subject factor for the distinct ERP components and measures presented above. No significant interaction between Congruency and subtype was present for the P1, N2 and P3b component at Pz, for the P3a component at Fz, or for the N170 component at the electrodes PO7, PO8 and Oz.

In addition to the phenomenological classification into projector and associator synesthetes, Hubbard *et al.* (2005) showed that synesthetes appeared to be distinguishable on the basis of their behavioral results. In this study, they demonstrated a strong correlation between their behavioral effect and a physiological

[functional magnetic resonance imaging (fMRI)] measure. Consistent with their reports, in our study, two distinct groups of synesthetes were dissociable on the basis of the behavioral results as well: one containing the synesthetes with a small, and one containing the synesthetes with a large priming effect (see Table 1). In our sample, these groups were equal in size ($n = 7$, for both groups). [Coincidentally, both groups contained three projectors and four associators.] Even though the priming effects were small in the former group they were significant for both the number–color ($t_6 = -4.871$, $P = 0.003$) and the color–number ($t_6 = -2.052$, $P = 0.046$) priming task. Not surprisingly, significant behavioral results were obtained for the group with the large priming effects as well for the number–color ($t_6 = -3.592$, $P = 0.011$) and for the color–number priming task ($t_6 = -6.603$, $P = 0.001$). We subsequently tested whether this division is mirrored by any of our physiological measures. Therefore, a repeated-measures ANOVA was performed with Task (number–color and color–number priming) \times Congruency (congruent and incongruent) as within-subjects factors, and Group (small and large behavioral priming effect) as a between-subjects factor for both the P3a amplitude as well as the P3b latency data. For the P3a amplitude, no interaction between Congruency and Group was present ($F_{2,6} = 2.486$, $P = 0.141$). However, a significant interaction between Congruency and Group was obtained for the P3b latency ($F_{2,6} = 15.734$, $P = 0.002$). *Post hoc* paired *t*-tests revealed that a significant congruency effect was present in the group with large behavioral effects for both the number–color ($t_6 = -2.462$, $P = 0.049$) and the color–number ($t_6 = -3.435$, $P = 0.014$) priming task. In contrast, no significant congruency effects for the number–color ($t_6 = -1.225$, $P = 0.266$) or the color–number priming task ($t_6 = -1.709$, $P = 0.138$) were present in the group with small behavioral effects. Together, these results indicate that within the group of synesthetes, two classes can be distinguished: synesthetes revealing congruency effects at the frontal and parietal electrode sites; and a group displaying a modulation at the frontal electrode site only. Within the group of controls we found no dissociable congruency effect. Therefore, no comparable statistical analysis was performed on the control data.

Finally, we also investigated whether the congruency effect of the P3b latency and P3a amplitude was of similar magnitude in both priming tasks for the two dimensions of synesthetes. No significant results were obtained suggesting that the task at hand did not influence the size of the congruency effect for both the projector and associator, as well as higher and lower synesthetes.

Discussion

Bi-directionality

In this study, our main aim was to investigate the time course of bi-directional interactions in synesthesia using a number–color and a color–number priming task. The reaction time data revealed a priming effect (present only for the synesthetes) that was of similar magnitude in both directions, thus replicating the results of our previous study (Gebuis *et al.*, in press). This outcome already hints at similar neural correlates underlying both directions of information flow in synesthesia, yet more conclusive evidence was derived from the ERP components affected. For both priming tasks, the congruency effect modulated the same ERP components. The incongruent trials resulted in larger P3a ‘amplitudes’ at frontal and longer P3b ‘latencies’ at parietal electrodes for the incongruent compared with the congruent trials. The P3a amplitude reflects orienting of attention (Schroger & Wolff, 1998; Polich & Comerchero, 2003) or the inhibition of response

processes (Goldstein *et al.*, 2002), whereas the P3b latency effect is thought to be related to processes leading up to stimulus evaluation such as lower-level sensory processes (Donchin *et al.*, 1986; Luck, 2005). Consequently, both early perceptual as well as later attentional or inhibitory processes appear to play a role in synesthesia.

Our results concerning the influence of number on color processes are consistent with previous studies (Schiltz *et al.*, 1999; Mattingley *et al.*, 2001, 2006). The presence of the modulation of attentional processes in synesthetes is in line with the results of Mattingley *et al.* (2001) who reported the necessity of overt recognition of the prime in synesthetic priming. In their study, priming effects were obtained only after initial processing of visual form. In addition, Schiltz *et al.* (1999) found amplitude differences at the frontal electrodes and large positive peaks at the parietal electrodes as well. They suggested that the frontal amplitude effects were related to inhibitory mechanisms that modulated the parietal activation, an idea that is most consistent with the disinhibited feedback model (Grossenbacher & Lovelace, 2001). This model postulates that feedback of information is inhibited in normal subjects but not in synesthetes resulting in synesthetic experiences.

Our results concerning bi-directional processing suggest that similar mechanisms subservise both directions of information flow in synesthesia, extending the results of Cohen Kadosh *et al.* (2007). In their study, an 'explicit' synesthete revealed bi-directional congruency effects at the perceptual as well as a late attentive stage. As these authors already suggested, the usage of an explicit synesthete could lead to distinct results when compared with the implicit form of bi-directional synesthesia, which is consistent with the results presented here. The results of the implicit synesthetes revealed that the same processes were affected independent of the direction of information flow.

Multiple dimensions in synesthesia

Synesthetes have been classified along two dimensions: (i) projectors vs. associators; and (ii) higher vs. lower synesthetes. Dixon & Smilek (2005) recently suggested that both dimensions might be equivalent. The neurophysiological responses obtained during the priming tasks allowed us to dissociate distinct processes in time, which together with the inclusion of projector and associator synesthetes made it possible to differentiate between these two dimensions.

For the projector–associator dimension, a significant difference was found neither at the behavioral nor at the neurophysiological level. The absence of a significantly larger priming effect in the reaction time data for projectors is at odds with results obtained by Dixon *et al.* (2004). They reported that projectors were more hindered by the elicited color experience compared with associators in a synesthetic Stroop task. In such a paradigm graphemes are presented in an ink color congruent or incongruent with the synesthetic color experience. The difference in (either grapheme- or color-) naming latency of the incongruent and congruent trials is referred to as the congruency effect and is indicative of automatic interference of the unattended dimension (e.g. the elicited synesthetic color or the ink color). Johnson *et al.* (2007) reported a similar finding. The results of the projector in their study revealed the largest congruency effect on a color-naming task and belonged to one of the three synesthetes with the largest effect in the digit-naming task. As already suggested by Cohen Kadosh *et al.* (2007), task differences (in this particular case priming vs. conflict processing) might underlie these different outcomes. In the synesthetic Stroop task, for instance, the color and a number are presented at the same time, which might result in a visual conflict leading to longer reaction times in the incongruent condition. It is not surprising that in this case projectors suffer more from the visual conflict induced compared with associators.

In contrast, in our study, both stimulus properties were presented sequentially, which prevented such a visual conflict.

For the higher–lower synesthesia dimension we applied a similar method of analyses as Hubbard *et al.* (2005). They demonstrated that consistent patterns within two groups of synesthetes were present between two measures (behavioral and fMRI data). In our study, the synesthetes could be divided into a group with small and a group with large behavioral priming effects. Interestingly, as was the case in the Hubbard *et al.* (2005) study, these two groups of synesthetes partly differed in their physiological responses as well. The group with large behavioral priming effects revealed priming effects at both frontal and parietal electrodes, whereas the group with small behavioral effects revealed frontal effects only. [Although stimulus categorization processes can be reflected in both the P3b latency and reaction time, suggesting a close relation between both measures (Luck, 2005), the presence of significant priming effects in both groups of synesthetes combined with an absence of a P3b latency effect in one group only, implies that there is no direct causal relationship between our behavioral and electrophysiological measure. Rather it suggests that the behavioral results of the group with small priming effects but no P3b latency effects are induced by the processes underlying the frontal amplitude effects.] Together, these results are indicative of the existence of distinct groups of synesthetes. Synesthetic experiences can apparently arise as a result of both bottom up (perceptual) and top-down (attentional/inhibitory) processes, or as a result of top-down (attentional/inhibitory) effects only. Our results fit well with the classification proposed by Ramachandran & Hubbard (2001), who suggested that besides the classification of synesthetes on the basis of their phenomenological experience, synesthetes could be classified on the basis of the inducers or the triggers of the synesthetic experience. They referred to synesthetes that reveal effects at lower perceptual processes as 'lower' synesthetes and to synesthetes with higher cognitive effects as 'higher' synesthetes. Our results indicate that attentional or inhibitory processes appear to play a role in bi-directional priming in all synesthetes, whereas only some (possibly 'lower') synesthetes reveal a priming effect at a lower, possibly perceptual level, as well.

Dixon & Smilek (2005) already emphasized the necessity of scrutinizing effects at the single subject level. They stated that if synesthesia is not a unitary phenomenon, possible patterns might be masked when all synesthetes are grouped together, resulting in conflicting reports or erroneous conclusions. Our results underline this suggestion and might explain some of the conflicting results reported concerning the stage at which the synesthetic experience arises. Involvement of both early pre-attentive as well as later attentional processes has been demonstrated in psychophysical (see for a critical review, see Gheri *et al.*, 2008) as well as imaging research (Paulesu *et al.*, 1995; Schiltz *et al.*, 1999; Nunn *et al.*, 2002; Elias *et al.*, 2003; Weiss *et al.*, 2005; Rich *et al.*, 2006; Barnett *et al.*, 2008; Beeli *et al.*, 2008; Brang *et al.*, 2008). In accordance with the study of Hubbard *et al.* (2005), the present study demonstrated that (grapheme-color) synesthesia is far from a unitary phenomenon.

Conclusions

Our results demonstrate, for the first time, that the same mechanisms underlie bi-directional interactions in synesthesia, at least for implicit synesthetes. At the group level, the priming effect for number to color as well as color to number was present at parietal (possibly perceptual processes) as well as frontal electrode sites (possibly attention or inhibitory processes). The ERP-components affected did not differ

between the often-described synesthetic subtypes (projectors and associators). Instead, when subjects were classified according to their behavioral performance, a dissociation between 'lower' and 'higher' synesthetes emerged. It is tempting to suggest that the attentional or inhibitory processes are important for higher and lower synesthetes alike, while for lower synesthetes perceptual processes play a role as well.

Acknowledgements

We would like to thank Sarah Plukaard for helping to test the subjects as well as Jonathan Carriere and an anonymous reviewer for helpful comments on the manuscript. This research was supported by NWO Grant 051.04.050 of the Cognition Program of the Netherlands Organization for Scientific Research (NWO).

Abbreviations

EEG, electroencephalogram; EOG, electrooculogram; ERP, event-related potential; fMRI, functional magnetic resonance imaging.

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