Research Report

Is the Sky 2?

Contextual Priming in Grapheme-Color Synaesthesia

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ABSTRACT—*Grapheme-color synaesthesia is a neurological phenomenon in which particular graphemes, such as the numeral 9, automatically induce the simultaneous perception of a particular color, such as the color red. To test whether the concurrent color sensations in grapheme-color synaesthesia are treated as meaningful stimuli, we recorded event-related brain potentials as 8 synaesthetes and 8 matched control subjects read sentences such as "Looking very clear, the lake was the most beautiful hue of 7." In synaesthetes, but not control subjects, congruous graphemes, compared with incongruous graphemes, elicited a more negative N1 component, a less positive P2 component, and a less negative N400 component. Thus, contextual congruity of synaesthetically induced colors altered the brain response to achromatic graphemes beginning 100 ms postonset, affecting pattern-recognition, perceptual, and meaning-integration processes. The results suggest that grapheme-color synaesthesia is automatic and perceptual in nature and also suggest that the connections between colors and numbers are bidirectional.*

Although somewhat bizarre to most people, statements such as "The southern California sky is almost always a beautiful shade of 2" are quite meaningful to people with grapheme-color synaesthesia. In these individuals, achromatic graphemes, such as the numeral *2* or the letter *P*, automatically elicit the concurrent perception of a particular color, such as bright blue or a metallic shade of green. Grapheme-color synaesthesia typically begins in early childhood and displays a remarkable degree of consistency over time (Cytowic & Wood, 1982). Although researchers have studied synaesthesia for well over a century (Galton, 1880), key aspects of this phenomenon remain unclear. One basic question is whether synaesthesia is simply a set of overlearned associations that have persisted since childhood (Cytowic & Wood, 1982), or whether it has a perceptual basis grounded in altered cortical connectivity (Ramachandran & Hubbard, 2001). Further, although the phenomenology of synaesthesia is unidirectional—that is, graphemes induce color sensations, but colors do not induce the sensation of their corresponding graphemes—some researchers have suggested that connections between color- and form-processing areas in synaesthetes might be bidirectional (Cohen Kadosh, Cohen Kadosh, & Henik, 2007; Knoch, Gianotti, Mohr, & Brugger, 2005).

Although the neural substrate of grapheme-color synaesthesia has been elegantly studied with functional magnetic resonance imaging (Hubbard, Arman, Ramachandran, & Boynton, 2005; Nunn et al., 2002) and diffusion tensor imaging (Rouw & Scholte, 2007), few studies have addressed the real-time processing of graphemes in this population (though see Sagiv & Ward, 2006; Schiltz et al., 1999). In order to explore the extent to which grapheme-color synaesthesia invokes perceptual versus conceptual processes, we employed electrophysiological techniques to examine grapheme-color synaesthetes' brain response to graphemes embedded in sentence contexts. Whereas previous researchers used mental arithmetic to invoke the concept of an inducer (e.g., "7") and showed that it affected the processing of its corresponding color (e.g., yellow) in a color-naming task (Dixon, Smilek, Cudahy, & Merikle, 2000), in the present study we utilized linguistic context (e.g., "The sky is") to invoke the concept of a color ("blue") in order to examine its impact on event-related potential (ERP) responses to an inducer grapheme.

In particular, we focused on the N400 contextual-priming effects observed for meaningful linguistic stimuli (color terms), nonlinguistic stimuli (color patches), and color-inducing graphemes presented in the same sentence contexts. A negative-going wave that peaks approximately 400 ms after the onset of a contextually relevant stimulus, the N400 is sensitive to the degree to which a meaningful stimulus is primed by the preceding context (Hagoort, Hald, Bastiaansen, & Petersson, 2004; Kutas & Hillyard, 1984). The N400 is elicited by all words, whether spoken, written, or signed, though different stimulus modalities alter its scalp topography in a way that suggests the contribution of different neural generators. The size of the N400

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elicited by words is reduced by the presence of congruous context. Consequently, the N400 to a word such as *cat* is smaller when the word is preceded by a related word (*dog*) than when it is preceded by an unrelated word (*sugar*), and is also reduced in a congruous sentence context (*Growing up, every kid should have either a dog or a cat*) relative to an incongruous sentence context (*I take my coffee with cream and cat*; Kutas & Hillyard, 1980). Meaningful nonlinguistic stimuli, such as line drawings, photographs, cospeech gestures, and even environmental sounds, also elicit N400 components whose amplitude is similarly affected by contextual priming (i.e., reduced by the presence of a congruous context; Wu & Coulson, 2005).

In contrast, musically incongruous stimuli typically elicit a positive-going response in the ERP (Besson & Macar, 1987). This response has been linked to both the P300 (Donchin & Coles, 1998), a general response to unexpected events, and the P600 (Patel, Gibson, Ratner, Besson, & Holcomb, 1998), which is often elicited by ungrammatical language. These positive-going ERP responses to incongruities are thought to reflect arbitrary or overlearned rules, and differ from semantic-integration processes indexed by the N400 (Besson & Macar, 1987).

To test whether grapheme-color synaesthetes' concurrent sensations of color when perceiving graphemes are subject to contextual integration effects, we recorded ERPs as participants read sentence frames that suggested a particular color term as the sentence-final item (e.g., "Looking very clear, the lake was the most beautiful hue of . . . "). These sentences were completed with congruous or incongruous color words ("blue" or "yellow"), congruous or incongruous color patches (blue rectangle or yellow rectangle), or graphemes known to elicit congruous or incongruous colors for a given synaesthete (e.g., in the case of 1 of our synaesthetes, "2," which appears blue, or "7," which appears yellow). If synaesthetic experiences are meaningful stimuli, then the congruity manipulation in the grapheme condition would be expected to give rise to N400 effects. Alternatively, if synaesthetic percepts are overlearned associations, then incongruous graphemes would be expected to elicit a positive-going wave.

METHOD

Participants

Eight grapheme-color synaesthetes and 8 age- and handedness-matched control subjects participated either for cash or in fulfillment of a course requirement. All were healthy fluent English speakers, all had normal or corrected-to-normal color vision, and none had any history of psychiatric or neurological disorder. Participants' age ranged between 18 and 31 ($M = 22.3$ years for synaesthetes and 21.0 years for control subjects). Handedness was assessed via the Edinburgh Inventory (Oldfield, 1971), which yields a laterality quotient ranging from +1 (strongly right-handed) to −1 (strongly left-handed). The majority of our participants were right-handed (6 right-handed and 2 left-handed in both groups), as suggested by the average laterality quotient of +.34 for synaesthetes and +.31 for control subjects. Synaesthesia was confirmed by means of consistency matching (on-line testing with the Synesthesia Battery; Eagleman, Kagan, Sagaram, & Sarma, 2007), including reaction time testing for color consistency.

Materials and Procedure

Stimuli consisted of 240 sentences ending in one of three ways. In *text* blocks, sentence frames (e.g., "Looking very clear, the lake was the most beautiful hue of . . .") were completed either with the predictable, contextually congruous color term ("blue") or with an incongruous color term ("yellow"). In *color* blocks, sentences ended with a rectangular color patch that was either congruous (blue) or incongruous (yellow). In *grapheme* blocks, sentences ended with an achromatic grapheme known to induce a particular concurrent color in a given synaesthete. For example, in 1 of our synaesthetes, "2" induces the color blue and "7" induces the color yellow, so for this synaesthete, "2" was considered to be a congruous completion of the sentence about the lake, whereas "7" was considered to be an incongruous completion. Half of the sentences in each block ended as expected (congruous completions), and half ended with an unexpected color word, an unexpected color patch, or (for the synaesthetes) a grapheme that induced an unexpected color (see Fig. 1). (Congruity of sentence-final words was established in a separate normative study.) Sentences were presented one word at a time at the rate of 2 words per second. Each sentence-final word, color patch, or grapheme was presented for 200 ms and followed by a blank screen for 1,300 ms.

To control for effects of surprise due to nonlinguistic stimuli being introduced into sentence contexts, we presented the three types of sentence endings in separate blocks (two blocks of each condition, for a total of six blocks). Block order was pseudorandomized for each subject such that blocks of the same type were not presented sequentially. Block order was approximately counterbalanced across subjects (3 synaesthetes viewed a text block first, 3 viewed a color block first, and 2 viewed a grapheme block first). Each synaesthete was matched with a control subject who viewed exactly the same stimulus list (in the same order).

The experiment took place in a sound-attenuated room. Participants were seated in a comfortable chair and viewed the computer monitor from a distance of 37 in. During the initial instructions, participants were told that they would be reading sentences presented one word at a time in the center of the screen, and they were instructed to fixate the centrally presented words, whose location would be indicated by the initial appearance of a fixation cross.

Electroencephalographic and Electro-Oculographic Recording

Participants' electroencephalogram (EEG) was monitored with a commercial electrode cap with 29 scalp sites arranged according

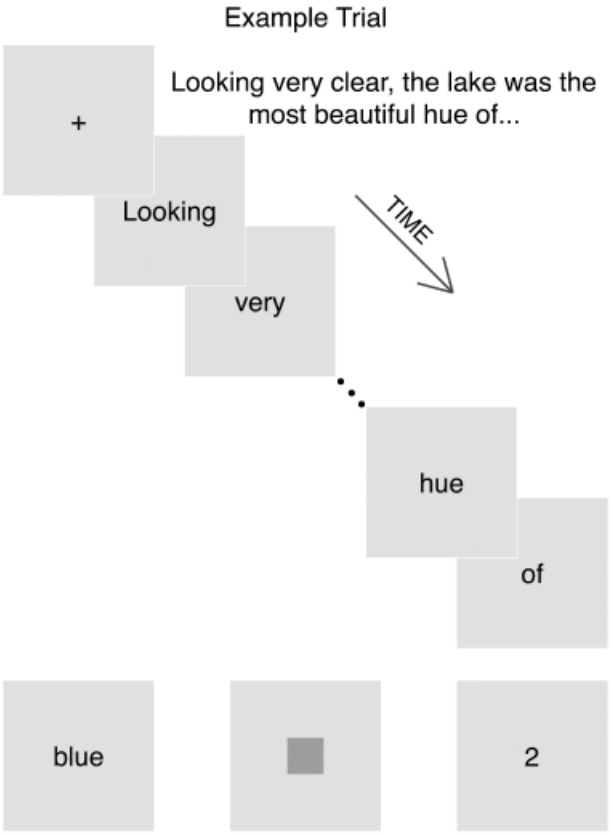

Fig. 1. Illustration of the display sequence in a trial. Depending on the condition, the final display showed a color word, color patch, or grapheme.

to the International 10–20 system. Horizontal eye movements were measured with a bipolar derivation of electrodes placed at the outer canthi. Vertical eye movements and blinks were monitored with an electrode under the right eye. All electrodes were referenced on-line to the left mastoid, and all impedances were maintained below 5 kΩ. The EEG at a band pass from 0.01 to 100 Hz was amplified with SA Instruments (Stony Brook, NY) 32-channel bioamplifiers, digitized at 250 Hz, and stored on a computer hard disk for later averaging.

Analysis of ERPs

ERPs were time-locked to the onset of the sentence-final stimulus. Analyses focused on a time window from 100 ms before through 920 ms after that onset. The 100-ms period preceding the onset of the sentence-final stimulus served as the baseline. Epochs containing blinks, eye movements, amplifier drift, or blocking were rejected prior to averaging, resulting in the exclusion of 18.85% of trials, on average, for synaesthetes and 12.63% of trials, on average, for control subjects, $F(1, 14) = 2.89$, n.s.

Unless noted otherwise, analysis involved mean amplitude measurements of each participant's ERPs elicited in three time windows: 100 to 150 ms after onset of the sentence-final stimulus (intended to capture the N1 component), 150 to 250 ms after onset of the sentence-final stimulus (intended to capture the P2 component), and 300 to 450 ms after onset of the sentence-final stimulus (intended to capture the N400 component). Measurements were subjected to repeated measures analyses of variance with the between-subjects factor of group (synaesthetes vs. control subjects) and within-subjects factors of congruity (congruous vs. incongruous), probe type (text vs. color vs. grapheme), and scalp distribution. In the analysis of midline sites (FPz, Fz, FCz, Cz, CPz, Pz, Oz), the distribution factor was electrode (seven levels, from anterior to posterior); in the analysis of medial sites (FP1/FP2, F3/F4, FC3/FC4, C3/C4, CP3/CP4, P3/P4, O1/O2), the distribution factors were hemisphere (left vs. right) and electrode (seven levels, from anterior to posterior); and in the analysis of lateral sites (F7/F8, FT7/FT8, TP7/TP8, T5/T6), the distribution factors were hemisphere (left vs. right) and electrode (four levels, from anterior to posterior). Although the original degrees of freedom are reported here for clarity, p values were subjected to Greenhouse-Geisser correction (Greenhouse & Geisser, 1959), when appropriate. Results of analysis are presented in the tables, which list theoretically meaningful effects. The hemisphere factor had no significant main effects and was not involved in any significant interactions, so is not discussed further.

RESULTS AND DISCUSSION

Tables 1 through 3 present results of analyses of mean amplitude in three time windows, corresponding to the N400, N1, and P2 ERP components, respectively.

Results for the text blocks were in keeping with previous ERP language research. In both groups of participants, congruous completions elicited a less negative N400 than did incongruous completions (see Fig. 2), as revealed by overall effects of the congruity factor, as well as by a reliable interaction between the congruity and electrode factors in the analysis of midline electrode sites (see Table 1).[1] In both groups, the N400 was broadly distributed across the scalp, began 200 ms after the onset of the sentence-final word, and returned to baseline by 600 ms postonset. These findings suggest that the altered perceptual experience that can accompany reading in grapheme-color synaesthesia, namely, the perception of colored letters, has little detectable impact on the contextual integration processes indexed by the N400 component in the ERP.

The two groups of participants also displayed a similar N400 response to the critical items in the color blocks (see Fig. 2). Congruous color patches elicited a less negative N400 than did incongruous ones (see Table 1). The time course of the color-congruity effect was similar between the two groups, beginning

[1]Because the N400 component is larger over some electrode sites than others, differences in N400 amplitude are often revealed by interactions between experimental conditions and electrode factors. In the present study, congruity effects on the N400 were revealed by congruity-by-electrode interactions in the statistical analyses.

TABLE 1

Analysis of Mean Amplitude 300 to 450 Ms After Onset of the Sentence-Ending Stimulus (N400)

	Midline sites		Medial sites		Lateral sites	
Analysis and effect	*F*	*p*	*F*	*p*	*F*	*p*
Text condition: between groups						
Group	$F(1, 14) = 5.76$	$< .05$	$F(1, 14) = 5.40$	$< .05$	$F(1, 14) = 2.73$	n.s.
Congruity	$F(1, 14) = 31.03$	$< .001$	$F(1, 14) = 28.76$	$< .001$	$F(1, 14) = 23.53$	$< .001$
Group × Congruity	$F(1, 14) = 0.91$	n.s.	$F(1, 14) = 0.45$	n.s.	$F(1, 14) = 0.02$	n.s.
Congruity × Electrode	$F(6, 84) = 4.85$	$< .05$	$F(6, 84) = 1.14$	n.s.	$F(3, 42) = 0.07$	n.s.
Group × Congruity × Electrode	$F(6, 84) = 1.77$	n.s.	$F(6, 84) = 3.16$	n.s.	$F(3, 42) = 0.37$	n.s.
Color condition: between groups						
Group	$F(1, 14) = 1.36$	n.s.	$F(1, 14) = 0.73$	n.s.	$F(1, 14) = 0.01$	n.s.
Congruity	$F(1, 14) = 8.24$	$< .05$	$F(1, 14) = 8.69$	$< .05$	$F(1, 14) = 9.92$	$< .01$
Group × Congruity	$F(1, 14) = 0.30$	n.s.	$F(1, 14) = 0.28$	n.s.	$F(1, 14) = 0.03$	n.s.
Congruity × Electrode	$F(6, 84) = 5.37$	$< .05$	$F(6, 84) = 6.08$	$< .05$	$F(3, 42) = 0.48$	n.s.
Group × Congruity × Electrode	$F(6, 84) = 0.18$	n.s.	$F(6, 84) = 0.01$	n.s.	$F(3, 42) = 0.09$	n.s.
Grapheme condition: between groups						
Group	$F(1, 14) = 5.06$	$< .05$	$F(1, 14) = 5.39$	$< .05$	$F(1, 14) = 2.00$	n.s.
Congruity	$F(1, 14) = 5.79$	$< .05$	$F(1, 14) = 4.46$	n.s.	$F(1, 14) = 2.11$	n.s.
Group × Congruity	$F(1, 14) = 0.22$	n.s.	$F(1, 14) = 0.24$	n.s.	$F(1, 14) < 1$	n.s.
Congruity × Electrode	$F(6, 84) = 8.62$	$< .01$	$F(6, 84) = 6.73$	$< .05$	$F(3, 42) = 6.21$	$< .05$
Group × Congruity × Electrode	$F(6, 84) = 3.95$	$< .05$	$F(6, 84) = 4.17$	n.s.	$F(3, 42) = 5.85$	$< .05$
Grapheme condition: synaesthetes						
Congruity × Electrode	$F(6, 42) = 7.33$	$< .01$	$F(6, 42) = 6.47$	$< .05$	$F(3, 21) = 8.91$	$< .05$
Grapheme condition: control subjects						
Congruity × Electrode	$F(6, 42) = 2.62$	n.s.	$F(6, 42) = 1.21$	n.s.	$F(3, 21) = 0.07$	n.s.

Note. The electrode factor refers to the anterior-posterior location of the electrode.

250 ms postonset and ending 450 ms postonset, as was the scalp topography.

In contrast to the similarities observed in the two groups for the text and color blocks, responses of synaesthetes and control subjects differed in the grapheme blocks (see Fig. 2). In control subjects, N400 amplitude did not vary as a function of sentence congruity (see Table 1). Given that recognition of sentence congruity was specifically designed to require that the grapheme induce an experience of color, our failure to observe an N400 effect in control subjects in the grapheme block is unsurprising. In synaesthetes, however, congruous graphemes elicited a less negative N400 than incongruous graphemes, as shown in a follow-up analysis of data recorded from the synaesthetes (see Table 1).

Although the congruous and incongruous inducer graphemes were equally incompatible with the sentence context (i.e., it makes as much sense to say that the lake is "2" as it does to say that the lake is "7"), the contextual congruity of the color sensation synaesthetes experienced modulated the size of the N400 elicited by the graphemes. This finding supports the idea that the color-induction process in grapheme-color synaesthesia is automatic and suggests that the concurrent color sensation is treated by the brain as a meaningful stimulus subject to contextual integration processes.

Further, the synaesthetes' N400 effect in the grapheme blocks was preceded by congruity effects on two earlier ERP components: the N1 and the P2. The N1 is an occipitotemporal negativity that typically peaks between 140 and 180 ms after onset of the stimulus (Vogel & Luck, 2000). Between 100 and 150 ms after onset of the sentence-final stimulus, ERPs to congruous graphemes were more negative than ERPs to incongruous graphemes in the group of synaesthetes (see Table 2). This effect was not present in the text or color blocks or in control subjects (see Table 2). This negativity peaked at approximately 153 ms in grapheme blocks. An additional analysis of the peak amplitude observed between 140 and 180 ms at lateral sites revealed a reliable congruity effect in grapheme blocks among synaesthetes only, $F(1, 7) = 19.27$, $p < .01$ (see Fig. 3), but not in text blocks, $F(1, 7) = 0.06$, n.s., or color blocks, $F(1, 7) = 0.23$, n.s.

TABLE 2

Effect of Congruity at Lateral Sites 100 to 150 Ms After Onset of the Sentence-Ending Stimulus (N1)

Group and condition	*F*(1, 7)	*p*
Synaesthetes		
Text condition	4.98	n.s.
Color condition	1.67	n.s.
Grapheme condition	5.78	$< .05$
Control subjects		
Text condition	0.04	n.s.
Color condition	3.52	n.s.
Grapheme condition	0.96	n.s.

TABLE 3

Analysis of Mean Amplitude in the Grapheme Condition 150 to 250 Ms After Onset of the Sentence-Ending Stimulus (P2)

	Midline sites		Medial sites		Lateral sites	
Analysis and effect	*F*	*p*	*F*	*p*	*F*	*p*
Between groups						
Group	$F(1, 14) = 4.94$	$< .05$	$F(1, 14) = 2.87$	n.s.	$F(1, 14) = 0.17$	n.s.
Congruity	$F(1, 14) = 4.11$	n.s.	$F(1, 14) = 4.69$	$< .05$	$F(1, 14) = 6.89$	$< .05$
Group × Congruity	$F(1, 14) = 10.08$	$< .01$	$F(1, 14) = 12.38$	$< .005$	$F(1, 14) = 11.8$	$< .005$
Congruity × Electrode	$F(6, 84) = 1.63$	n.s.	$F(6, 84) = 1.22$	n.s.	$F(3, 42) = 0.44$	n.s.
Group × Congruity × Electrode	$F(6, 84) = 3.85$	$< .05$	$F(6, 84) = 1.93$	n.s.	$F(3, 42) = 0.34$	n.s.
Synaesthetes						
Congruity	$F(1, 7) = 12.35$	$< .01$	$F(1, 7) = 15.21$	$< .01$	$F(1, 7) = 27.85$	$< .01$
Congruity × Electrode	$F(6, 42) = 5.50$	$< .05$	$F(6, 42) = 3.36$	n.s.	$F(3, 21) = 0.93$	n.s.
Control subjects						
Congruity	$F(1, 7) = 0.73$	n.s.	$F(1, 7) = 0.73$	n.s.	$F(1, 7) = 0.23$	n.s.
Congruity × Electrode	$F(6, 42) = 0.19$	n.s.	$F(6, 42) = 0.26$	n.s.	$F(3, 21) = 0.16$	n.s.

Note. The electrode factor refers to the anterior-posterior location of the electrode.

Remarkably, the onset of reliable grapheme-congruity effects in synaesthetes emerged 150 ms before the onset of color-congruity effects, as the N400 diverged from the baseline between 250 and 300 ms after the onset of the color patch in the color blocks.

Thus, as in prior N1 research, the N1 response to target stimuli (in this case, contextually congruous graphemes) was more negative than the N1 response to nontarget stimuli (contextually incongruous graphemes). The amplitude of the occipitotemporal N1 has been shown to be modulated by tasks involving form or color discrimination, has been implicated in the perceptual categorization of visual stimuli (Curran, Tanaka, & Weiskopf, 2002), and is also modulated by attention (for a

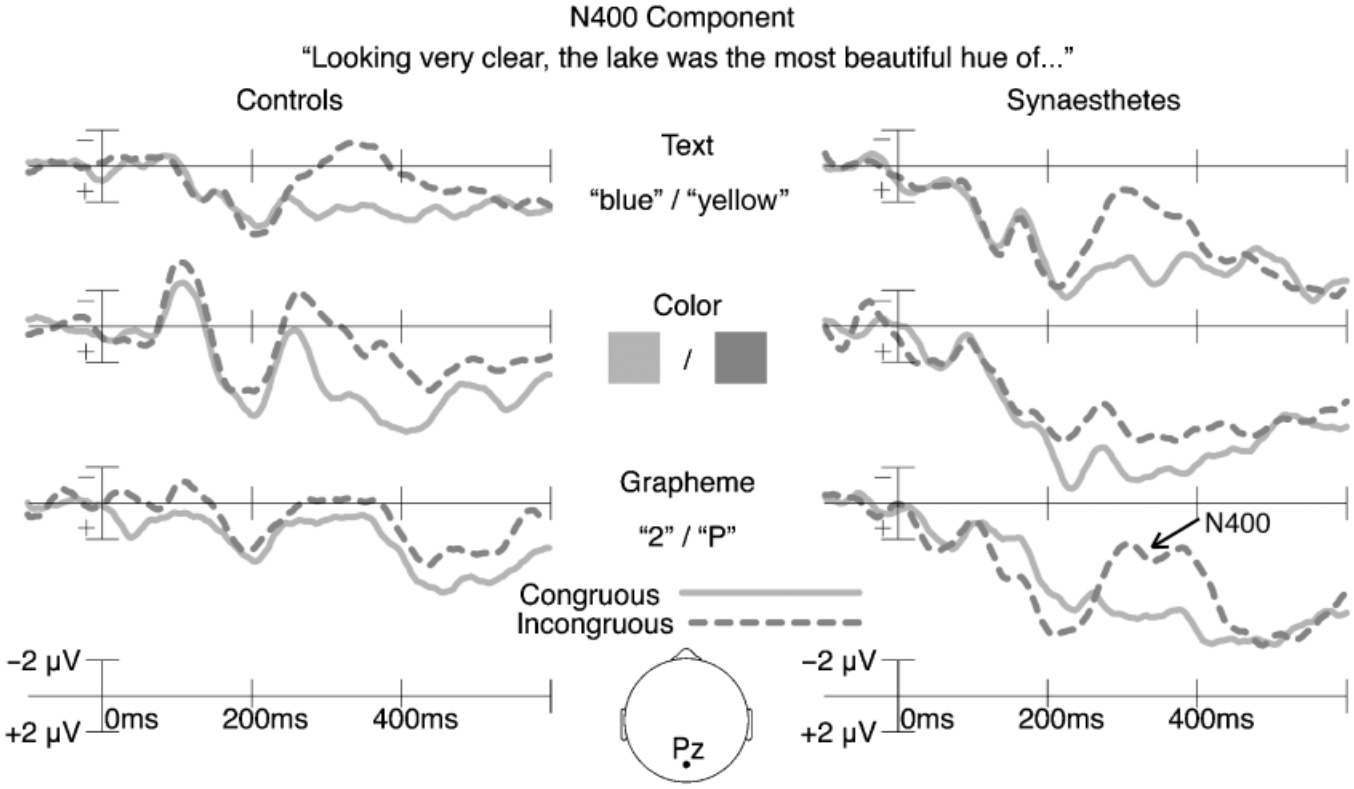

Fig. 2. Grand-average event-related potentials at posterior electrode Pz for congruous and incongruous sentences. Results are shown separately for the three probe types (text, color, grapheme), for both synaesthetes ($n = 8$) and control subjects ($n = 8$). The N400 for synaesthetes in the grapheme condition is labeled. For purposes of display (but not analysis), these data were digitally low-pass-filtered at 20 Hz. Negative voltage is plotted upward.

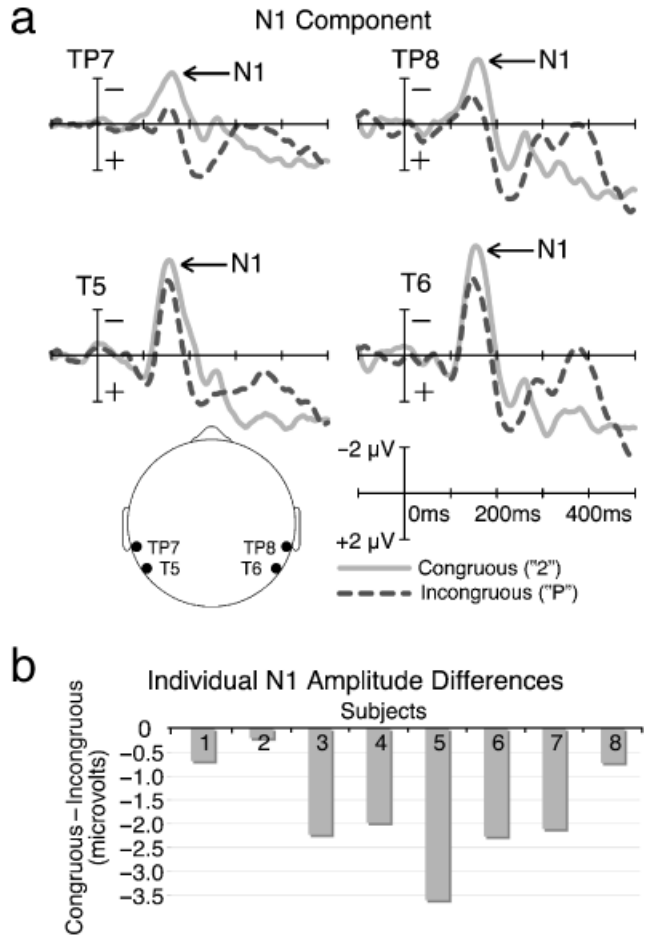

Fig. 3. The N1 observed in synaesthetes (n = 8). The upper panel (a) shows grand-average event-related potentials to congruous and incongruous graphemes at four electrode sites. For purposes of display (but not analysis), these data were digitally low-pass-filtered at 20 Hz. Negative voltage is plotted upward. The lower panel (b) presents the difference in N1 amplitude between congruous and incongruous graphemes for each synaesthete individually.

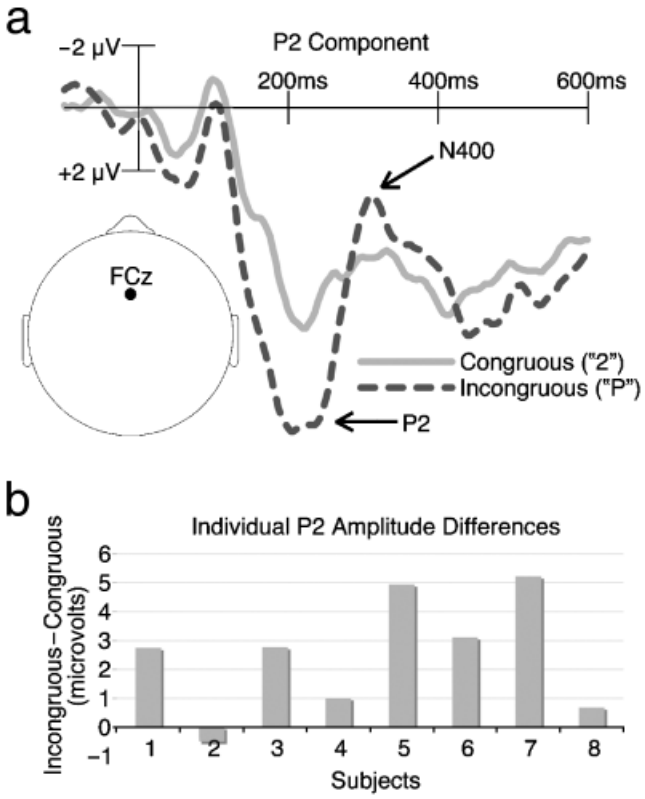

Fig. 4. The P2 observed in synaesthetes (n = 8). The upper panel (a) shows grand-average event-related potentials to congruous and incongruous graphemes at FCz. For purposes of display (but not analysis), these data were digitally low-pass-filtered at 20 Hz. Negative voltage is plotted upward. The lower panel (b) presents the difference in P2 amplitude between congruous and incongruous graphemes for each synaesthete individually.

review, see Vogel & Luck, 2000). Observed N1 effects in the present study may reflect enhanced visual processing of contextually appropriate graphemes, as semantic expectations engendered by the preceding sentence context served to facilitate form discrimination of expected graphemes and synaesthetic color induction arising from them.[2]

The P2, a frontal positivity evident between 150 and 250 ms after stimulus onset, was modulated by congruity in synaesthetes, but not in control subjects (see Table 3). In synaesthetes, the mean amplitude of the P2 was approximately 2.5 μV larger for incongruous graphemes than for congruous ones (Fig. 4). In control subjects, P2 amplitude was similar for congruous and incongruous graphemes, differing only by 0.5 μV (see Table 3).

The frontal positivity we observed is partially consistent with results of a prior electrophysiological study of grapheme-color synaesthetes using a target-detection paradigm (Schiltz et al., 1999). Although the experimental manipulation in that study did not modulate P2 amplitude, both target and nontarget stimuli elicited larger positivities in synaesthetes' than control subjects' ERPs between 200 and 300 ms after grapheme onset.

Though the neural generators for the anterior P2 component are currently unknown, Kranczioch, Debener, and Engel (2003) argued that this component reflects perceptual processing. The P2 has previously been observed in target-detection paradigms that address the role of spatial attention in vision. In these paradigms, the P2 is larger for targets than nontargets (Hillyard & Münte, 1984; Kenemans, Kok, & Smulders, 1993). Because the P2 has been shown to be enhanced for targets defined by orientation, size, or color, Luck and Hillyard (1994) argued that it reflects a multidimensional feature-detection process. In view of its sensitivity to attentional manipulations (Kranczioch et al., 2003; Luck, Vogel, & Shapiro, 1996) and to multiple distinct visual attributes, the P2 observed in our synaesthetes' ERPs to graphemes may index processes relevant to the synaesthetic

[2]In a case study of a grapheme-color synaesthete, Sagiv and Ward (2006) also observed that N1 amplitude in response to graphemes differed depending on whether the graphemes' printed color was consistent or inconsistent with their induced color.

binding of shape and induced color. The observed congruity effect, then, might reflect the difficulty of generating the synaesthetic percept when contextual cues prime a different color.

This explanation receives partial support from ERP data reported by Beeli, Esslen, and Jäncke (2008) from a study of color-hearing synaesthetes, in whom spoken words and letters give rise to concurrent color sensations. Beeli et al. found that the P2 elicited by spoken letters was smaller in synaesthetes than in control subjects, and during the 10 ms surrounding the P2 peak, Beeli et al. observed brain activity in synaesthetes in left superior frontal gyrus, left precuneus, and right intraparietal sulcus. Though such localization claims about EEG activity should always be approached with caution, these activations are consistent with brain areas putatively involved in perceptual binding. However, the precise relationship between the auditory potentials reported by Beeli et al. and the visual potentials observed in the present study is unknown, and further work will be required to ascertain the functional significance of observed P2 congruity effects in grapheme-color synaesthetes.

In sum, contextual congruity of synaesthetic colors altered synaesthetes' brain response to achromatic graphemes beginning 100 ms postonset, affecting form-recognition, perceptual, and meaning-integration processes. The early effects observed in this study support accounts of synaesthesia as caused by nonstandard neuroanatomy, such as altered connectivity in the visual system (Ramachandran & Hubbard, 2001; Rouw & Scholte, 2007) or disinhibited feedback (Grossenbacher & Lovelace, 2001), and further support the idea that synaesthesia is perceptual in nature. The present study expands the notion of synaesthesia as a psycholinguistic phenomenon in which many inducer stimuli are linguistic (Simner, 2007), by showing that synaesthetic colors are subject to linguistically mediated contextual-priming effects. In addition, these results support the suggestion that there are bidirectional connections between colors and numbers in synaesthetes (Cohen Kadosh et al., 2007; Knoch et al., 2005), as the conceptual expectation of colors, evoked by the sentence frames, successfully mediated the processing of graphemes at multiple levels. The observed N1 effects (100 to 150 ms) are particularly remarkable, as they indicate that the sentence contexts (e.g., "Looking very clear, the lake was the most beautiful hue of . . .") successfully modulated visual discrimination of graphemes presented in black. However, our findings do not indicate whether these bidirectional mappings in synaesthetes result from cross-activation between V4 and fusiform gyrus or are mediated by higher-level areas.

Indeed, our results have implications beyond synaesthesia, extending to the flexibility of multimodal meaning-integration processes. Participating in a conversation, for example, often requires combining linguistic information in speech with contextually salient visual information, such as an image on a television or computer screen, the affective facial expressions of interlocutors, and information in cospeech gestures. Our demonstration that synaesthetic colors were integrated into participants' representation of sentence meaning is consistent with recent evidence that the brain simultaneously integrates information from spoken words and cospeech gestures (Ozyurek, Willems, Kita, & Hagoort, 2007).

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